UNIVERSITY OF CALIFORNIA, SAN DIEGO

Gene-culture coevolution in a social cetacean: integrating acoustic and genetic data to understand population structure in the short-finned pilot whale (*Globicephala macrorhynchus*)

A dissertation submitted in partial satisfaction of the
requirements for the degree
Doctor of Philosophy

in

Oceanography with a Specialization in Interdisciplinary Environmental Research

by

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2017

The dissertation of Amy Van Cise is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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University of California, San Diego

2017

To Bean and Kiwi.

And my SIO Family.

This wouldn't have happened without you.

Or it would have, but I wouldn't have had near as much fun.

EPIGRAPH

In a way, science might be described as paranoid thinking applied to Nature:

we are looking for natural conspiracies.

— Carl Sagan, Dragons of Eden: Speculations on the Evolution of Human Intelligence

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ACKNOWLEDGEMENTS

Before any of this, someone had to agree to teach me. For that, I will be forever incredibly grateful to Jay Barlow and Phil Morin, for taking me on as a student. You knew little more of me than my enthusiasm, and yet you took the risk. From you I learned as much about life, art, natural history, and who I would like to be as I did about science. Thank you for letting me pursue a risky research project, that required a lot of collaboration on your part and a lot of learning on mine. Thank you for being flexible when I constantly asked to do field work "just one more time." Thank you for always looking out for me - whether it was helping me to get funding, or get to an important conference, or meet a potential collaborator, it means a lot to know that you've kept my best interest at heart. And, really, thank you for treating me as a colleague, because it was your example that helped me understand the scientific community I was joining. Your generosity has permanently changed me.

To my committee, for guiding me and supporting me along the way, I am thankful. Your work required the patience to let me run with ideas, and the ability to guide those ideas and make them useful. At different points along the way I've leaned on each of you for technical expertise and guidance, and you always made time for me. Lisa Levin, as my Scripps co-chair, thank you for all of the scientific and career advice you've given me over the years, and thank you for working with Jay and Phil to advise me. Ron Burton, Bill Hodgkiss, and James Fowler, thank you for always letting me come to you with my many questions - whether they were about science, grants, or life after grad school. Thank you, to all my committee, for reviewing paper drafts and sitting in meetings and answering all the doodle polls. At first, it seemed incredible to me that such powerhouse scientists could make time for a random gradate student. I got used to it, but I'm still amazed and grateful. It means the world to me.

I have been lucky to learn from some inspirational and collaborative women, who took me under their wing. Thank you, Karen Martien and Marie Roch, for teaching me,

working with me, and being strong professional role models that I could look up to.

Robin Baird, you and your team at Cascadia Research Collective were generous not only with your data but with your time. From you I gained so much, including field research skills, a well-rounded understanding of the Hawaiian marine ecosystem, and some of the rarest and most cherished experiences a person can have. Thank you for sharing your world with me.

Eric Archer, you once told me that you got to where you are today by being in the right place at the right time. I'm lucky to have been here these last six years - from my first R class, and through every paper I've written, you've patiently taught me coding language, statistical theory, and scientific concepts that I will use for the rest of my life. Thank you for letting me pepper you with questions for six years. I am a better person for it.

Barb Taylor, when I first started at SIO you said that, if I studied pilot whales, my research might force me to work in Hawai'i, "and that would be just terrible!" Thank you so much for the push in the right direction. I can't imagine a better research project. Thank you for being inspiring and welcoming and supportive over the years.

Lisa Ballance, thank you for creating a space within the Marine Mammal and Turtle Division for students to learn alongside such amazing scientists, and for taking such good care of the SIO student community. I am so grateful for the opportunities you've created for me.

All of the people in NOAA's Marine Mammal Genetics and Acoustics groups could not have been more supportive or patient throughout my entire PhD process. Brittany Hancock-Hanser, Kelly Robertson, Vicki Pease, Morgane Lauf, Gaby Serra-Valente, and Shannon Rankin - thank you for all of your help. You got me through some of my toughest days.

This dissertation is as much a product of the scientific community that welcomed me and guided me as it is my own work, and I appreciate the chance to stand on the shoulders

of such giants.

Chapter 2, in full, is a reprint of the material as it appears in Marine Mammal Science, Van Cise, Amy M., Morin, Phillip A., Baird, Robin W., Lang, Aimee R., Robertson, Kelly M., Chivers, Susan J., Brownell, Robert L., Martien, Karen K. **2016**, volume *32*, pages 1177-1199. The dissertation author was the primary investigator and author of this paper.

Chapter 3, in full, is a reprint of the material as it appears the in Journal of the Acoustical Society of America, Van Cise, Amy M., Roch, Marie A., Baird, Robin W., Aran Mooney, T., Barlow, Jay. **2017**, volume *141*, pages 737-748. The dissertation author was the primary investigator and author of this paper.

Chapter 4, in full, has been submitted for publication of the material as it may appear in Molecular Ecology, **2017**, Van Cise, Amy M., Martien, Karen. K., Mahaffy, Sabre D., Baird, Robin W., Webster, Daniel L., Fowler, James H., Oleson, Erin M., Morin, Phillip A. Familial social structure and socially-driven genetic differentiation in Hawaiian short-finned pilot whales. The dissertation author was the primary investigator and author of this paper.

Chapter 5, in full, is currently being prepared for submission for publication of the material. Van Cise, Amy M., Mahaffy, Sabre D., Baird, Robin W., Mooney, T. Aran, Barlow, Jay. Song of my people: Dialect differences among sympatric social groups of Hawaiian short-finned pilot whales. The dissertation author was the primary investigator and author of this paper.

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Van Cise, A. M., Martien, K. K., Mahaffy, S. D., Baird, R. W., Webster, D. L., Fowler, J. H., Oleson, E., Morin, P. A., "Familial social structure and socially-driven genetic differentiation in Hawaiian short-finned pilot whales" *Molecular Ecology* - In Review.

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ABSTRACT OF THE DISSERTATION

Gene-culture coevolution in a social cetacean: integrating acoustic and genetic data to understand population structure in the short-finned pilot whale (*Globicephala macrorhynchus*)

by

Amy Van Cise

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The evolutionary ecology of a species is driven by a combination of random events, ecological and environmental mechanisms, and social behavior. Gene-culture coevolutionary theory attempts to understand the evolutionary trajectory of a species by examining the interactions between these potential drivers. Further, our choice of data type will affect the patterns we observe, therefore by integrating several types of data we achieve a holistic understanding of the various aspects of evolutionary ecology within a species.

In order to understand population structure in short-finned pilot whales, I use a combination of genetic and acoustic data to examine structure on evolutionary (genetic) and cultural (acoustic) timescales. I first examine structure among geographic populations in the Pacific Ocean. Using genetic sequences from the mitochondrial control region, I show that two genetically and morphologically distinct types of short-finned pilot whale, described off the coast of Japan, have non-overlapping distributions throughout their range in the Pacific Ocean. Analysis of the acoustic features of their social calls indicates that they are acoustically differentiated, possibly due to limited communication between the two types. This evidence supports the hypothesis that the two types may be separate species or subspecies.

Next, I examine structure among island communities and social groups within the Hawaiian Island population of short-finned pilot whales. Using a combination of mitochondrial and nuclear DNA, I showed that the hierarchical social structure in Hawaiian pilot whales is driven by genetic relatedness; individuals remain in groups with their immediate family members, and preferentially associate with relatives. Similarly, social structure affects genetic differentiation, likely by restricting access to mates. Acoustic differentiation among social groups indicates that social structure may also restrict the flow of cultural information, such as vocal repertoire or dialect.

The qualitative correlation between social structure, cultural information transfer, and genetic structure suggest that gene-culture coevolution may be an important mechanism to the evolutionary ecology of short-finned pilot whales. Further research may reveal a similar structure in the transmission of ecological behaviors, such as diet preference, habitat use, or movements. The results of this research underscore the applicability of gene-culture coevolutionary theory to non-human taxa.

Chapter 1

Introduction

An individual's behavior can be described as a combination of its interactions with others of the same species (social behaviors), interactions with its environment and other species (ecological behaviors), and the influence of its genetic material (evolutionary behaviors). Each of these three elements interacts with and influences the others, in ways that can either stabilize or destabilize population-level structure.

Although social behavior influences ecological and evolutionary behaviors in many species, theoretical studies that integrate social behavior with the interactions between ecology and evolution in a species have historically been focused on humans. Based on evidence from the archaeological record scientists could point to traditions, such as tool use and written language, that were passed down from one generation to the next, much in the same way that genetic information is passed on from parents to offspring. This led to the development of gene-culture coevolutionary theory, a branch of population genetic theory that attempted to integrate an understanding of the mechanisms underlying population structure, divergence, and speciation such as gene flow, drift, and adaptation with an understanding of how the same mechanisms affect cultural information rather than genetic information (Feldman and Laland, 1996).

Under this branch of population genetics, several types of theoretical models have

been developed to improve our understanding of the interaction between socio-cultural behaviors and evolution. These include models that consider cultural transmission as a parameter when partitioning variance in phenotypic behaviors (Cavalli-Sforza and Feldman, 1973). They also include models that broadly consider the interaction between genetic and cultural shifts in a population or species (Rice et al., 1978; Boyd and Richardson, 1985; Aoki and Feldman, 1987; Fowler et al., 2009; Richerson et al., 2010), and models that specifically consider the interaction between a single cultural trait and a handful of genes that influence that trait (Feldman and Cavalli-Sforza, 1976, 1980; Fowler et al., 2011; Apicella et al., 2012).

The restriction of gene-culture coevolutionary theory to humans was based on the premise that, outside of humans, social behaviors could not be stable enough to allow information transfer and accumulation from one generation to the next (Feldman and Laland, 1996). However, as evidence of cultural traditions across many vertebrate taxa accumulated, cultural evolutionary theory began to expand to include non-human animal cultures (Mundinger, 1980; Laland and Janik, 2006). The use of gene-culture coevolution models to describe non-human system revealed some universal similarities in the development of traits across taxa. For example, cultural communication and evolution of genes involved with learning preferences can be modeled in the same way in birds and humans (Lachlan and Feldman, 2003). Similarly, in males across several vertebrate taxa, including humans, social status is tied to immune response and levels of parasitism (Habig et al., 2015).

These complex interactions between sociality and genetics mean that by integrating our understanding of each of these elements, we can improve our understanding of the life history of individuals or species. For example, a study of acoustic and genetic structure in the Okinawa least horseshoe bat revealed strong female philopatry and vertical transmission of echolocation frequencies, and suggests maternally-transmitted cultural and genetic drift among segregated populations (Yoshino et al., 2008). Similar studies in multiple bird

species have shown that in some species culturally-learned bird song is vertically transmitted along genetic lines, from parent to offspring, while in other species regional songs are learned by immigrants through horizontal transmission among peers, possibly indicating an environmental influence on song within these species (Wright and Wilkinson, 2001). In some whales, especially those with long migration routes such as humpback and blue whales, differences in call type or song type may differ among genetically-similar groups that use different breeding grounds or inhabit different ocean basins, resulting in differences between acoustic and genetic structure (e.g. McDonald et al. (2006), Garland et al. (2015)). In others, cultural differences among groups act to promote reproductive isolation and genetic divergence, accelerating the rate of speciation (Riesch et al., 2012).

Studying a species using culturally transmitted traits may reveal anthropogenic effects on diversity or connectivity before they have an impact on genetic structure, as was shown in the grey shrike-thrush. In this species of woodland bird, habitat fragmentation had not yet affected genetic connectivity, but had decreased song sharing and created dissimilarities in song types among fragmented regions (Pavlova et al., 2012), which could ultimately become a barrier to mating between individuals in different regions.

One component of culture, social structure, has been shown to affect ecology and evolution across a growing number of taxa. Social structure has been employed to understand disease transmission in humans (Cauchemez et al., 2011) and wild populations (Loehle, 1995), including a number of social vertebrates (e.g. elephants (Chiyo et al., 2014), and primates (Griffin and Nunn, 2012)). In several mammalian species, social structure has caused prezygotic isolation that leads to genetic drift, resulting in a high degree of genetic structuring at a sub-population level, which, if stable for long periods of time, may increase differentiation among populations within a species (Storz, 1999). Over evolutionary time periods, social structure can promote ecological and evolutionary divergence, and possibly speciation (Riesch et al., 2012; Foote and Morin, 2016).

Because population structure is dependent on the temporal stability and type of mechanisms driving it, our understanding of population structure within a species will be affected by the type of data used to examine that structure. Traditionally, taxonomists have used morphological data to describe species or populations. The advent of population genetics led to the description of new cryptic species across many taxa. Similarly, integrating data types such as social structure, acoustic, diet, or movement data may reveal additional structure within a species or population, detectable at ecological rather than evolutionary temporal scales, that is relevant to the conservation of the species.

In many vocal species, acoustic differentiation indicates barriers to information transfer between groups - such as social units, populations, or sub-species. These barriers could be geographic or ecological, or, in some cases, among sympatric groups, variability in the vocal repertoire could be due to socially-structured barriers (Conner, 1982). Acoustic differentiation among geographically disparate populations represents a barrier to communication, or information transfer, between those two populations. On the other hand, acoustic differentiation among sympatric or allopatric populations, occurring despite a lack of geographic barriers to communication or information transfer, is likely to indicate the purposeful social segregation of groups or populations. It is often the case that this pattern of acoustic differentiation arises when vocal repertoires are used as a mechanism to maintain social segregation among groups, and may act to accelerate genetic divergence among groups.

Comparing acoustic structure, which represents population structure over relatively shorter time periods, with genetic structure, which can represent population structure over relatively longer time periods, may help us understand the temporal stability of socially-driven structure, and allow us to better understand how ecology and social structure affect genetic differentiation and divergence within a species. Although divergence in both data types is driven by the same mechanisms, including drift, flow (through mixing or introgres-

sion), and adaptation, the rate at which each of these mechanisms drives differentiation is likely to be different for each data type. To understand the relationship between genetic and acoustic structure within a social species, we can first compare patterns of differentiation in the two data types, and second quantify the magnitude of differentiation in the two data types.

In the marine environment, there are few barriers to dispersal for highly mobile or migratory species, including most marine mammals and a number of large predatory fishes. For some of these species, social structure may play an important role in driving differences in the ecology and genetics of a species, at a sub-population, population, or sub-species level.

One such social species, the short-finned pilot whale (*Globicephala macrorhynchus*), is known to live in stable social units for periods of a decade or more (Mahaffy et al., 2015; Baird, 2016). Those social units have long been hypothesized to be matrilineal Whitehead (1998), based on the species social evolution (Connor et al., 1998) and similarity to closely-related killer whales and long-finned pilot whales, both of which have matrilineal social organization (Bigg et al., 1990; Amos et al., 1991).

Short-finned pilot whales primarily inhabit coastal and neritic waters in the tropical and sub-tropical regions of the Atlantic, Pacific, and Indian Oceans. Early taxonomists described several species in the genus *Globicephala*, which were later synonymized, leaving two species: *Globicephala macrorhycnhus*, or short-finned pilot whale, and its sister species, *Globicephala melas*, or long-finned pilot whale, which has an anti-tropical distribution throughout the worlds oceans, except in the North Pacific Ocean. However, in the 1980s, Japanese scientists described two distinct morphological types of short-finned pilot whale using specimens collected during the drive fishery in Japan (Kasuya et al., 1988). These two types, which differed in body length, skull shape, and coloration pattern, were also found to be genetically distinct based on mitochondrial control regions (Wada, 1988; Kage,

1999; Oremus et al., 2009). Their ranges are thought to be non-overlapping off the coast of Japan, inhabiting regions to the north and south of the Kuroshio-Oyashio Extension Current, and they exhibit demographic differences such as the seasonal timing of reproduction and mating (Kasuya and Marsh, 1984). Based on their ranges off the coast of Japan, scientists have hypothesized that short-finned pilot whales may be distributed according to sea surface temperature, with morphologically and genetically distinct tropical and temperate population or sub-species (Polisini, 1980).

Conservation management for short-finned pilot whales is limited. They are currently managed in the United States as a single species with two stocks: a California Current stock and a Hawaiian stock (Carretta et al., 2016). In the Southern California Bight, a large population that once inhabited the region (Dohl et al., 1980) largely disappeared from the region for unknown reasons, coincident with the 1982/1983 El Niño. Sightings after that time period were rare, and primarily occurred during warm-water years (Barlow, 2016). The Bight population is thought to have been competitively displaced by Risso's dolphins, which have a similar ecological niche (Shane, 1995). Today, a small population of approximately 836 individuals inhabits the California Current (Barlow, 2016; Carretta et al., 2016). South of the California Current, there is a large gap in the distribution of the species (Figure 1) (Hamilton et al., 2009). Another population of short-finned pilot whales, with an abundance of 160,200 individuals, inhabits the coastal and pelagic waters of the Eastern Tropical Pacific (Wade and Gerrodette, 1993).

The Hawaiian stock consists of about 19,500 short-finned pilot whales (Bradford et al., 2017), with a range extending from the coastal and neritic waters surrounding the Main Hawaiian Islands to the Northwest Hawaiian Islands and nearby pelagic waters. Longitudinal observations and photo identification studies of animals in this area, conducted since 2000, indicate strong island philopatry and a high degree of social structure within island groups, driven by natal-group philopatry (Figure 2) (Mahaffy et al., 2015). It is
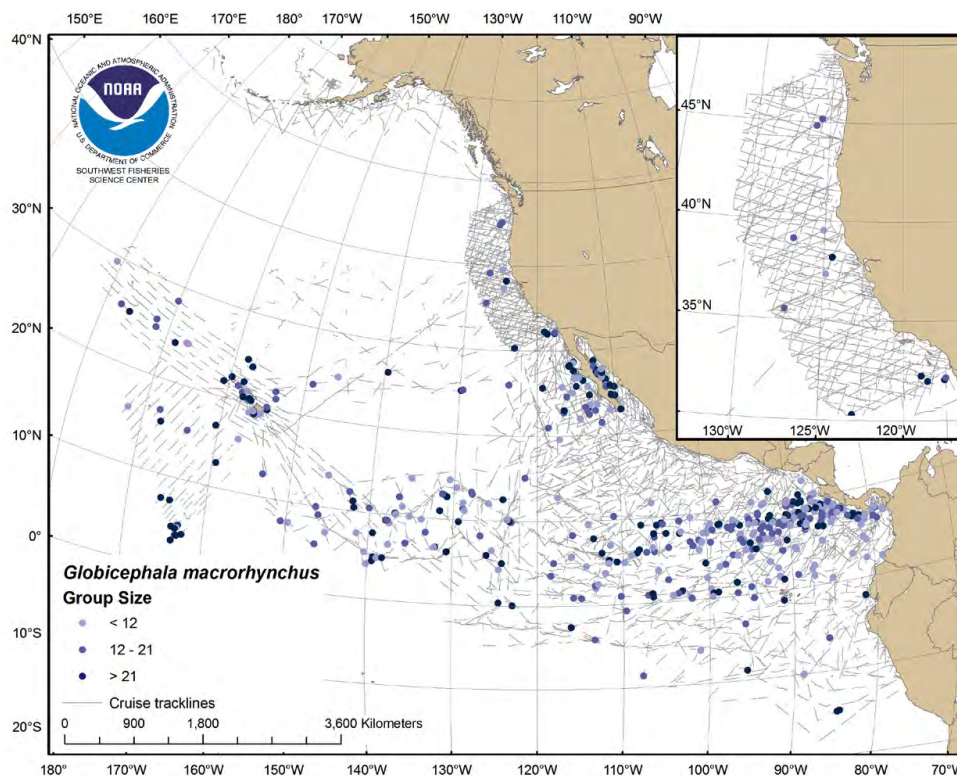
Figure 1.1: *Distribution of observations of short-finned pilot whales (circles) during NOAA marine mammal surveys (gray lines) conducted from 1986-2005. Figure from Hamilton et al. (2009).*

possible that social structure is driven in part by genetic relatedness, as is thought to occur in a similar population off Madeira Island (Alves et al., 2013), although the extent to which genetic similarity drives social structure in short-finned pilot whales is unknown. These data also indicate the presence of an insular, resident population around the Main Hawaiian Islands, based on a high occurrence of multi-year re-sights (Baird et al., 2013; Baird, 2016).

Population structure and divergence within short-finned pilot whales are poorly understood, at both regional and local spatial scales. At a regional scale, the taxonomic status of the two morphotypes identified off Japan, as well as the relationships among global populations of short-finned pilot whales, remains unclear. It is possible that short-finned pilot whales comprise two or more sub-species or species globally; additional data are needed throughout the range of the species to test this hypothesis, including genetic and
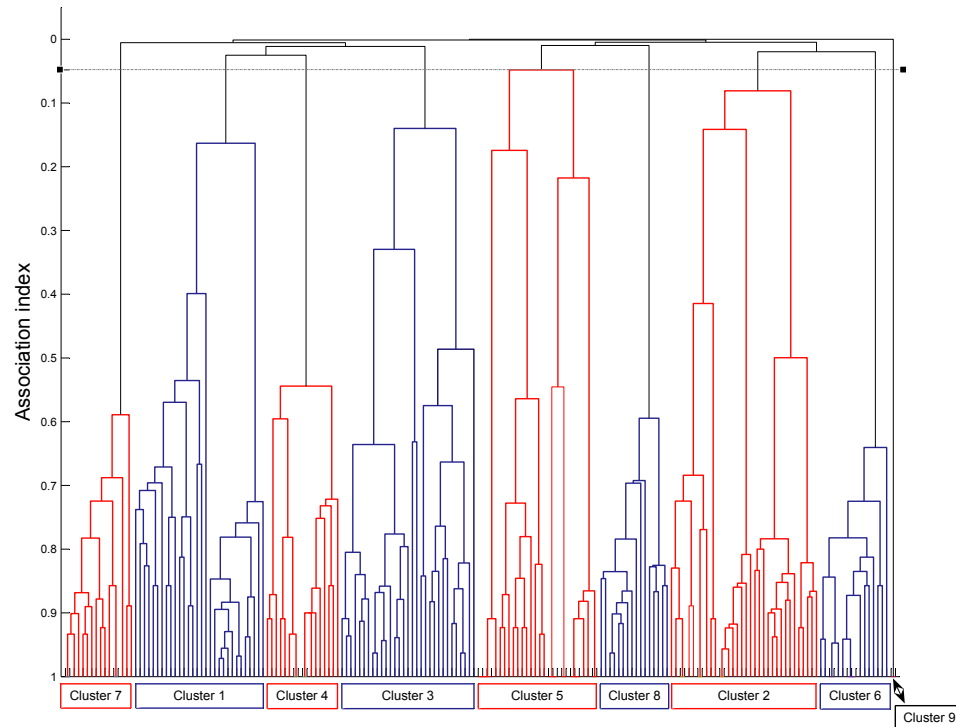
Figure 1.2: *Social structure of short-finned pilot whales off Hawaii Island, which preferentially associate with specific individuals their entire lives. Figure from Mahaffy et al. (2015).*

other supporting data (e.g. acoustic data, photo identification data, or morphometric data).

The Hawaiian stock of short-finned pilot whales may comprise multiple populations, including an insular population close to the islands and a pelagic population. Additional genetic or acoustic structure may be found among communities or social groups within the Hawaiian Islands; however, it is unknown whether the social organization of short-finned pilot whales is driven by genetic relatedness or other mechanisms, including environmental, ecological, or oceanographic factors.

In the next four chapters, I explore genetic and acoustic structure in short-finned pilot whales, both globally and locally, within the Hawaiian stock, in order to better understand short-finned pilot whale population structure and drivers of divergence. The results of this thesis improve our knowledge of the links between social and genetic structure in short-finned pilot whales, and allow us to compare the flow of genetic versus cultural information.

Finally, as empirical data to test gene-culture evolutionary theory are limited outside humans, this research lays the foundation for applying that theory to short-finned pilot whales, and provides a dataset that can be used to improve our theoretical understanding of the links between social and genetic structure.

Globally, I examine genetic population structure in the Pacific, Indian, and Atlantic Oceans using mitochondrial markers, and examine the relationship between these populations and the two morphotypes described off the coast of Japan. I further test the hypothesis that sea surface temperature drives the distribution of morphologically/genetically distinct types or populations of short-finned pilot whales.

The results of this genetic analysis informs an analysis of acoustic structure in the Pacific Ocean. I stratify acoustic recordings collected throughout the eastern and central Pacific Ocean, as well as around the Hawaiian Islands, into populations defined using genetic data, and test for acoustic differentiation among them. Acoustic differentiation would indicate geographic isolation among these populations. Using acoustic data from genetically-defined populations, I develop an algorithm to classify acoustic recordings from areas where genetic data are lacking, which may improve our knowledge of distributional boundaries among populations, and allow us to define areas of potential overlap.

In the second half of my thesis I focus on the Hawaiian stock of short-finned pilot whales, where longitudinal observations and photo ID analyses provide a comprehensive description of social structure and habitat use by individuals around the Main Hawaiian Islands, to explore local drivers of population structure at a population and sub-population level. I use a combination of mitochondrial and nuclear markers to look for oceanographically- or ecologically-stratified populations within the Hawaiian stock, as well as socially-stratified structure within populations. I examine relatedness to test the hypothesis that social structure is genetically driven, i.e. that individuals preferentially associate with close relatives; conversely, I test whether social structure drives genetic structure, i.e. that preferential

association among social groups restricts access to potential mates.

Finally, I examine the variability in the vocal repertoire of short-finned pilot whales in Hawaii, to test the possibility that vocal repertoire is a proximate mechanism used in the maintenance of social structure. Using recordings collected around the Main Hawaiian Islands, I document acoustic differentiation among social groups and island communities.

Differences in acoustic and genetic structure, either at a regional or local level, may indicate a difference in the rate of genetic or cultural divergence. On the other hand, an agreement between the two data types would indicate that cultural/ecological and genetic divergence are occurring in concert, possibly in a manner that acts to sustain the continued divergence at a population or sub-population level within the species. As in other social marine mammals, most notably the killer whale (e.g. Foote et al., 2016), the existence of groups that are socially/ecologically distinct as well as genetically distinct, may be an indicator of an ongoing process of ecological and cultural speciation occurring within short-finned pilot whales.

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Chapter 2

Redrawing the map: mtDNA provides new insight into the distribution and diversity of short-finned pilot whales in the Pacific Ocean

Redrawing the map: mtDNA provides new insight into the distribution and diversity of short-finned pilot whales in the Pacific Ocean

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Abstract

Correlations between morphological and genetic data provide evidence to delineate species or evolutionarily significant units, which then become the units to conserve in management plans. Here, we examine the distribution and genetic differentiation of two morphotypes of short-finned pilot whale (*Globicephala macrorhynchus*) in the Pacific Ocean. Mitochondrial control region sequences from 333 samples were combined with 152 previously published sequences to describe genetic variability globally and population structure in the Pacific. Although genetic variability is low, we found strong differentiation at both broad and local levels across the Pacific. Based on genetics, two types are distributed throughout the Pacific, one predominantly in the eastern Pacific and the other in the western and central Pacific. In the eastern Pacific Ocean, no correlation was found between distribution and sea surface temperature. The two types have broad latitudinal ranges, suggesting their distributions are likely driven by more complex factors, such as prey distribution, rather than sea surface temperature.

Key words: short-finned pilot whale, *Globicephala macrorhynchus*, phylogeography, distribution, genetics, southern form, northern form.

Comparative morphology has traditionally been the primary method for the identification of species. In recent years, however, genetic data have played an increasingly important role in taxonomic studies. Though genetic and morphological data are often complementary, the relationship between genotype and phenotype can be complex. Morphological traits, for example, have been found to be ecologically plastic in many cases (*e.g.*, Inoue *et al.* 2013, Scharnweber *et al.* 2013), and convergent evolution can confound the relationship between morphology and genetic structure. For example, dolphin species in four different families have evolved similar phenotypes to live in freshwater, and echolocation has developed twice in mammals through similar

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evolutionary pathways (Parker *et al.* 2013). For these and a variety of other reasons, some geneticists caution against using differences in morphology alone to classify populations (Allendorf and Luikart 2011).

However, in many cases genetic and morphological patterns are correlated (*e.g.*, Punnett 1904), making it possible for morphological variability to be used as a proxy for genetic variability and *vice versa*. These correlations can be useful in identifying barriers to dispersal or gene flow in elusive species such as cetaceans, and in some cases can support the taxonomic delineation of undiscovered or cryptic species, subspecies, or evolutionarily significant units (Taylor 2005).

The short-finned pilot whale (*Globicephala macrorhynchus*) inhabits both coastal and pelagic waters in tropical and subtropical regions globally. Two morphotypes have been identified in the Pacific Ocean (Yamase 1760, Kasuya *et al.* 1988). These morphotypes have been referred to as the northern and southern types based on their distribution off Japan, where they were first described (Kasuya *et al.* 1988). However, because their distribution outside of Japan is poorly known, we will refer to them by names originally ascribed to them by Yamase (1760): the northern type is called *Shiho goto* (goto meaning short-finned pilot whale) and the southern type is called *Naisa goto*. They differ in body size, melon shape, color pattern, and number of teeth. The Shiho type is larger and has a round melon and light saddle patch with a distinct posterior boundary, while the Naisa type is smaller with a square melon and a darker, indistinct saddle patch (Yonekura *et al.* 1980, Kasuya *et al.* 1988, Miyazaki and Amano 1994). Gray (1846) designated these forms as different species. The Naisa type was called *G. sieboldii* (Gray 1846), and the Shiho type was named *G. sibo* (Gray, 1846). A third species, *G. scammonii* (Cope 1869) with a skull morphology similar to that of the Shiho type of northern Japan, was described from a pilot whale collected off Baja California, Mexico. These three nominal species were all subsequently considered as junior synonyms of *G. macrorhynchus* (van Bree 1971).

Off the coast of Japan, the distributions and breeding phenology of the Shiho and Naisa types are well documented and largely nonoverlapping (Kasuya and Marsh 1984, Kasuya *et al.* 1988, Yonekura *et al.* 1980). Several studies indicate that they are separated by the Kuroshio-Oyashio Extension (KOE) Current, which influences the distribution of several other species (Briggs 1974, Kasuya *et al.* 1988), with the Naisa type inhabiting the warm-temperate waters of the Kuroshio Current while the Shiho type inhabits areas with cold-temperate waters of the Oyashio Current (Kasuya *et al.* 1988). The closely related long-finned pilot whale (*Globicephala melas*) has been shown to exhibit similar temperature-driven population structure in the North Atlantic (Fullard *et al.* 2000). However, some evidence suggests that the relationship between sea surface temperature (SST) and the geographic boundaries of these two types off Japan is weak, and is likely a proxy for other drivers (Kasuya *et al.* 1988). In addition to being geographically segregated off Japan, their breeding seasons do not overlap: the peak breeding season of the Shiho type animals (September) is later than that of the Naisa type animals (May) (Kasuya and Marsh 1984). These aspects of their ecology indicate that the animals are likely reproductively isolated, and it has been suggested that the two types may be distinct subspecies off the coast of Japan (Kasuya 1986, Kasuya *et al.* 1988, Wada 1988).

Previous studies suggest that the distributions of the Shiho and Naisa morphotypes extend beyond Japan. Naisa morphotypes have been found in Southeast Asia (Chen *et al.* 2014), Hawai'i (Polisini 1980; RWB, unpublished data) and the North Atlantic Ocean (RLB, unpublished data), and Shiho morphotypes have been found in the California Current and off Peru (Cope 1869, Polisini 1980, Reyes-Robles 2009).

These studies suggest a tropical form with Naisa type morphology and a cold-temperate form with Shiho type morphology (Polisini 1980, Kasuya et al. 1988). However, the full ranges of the morphotypes are not known due to a lack of morphological data in much of their geographic range, and published data to support this hypothesis are limited from many areas (e.g., Eastern Tropical Pacific [ETP] and Hawai'i).

Kage (1999) found that morphology was strongly correlated with genetics for the two morphotypes off the coast of Japan, although his sample size was small for the Shiho morphotype. Oremus et al. (2009) showed that all Naisa haplotypes were characterized by a diagnostic substitution, and therefore suggested that the Naisa type may be a distinct subspecies. While these studies provide support for the delineation of Shiho and Naisa type short-finned pilot whales off the coast of Japan, they did not have data to describe the distribution of the two types of short-finned pilot whales in other parts of the North Pacific. Genetic analysis of short-finned pilot whales from throughout the Pacific Ocean could improve our understanding of the distribution of these two types, especially in data-deficient areas such as Hawai'i and the eastern Pacific Ocean (ETP and California Current).

In this study, we examine the population structure of short-finned pilot whales in the Pacific Ocean using new genetic samples, primarily available from the eastern Pacific Ocean and Hawai'i, as well as SE Asia and the South Pacific, Indian and western North Atlantic Oceans. We combine these new genetic samples with existing sequence data (Oremus et al. 2009) to examine global patterns of genetic diversity and distribution. We further investigate whether any patterns of genetic differentiation corroborate the current hypothesis of a SST-based distribution of the Shiho and Naisa types (e.g., Kasuya et al. 1988), with special consideration for areas where morphological data are limited, such as the ETP and Hawai'i. Finally, we use our combined data set to improve our understanding of interbasin divergence in addition to divergence within the Pacific Ocean. Geographically separated distributions could support the classification of these two types as distinct species or subspecies.

Methods

Sample Collection

DNA sequences from *G. macrorhynchus* were generated from samples in the Southwest Fisheries Science Center (SWFSC) Marine Mammal and Turtle Molecular Research Sample Collection or obtained from GenBank (Benson et al. 2006). The samples archived at SWFSC (*n* = 333, Fig. 1) were collected between 1984 and 2011, primarily from biopsies taken during SWFSC research cruises along the west coast of the United States, in the ETP, the Northwest Hawaiian Islands, and Guam. Seventy-two samples were collected by Cascadia Research Collective from the main Hawaiian Islands as part of a long-term photo-identification study (Mahaffy et al. 2015, Baird et al. 2013). Additional samples were collected from strandings in New Zealand, Cambodia, Hawai'i, and the Pacific, Atlantic, and Gulf of Mexico coasts of the United States, and from fisheries bycatch off the coast of California and in the Phillipines. Field sampling protocols included identifying individuals visually or with photographs to minimize resampling of individuals. Samples were stored at –80°C, or fixed in either a salt-saturated 20% DMSO solution or 100% ethanol and permanently archived in a –20°C freezer.
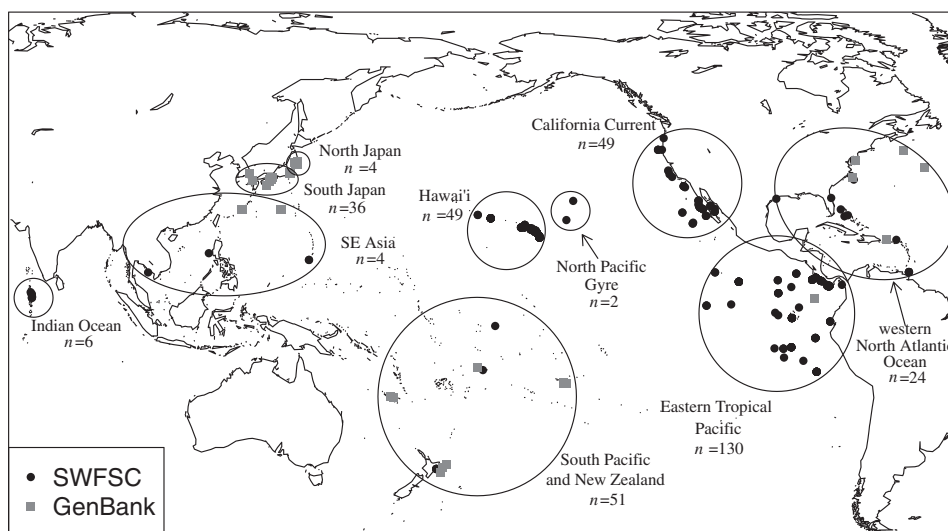
Figure 1. Sampling locations for all samples of short-finned pilot whale used in the present study. Circles represent the location of samples from the SWFSC Marine Mammal and Turtle Molecular Research Sample Collection. Squares indicate the approximate location of sequences taken from GenBank, based on locations published in Oremus *et al.* (2009). Ellipses delineate the strata used for tests of population differentiation; the break between the ETP and California Current represents a natural break in the known distribution of short-finned pilot whales. The two samples collected northeast of the Hawaiian Archipelago ("North Pacific Gyre"), and the market samples from Japan, were excluded from all statistical analyses except for the Median Joining Network.

Additionally, 15 tooth samples were obtained from skulls housed at the Los Angeles County Museum, and one from the American Museum of Natural History, in order to test the connection between morphology and haplotype in short-finned pilot whales outside of Japan.

DNA Sequencing

DNA was extracted from skin and muscle samples using a sodium chloride precipitation protocol (Miller *et al.* 1988), Qiagen DNeasy Blood and Tissue Kit (#69506, Qiagen, Germantown, MD) or a phenol-chloroform protocol (Sambrook *et al.* 1989). The hypervariable mtDNA control region was amplified and sequenced in two parts of approximately 420 bp and 560 bp, with approximately 20 bp of overlap between the two sequences. Primers, PCR, and sequencing methods have been described previously by Martien *et al.* (2014). The resulting combined sequence was 962 base pairs long, and was assembled using SEQED, version 1.0.3 (ABI), Sequencher software (versions 4.1 and 4.8; Gene Codes, Ann Arbor, MI) or Geneious (version 6.1.5, Biomatters Ltd, Auckland, New Zealand). New sequences were accessioned into NCBI GenBank with accession numbers KM624040-KM624062.

Short-finned pilot whale sequences from the 5′ end of the control region that were already published in GenBank ($n = 152$, Fig. 1) were included to better represent global pilot whale haplotypic diversity. The majority of these sequences were from a study of the phylogeography of pilot whales in the western Pacific Ocean (Oremus

et al. 2009; FJ513328.1-FJ513341.1), with additional sequences from Vilstrup *et al.* (2011; JF339974-JF339976), Siemann (1994; U20921-U20923), Baker (direct submission, DQ145030-DQ145033), and Caballero *et al.* (2008; EU121124). The sequences acquired from GenBank were 345 bp in length; for the analyses that included these samples, all SWFSC sequences were truncated to match.

Tooth samples were extracted and sequenced according to the methods outlined in Morin *et al.* (2006). Two primer sets were used to sequence a 300 bp segment of the 5′ mitochondrial control region: TRO (5′-CCTCCCTAAGACTCAAGGAAG-3′, developed at SWFSC) and A3 (5′-AATACGRGCTTTAACT-3′, Rosel *et al.* 1994) formed the first set; the second set consisted of D (5′-CCTGAAGTAAGAACA-GATG-3′, Rosel *et al.* 1994) and A3r (5′-GATAAGTTA AAGCTCGTATT-3′, developed at SWFSC).

Data Analysis

New sequences were aligned using a MAFFT alignment with default parameters (scoring matrix: 200PAM/k = 2, gap open penalty: 1.53, offset value: 0.123) in the Geneious software package (Katoh and Kuma 2002). Once the alignment was completed, sequences were reexamined. Any haplotypes represented by only a single sequence or haplotypes with a single base-pair difference from the most similar haplotype were reviewed for accuracy. Unique haplotypes were repeat sequenced in order to ensure the accuracy of the sequence. Once the newly generated sequences were verified, they were aligned with previously published GenBank sequences using the MAFFT alignment described above.

Samples were stratified according to their sampling location, resulting in nine broad geographic strata that were used for analysis of genetic differentiation (Fig. 1). These strata were chosen, wherever possible, based on natural breaks in the distribution of short-finned pilot whales (*e.g.*, the break in distribution between the ETP and California Current (Hamilton *et al.* 2009), and the break between north and south Japan); where this information was not available, strata were defined based on breaks in the sampling distribution. Two samples collected between Hawai'i and the North American coast ("North Pacific Gyre," Fig. 1) were not included in any statistical analyses due to their geographic isolation from all other samples. Sequences from Japanese market samples (Oremus *et al.* 2009) were also excluded from all statistical analyses because neither the geographic origin nor morphology of the animals from which they came was known. Therefore, the two North Pacific Gyre samples and all Japanese market samples were used only in the geographic analysis and median-joining network. Because short-finned pilot whales are known to exhibit social structure and may associate closely with relatives, there exists the potential for nonindependence in the full data set. Therefore, the data set was adjusted to include one sample of each haplotype from each encounter, in order to control for nonindependence, for the diversity and pairwise distance calculations.

Haplotype (*h*) and nucleotide (*π*) diversity, theta (θ_H, a measure of genetic diversity based on population size and mutation rate), and pairwise estimates of population differentiation (F_{ST}, Φ_{ST}) were calculated in Arlequin (Excoffier and Lischer 2010) for the adjusted data set using the short sequences (345 bp). The North Japan stratum was removed from pairwise analyses due to small sample size in the adjusted data set ($n = 1$). For F_{ST}, we calculated the genetic distance between haplotypes using the Tamura-Nei model with invariant sites, without a gamma correction (Tamura and Nei 1993), which was identified by jModelTest2 (Guindon and Gascuel 2003,

Darriba *et al.* 2012) as the substitution model that best fit our data. We assessed the statistical significance of the F_{ST} and F_{ST} values through permutation tests with 10,000 permutations. We also used Fisher's exact tests of differentiation (Raymond and Rousset 1995) with 10,000 permutations to test the null hypothesis of no population structure among the strata, also conducted in Arlequin.

In the eastern Pacific, long-sequence (962 bp) samples from the adjusted data set were pooled and divided into temperate (SST < 25°C) and tropical (SST > 25°C) strata (Fig. 2) based on the definition of temperate and tropical waters in the eastern Pacific (Fiedler and Talley 2006). Mean monthly 0.5°-square SST values for the date and location where each sample was collected were acquired from the Simple Ocean Data Assimilation version 2.2.4 reanalysis (Carton and Giese 2008) for the purpose of binning samples into temperate (SST < 25°C) and tropical (SST > 25°C) strata. Differentiation analyses (F_{ST}, Φ_{ST}) were conducted between temperate and tropical strata to examine the correlation between sea surface temperature and local structure in the eastern Pacific Ocean.
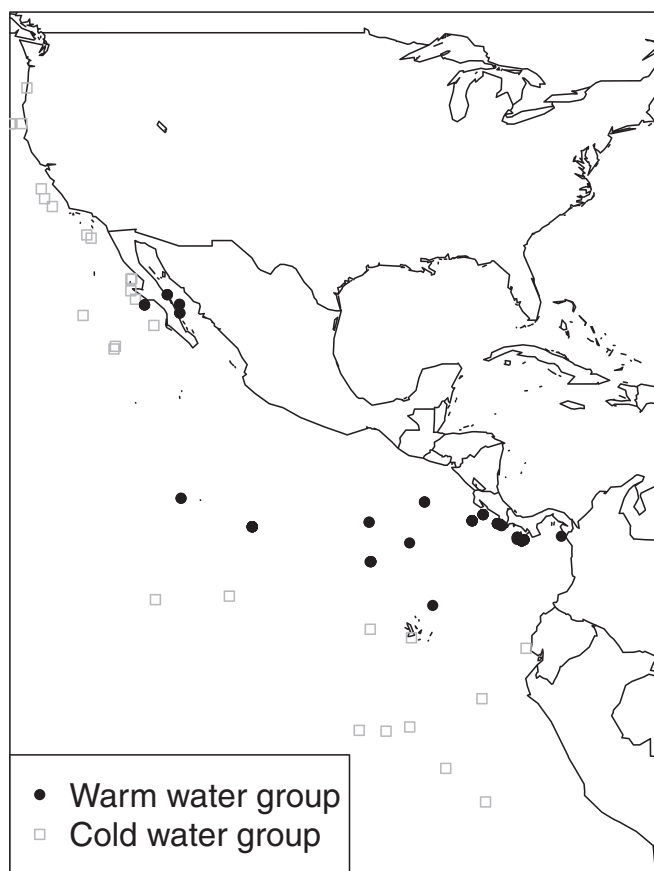
Figure 2. Distribution of temperate and tropical water groups of short-finned pilot whales in the eastern Pacific Ocean, showing the sample stratification used to test for localized structure driven by sea surface temperature. Temperate and tropical water samples were separated at 25°C based on the estimated SST at their collection location on the date they were collected. Circles represent warm water samples while squares represent cold water samples. Only long-sequence (962 bp) samples were used for this analysis. Warm water group $n = 22$, Cold water group $n = 34$.

Finally, a hierarchical AMOVA was conducted on the adjusted data set of short sequences (345 bp) to determine how much of the total variance is described by differences among regions *vs.* among strata within regions. For this analysis, strata outside the Pacific Ocean were excluded. The Pacific Ocean strata were divided into three regions: North/East Pacific (California Current, ETP, and North Japan strata), Central Pacific (Hawai'i, South Japan, and SE Asia strata) and South Pacific. The first two regions correspond to the known geographic distributions of the Naisa and Shiho types (see Results), while the third corresponds with the area where most haplotypes are unknown.

We constructed median-joining networks (MJN) from the full data set using the algorithm of Bandelt *et al.* (1999), implemented in the software package Network 4.6.1.2 (available at http://www.fluxus-engineering.com/sharenet.htm), with none of the optional analyses. A median-joining network was first constructed using the 962 bp mtDNA haplotypes sequenced at the SWFSC. A second median-joining network was constructed using combined haplotypes from the SWFSC and GenBank using the shorter portion of the control region (345 bp).

Using previously published sequence data from animals of known morphology (based on skull and body measurements), we identified four haplotypes from known Naisa type animals and one haplotype from known Shiho type animals (Kage 1999). These previously published haplotypes were designated as "known Shiho" or "known Naisa" haplotypes, and are referred to as such in the Results and Discussion. We consider individuals with either a known Shiho or known Naisa haplotype to be either Shiho or Naisa type short-finned pilot whales, respectively. The distribution of all individuals with known Shiho or Naisa haplotypes was mapped to examine the range of each type of animal.

Results

A total of 333 tissue samples from the SWFSC archive were sequenced and analyzed (Fig. 1, Table S1). Using the full 962 bp sequences, we detected 23 unique haplotypes (Table 1) with 24 polymorphic sites. When the sequences generated at SWFSC were truncated to 345 bp for comparison to the GenBank sequences the number of unique haplotypes was reduced to 20. Fourteen haplotypes, representing 152 samples, were obtained from GenBank, representing samples from the North Japan, South Japan, SE Asia, South Pacific, ETP, and western North Atlantic strata. Eight of the haplotypes obtained from GenBank were not present in the samples sequenced at SWFSC, resulting in a total of 28 short (345 bp) haplotypes. A complete list of tissue samples, with their short haplotypes and corresponding long haplotypes, can be found in Table S1.

Using unadjusted short sequence data, the ETP stratum exhibited the largest number of haplotypes in the sample set ($n = 8$, Table 1). There was a large number of haplotypes in the Japanese market samples ($n = 10$), but this group likely include haplotypes from both Naisa and Shiho type short-finned pilot whales. The Hawaiian Islands were unique in that only four haplotypes were found there despite a large sample size ($n = 123$). Of those four haplotypes, two were known Naisa haplotypes, J and K, with J representing 94.3% (116) of the sampled individuals (Table 1). One individual sampled west of Ni'ihau had haplotype C, a haplotype common to the South Pacific and Japanese market samples. Haplotype 12 was found only in the Northwestern Hawaiian Islands (NWHI), which had

Table 1. Short-finned pilot whale haplotype frequencies by strata (Fig. 1), determined using the 345 bp consensus region from SWFSC and GenBank sequences. Haplotypes A through N are labeled according to Oremus et al. (2009); additional haplotypes are numbered 2–15. Haplotypes A, D, and E from Oremus et al. (2009) were subdivided into seven haplotypes using the 962 bp samples from SWFSC; these haplotypes and their frequencies are shown below the line.

Haplotype	California Current	Eastern Tropical Pacific	North Japan (Shiho type)	Market Japan	South Japan (Naisa type)	Hawai'i	North Pacific Gyre	South Pacific	SE Asia	Indian Ocean	Western North Atlantic Ocean	Total
2	2	14										16
3	1											1
4		1										1
5		2										2
6		8										8
7		1										1
8		3										3
9	1											1
10		5										3
11							1					1
12						5						5
13								1				1
14									1			1
15											1	1
A								25	2	5	5	38
B								1				1
C				10		1		23				34
D											18	18
E	45	96	4	6								151
F				1								1
G				3								3
H				1								1
I				7	8							15

(*Continued*)

Table 1. (Continued)

Haplotype	California Current	Eastern Tropical Pacific	North Japan (Shiho type)	Market Japan	South Japan (Naisa type)	Hawai'i	North Pacific Gyre	South Pacific	SE Asia	Indian Ocean	Western North Atlantic Ocean	Total
J				3	1	116						120
K				6	7	1	1	1	1	1		18
L				3								3
M				14	20							34
N				2								2
Total	49	130	4	56	36	123	2	51	4	6	24	486
A1								3[a]		5		8
A2									2		4[a]	6
D1											2	2
D2											2	2
E1	2											2
E2	6											6
E3	37	95[a]										132

[a]Note that the total of these haplotypes does not equal the haplotype total above the line, as additional samples from Oremus *et al.* (2009) are included in the totals above line.

14 of the total 123 samples from Hawai'i. Short-finned pilot whales from the ETP and California Current exhibited two shared haplotypes, E and 2. They shared one haplotype with North Japan (E), which until this study was the only known Shiho haplotype in all ocean basins in which short-finned pilot whales occur, and represented 73.8% of the samples in the ETP and 90% of the samples in the California Current (Table 1).

Ten tooth samples from animals with known morphology and sampling location were successfully sequenced (Table 2). The 300 bp segment was compared to the 345 bp haplotypes to identify genetic type for each individual. All Naisa morphotypes had haplotypes matching previously known Naisa haplotypes. Five of the six Shiho morphotypes had haplotype E, the only known Shiho haplotype. The sixth Shiho morphotype had haplotype 5, a haplotype found in the eastern Pacific, which differs from haplotype E by a single substitution.

The SE Asia stratum ($n = 3$) exhibited high haplotypic and nucleotide diversity (Table 3), while North Japan had the lowest, due to small sample size ($n = 1$). All three estimates of diversity were also low in Hawai'i and the eastern Pacific relative to other strata, despite the large samples from these two strata.

Pairwise estimates of differentiation ranged from 0.02 to 0.77 for F_{ST} and 0.00 to 0.88 for Φ_{ST} (Table 4). F_{ST} and Φ_{ST} values were lowest between the ETP and California Current. Values were also lower among SE Asia (*i.e.,* Philippines, Cambodia, and Guam), the South Pacific and New Zealand, and the Indian Ocean, though the small sample size from these areas reduces power to detect differentiation and increases uncertainty in these estimates. F_{ST}, Φ_{ST}, and Fisher's exact tests for differentiation (Table 4, 5) were not significant between the ETP and California Current, nor between South Japan (Naisa) and SE Asia. F_{ST} and Fisher's exact tests for differentiation were nonsignificant among the Indian Ocean, South Pacific and New Zealand, and SE Asia; however, lack of differentiation between these three strata could be due to small samples sizes. It is important to note that we did not calculate differentiation between the North Japan (Shiho) stratum and any other strata due to subsampling that reduced the sample size in that stratum to $n = 1$. However, using the full data set, the North Japan

Table 2. Haplotypes and morphological types (determined from skull measurements) of ten short-finned pilot whales. Note that haplotypes were determined by comparing 300 bp sequences to 345 bp sequences, but there are variable sites in some haplotypes in base pairs 301-345.

ID	Source ID	Morphotype	Haplotype	Sample location
136113	LACM027408	Naisa	J	Hawai'i
136114	LACM054112	Shiho	E	California
136116	LACM054119	Shiho	E	California
136118	LACM054121	Naisa	M	Japan
136119	LACM054122	Naisa	M	Japan
136121	LACM054124	Naisa	M	Japan
136122	LACM054125	Shiho	E	California
136123	LACM054130	Shiho	E	California
136124	LACM054139	Shiho	E[a]	California
136126	LACM054184	Shiho	5	California

[a]This sample is likely haplotype E; it had one ambiguous base pair at a site that was invariable for all other haplotypes.

Table 3. Diversity indices for nine global strata (Fig. 1) calculated using short sequences from the adjusted data set. Standard deviation for haplotype diversity, nucleotide diversity, and θ_H (genetic diversity calculated using observed homozygosity) are shown beneath the values as a $\pm$ value.

	California Current	Eastern Tropical Pacific	North Japan (Shiho type)	South Japan (Naisa type)	Hawai'i	South Pacific and New Zealand	SE Asia	Indian Ocean	Western North Atlantic
Sample size	25	35	1	10	29	23	3	5	21
No. haplotypes	4	8	1	4	4	5	3	2	3
No. variable sites	5	9	0	3	8	7	4	3	2
Haplotype diversity (h)	0.297 ± 0.115	0.560 ± 0.095	1.000 NA	0.778 ± 0.091	0.200 ± 0.10	0.640 ± 0.065	1.000 ± 0.272	0.400 ± 0.237	0.267 ± 0.120
Nucleotide diversity (π)	0.002 ± 0.002	0.002 ± 0.002	0.000 NA	0.004 ± 0.003	0.002 ± 0.002	0.004 ± 0.003	0.008 ± 0.007	0.004 ± 0.003	0.008 ± 0.001
θ_H	0.314 ± 0.172	0.952 ± 0.375	NA	2.746 ± 1.548	0.186 ± 0.113	1.346 ± 0.390	NA	0.496 ± 0.492	0.270 ± 0.165

Table 4. Pairwise differentiation values for eight geographical strata (Fig. 1) calculated using short sequence data from the adjusted data set. F_{ST} is shown below the diagonal, Φ_{ST} is shown above the diagonal. P-values are shown in parentheses. Significant P-values are in bold.

	California Current $n = 25$	Eastern Tropical Pacific $n = 35$	South Japan (Naisa) $n = 10$	Hawai'i $n = 29$	South Pacific and New Zealand $n = 23$	SE Asia $n = 3$	Indian Ocean $n = 5$	Western North Atlantic $n = 21$
California Current		−0.023 (<0.87526)	0.809 (**<0.00001**)	0.852 (**<0.0001**)	0.521 (**<0.0001**)	0.736 (**<0.00079**)	0.549 (**<0.00059**)	0.78 (**<0.0001**)
Eastern Tropical Pacific	0.02 (<0.17038)		0.777 (**<0.00001**)	0.823 (**<0.00001**)	0.479 (**<0.0001**)	0.685 (**<0.00079**)	0.47 (**<0.0004**)	0.712 (**<0.0001**)
South Japan (Naisa)	0.527 (**<0.00001**)	0.359 (**<0.00001**)		0.574 (**<0.0001**)	0.655 (**<0.0001**)	0.105 (<0.21602)	0.534 (**<0.00218**)	0.851 (**<0.0001**)
Hawai'i	0.755 (**<0.00001**)	0.609 (**<0.00001**)	0.561 (**<0.00001**)		0.744 (**<0.0001**)	0.639 (**<0.0001**)	0.738 (**<0.00416**)	0.882 (**<0.0001**)
South Pacific and New Zealand	0.536 (**<0.00001**)	0.404 (**<0.00001**)	0.296 (**<0.0002**)	0.59 (**<0.00001**)		0.48 (**<0.0099**)	0.202 (<0.09128)	0.58 (**<0.0001**)
SE Asia	0.567 (**<0.00495**)	0.331 (<0.02277)	0.082 (<0.27304)	0.67 (**<0.00535**)	0.082 (<0.27591)		0.157 (<0.36967)	0.816 (**<0.00168**)
Indian Ocean	0.679 (**<0.0001**)	0.482 (**<0.0001**)	0.347 (**<0.00515**)	0.76 (**<0.00001**)	0.103 (<0.18879)	0.022 (<0.45956)		0.674 (**<0.0002**)
Western North Atlantic	0.717 (**<0.00001**)	0.564 (**<0.00001**)	0.536 (**<0.00001**)	0.771 (**<0.00001**)	0.52 (**<0.00001**)	0.571 (**<0.01119**)	0.675 (**<0.00059**)	

Table 5. Results of Fisher's exact test of differentiation, testing the null hypothesis of nondifferentiation between nine strata of short-finned pilot whale, from the adjusted data set of short sequences. Results shown as permutation values ± standard deviation. Significant values are in bold. Sample sizes used are the same as Tables 3 and 4.

	California Current	Eastern Tropical Pacific	South Japan (Naisa)	Hawai'i	South Pacific and New Zealand	SE Asia	Indian Ocean
Eastern Tropical Pacific	0.423 ± 0.01						
South Japan (Naisa)	0.000 ± 0.00	0.000 ± 0.00					
Hawai'i	0.000 ± 0.00	0.000 ± 0.00	0.000 ± 0.00				
South Pacific and New Zealand	0.000 ± 0.00	0.000 ± 0.00	0.000 ± 0.00	0.000 ± 0.00			
SE Asia	0.005 ± 0.00	0.008 ± 0.00	0.136 ± 0.00	**0.004 ± 0.00**	0.080 ± 0.00		
Indian Ocean	0.000 ± 0.00	0.000 ± 0.00	0.009 ± 0.00	0.000 ± 0.00	0.274 ± 0.00	0.643 ± 0.00	
Western North Atlantic	0.000 ± 0.00	0.000 ± 0.00	0.000 ± 0.00	0.000 ± 0.00	0.000 ± 0.00	**0.011 ± 0.00**	**0.001 ± 0.00**

(Shiho) stratum is significantly different from all other strata except the ETP and California Current (data not shown).

The hierarchical AMOVA among regions in the Pacific suggested that most genetic variance occurs among regions, with some differentiation among strata within regions (Table S2). Variation among regions accounted for 63% of genetic variance, while approximately 11% of variation occurred among strata within regions and 27% of the variation occurred within strata.

We tested the hypothesis that populations in the eastern Pacific were distributed according to sea surface temperature using full long-sequence data (Fig. 2), and found that the temperate and tropical groups were not significantly differentiated (Fisher's exact $P = 0.7933$), and the magnitude of differentiation between them ($F_{ST} = -0.007$, $P = 0.48$; $F_{ST} = -0.019$, $P = 0.79$) was similar to the comparison between the California Current and ETP strata (Table 4).

The full data set of short-sequence data from SWFSC was compared with previously published data using a median joining network (Fig. 3). The resulting global phylogeography supports the hypothesis that California Current short-finned pilot whales are Shiho type (Oremus *et al.* 2009), with the known Shiho haplotype (E) making up 78% of the stratum. The known Shiho haplotype also represents 73.8% of the ETP stratum. Most of the other ~25% of individuals in the eastern Pacific are only 1–2 base pairs removed from the known Shiho haplotype (*e.g.*, haplotypes
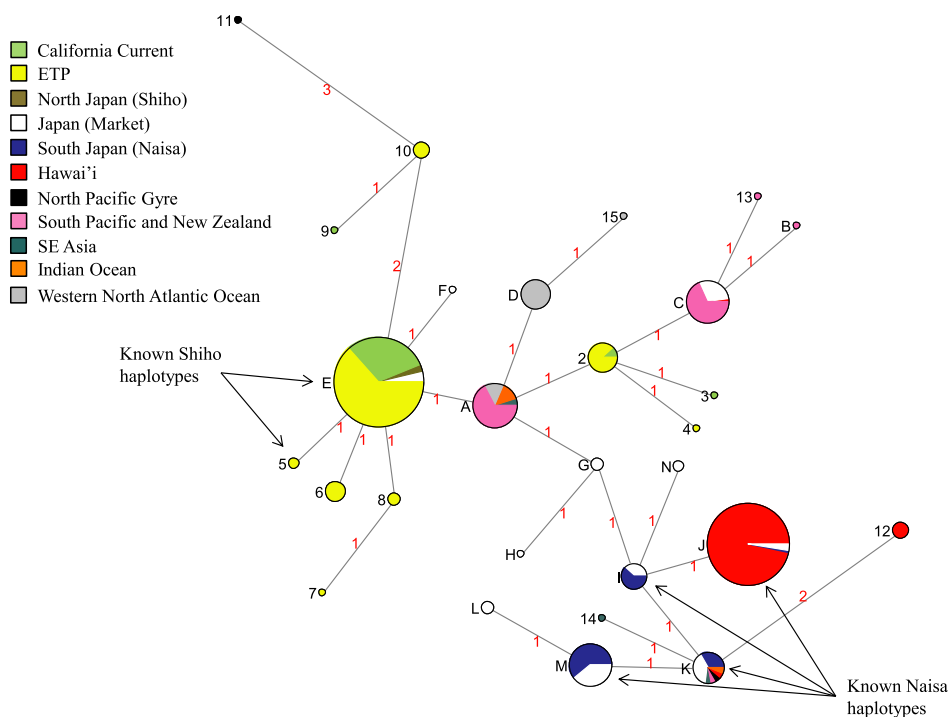
Figure 3. Median joining network created using short (345 bp) sequences from SWFSC and GenBank, including those from Oremus *et al.* (2009). Samples are segregated geographically. Red numbers indicate the number of base pair differences between each haplotype, black labels indicate haplotype. The size of each circle represents the number of individuals with the respective haplotype in the study.

5, 6, 7, 8, 10), and one of these (haplotype 5), was determined to belong to the Shiho morphotype using skulls collected in the eastern Pacific Ocean (Table 2). A few haplotypes found in the eastern Pacific Ocean (haplotypes 2, 3, and 4) were only 2–3 base pairs removed from the known Shiho haplotype (E); it is interesting to note, though, that the path between haplotypes 2–4 and haplotype E, all found in the eastern Pacific Ocean, is through a common haplotype found in the South Pacific and New Zealand stratum. Of the four Hawaiian haplotypes, three were closely related to each other, two of which were known Naisa haplotypes. Most haplotypes from the South Pacific and New Zealand, Indian Ocean, and western North Atlantic strata were grouped together, and clustered with some haplotypes found in the eastern Pacific. Haplotype K, one of the known Naisa haplotypes, was widely dispersed in the Hawai‘i, SE Asia, South Pacific and New Zealand, South Japan, market Japan, North Pacific Gyre and Indian Ocean strata. A median-joining network of the longer 962 bp sequences from the SWFSC samples (Fig. S1) shows no change in the overall pattern seen in the dataset of smaller sequences.

The distribution of the known Shiho haplotype extended from northern Japan to the California Current, and throughout the range of pilot whales in the eastern Pacific Ocean (Fig. 4). The known Naisa haplotypes were found in southern Japan, SE Asia, the South Pacific, and Hawai‘i. No known Shiho or Naisa haplotypes were found in the western North Atlantic Ocean, but the known Naisa haplotype K was found in the Indian Ocean.
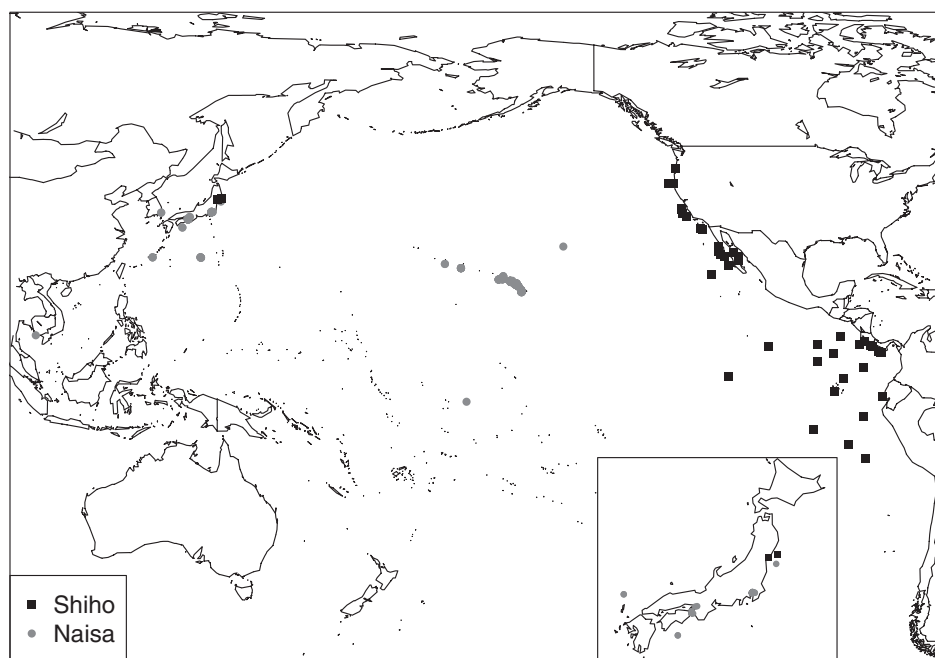
Figure 4. Global distribution of only the known short-finned pilot whale Naisa and Shiho haplotypes, based on previously published DNA sequences from animals of known morphology (skull and body measurements). Shiho type samples are shown as black squares; Naisa type samples are gray circles. Inset: enlarged map of Japan showing details of approximate sample locations (from Oremus *et al*. 2009).

DISCUSSION

Distribution of Shiho and Naisa Types

The taxonomic status of short-finned pilot whales in the Pacific Ocean has been in question since the identification of possible subspecies off of coastal Japan (*e.g.*, Kasuya *et al.* 1988, Oremus *et al.* 2009). While the link between mtDNA haplotypes and morphology is correlative and not causative, it has been used in many taxa to help identify population divergence and speciation (*e.g.*, Avise 1992, Palumbi *et al.* 1997, Oremus *et al.* 2009, Foote *et al.* 2011). The genetic data presented in this paper are not sufficient to resolve the taxonomic question, due to the fact that in highly social cetaceans such as short-finned pilot whales there might be male-mediated gene flow, which mtDNA alone cannot rule out. However, this study provides strong evidence that the distributions of the Shiho and Naisa types are spatio-temporally nonoverlapping in the Pacific Ocean (Fig. 4); this result is consistent with the traditional definition of subspecies as diagnosable geographic forms (Reeves *et al.* 2004).

Our sequences of 10 samples of known morphology provide additional support for the connection between genetic haplotype and morphology in short-finned pilot whales. Notably, this is the first time individuals of known morphology have been sequenced from the eastern Pacific, supporting the conclusion that eastern Pacific short-finned pilot whales are Shiho type animals. Our results also add a new haplotype (5) to those that have been morphologically identified as Shiho haplotypes.

This genetic evidence indicates that the distribution of the two types of pilot whales throughout the Pacific does not follow the north-south distribution found in Japan, therefore the commonly accepted "northern" and "southern" type naming system no longer accurately describes these two types. We recommend that Naisa and Shiho, the historical names used by Yamase (1760) in his original description of these two types, as well as in this study, be re-adopted when referring to the two types of pilot whale in the Pacific Ocean.

Until now the accepted hypothesis has been that the two types of short-finned pilot whale are distributed according to sea surface temperature. In Japan, some evidence suggests that SST may be a proxy for other driving factors (Kasuya *et al.* 1988, Kasuya and Marsh 1984). In the rest of the Pacific Ocean, the morphological and genetic data previously available were limited in number and patchy in their distribution. Using mtDNA we found Naisa type animals in Hawai'i, but Shiho type animals in both tropical and temperate waters in the eastern Pacific Ocean (*i.e.*, in the California Current and ETP strata). Based on this evidence, and the lack of differentiation found when samples in the eastern Pacific Ocean were stratified according to sea surface temperature, the distribution of these two types does not appear to be driven by sea surface temperature. Rather, it is probable that a combination of ecological, environmental, and possibly social factors drives the distribution of short-finned pilot whales.

The expanse of the oligotrophic central Pacific Ocean could act as a barrier to the dispersal of short-finned pilot whales, thus driving the distribution of the two types. Previous evidence has shown that insular populations of this species prefer slope waters (Baird *et al.* 2013, Mahaffy *et al.* 2015), and therefore movements into more offshore pelagic waters may be limited. Furthermore, while short-finned pilot whales do occur continuously between Hawai'i and the eastern Pacific Ocean, there is a large area of low density of pilot whales between Hawai'i and the more productive waters of the ETP (Hamilton *et al.* 2009, Forney *et al.* 2012). However, the presence of

Shiho type pilot whales off of northern Japan and in the eastern Pacific Ocean suggests some past or current gene flow across the ocean basin.

Prey preference may influence the distribution of Shiho and Naisa type pilot whales. The distribution of pilot whales has been shown to be highly correlated with squid, their primary prey (Shane 1995). The two types exhibit differences in dietary preference off Japan (Kubodera and Miyazaki 1993), although in one area the Shiho type has been reported eating the most common squid species (Okutani and McGowan 1969, Sinclair 1992). Little is known of the diet of either type of pilot whale, but it is possible that differences in dietary preference influence the distribution of each type. For example, the geographic range of Humboldt squid (*Dosidicus gigas*), a possible prey item, is similar to the distribution of Shiho type short-finned pilot whales in the eastern Pacific Ocean, while the distribution of Naisa type short-finned pilot whales is similar to that of a closely related squid species, *Sthenoteuthis oualaniensis*, extending eastward from Japan and SE Asia through Hawai'i waters and into the eastern Pacific Ocean (Staaf *et al.* 2010). Both squid species live at 200–700 m, while short-finned pilot whales are known to dive as deep as 800 m (RWB, unpublished data). If Naisa and Shiho type short-finned pilot whales exhibit prey preferences throughout their range, as they do off Japan, it is possible that the extent of the range of each type is influenced by the range of their preferred prey items.

Many of the short-finned pilot whales in this study, including most from the South Pacific, Indian, and western North Atlantic Oceans, do not have known Shiho or Naisa haplotypes. The haplotypes found in these areas may represent one of the two types, which could be elucidated by further genetic analysis. It is also possible that some of these haplotypes represent a third type of short-finned pilot whale. Kasuya *et al.* (1988) suggested the possibility of a second stock of Naisa type short-finned pilot whales, representing a pelagic population of that type separated from the insular stock by the Kuroshio Current. Oremus *et al.* (2009) genetically identified market samples that were otherwise unrepresented in southern Japan, and therefore may belong to a third stock, with a distribution extending into the South Pacific. Our study found a Naisa type haplotype in the Indian Ocean, but failed to find any known Naisa or Shiho haplotypes in the Atlantic Ocean. It remains possible that a third type inhabits part of the South Pacific, Indian, or Atlantic Oceans.

Although short-finned pilot whales are known to occur in the pelagic waters between the ETP and Hawai'i (Hamilton *et al.* 2009), no known genetic or morphological data exist from the area that can be used to determine which type occurs there. In this area and others like it, where genetic and morphological sampling can be difficult, alternative data sources such as acoustic or photo ID data could aid in examining the distribution of the Naisa and Shiho type short-finned pilot whale.

Population Structure and Diversity

Three populations were of primary interest in this analysis: the Hawaiian Islands, the California Current, and the ETP. Short-finned pilot whales in Hawai'i were found to be genetically distinct from all other strata in the Pacific as well as globally, with F_{ST} and Φ_{ST} values ≥ 0.56, indicating very restricted female-mediated gene flow. For the California Current and ETP strata, samples were not significantly differentiated when stratified either according to geography or SST, suggesting a single population throughout the eastern Pacific Ocean.

There may be further population structure within each of our strata that could be elucidated with more samples, longer DNA sequences or nuclear markers. For

example, 36% of the short-finned pilot whales sampled in the Northwestern Hawaiian Islands shared a single haplotype not found anywhere else. Similarly, both of the samples included in this study from Clipperton Island shared a haplotype unique to that island. Eight of the nine Galapagos samples included in this study share a haplotype only found around those islands. These findings are consistent with the presence of insular populations around Clipperton and the Galapagos Islands, similar to the insular population known to reside in Hawaiian waters (*e.g.,* Baird *et al.* 2012, Mahaffy *et al.* 2015). The SE Asia stratum, which covers a broad geographic area, exhibited the greatest genetic diversity with relatively few samples, suggesting the possibility that greater population structure may be found within that stratum. Our findings highlight the need for higher resolution analyses of population structure within each of the strata included in this study.

Short-finned pilot whales have previously been shown to exhibit strong genetic differentiation between ocean basins, and between populations in Japan (Oremus *et al.* 2009). Here we have shown, using a hierarchical AMOVA, that there is strong differentiation within the Pacific Ocean among the North/East Pacific, Central Pacific, and South Pacific regions. Although sample sizes are small in the Indian Ocean and SE Asia, estimates of F_{ST} and Φ_{ST} differentiation suggest higher levels of gene flow between the Indian Ocean and the western Pacific Ocean than between the eastern and western Pacific Ocean. Although our F_{ST} and Φ_{ST} statistics corroborate previous evidence indicating population differentiation between ocean basins, the occurrence of a shared haplotype among the western North Atlantic Ocean, the Indian Ocean, SE Asia, and the South Pacific Ocean suggests that there may still be continued gene flow among the three ocean basins, or that there may be incomplete lineage sorting due to recent divergence.

Higher haplotypic diversity is found in many of the Pacific Ocean populations than in the western North Atlantic Ocean. Our sample size is small in the Atlantic Ocean, but current evidence from the western North Atlantic suggests that low overall diversity is not an artifact of sample size (Oremus *et al.* 2009, Téllez *et al.* 2014, P. Rosel[2]). Two differences between the western North Atlantic and Pacific that may influence diversity are immediately notable: the first is the size of the Pacific Ocean compared with the western North Atlantic, and the second is the absence of long-finned pilot whales in the North Pacific Ocean since the 12th century (Kasuya 1975). The two factors combined may have allowed short-finned pilot whales to expand to a presumably greater abundance and into a greater variety of habitats in the Pacific Ocean, thus increasing their haplotypic diversity.

The overall low mtDNA diversity in short-finned pilot whales may inhibit the detection of genetic structure, leading to the conclusion that short-finned pilot whales are a single species globally. However, their complex social structure and regional genetic differentiation suggests that this species may have a higher degree of structure than is immediately evident. Killer whales (*Orcinus* spp.) exhibit similarly low levels of mitochondrial genetic diversity, but analyses of the full mitogenome and multiple nuclear loci (Morin *et al.* 2010, 2015; Foote *et al.* 2011) as well as integrative studies (Foote 2012, Beck *et al.* 2011) have shown that the current species may actually comprise as many as nine geographically, ecologically or socially distinct subspecies or species. The complicated patterns of morphological and genetic

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[2]Personal communication from Patricia Rosel, NOAA NMFS, Southeast Fisheries Science Center, 646 Cajundome Boulevard, Lafayette, LA 70506, 14 July 2014.

diversity in short-finned pilot whales may also be better explained by using mitogenomes and nuclear DNA. Additionally, integrating genetic data with diet data (*e.g.*, stable isotopes) or social structure data (*e.g.*, acoustics, photo ID) could improve our understanding of possible ecological or cultural drivers of the distribution of the Naisa and Shiho types.

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Supporting Information

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12315/suppinfo.

Figure S1. Median joining network created using long (962 bp) sequences from SWFSC samples. Samples are segregated geographically; legend entries are: Asia = Southeast Asia and Guam, ENP = California Current, ETP = Eastern Tropical Pacific, HI = Hawai'i. Red numbers indicate the number of base pair differences between each haplotype, black labels indicate haplotype.

Table S1. Complete list of samples used, including short and long haplotye designations and GenBank accession numbers for sequences obtained from GenBank.

Table S2. Variance components of hierarchical AMOVA to test for regional differences among Pacific short-finned pilot whale populations, with Naisa type, Shiho type, and the South Pacific each considered a separate region. The adjusted data set was divided into strata as for the pairwise and diversity measurements, then grouped into regions.

Chapter 2, in full, is a reprint of the material as it appears in Marine Mammal Science, Van Cise, Amy M., Morin, Phillip A., Baird, Robin W., Lang, Aimee R., Robertson, Kelly M., Chivers, Susan J., Brownell, Robert L., Martien, Karen K. **2016**, volume *32*, pages 1177-1199. The dissertation author was the primary investigator and author of this paper.

Chapter 3

Acoustic differentiation of Shiho- and Naisa-type short-finned pilot whales in the Pacific Ocean

Acoustic differentiation of Shiho- and Naisa-type short-finned pilot whales in the Pacific Ocean

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Divergence in acoustic signals used by different populations of marine mammals can be caused by a variety of environmental, hereditary, or social factors, and can indicate isolation between those populations. Two types of genetically and morphologically distinct short-finned pilot whales, called the Naisa- and Shiho-types when first described off Japan, have been identified in the Pacific Ocean. Acoustic differentiation between these types would support their designation as sub-species or species, and improve the understanding of their distribution in areas where genetic samples are difficult to obtain. Calls from two regions representing the two types were analyzed using 24 recordings from Hawai'i (Naisa-type) and 12 recordings from the eastern Pacific Ocean (Shiho-type). Calls from the two types were significantly differentiated in median start frequency, frequency range, and duration, and were significantly differentiated in the cumulative distribution of start frequency, frequency range, and duration. Gaussian mixture models were used to classify calls from the two different regions with 74% accuracy, which was significantly greater than chance. The results of these analyses indicate that the two types are acoustically distinct, which supports the hypothesis that the two types may be separate sub-species. [http://dx.doi.org/10.1121/1.4974858]

I. INTRODUCTION

Divergence in animal vocalizations can be a marker of population divergence or speciation. Such acoustic divergence between geographic regions, or geographic variability (Conner, 1982), has been correlated with genetic differentiation due to reduced dispersal between regions, female-driven assortative mating, or exclusion by males (e.g., Baker and Cunningham, 1985). This type of divergence has been identified in bats [e.g., horseshoe bats (Yoshino *et al*., 2008)], birds [e.g., rufous-collared sparrow (Tubaro *et al*., 1993)] and cetaceans [e.g., blue whales (McDonald *et al*., 2006), humpback whales (Winn *et al*., 1981), and striped dolphins (Papale *et al*., 2013)]. This variation can be caused by a variety of factors, including isolation and subsequent adaptation to a local environment (e.g., Graycar, 1976; Ding *et al*., 1995), morphological or genetic differences between populations (Janik and Slater, 2000; Slabbekoorn and Smith, 2002),

socially maintained differences between sympatric or parapatric populations, called dialects [e.g., sperm whales (Rendell and Whitehead, 2003; Rendell *et al*., 2012; Gero *et al*., 2016), killer whales (Ford, 1989, 1991; Filatova *et al*., 2012)], or acoustic drift between geographically separated populations (Conner, 1982).

Vocal repertoires are often learned through vertical transmission from parent to offspring (e.g., Yurk *et al*., 2002), or by learning when an immigrant individual adopts the vocalizations of the new group or population (Mundinger, 1980; Conner, 1982; Musser *et al*., 2014). Geographic variability in the vocal repertoire could result in a positive feedback loop with genetic divergence, for example, when habitat-dependent selection of song characteristics promotes divergence or speciation among populations of songbirds living in different habitats (Slabbekoorn and Smith, 2002).

Pilot whales are distributed in the open ocean and along continental slopes throughout tropical and temperate oceans. In the Pacific Ocean, two morphologically and genetically distinct types of short-finned pilot whale are also

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geographically non-overlapping and may be distinct sub-species or species (Kasuya *et al.*, 1988; Oremus *et al.*, 2009; Van Cise *et al.*, 2016). These two types have been called the Naisa- and Shiho-type short-finned pilot whale, after their original description (Yamase, 1760). The Naisa-type occurs off southern Japan, southeast Asia, the Indian Ocean, and Hawai'i. The Shiho-type occurs off northern Japan and in the eastern Pacific Ocean between 45°N and 15°S latitude. Mitochondrial evidence suggests strong female fidelity to geographic regions, with little or no female-mediated genetic exchange between these two types (Van Cise *et al.*, 2016). A third genetic clade has been identified, recently diverged from the Naisa-type, and is broadly distributed throughout the Indian, Atlantic, and tropical Pacific Oceans (Hill *et al.*, 2015). The distribution of this unnamed third clade overlaps the Shiho-type in the eastern Pacific and the Naisa-type in southeast Asia and in the Mariana Islands (Hill *et al.*, 2015).

In some regions, the distribution of the Naisa- and Shiho-types remains poorly described. This is true in the eastern/central Pacific Ocean, where short-finned pilot whales are continuously distributed between the west coast of the Americas and Hawai'i (Hamilton *et al.*, 2009), but morphological and genetic samples from the pelagic ocean between the eastern Pacific region and Hawai'i are rare and difficult to collect. Where genetic samples are missing, geo-graphic variability in acoustic signals could help to differentiate between the types and improve our understanding of their distribution.

Although little is known of the short-finned pilot whale vocal repertoire, they have been shown to exhibit distinct, repeated call types (Sayigh *et al.*, 2013). Sayigh *et al.* (2013) went on to determine that about 42% of calls produced in their study could be classified as distinct calls. Seventy percent of those were repeated more than ten times during the study and thus considered to be predominant call types. These calls, including both whistles and burst pulses, can be identified and quantified in order to examine variability in call composition, i.e., variability in which calls and components are being used, as well as variability in level of call complexity [number of components in a single call (Kershenbaum *et al.*, 2014)], between the Naisa- and Shiho-types.

Here, we examine geographic variability in short-finned pilot whale call composition, as well as acoustic features of call contours, with two main goals. The first is to determine whether Naisa- and Shiho-type short-finned pilot whales are acoustically distinct. Acoustic differentiation within a spe-cies can imply a lack of social interaction or transmission of cultural information, which may be considered an implica-tion of sub-species or species-level differentiation. The sec-ond goal is to determine whether calls from the central Pacific can be acoustically categorized as belonging to the Naisa- or Shiho-type, in order to clarify the distributions of each type in the region where no genetic or morphological information exists to assess type.

In addition to an analysis of the composition of distinct, repeated call types, we undertake an analysis of the acoustic features (i.e., peak frequency, duration, frequency range) of all calls identified in the study (i.e., whistles and pulsed calls). Because it is difficult to know *a priori* whether call composition or acoustic features are more ecologically plas-tic (Slabbekoorn and Smith, 2002), a study of both aspects provides a comprehensive analysis of acoustic divergence in Pacific Ocean short-finned pilot whales.

II. METHODS

A. Data collection

In Hawai'i, recordings were obtained between 2009 and 2013 during Cascadia Research Collective surveys (Baird *et al.*, 2013) near the islands of Hawai'i and Lāna'i using two instruments: a DMON-Towfish and a Biological Underwater Recording Package [BURP 3.2, developed at Southwest Fisheries Science Center (SWFSC); see Table I for specifications of all recording instruments]. The BURP was deployed by tethering it to a buoy for periods of 15 min–1 h, while short-finned pilot whales were in the near area (<500 m). The Towfish contained a DMON acoustic recorder (e.g., Kaplan *et al.*, 2015) developed at Woods Hole Oceanographic Institution (WHOI) in a custom-built towfish body, towed ca. 15 m behind an 8.2 m Boston Whaler (Edgemont, FL) with two 150 hp outboard motors while the boat was within 30–200 m of short-finned pilot whales.

TABLE I. Specifications for recording packages used in the present study.

	BURP 3.2 (buoy)	DMON Towfish (towed)	SWFSC 2000 (towed)	SWFSC 2003 (towed)	SWFSC 2006 (towed)	SWFSC (CalCurCEAS) 2014 (towed)	SoundTrap ST200 STD (buoy)
Sampling rate	192 kHz	512 kHz	48 kHz	48 kHz	48 kHz	500 kHz	188 kHz
Functional bandwidth	2–60 kHz ± 5 dB	160 kHz	2–24 kHz ± 4 dB	2–24 kHz ± 5 dB	2–24 kHz ± 5 dB	2 kHz–100 kHz ± 5 dB	20 Hz–60 kHz ± 3 dB
Recorder flat response range	2–60 kHz	5–160 kHz	1200 Hz–40 kHz	1200 Hz–40 kHz	1200 Hz–40 kHz	2 kHz–100 kHz	20 Hz–60 kHz
Pre-amplifier flat response range	>2 kHz	NA	>2 kHz	>2 kHz	>2 kHz	>2 kHz	NA
Recorder bit-depth/resolution	24-bit	16-bit	16-bit	16-bit	16-bit	16-bit	16-bit
Hydrophone manufacturer and model	HTI, Inc.	Navy type II ceramics	Sonatech, Inc. Norris	EDO E65	EDO E65	HTI, Inc.	Ocean Instruments
Number of encounters	12	11	1	1	7	2	1
Recording period	2012	2012–2013	2000	2003	2006	2014	2015
Type recorded	Naisa	Naisa	Shiho	Shiho	Shiho	Shiho	Shiho

Recordings from the eastern and central Pacific Ocean were collected and manually annotated during National Oceanic and Atmospheric Administration (NOAA) SWFSC surveys between 2000 and 2015 using either a custom-built towed array (Rankin *et al.*, 2013) or an Ocean Instruments (Aukland, New Zealand) SoundTrap 201 (Table I). Arrays were towed ∼300 m behind a research vessel traveling 10 kn. The SoundTrap 201 also was tethered to a surface buoy and deployed from a recreational fishing vessel contracted by SWFSC, which then moved to a distance of ∼500 m from the buoy to decrease noise levels as the animals passed the buoy. Data collected before 2006 were recorded onto digital tapes using a Tascam (Montebello, CA) recorder with a sampling rate of 48 kHz. Digital playbacks from Tascam recordings were re-digitized using a 24-bit Creative Labs (Milpitas, CA) Sound Blaster Extigy sound card with a 96 kHz sampling rate and 100 dB SNR, and recorded using Raven (Cornell Lab of Ornithology, Ithaca, NY) 4.1 software.

Recordings were used for this study if pilot whales were the only species seen in the vicinity. Trained observers identified any species that came within the horizon during encounters. Recordings were not used from conditions worse than Beaufort 5, both to minimize the impact of noise from the surface and to reduce the possibility of animals passing through the recording area undetected. Acoustic recordings were separated into three regions (Fig. 1): Hawaiʻi, the eastern Pacific Ocean, and the central Pacific Ocean. Hawaiian recordings are considered to be from Naisa-type short-finned pilot whales, and eastern Pacific recordings are considered to be from Shiho-type short-finned pilot whales, based on evidence that the distribution of these two types is non-overlapping in this region (Van Cise *et al.*, 2016). Recordings from the central Pacific Ocean cannot be designated as belonging to one type or another, due to a lack of information on the distribution of these two types in that region.

B. Call extraction

Burst pulses and whistles were considered "calls" and analyzed together, based on evidence that burst pulses and
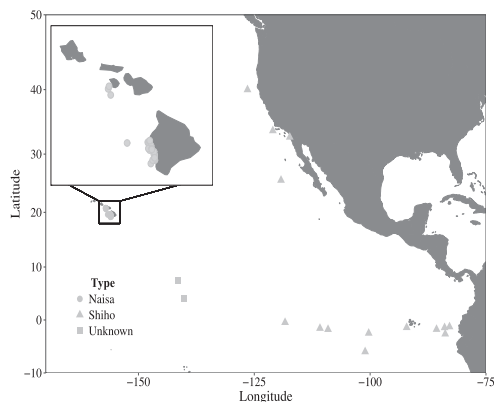
FIG. 1. Distribution of acoustic encounters throughout the Pacific Ocean. Samples were collected by the SWFSC and Cascadia Research Collective (CRC).

whistles can be described on a continuous spectrum (Murray *et al.*, 1998), as well as evidence that pilot whales exhibit smooth transition and simultaneous use of whistles and burst pulses (Sayigh *et al.*, 2013). Spectrograms were created for each recording in Raven 1.4, using a discrete Fourier transform (DFT) with a Hamming window and 50% frame advance. DFT frame lengths were set to provide similar temporal and spectral resolution across recordings irrespective of sample rate [BURP $N_{DFT} = 2048$ samples, Towfish $N_{DFT} = 1280$, SWFSC towed array $N_{DFT} = 512$, SWFSC (CalCurCEAS) 2015 towed array $N_{DFT} = 5333$, SoundTrap $N_{DFT} = 2005$]. Although recordings were collected using a variety of hydrophones, all had flat frequency response from 2 to 40 kHz. Analyses focused on frequency, range, and duration of calls to preclude any amplitude-specific influence of specific recording systems. We tested this hypothesis using an analysis of variance (ANOVA) with recorder as a random effect implemented in R (version 3.2.3).

Calls were visually characterized based on sub-units, or components, separated from each other by a short pause (>0.1 s) in sound production or a rapid change in frequency (>500 Hz in 0.25 s; Shapiro *et al.*, 2011), examples of which can be seen in Fig. 3. Call components were classified alphanumerically in the order in which they were identified; each call consisted of one or more components. Calls made by several individuals vocalizing at the same time could potentially be mistaken for a multi-component call; in order to avoid this bias, a call was labeled as multi-component only if it occurred more than three times with the same component order and timing. We use the word "non-tonal" to refer to calls without any distinct structural component, such as buzzes. Calls that occurred more than five times in the study are considered predominant call types, following the methods outlined in the study of short-finned pilot whale vocal repertoire by Sayigh *et al.* (2013); however, we modified the threshold for predominant call types from ten occurrences to five because the number of calls in our dataset is smaller.

Once calls were annotated and extracted from Raven, they were imported into PAMGUARD version 1.11.12 (Gillespie *et al.*, 2009; Gillespie *et al.*, 2013). We traced the fundamental frequency contour of each whistle, that is, the lowest frequency band associate with a whistle and its harmonics. Pulsed calls were characterized by tracing the lowest frequency band for which the entire call was visible (usually the first or second frequency band), which was determined to be the energy contour associated with the pulse repetition rate, equivalent to the fundamental frequency of whistles. This was also the frequency band with the most power in pulsed calls where one band had visibly more power than others. Up to 50 randomly selected calls were traced per encounter (Fig. 2) using ROCCA for PAMGUARD (Oswald and Oswald, 2013).

C. Data analysis

To validate the call classification system used in this study, we trained a group of five non-expert volunteers to characterize a subset of the data using a catalogue of call components developed during the initial call classification
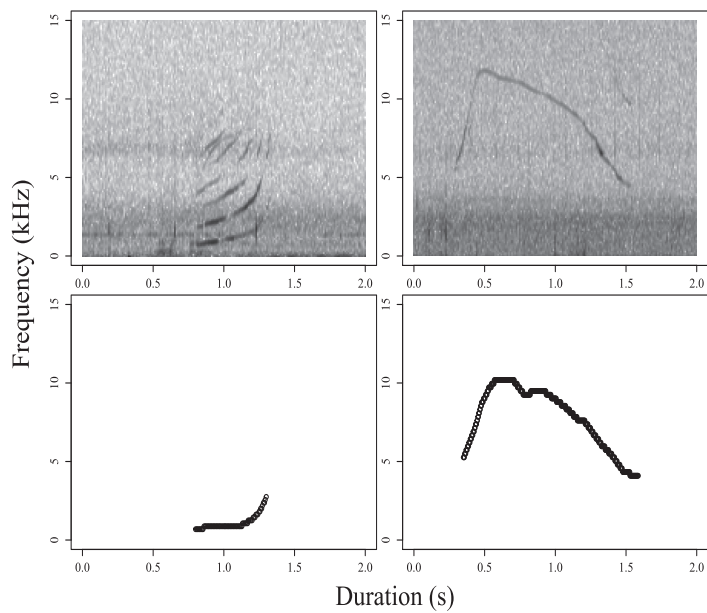
FIG. 2. Example results of manual call contour traces for a pulsed call (left) and a whistle (right). Original spectrograms are shown above; the traced contour is shown below.
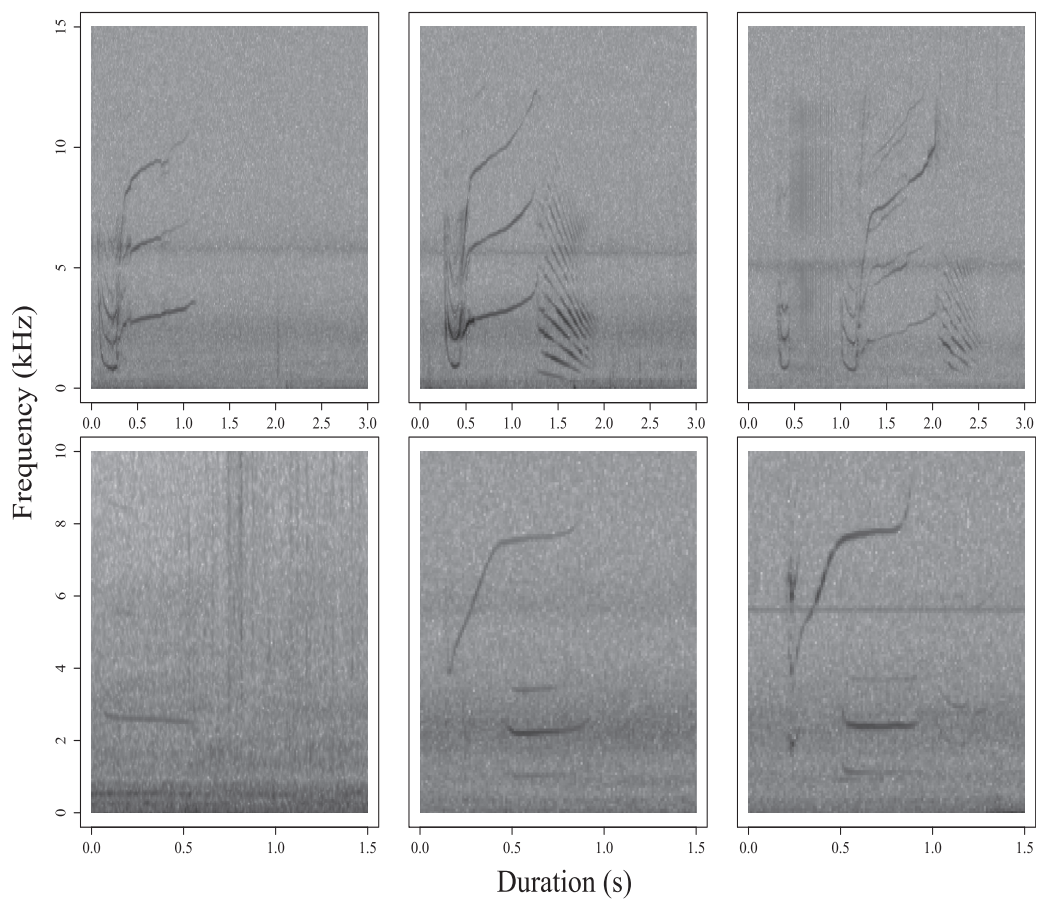
FIG. 3. Example spectrograms from vocalizations of Naisa-type short-finned pilot whales. The top and bottom rows each show a sequence of calls that increase in complexity from left to right.

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process. Volunteers gave all calls alphanumeric classification codes based on the components identified within each call. Classifications by these volunteers were compared to the original classification for each call (by A.M.V.C.), and match rates were calculated to determine the repeatability of this method.

Call types were quantified in each region, and call type diversity analyzed in each region using a Shannon diversity index and rarefaction curve, implemented using the *vegan* package in R (Oksanen *et al.*, 2016). The difference in number of multi-component calls and non-tonal calls such as buzzes used in each region was compared using a standard ANOVA, also implemented in R.

Call contours were characterized using two methods. First, we measured the start, minimum, maximum, and mean frequencies, as well as duration and frequency range of each call contour, and stored the results in what we will refer to as the summary statistics dataset. The second method used the intercept and four coefficients of a fourth-order Legendre polynomial fit to each call component after translating the start time to 0, a method that has been successfully used in killer whale call and sub-unit recognition (Shapiro *et al.*, 2011) and human speech processing (Bonafonte *et al.*, 1996; Dehak *et al.*, 2007). These data were stored in what we will refer to as the call contour dataset.

We used three different methods to test for acoustic differences between Naisa- and Shiho-type short-finned pilot whales in Hawai'i and the eastern Pacific Ocean. First, we tested for statistical differences between the two types. Second, we used a mixture-model-based classification algorithm. Finally, we calculated divergence between encounters and regions using Kullback-Leibler (KL) divergence (Joyce, 2011).

Using the summary statistics dataset, we first tested for statistical differences in distributions of frequency, duration, and frequency range using two tests: a Kolmogornov-Smirnoff test of differences in cumulative frequency distributions of calls from each region, and a Kruskal-Wallis test of differences in the median values for each region (assuming homogeneity of variance). Then, because short-finned pilot whales are known to form stable social groups (Mahaffy *et al.*, 2015), we used a nested, non-parametric multivariate analysis of variance (MANOVA) to test whether encounters (roughly equal to social groups) might cause statistical differences between regions, implemented in R using the *BiodiversityR* package (Kindt and Coe, 2005).

Two sets of mixture models were trained using the *mclust* package (Fraley and Raftery, 2002; Fraley *et al.*, 2012). The first set of models used the summary statistics data as call features, while the second used call contours. We used 90% of the encounters to train a mixture model for each region, using calls that were known to be from that region (i.e., Naisa- or Shiho-type animals), allowing for 1–7 components in each mixture model and choosing the best number of components using Bayesian information criterion (BIC). We then tested those models by classifying the final 10% of the data. We replicated this procedure ten times, each time using a different 10% of the data to test the model. Each call was classified individually rather than grouping

calls, as is common in most acoustic classifiers, because here our goal was not to improve classification rate but to understand the magnitude of acoustic differentiation between the Naisa- and Shiho-type short-finned pilot whales in Hawai'i and the eastern Pacific. A Fisher's exact test of differentiation was used to determine whether the classification error rate was significantly different from a classification error rate achieved by chance.

Using the summary statistics mixture models only, we attempted to classify acoustic encounters from the central Pacific, where the distribution of the two types is unknown. Data from this region were available from two encounters collected during a SWFSC cruise in 2000. We performed a bootstrap analysis of the classification algorithm with 10 000 repetitions, using 90% of the calls from the summary statistics dataset, selected randomly across all encounters, to train mixture models for each region, then classifying each encounter using all calls from that encounter.

Finally, we used the summary statistics dataset to calculate the symmetric KL divergence (Joyce, 2011) between Naisa- and Shiho-type short-finned pilot whales. KL divergence is an asymmetric information theory measure of how much extra information would have to be used to represent another distribution using the first one. As such, identical distributions have KL divergence of zero and distributions that are relatively similar have low divergence. KL divergence measures only the additional information needed to describe one model using another, and is therefore non-symmetric: the symmetric KL divergence is obtained by averaging the KL divergence in each direction. We computed the symmetric KL divergence between a pair of mixture models trained to represent the Naisa- and Shio-type data (Hershey and Olsen, 2007), again using the *mclust* package in R (Fraley *et al.*, 2012). To test for within-type divergence we then constructed two datasets from the encounters within each type by generating ten random partitions of encounters from each pilot whale type. The KL divergence of within-type partitions was computed and compared with divergence between the two types.

III. RESULTS

Vocalizations were obtained from 24 encounters with Naisa-type pilot whales in Hawai'i and 12 encounters with Shiho-type pilot whales in the eastern Pacific (Fig. 1). In Hawai'i, these recordings come from at least 15 known social clusters (as defined in Mahaffy *et al.*, 2015), within at least two hypothesized island communities in the insular population of short-finned pilot whales. Social structure data are not available from the eastern Pacific Ocean; however, it is likely, due to both the spatial and temporal distance between encounters and the large population size in the region, that each encounter represents a different social group in that region. An additional two recordings, which cannot be classified as Naisa- or Shiho-type based on existing data, were collected from the central Pacific, also likely from different social groups.
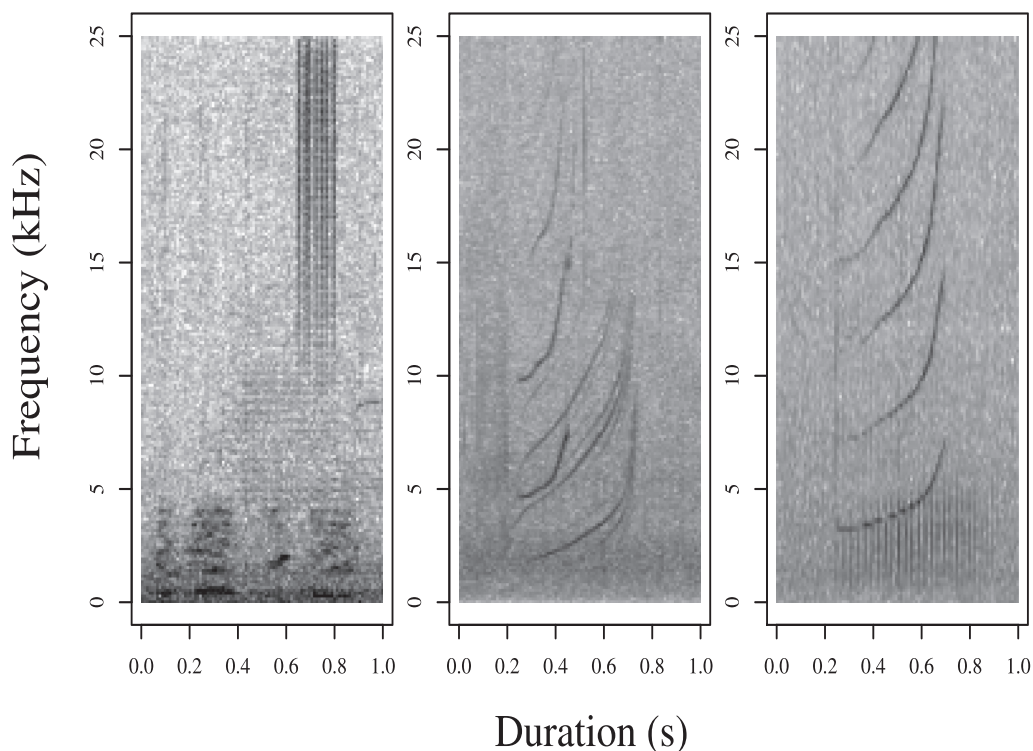
FIG. 4. Example spectrograms from vocalizations of Shiho-type short-finned pilot whales. Non-tonal calls were more common in this type (left), as well as repeated simultaneous calls (center). A low frequency, staccato, pulsed sound, not seen in the recordings of Naisa-type short-finned pilot whales, was found in several encounters in combination with an upsweep call (right, supplementary wav file S1; footnote 1).

A. Call composition

A total of 1745 calls were classified from Naisa-type pilot whale recordings in Hawai'i, and 1178 Shiho-type pilot whale calls were classified from eastern Pacific recordings. Manual call classification resulted in 31 discrete, repeated call types from the Naisa-type pilot whales, representing 1508 of the classified calls from that type, and 16 discrete, repeated call types from the Shiho-type pilot whales, representing 736 of the classified calls from that type (Figs. 3 and 4). The Naisa-type vocal repertoire had a Shannon diversity index value of 3.39, while the Shiho-type vocal repertoire had a value of 2.25. A rarefaction curve indicates that call diversity is divergent between the two regions (Fig. 5). Volunteer analyst classification of a subset of the data (1948 observations) had a 79% match rate with their original classification by AMVC, using example call types in a component-based call catalogue.

Naisa-type vocalizations had more multi-component calls, which made up 27% of the total vocalizations recorded in Hawai'i (Fig. 3) and only 6% of the total Shiho-type vocalizations recorded in the eastern Pacific Ocean. A nested ANOVA showed that both region and encounter were significant predictors of whether or not a call had multiple components ($p < 0.000001$ for both variables). Additionally, there were more non-tonal calls observed in recordings from the Shiho-type (27%) than from the Naisa-type (2%); again, region and encounter were both significant predictors of whether or not a

call was non-tonal ($p < 0.000001$ for both variables). A unique vocalization, characterized by rapid, staccato, low-frequency pulses, was found only in the Naisa-type short-finned pilot whales, and always simultaneously expressed with an upsweep pulsed call (Fig. 4 supplementary wav file S1).[1]

Of the discrete, repeated call types identified in each region, 12 were shared between regions. Those 12 calls comprise 74% of all calls in the Hawai'i dataset, even though a total
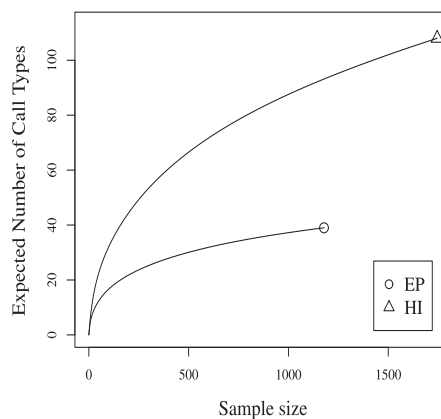
FIG. 5. Rarefaction curve depicting richness of the vocal repertoire in each type. Sub-sample was taken from the entire call repertoire, including calls that were considered repeated call types and calls that were not.
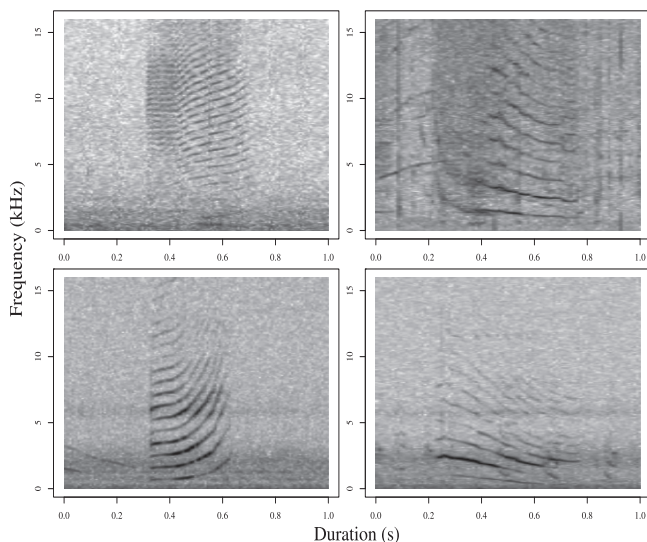
FIG. 6. Example spectrograms of components that were shared between Shiho- (top) and Naisa- (bottom) types, showing the variability within a component type. Call type 10, a pulsed upsweep call, is on the left, and call type 6, a pulsed downsweep, is on the right.

of 31 call types were identified, indicating a high rate of repetition of those 12 call types. Similarly, in the eastern Pacific these 12 call types represent 92% of all discrete, repeated calls in the eastern Pacific dataset, although a total of 16 call types were identified. The 12 discrete call types, although identified in recordings from both regions, were variable both between recordings and between regions (i.e., between the Naisa- and Shiho-type short-finned pilot whales, Fig. 6).

B. Differentiation using acoustic features

Our call traces resulted in measurements of start frequency, mean frequency, minimum and maximum frequencies, frequency range, and duration for each call. A pairwise correlation test showed that all of the measured frequency variables were highly correlated with each other ($R^2 = 0.80$–0.92); therefore, we included only start frequency as a representative of the suite of frequency variables that were measured. Start frequency, frequency range, and duration of vocalizations from Naisa- and Shiho-type pilot whales were significantly different in both their medians and cumulative distributions (Fig. 7, Table II). However, when the encounter effect was nested within each region using a nested, non-parametric MANOVA, the encounter effect was found to be significant ($p < 0.01$), while the region effect was not ($p = 0.67$). The recorder used did not to have a significant effect on differentiation in acoustic features.
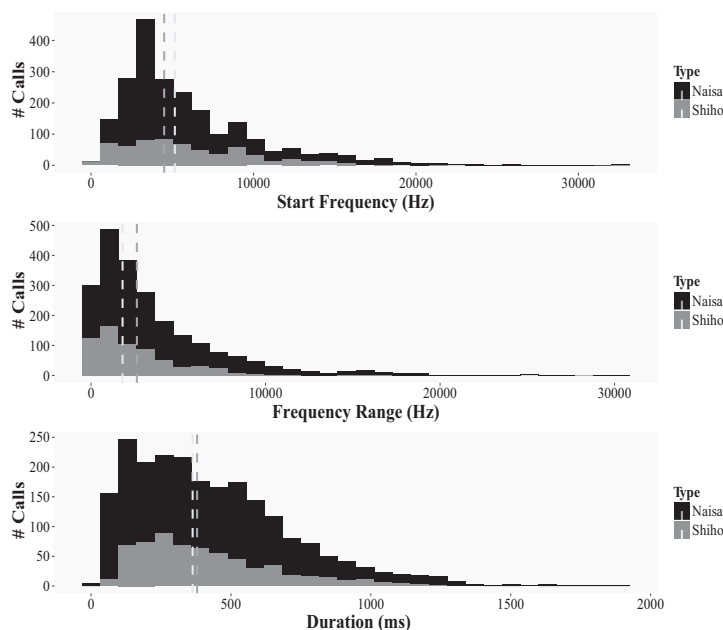
FIG. 7. Histograms of start frequency, frequency range, and duration of calls from Naisa- and Shiho-type short-finned pilot whales. Dashed lines represent median values for both types.

TABLE II. Kruskal-Wallis and Kolmogorov-Smirnoff tests of differentiation between Naisa- and Shiho-type short-finned pilot whales, using start frequency, frequency range, and call duration as input parameters for each test.

	Start Frequency	Frequency range	Duration
Kolmogornov-Smirnoff test			
p-value	0.0004	<0.0001	0.0002
Kruskal-Wallis test			
p-value	0.008	0.0001	0.0002

Two mixture-model based classification algorithms were built, the first using the call contour dataset and the second using the summary statistics dataset. No difference in vocalizations was found between the two types using the call contour dataset, while the models using the summary statistics were able to classify individual calls with a mean error rate of 26% (95% CI = 15%–37%, Fig. 8). Using the summary statistics dataset, mixture models for Hawai'i (Naisa-type) had seven components for nine out of ten models, while mixture models for the eastern Pacific (Shiho-

type) had six components for nine out of ten models. A Fisher's exact test indicated that this classification rate was significantly different from chance ($p = 0.0013$).

Using the classification algorithm developed for the summary statistics dataset, two encounters from the central Pacific Ocean were classified using a tenfold cross-validation model. One was classified as Naisa-type in 97% of the classification attempts, while the other was classified as Shiho-type in 60% of the classification attempts.

Intra-type KL divergence within the Shiho-type made up 15% of the divergence between the two types, while KL divergence within the Naisa-type made up 11% of the divergence between types.

IV. DISCUSSION

The call composition and acoustic features of Naisa- and Shiho-type vocal repertoires were found to be differentiated in all analyses. We found statistically significant differences in the type and number of call components per call used by each type, as well as the start frequency, frequency
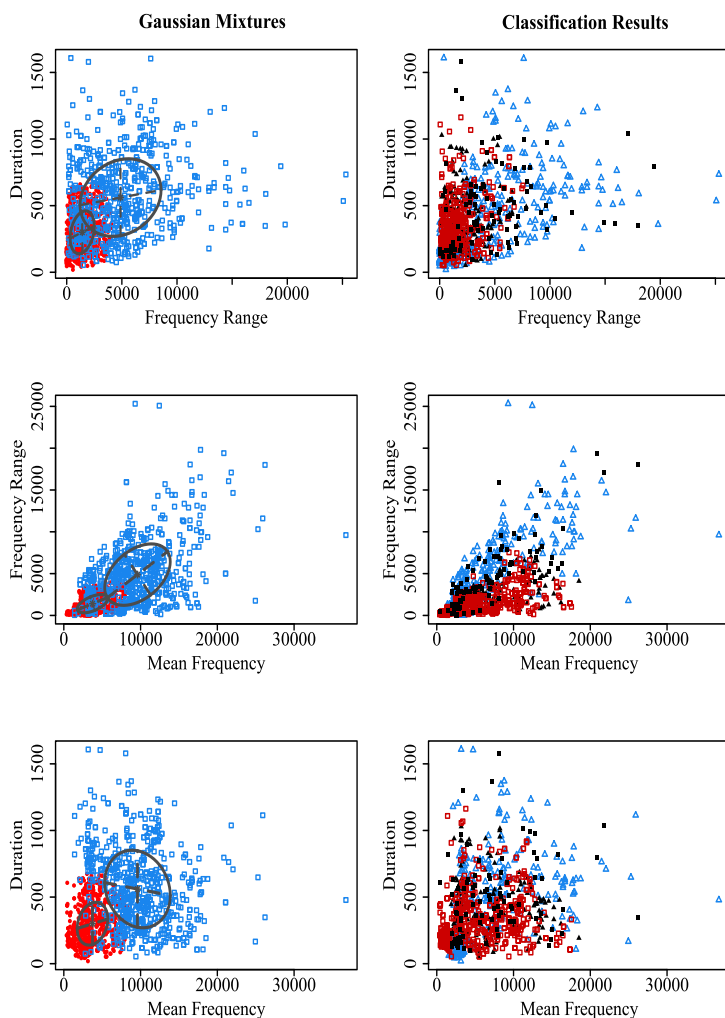
FIG. 8. (Color online) Mixture-model based classification of acoustic vocalizations as either Naisa- or Shiho-type vocalizations using the *summary statistics* data set. Two-dimensional plots of model-based classifications based on mean peak frequency (Hz), frequency range (Hz), and duration (s). (Left) Gaussian mixtures created using training data, labeled as Naisa (blue) or Shiho (red). Ellipses are centered on the mean of the most important mixture (mean number of mixtures for Naisa-type = 7 and Shiho-type = 6). (Right) Results of classifying the training data. Calls that were correctly classified are labeled as Naisa (blue) or Shiho (red). Misclassified calls are labeled in black.

range, and duration of calls. We were further able to use the differences in acoustic features to build a classification algorithm using mixture models, and quantify divergence within and between types using KL divergence.

A. Call composition

The vocal repertoires of the Naisa- and Shiho-types were distinct both in call diversity and number of call components (e.g., Fig. 5). The social complexity hypothesis suggests that more complex communication systems are needed as social structure becomes more complex (Freeberg et al., 2012). The larger number of multi-component calls observed in the Hawaiian vocal repertoire may indicate a more complex social structure, as communication signals tend to be more complex in contexts that require greater information transfer, such as social interactions (Bradbury and Vehrencamp, 1998). There is evidence of both pelagic and insular populations of pilot whales around the main Hawaiian Islands, and multiple communities within the insular population (Baird, 2016), and the greater number of multi-component calls may reflect this complexity in social structure. However, it is also possible that this difference is due to sampling bias, if we simply encountered groups during periods of foraging or social interaction more often in the Hawaiian Islands than we did in the eastern Pacific Ocean, as differences in the number of multi-component calls we identified may reflect behavioral state or social context during an encounter.

Untrained analysts used the call catalogue we developed to correctly classify 79% of the calls they were provided, which is similar to results from a similar study on short-finned pilot whale vocalizations in the Bahamas (Sayigh et al., 2013). That study identified calls as a single unit, unlike the present study, which identified calls as combinations of different sub-units or components. The similar success rate between the two methods suggests convergence and could support a component-based classification system of discrete, repeated call types for short-finned pilot whales, similar to a component-based classification system developed for killer whales (Shapiro et al., 2011). The identification of components within each call may prove useful in future studies of vocal behavior or social structure. For example, killer whales' repertoire of monophonic calls is more diverse in larger populations, while biphonic calls are less diverse, suggesting that they are driven by different evolutionary factors (Filatova et al., 2012).

B. Differentiation using acoustic features

Significant statistical differentiation in start frequency, duration, and frequency range of Naisa- and Shiho-type vocalizations indicates that these two types have distinct acoustic features in their vocal repertoires (Table II, Fig. 8). Inter-type KL divergence was also greater than intra-type KL divergence, confirming divergence of acoustic features between the two types. Similar results have been reported for short-finned pilot whales in the Atlantic Ocean, where Caribbean and Canary Island populations have been shown to exhibit divergence in the acoustic features of their

tonal calls (Rendell et al., 1999), although it is unknown whether there are morphological differences between these populations.

A significant effect of encounter (a proxy for social group) in the nested MANOVA indicates that divergence between the two regions may be affected by differences between social groups. Cultural factors, such as vertical transmission, may be working in combination with acoustic drift to drive differentiation between the vocal repertoires of these two types.

The classification algorithm was able to correctly classify Naisa- and Shiho-type vocalizations with an accuracy of 74% (Fig. 8). Acoustic differentiation, therefore, may be an important tool in rapidly identifying Naisa- and Shiho-type short-finned pilot whales in the field, especially in areas where the distribution of the two types is unknown and possibly overlapping (e.g., the central Pacific Ocean). As additional data are collected from areas where genetic samples are not available, this classification algorithm will be useful in further delineating boundaries between the two types, as well as identifying areas of possible overlap or temporal variability in distribution.

While the classification algorithm based on summary statistics was able to distinguish between Naisa- and Shiho-type calls ~74% of the time, the algorithm based on call contours did not show a difference between the two types. This may indicate that the call contours did not capture the information necessary to differentiate between the two types; adding variables such as duration may improve this method. It is also possible that any signal in this data set was masked by the large amount of variability in call contours within each type, which may be caused by a combination of social structure within each type and variability in behavior, both of which have been shown to occur in social cetaceans such as killer whales (Deecke et al., 2010; Holt et al., 2013). Therefore, when analyzing groups of animals with suspected acoustic variability due to structure within the group, basic summary statistics may perform better than call contours. Call contours may be better used as a higher-resolution test for acoustic structure within a group, for example, due to social structure or acoustic behavior (e.g., Deecke et al., 2010), or in classifying call types (e.g., Shapiro et al., 2011).

C. Classification of unknown encounters

Two encounters with pilot whales of unknown type from the central Pacific Ocean were classified, one as Naisa-type and the other as Shiho-type. Acoustic data from additional encounters could aide in the determination of distributional boundaries between the two types in this area, or other areas where genetic and morphological data are scarce and difficult to collect (e.g., Van Cise et al., 2016). Acoustic data have been used to describe population boundaries of several other cetaceans, for example, blue whales (McDonald et al., 2006; Balcazar et al., 2015) and humpback whales (Garland et al., 2015). Here, acoustic data correlate with the two morphologically and genetically distinct types; if they are determined to be sub-species or species,

acoustic data may be important to their management and conservation.

In the central Pacific, the distribution of the two types may be parapatric or temporally distinct, as is the case off Japan where both types are found separated by the Kuroshio-Oyashio Extension Current and move north-south throughout the year following the boundary set by this current (Kasuya, 1986; Kasuya et al., 1988). However, if the two types are sympatric in their distributions in the central Pacific Ocean, then it could be a region of acoustic mixing between the two types, which will decrease the effect of acoustic drift between them through horizontal learning, a phenomenon that has been described in several taxa, including birds and marine mammals (e.g., Slabbekoorn and Smith, 2002; Crance et al., 2014).

Alternatively, acoustic structure may be important to the maintenance of genetic structure in this area, i.e., individuals prefer mates that sound similar to themselves over potential mates with different vocal repertoires. This acoustic sorting could cause a positive feedback loop in which animals only mate with similar sounding animals, thus increasing the differentiation between the two types. This has been demonstrated to occur in several bird species using playback experiments (Slabbekoorn and Smith, 2002), and could be similarly tested in pilot whales.

D. Future work

The results of this study suggest that short-finned pilot whale vocal repertoires are variable at a local level within each region, possibly driving the differentiation we see between the two types; this was illustrated by a significant effect of encounter in the nested, non-parametric MANOVA. Evidence suggests that, for other social cetaceans, variability in the vocal repertoire can be both socially driven [e.g., killer whales (Yurk et al., 2002; Riesch et al., 2006; Deecke et al., 2010; Filatova et al., 2012; Crance et al., 2014; Musser et al., 2014) and sperm whales (e.g., Rendell et al., 2012; Cantor et al., 2015)] and behaviorally driven [e.g., killer whales (Filatova et al., 2013; Holt et al., 2013)]. Short-finned pilot whales are a highly social cetacean, known to form stable social groups for a decade or more (Heimlich-Boran and Hall, 1993; Mahaffy et al., 2015). In the Hawaiian Islands, these social groups form island-associated communities within a Main Hawaiian Island insular population (Baird, 2016). Acoustic differences among these communities, or the social groups within these communities, may be important to driving the acoustic variability we see within the Hawaiian region (Janik and Slater, 2000). This could be tested by conducting a higher resolution comparison of acoustic and photo ID data within the region to differentiate acoustically among identified social groups.

Differences in behavioral state may also be a driver of the acoustic divergence within regions, as has been documented in a number of cetaceans, including killer whales (e.g., Holt et al., 2013). Differences in group behavior during the recording (e.g., foraging, socializing, or resting), which may be, in turn, affected by environmental factors (e.g., seasonality, time of day, productivity) will introduce variability into low resolution studies of vocal repertoire such as this one. Similar to the variability introduced by acoustic differences among social groups within a region, this pattern could be tested with a high resolution study of vocal activity recorded during distinct behavioral states.

Additionally, the present study does not cover the entire range of either of the two types. Continued sampling from their entire Pacific (or global) range is needed to determine whether this pattern of acoustic divergence between the two types is consistent throughout their range, especially in areas of possible overlap between the two types. Further study of acoustic divergence between social groups would provide insight into the role vocal repertoire may have in maintaining divergence between groups.

E. Conclusion

Geographic variability in acoustic structure between Naisa- and Shiho-type short-finned pilot whales suggests that these two groups are acoustically differentiated. A nested MANOVA indicates that the difference between regions is largely driven by differences between encounters within regions, possibly due to sub-population structure or social structure. This evidence can be added to previous studies of their genetics, morphology, and geographic distribution (Kasuya and Marsh, 1984; Wada, 1988; Oremus et al., 2009; Van Cise et al., 2016) to suggest that the two types may be separate sub-species or species. The classification algorithm developed here shows that acoustic divergence between the two types can be used to improve our understanding of their spatial and temporal distribution in areas where genetic or morphological samples are difficult to acquire, such as the central Pacific Ocean.

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[1]See supplementary material at http://dx.doi.org/10.1121/1.4974858 to hear an audio recording of the unique vocalization described herein.

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Chapter 3, in full, is a reprint of the material as it appears the in Journal of the Acoustical Society of America, Van Cise, Amy M., Roch, Marie A., Baird, Robin W., Aran Mooney, T., Barlow, Jay. **2017**, volume *141*, pages 737-748. The dissertation author was the primary investigator and author of this paper.

Chapter 4

Familial social structure and socially driven genetic differentiation in Hawaiian short-finned pilot whales

4.1 Abstract

Social structure has been shown to have a significant impact on divergence and evolution within social species, especially in the marine environment, which has few environmental boundaries to dispersal for large marine mammals. Genetic structure has also been shown to affect social structure in social species, through and individual preference toward associating with relatives. One social species, the short-finned pilot whale, has been shown to live in stable social groups for periods of at least a decade. Here, we examine population structure among geographic and social groups of short-finned pilot whales in the Hawaiian Islands, and test whether social structure is a driver of genetic structure and vice versa, using a combination of mitochondrial sequences and nuclear SNPs. Our results show that there are at least two geographic populations in the Hawaiian Islands: a Main

Hawaiian Island (MHI) population and a Northwest Hawaiian Island/Pelagic population. We additionally show evidence for two island communities within the main Hawaiian Island population: an eastern MHI community and a western MHI community. We find evidence for genetically-driven social structure in the high relatedness among social units and clusters, as well as a positive relationship between relatedness and association index between individuals. Further, we find that socially-organized clusters are genetically distinct, indicating that social structure is a driver of genetic divergence within Hawaiian pilot whales. This genetic divergence among social groups can make specific groups less resilient to anthropogenic or ecological disturbance. Conservation of this species therefore depends on understanding genetic, social and ecological variability among social groups within the species.

4.2   Introduction

While the concept of culture has traditionally been reserved for human societies, since the early 1900s biologists have identified and described aspects of culture in non-human species, such as elephants, birds, primates, pinnipeds, and cetaceans (e.g. Mundinger, 1980; Lachlan and Slater, 1999; Whitehead, 2007a; Rendell and Whitehead, 2003; McComb and Semple, 2005; Laland and Janik, 2006; Wittemyer et al., 2009; de la Torre and Snowdon, 2009; Kershenbaum et al., 2012; Riesch et al., 2012; Kessler et al., 2014). Theoretical studies have long suggested the existence of gene-culture coevolution outside humans, and integrative studies of genomic and cultural traits are beginning to provide evidence of gene-culture coevolution in social mammals, both in a narrow sense (i.e. direct links between genes and cultural phenotypic traits), and a broad sense (i.e. population-level genetic differences among groups with different cultures or societies). Sociality has been shown to increase inclusive fitness in cooperative species (e.g. Connor et al., 1992; Whitehead, 2007a), and therefore be an evolutionarily advantageous trait. Socially-driven, fine-scale genetic structure has been documented in primates and some other social mammals, such

as elephants, rock wallabies, prairie dogs, killer whales and sperm whales (e.g. Pope, 1992; Dobson et al., 1998; Hazlitt et al., 2006; Wittemyer et al., 2009; Cantor et al., 2015; Foote et al., 2016). These species all form socially-defined groups that are genetically distinct due to nonrandom mating and dispersal patterns, and are often characterized by matrilineal societies with male-biased dispersal. These types of societies, if stable over many generations, could lead to the co-evolution of genes and culture.

Because cetaceans live in an environment with few boundaries to dispersal, social structure may play an important role in driving population structure and evolution. Stable social structures (i.e. hierarchical group associations that remain stable for decades to generations) have been identified in four species of cetacean - sperm whales, killer whales, long-finned pilot whales and short-finned pilot whales (e.g. Amos et al., 1993; Baird and Whitehead, 2000; Cantor et al., 2015). Whitehead (1998) suggests that the dearth of mitochondrial diversity in these four highly social cetaceans may be driven by selection for maternally-inherited cultural traits. In killer whales and sperm whales, the effects of social structure and cultural learning (e.g. foraging techniques, migration patterns, predator avoidance, and vocal traditions) as drivers of genetic structure have been well documented (e.g. Ford and Fisher, 1982; Janik and Slater, 1997; Weilgart and Whitehead, 1997; Foote et al., 2009, 2016; Filatova et al., 2012; Rendell et al., 2012; Riesch et al., 2012; Cantor et al., 2015). However, little is understood of the social and genetic structure of pilot whales, or the links between the two.

Just as social structure can affect genetic structure, genetic structure can have a driving effect on social structure, if individuals choose to associate with close relatives rather than disperse throughout their range, even though it may or may not provide an evolutionary advantage (Beck et al., 2011). The positive feedback loop created by these two complementary processes may stabilize social units or clusters, allowing co-evolutionary genetic and social divergence to occur. While many aspects of this theory have been

discussed (e.g. Findlay, 1991; Lachlan and Slater, 1999; Laland, 1992), empirical evidence of stable gene-culture coevolution outside of humans is limited (Whitehead, 2007a). Although research in this area is increasing (e.g. Foote et al., 2016), the relationship between ecology, culture, and genetics is poorly understood in all species (Laland et al., 2010). Short-finned pilot whales, due to their social nature, may be affected by this reciprocal link between social structure and genetic structure. Stable social units and a long period of post-reproductive senescence in females may contribute to gene-culture divergence in this species, both at the population and sub-population level, as is true of killer whales (Brent et al., 2015). In the Pacific Ocean, two types of short-finned pilot whale have been identified, distinct in their morphology, genetics, distribution and vocal repertoire (Kasuya et al., 1988; Oremus et al., 2009; Van Cise et al., 2016, 2017). Little is known of the mechanism of divergence between these two types, but due to their similarity to killer whales, we hypothesize that cultural adaption to distinct ecological environments (e.g. diet preference or foraging techniques) promoted the divergence of the two types (Riesch et al., 2006), which may be distinct sub-species or species.

The Hawaiian archipelago is home to one of these types, the Naisa-type short-finned pilot whale (Van Cise et al., 2016). Longitudinal observations and photo identification data collected since 2000 have been used to calculate the rate of association between pairs of individuals (called the association index), using a half-weight index to control for effort (?Mahaffy et al., 2015). This revealed that short-finned pilot whales in Hawaii form stable social units of approximately 12 individuals for periods of at least a decade, and that these social units will often associate with a number of other social units in affiliations called clusters, with an average of 23 individuals (Mahaffy et al., 2015). Social units, the smallest group in the social hierarchy, have a mean association index of 0.76. Clusters, the next hierarchical level, comprise one or more social units with mean association index of 0.48. Additionally, satellite tag and photo ID data indicate that, within the Main Hawaiian

Islands (MHI), three island-associated communities may exist: an eastern MHI community, around Hawaii Island, a western MHI community around Oahu and Kauai Islands, and central MHI community around Oahu and Lanaii Islands (Baird, 2016). The presence of these communities suggests that, in regions with highly heterogeneous habitat such as island archipelagos, geographic or environmental boundaries, or habitat preference, may be important drivers of local structure. Communities represent the highest level of social organization, comprised of multiple clusters. Based on studies from short-finned pilot whale populations in the Atlantic Ocean, social units are thought to be matrilineal (Heimlich-Boran, 1993; Alves et al., 2013). These two studies suggest that males remain in their natal social unit but mate outside of that group. However, in at least some cases, all-male groups have been observed (Baird, 2016), suggesting that males do not always exhibit natal philopatry. It is unknown whether males extra-unit mate choices are random or socially-driven, or whether genetic relatedness affects association or social structure at any level higher than that of social units. In this study, we aim to improve our understanding of local population structure and divergence in Hawaiian short-finned pilot whales. We analyze genetic differentiation between three geographic strata: the Main Hawaiian Islands, Northwest Hawaiian Islands and pelagic waters surrounding the Hawaiian Islands; we then examine genetic differentiation between observed island communities within the Main Hawaiian Islands, test for sex-biased dispersal between those communities, and look for evidence that geographic distance is a driver of the amount of time that individuals spend together. We further hypothesize that social structure is an important driver of genetic divergence within local populations, and that, in turn, group philopatry affects social structure. If genetic structure affects social structure, insomuch as close relatives form lifelong associations and travel in close-knit groups, we would expect to see higher relatedness within social units than expected at random. Similarly, if social structure affects genetic structure we might expect to see genetic divergence in the allele frequency among

clusters. These patterns, along with a statistical relationship between genetic and social structure, could indicate a reciprocal relationship between genetic and social structure in Hawaiian pilot whales.

4.3 Methods

4.3.1 Genetic data collection

Skin samples (n=254) were collected from short-finned pilot whales (*G. macrorhynchus*) throughout the Main Hawaiian Islands and Northwest Hawaiian Islands in collaboration with Cascadia Research Collective (CRC) and NOAAs Southwest Fisheries Science Center (SWFSC). Samples were collected opportunistically, as social groups were encountered in the field, with priority given to sampling as many adults in each social group as possible. Samples were archived in the SWFSC Marine Mammal and Sea Turtle Research Collection, and were either stored at -80C, or preserved in either a salt-saturated 20% DMSO solution or 100% ethanol and stored in a -20C freezer. In the Main Hawaiian Islands, known social units were heavily sampled in order to test for relatedness; additional samples were chosen randomly, with consideration given to ensuring that samples represented unrelated individuals from multiple social groups per stratum.

4.3.2 Photo ID/social network data collection

Photographs used to generate social stratification data as well as pairwise association indices between individuals were collected according to Mahaffy et al. (2015). Photo identification data from that publication and from subsequent field observations, between 2003 and 2015, are included in this study. Association indices were calculated using SOCPROG 2.4, with a sampling period of one day and a half-weight index (HWI) of association to control for effort (Whitehead, 2008, 2009). We used the photo identification,

association indices, and terms (social units, clusters, and communities) used by Mahaffy et al. (2015) to characterize the hierarchical nature of short-finned pilot whale social organization in the Main Hawaiian Islands.

4.3.3 Genetic sequencing and assembly

DNA was extracted from skin and muscle samples as previously described (Martien et al., 2014). The hypervariable mtDNA control region was amplified and sequenced in two parts of approximately 420 bp and 560 bp, with approximately 20 bp of overlap between the two sequences. Primers, PCR, and sequencing methods have been previously described by Martien et al. (2014). The resulting combined sequence was 962 bp, and was assembled using SEQED, version 1.0.3 (ABI), Sequencher software (versions 4.1 and 4.8; Gene Codes, Ann Arbor, MI, USA) or Geneious (Kearse et al., 2012). Mitochondrial sequences were aligned using a MAFFT alignment with default parameters (Scoring Matrix: 200PAM/k=2, Gap open penalty: 1.53, Offset value: 0.123) in the Geneious software package (Katoh and Kuma, 2002). Once the alignment was completed, sequences were re-examined. Any haplotypes represented by only a single sequence or haplotypes with a single base-pair difference from the most similar haplotype were reviewed for accuracy. Unique haplotypes were repeat sequenced in order to ensure the accuracy of the sequence. Sequences were combined with previously published sequences from Van Cise et al. (2016) to generate the final mtDNA data set.

Sequencing of 78 targeted nuclear loci for SNP analysis was completed using a custom capture enrichment array designed at SWFSC based on bottlenose dolphin (*Tursiops truncatus*) genome sequences, followed by highly-parallel sequencing (Hancock-Hanser et al., 2013; Morin et al., 2015). Four libraries of genomic DNA were prepared using protocols described in Meyer and Kircher (2010) and Hodges et al. (2009), with modifications described in Hancock-Hanser et al. (2013). Up to 400 ng of extracted DNA in 80 L total

volume was sonicated using a Bioruptor UCD-200 (Diagenode). Blunt-ends of the DNA were repaired using 20 L of the sonicated product, adaptors were ligated to the DNA, and indexes were added to each sample library via PCR with indexed primers (Meyer and Kircher, 2010). Once indexed, each sample was quantified using qPCR to estimate the number of nuclear DNA copies in each sample, and approximately 100,000 copies per sample were pooled and hybridized to a capture array. The capture-enriched product was amplified, then sequenced on Illumina HiSeq (1 x 100 bp) or NextSeq (1 x 75 bp) instruments by The DNA Array Core Facility (The Scripps Research Institute, La Jolla, CA).

Nuclear sequences were assembled as in Morin et al. (2015), using bottlenose dolphin (*Tursiops truncatus*) reference sequences (used for capture enrichment) for sequence assembly and SNP genotyping. The cutoff for calling a genotype at any position was set to 10 reads for both homozygous and heterozygous positions, to minimize genotype error (Fountain et al., 2016). Potential SNPs were identified using scripts developed at SWFSC (Dryad data repository doi:10.5061/dryad.cv35b) in the R computing environment (R Core Team 2016). From the pool of sequenced loci, candidate SNPs were selected if at least five individuals were heterozygous at that locus. Those SNPs with coverage at fewer than 55% of samples were removed, and samples with coverage at fewer than 70% of the SNP loci were also removed. Next, sequenced regions with multiple SNP loci were examined for signs of paralogous reads within the assembly (e.g., excess heterozygosity across multiple SNPs in a region, discrete regions of high coverage), and SNPs were removed if assembly of paralogous loci was determined to have occurred. Finally, quality control analyses were performed on this set of SNPs and samples using the strataG package for R (Archer et al., 2016). SNPs were removed if the quality control analysis indicated that the locus was an outlier for homozygosity (>80% homozygous, based on the distribution of homozygous genotypes across all loci), and we additionally tested for outliers from HWE, using a Bonferonni adjustment for multiple test. Loci that deviated significantly from HWE equilibrium were

closely re-examined for evidence of assembly of paralogous loci. Additionally, samples that had highly similar SNP genotypes and could be duplicates were checked against photo ID records to confirm that they were distinct individuals; if this could not be determined, one from each pair of duplicate samples was removed. Loci with multiple SNPs were phased based on allele frequencies in the three regional strata, with a phase cutoff probability of 0.5, to generate a single multi-SNP genotype per sample at each locus for analyses of genetic differentiation (Morin et al., 2012). For analysis of relatedness within Hawaiian social units, the highest heterozygosity SNP at each locus (N = 51 after removal of one locus that was invariant in these populations) was chosen for the analysis.

4.3.4   Data analysis

For mitochondrial DNA analysis, samples were divided into three strata: Main Hawaiian Islands (MHI), Northwest Hawaiian Islands (NWHI), and pelagic samples (Fig 1). Samples were placed in one of these three strata primarily based on their sampling location, with the exception that samples collected near the MHI were placed in the pelagic stratum if photo ID data verified that the individuals did not associate with MHI communities. MHI mtDNA samples were not further stratified because all samples except one have the same haplotype. We placed samples from the NWHI in a separate stratum because several studies have shown strong differentiation between the MHI and NWHI for other marine mammals (Andrews et al., 2010; Courbis et al., 2014; Martien et al., 2014).

SNP data were only available for the MHI and pelagic strata. Using previous knowledge of the social structure, habitat use, and movements (Baird et al., 2015; Mahaffy et al., 2015), SNP samples were divided into two strata within the MHI (eastern and western MHI communities) based on photo-identification and observation data (Figure 1). Several social units were heavily sampled in order to test for relatedness within social units; therefore, before conducting geographic analyses we subsampled the dataset to include no more than

two individuals from each social unit.

Molecular diversity indices for all samples and for each region were calculated for both mtDNA (Theta (Θ_H), haplotypic diversity (h), and mean nucleotide diversity (π)) and SNP genotypes (average number of alleles per locus, expected and observed heterozygosity (H_e, H_o)). All estimates of divergence and genetic diversity were conducted using the strataG package for R except haplotypic diversity, which was calculated in Arlequin (Excoffier and Lischer, 2010).

To calculate relatedness within and among social units in the MHI, samples were stratified according to previously inferred social structure (Mahaffy et al., 2015), and social unit relatedness was calculated if at least five individuals from a social unit had been sampled. Relatedness was estimated using a dyadic maximum likelihood estimator (Milligan, 2003) in the R package Related (Pew et al., 2014), which implements the software program COANCESTRY (Wang and Summers, 2010). Within-unit relatedness was compared to the expected relatedness by permuting a random sample 1,000 times and calculating relatedness. For one cluster in which two social units were sampled, we tested the hypothesis that genetic relatedness is a driver of association among social units by comparing within-cluster relatedness with the distribution of relatedness between 1,000 randomly selected pairs of social units.

Pairwise genetic differentiation was calculated among geographic strata using F_{ST} and ϕ_{ST} for mtDNA and F_{ST} for SNP genotypes. Pairwise SNP genetic differentiation (F_{ST}) was also tested among clusters, which represent one or more social units, using SNP genotypes only due to the lack of mtDNA haplotypic diversity. F_{ST} and ϕ_{ST} analyses were also performed using the strataG package in R. Clusters were only included if there were at least five samples collected from that cluster. To characterize the overall degree of differentiation among social clusters, we performed this test using all available samples. Then, to characterize the extent to which gene differentiation has been affected by social

structure, we removed highly related ($r > 0.6$) samples to remove bias due to genetic relatedness and recalculated FST among social clusters, now considering the underlying allele frequency of non-related individuals within each cluster. We tested for sex-biased dispersal among communities using the Hierfstat package in R (Goudet, 2005), which looks for first-generation immigrants within the sample set. To do this, we tested for differences among males and females in F_{ST}, F_{IS}, or the mean or variance of assignment probability (Goudet et al., 2002).

To determine whether genetically similar social units and clusters were more likely to associate, we compared pairwise cluster genetic differentiation (F_{ST}) with mean pairwise association between clusters, using a fixed effect linear model with cluster ID controlled as a fixed effect. Association between pairs of clusters was calculated by taking the mean of association between individuals in the first cluster and individuals in the second cluster.

We used Mantel tests and linear models to examine the relationship between geographic distance, genetic relatedness, and associations between individuals. To do this, we first calculated geographic distance (d) as the straight-line distance between sampling locations for each sample. Three Mantel tests were calculated between all pairs of individuals, comparing genetic distance (defined as 1 genetic relatedness, r), geographic distance (d), and the amount of time a pair spends together (association index, AI). We compared linear, exponential, and logarithmic models to test the importance of geographic distance (d), genetic relatedness (r), and an interaction term ($r \times d$) as potential drivers of association between individuals (AI). For these models, we converted geographic distance to a categorical variable with two categories (inter-island, $d < 50$ and intra-island, $d > 300$), due to the fact that, within each island community, sampling location is not representative of an individuals habitat use or distance to other individuals in the community. Further, in order to account for multiple observations of each individual, we included fixed effects for each pairwise individual (I). We iteratively built models by adding one predictor variable

with each iteration, for a final model that included all possible predictor terms:

$$E(f[AI_{ij}]) = \alpha + \beta_1 r_{ij} + \beta_2 d_{ij} + \beta_3 r_{ij} d_{ij}, + G(I_i) + G(I_j) \tag{4.1}$$

Significant parameters of the model that minimized Akaike's Information Criterion (AIC) considered to be potential drivers of association among pairs of individuals.

4.4 Results

The mtDNA dataset, including newly generated sequences and those from Van Cise et al. (2016), consisted of 242 samples from throughout the Hawaiian Islands, 100 of which were also included in the SNP dataset (Figure 4.1). A total of 163 SNPs at 50 nuclear loci from 112 individuals were successfully genotyped from four capture-enriched library pools. Six samples were determined to be duplicates and removed from the dataset, so that the final SNP dataset included 106 individuals (Supplemental Table B.1). Forty-four SNPs were removed during the quality analysis phase due to possible assembly of paralogous loci, resulting in 119 SNPs at 49 nuclear loci (Supplemental Table B.2). The subsampled SNP dataset (two samples per social unit) used for geographic differentiation analyses within the MHI included 63 samples (Supplemental Table B.3). Only seven samples with SNP data were available from the pelagic stratum, and no samples were successfully genotyped from the Northwest Hawaiian Islands; therefore, SNP analyses of genetic structure among these strata were not possible. Cluster assignments were available for 93 of the samples; analyses of differentiation among social clusters were performed using a dataset that included related individuals (n=93) and a dataset with individuals removed from pairs with relatedness estimates >0.6 ($n = 85$). Finally, pairwise relatedness based on the 51 unlinked SNPs was calculated for the full 106 sample SNP dataset, and group relatedness was calculated for three social units, five clusters and two communities.

We found very low mtDNA haplotype diversity in the Hawaiian Islands (Table 4.1). Six haplotypes were identified among the 242 samples (Table 4.2), all of which were previously reported by Van Cise et al. (2016); 231 of the 242 samples had haplotype J. With the exception of one sample collected off Kauai, all samples from the MHI stratum had haplotype J. Observed and expected heterozygosity for the phased multi-SNP genotypes in the MHI were 0.47 and 0.46, respectively, with slightly higher heterozygosity in the western MHI community than in the eastern MHI community (Table 4.1).

Mitochondrial differentiation was significant between the MHI and NWHI strata, as well as between the MHI and pelagic strata (F_{ST} and $\phi_{ST} P < 0.001$, 4.3). Within the MHI, SNP differentiation was small but significant between the eastern and western MHI communities. SNP differentiation was not tested between other strata (pelagic, NWHI) due to low sample size. We did not find any evidence of sex-biased dispersal between communities in the MHI (*P*-values for all indices ranged from 0.2 to 0.9).

Within each island community, stable social units have been identified based on an ongoing study throughout the Hawaiian Islands (Baird, 2016). We obtained SNP data from five or more samples from each of three stable social units identified by Mahaffy et al. (2015), allowing us to calculate within-group relatedness for these units. Within-unit relatedness estimates were all significantly higher than expected if groups were randomly organized (Figure 4.2). Overall, mean relatedness within social units ($r = 0.23$) was higher than expected across all groups ($P < 0.001$, Figure 4.2). Within-cluster relatedness for cluster H20, comprised of three social units, was also significantly higher than relatedness between randomly selected pairs of social units ($r = 0.33$, $P < 0.03$), as well as being higher than mean relatedness at the community level ($r = 0.11$).

When highly related individuals ($r > 0.6$) were removed, clusters with more than five individuals sampled were found to be significantly differentiated from each other in eight out of ten pairwise comparisons (Table 4.4). Global F_{ST} was also significant when

tested using all samples with cluster assignments ($n = 84$, $F_{ST} = 0.02$, $P = 0.05$). When the same analysis is performed using all samples regardless of relatedness, the number of significant pairwise differences between social clusters increases from eight to nine, likely due an increase in both sample size and relatedness within groups (Supplemental Table B.4).

Pairs of clusters that exhibited higher genetic differentiation associated less often (Figure 4.3). The results of a fixed effect linear regression indicate a negative causal relationship between pairwise F_{ST} differentiation and association between clusters ($P = 0.01$). Genetic differentiation explained 68% of the variance in association between clusters ($R^2 = 0.68$).

While there was no correlation between relatedness and geographic distance (Mantel test $P = 0.13$), association index was significantly correlated with both relatedness and distance (Mantel test $P < 0.001$ for both tests).

Regression model fits indicated that association between individuals increases with genetic relatedness. Genetic relatedness was found to be a significant driver of association time ($P < 0.0001$), while distance category (near or far), and the product of genetic relatedness and distance category, were not found to be significant ($P = 0.9$ and 0.2, respectively). AIC was minimized using a model in which association index increased with an exponential increase in relatedness ($AIC = -4169$), but a linear relationship was similar ($AIC = -4164$). Relatedness explained between 21% of the variance in association time between pairs of individuals ($R^2 = 0.21$).

4.5   Discussion

4.5.1   Genetics, sociality and ecological behavior

Our results show that short-finned pilot whales in Hawaii exhibit links between their genetic structure, social structure and at least one learned ecological behavior, island preference. Links between social behavior, learned ecological strategies, and genetic structure have been shown in other social animals, such as killer whales, sperm whales, and elephants (Yurk et al., 2002; Archie et al., 2006; Wittemyer et al., 2009; Rendell et al., 2012; Foote et al., 2016), and may have a stabilizing effect that promotes rapid genetic divergence among groups. In Hawaiian pilot whales, island preference and social unit philopatry influence genetic structure, and genetic relatedness in turn affects social organization.

The importance of genetic relatedness to social organization is evident when we examine the high level of relatedness within social units as compared to random (Figure 4.2), a pattern that has been demonstrated in pilot whales from other regions of the world (Alves et al., 2013), and may result from matrilineal fidelity. We additionally found that relatedness was higher within clusters than throughout the Hawaiian population, suggesting that relatedness plays a role in determining how groups are organized at hierarchical levels above the immediate family unit. We saw the same pattern in the regression comparing relatedness with association in pairs of individuals, which showed that animals that were more closely related were also more likely to associate.

If relatedness does not affect social structure at any level higher than that of the social unit, we would expect relatedness at the cluster level to fall to the level of relatedness within the entire population. Our results indicate that relatedness continues to drive social structure and association at higher levels in the hierarchical organization than just the matrilineal social unit. This may indicate that clusters are groups of related social units that underwent fission, similar to elephants (Archie et al., 2006) and killer whales (Williams and Lusseau,

2006). Genetic relatedness between groups can decay quickly in time due to the death of kin, and would be consistent with the lower relatedness within clusters than social units that we observed in this study. Higher relatedness within clusters than within island communities suggests that fitness benefits of association at the cluster level may be direct rather than indirect, such as cooperative foraging, mating, or predator avoidance (Archie et al., 2006), although the last is unlikely in Hawaiian pilot whales, which have little evidence of predators (Baird, 2016).

In elephants, social units that associate more often were shown to have recently split from each other due to the death of a matriarch (Archie et al., 2006). A larger, more comprehensive sample that includes all or most clusters, and a greater number of SNPs, would increase the resolution of the genetic structure among socially-divided units, clusters and communities, and may allow us to determine which clusters are more genetically similar, and whether specific clusters are facilitating gene flow between island communities.

On the other hand, we were able to show significant genetic differentiation among sympatric clusters even when highly related individuals were removed from our analyses, indicating restricted gene flow among sympatric clusters. Clusters that were more genetically differentiated also spent less time together (Figure 4.3). This would suggest that social structure inhibits gene flow among clusters, which could accelerate genetic divergence among clusters compared to a group of randomly mating individuals. It is important to note, however, that the observed genetic differentiation among clusters may also be caused by low effective population size, sampling stochasticity, or a combination of these factors.

This bi-directional influence between social structure and genetic structure creates a positive feedback between the two that may be self-stabilizing, thus encouraging continued genetic and social divergence. In birds, social song learning has been argued to restrain genetic divergence soon after a dispersal event, but promote divergence at later stages in the process (Slabbekoorn and Smith, 2002). In killer whales, social structure and social

learning are thought to have promoted rapid sub-species divergence into novel ecological niches (Foote et al., 2016). In a similar way, social structure in pilot whales may promote genetic divergence, and in turn genetic relatedness helps maintain a familial social structure.

Geographic distance is significantly correlated with association between individuals, or social structure, although it was not found to be a significant driver of association between individuals. Since geographic distance (d) cannot be interpreted as a continuous variable, due to the geographic overlap of social units within island communities, it instead represents individuals that were encountered in the same island community ($d < 50mi$) or different island communities ($d > 300mi$). The correlation between geographic distance and association among individuals likely indicates that individual preference for one island community and association with other individuals are both driven by similar mechanisms.

While the present study did not examine genetic or social structure as drivers of ecological behaviors such as island preference, there is evidence for social and parental (i.e. genetic) learning of ecological and other behaviors in other highly social cetaceans, such as killer whales and sperm whales (Cantor et al., 2015; Foote et al., 2016). Indeed, social learning of ecological behaviors may be important to the long-term resilience of oceanic predators (Whitehead, 2007b). Further studies of ecological and social behaviors in pilot whales, such as diet preference, foraging strategies, mating strategies, group movements, and vocal repertoire would help elucidate whether social and genetic structure also contribute to the learning and practice of these behaviors.

4.5.2   Hawaiian Islands population structure

The Main Hawaiian Islands stratum was distinct from the pelagic and NWHI strata, indicating the presence of an insular population around the Main Hawaiian Islands, as well as a pelagic/NWHI population. Insular or coastal populations have been observed in other odontocetes, such as false killer whales (Martien et al., 2014), bottlenose dolphins (Allen

et al., 2016) and spinner dolphins (Andrews et al., 2010). Pilot whales exhibit strong site fidelity (Mahaffy et al., 2015), and it is possible that the MHI population has become adapted to the slope habitat it prefers (Baird, 2016; Abecassis et al., 2015), and may have different dietary preferences to the pelagic population. However, tagging data indicate that pelagic social groups will sometimes travel through the slope region of the MHI (Baird, 2016) The lack of mtDNA gene flow between these two populations suggests that social structure prevents dispersal of females between these two populations when they come in contact with each other.

Although mtDNA differentiation between the pelagic and NWHI strata was non-significant, we expect that a larger sample size will differentiate the two populations. Samples from the pelagic stratum had haplotypes also found in SE Asia, the South Pacific, the Indian Ocean, and southern Japan, while NWHI haplotypes were either J (MHI) or an endemic haplotype with 4 bp difference from J, suggesting that the NWHI group may have diverged from the MHI insular population, possibly due to geographic isolation. This is similar to the pattern observed in Hawaiian false killer whales, where photo-identification, tagging, and mtDNA suggest three populations, with shared maternal ancestry between the MHI and NWHI, but nuclear data showing contemporary gene flow is highest between the NWHI and pelagic populations (Martien et al., 2014). However, our nuclear SNP sample size was not large enough to test for geographic differentiation between these strata, therefore the possibility still remains for male-mediated gene flow between the NWHI and Pelagic strata. A large dataset of both mtDNA haplotypes and SNP genotypes from the NWHI and pelagic strata may provide greater insight into the historical and contemporary rates of gene flow among these geographic areas.

Within the insular Main Hawaiian Island population, there are at least two genetically distinct island communities, with some continued gene flow between them. This may be driven by cluster philopatry to island communities, with some clusters key to gene flow

between communities. Satellite tag data indicate a third possible community, around Oahu/Lnai, known as the central MHI community. Additional samples from that community are needed to test whether it is genetically distinct from the eastern and western MHI communities. Individuals rarely leave their island community, instead spending the majority of their time around one island; however, on rare occasions clusters have been observed outside their island community ranges (Baird, 2016), and mating may occur during these rare excursions. There was no nuclear evidence for sex-biased dispersal among communities. Although sex-biased dispersal is commonly thought to be a mechanisms for inbreeding depression avoidance in socially-structured animals, studies have shown that social structure itself may be important to avoiding inbreeding depression (Parreira and Chikhi, 2015).

Short-finned pilot whales in Hawaiian waters are subjected to a variety of anthropogenic impacts, including interactions with fisheries, vessel strikes, and exposure to high-intensity Navy sonars (Baird, 2016). Social species such as this can be more vulnerable to the removal of a single individual, as it may precipitate the loss of an entire group (Wade et al., 2012). If some clusters contribute more to gene flow between communities, the loss of those clusters could act to fragment communities within the MHI, which would decrease genetic diversity and increase demographic isolation in each region, thus making those communities more vulnerable to environmental or anthropogenic perturbations. In order to avoid this vulnerability, conservation management of this species in the Hawaiian Islands could focus on maintaining gene flow between communities within the MHI populations, similar to migration corridors between fragmented terrestrial habitats.

4.6 Acknowledgements

We thank the NOAA/SWFSC Marine Mammal Genetics Group, including Brittany Hancock-Hanser, Vicki Pease, and Gabriela Serra-Valente for their support of this project. We also thank the Cascadia Research Collectives Daniel Webster and Greg Schorr for their

Chapter 4, in full, has been submitted for publication of the material as it may appear in Molecular Ecology, **2017**, Van Cise, Amy M., Martien, Karen. K., Mahaffy, Sabre D., Baird, Robin W., Webster, Daniel L., Fowler, James H., Oleson, Erin M., Morin, Phillip A. Familial social structure and socially-driven genetic differentiation in Hawaiian short-finned pilot whales. The dissertation author was the primary investigator and author of this paper.

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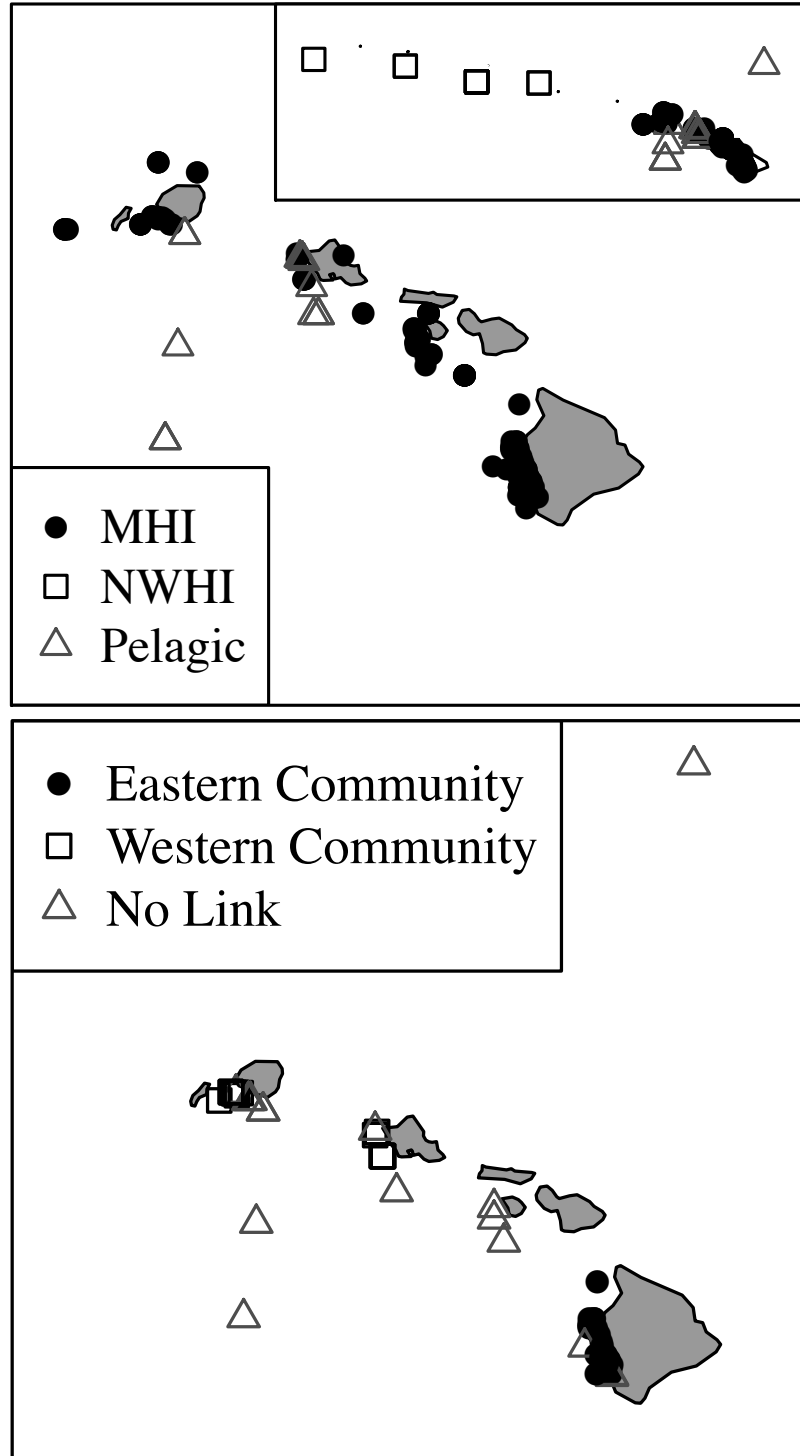
Figure 4.1: *Sampling locations for samples used in this study. Above: samples used in mtDNA analyses. Symbols represent their stratification for genetic structure analyses. Below: samples used in SNP analyses. Symbols represent their stratification for genetic structure analyses.*
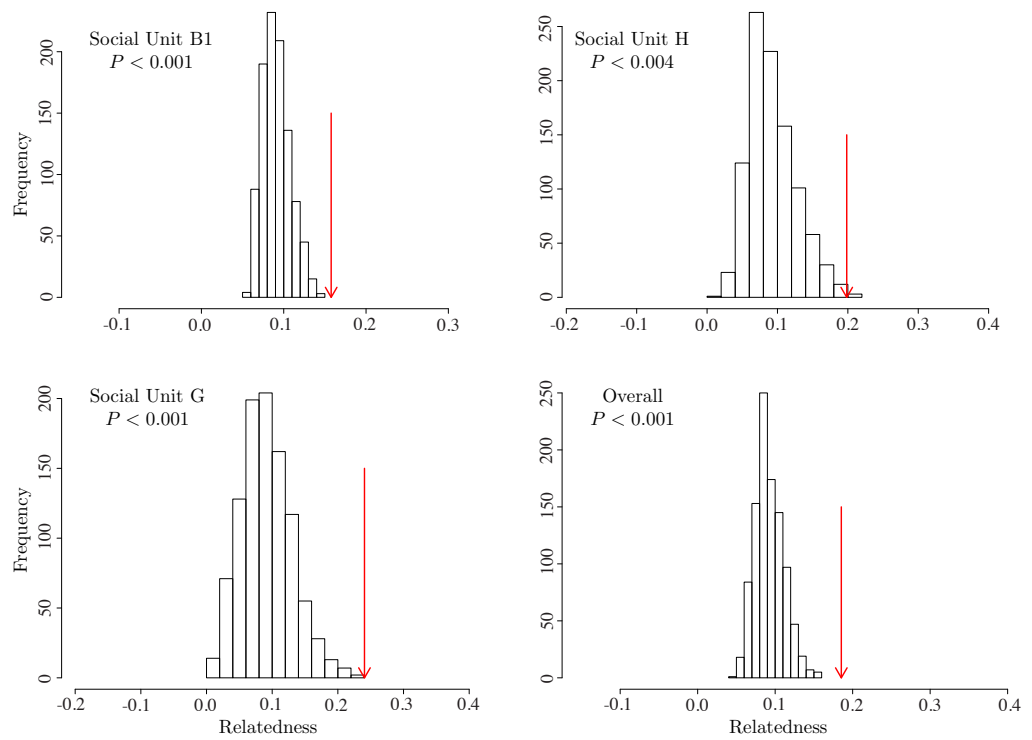
Figure 4.2: *Relatedness analysis for three social units with at least five individuals sampled, and overall relatedness within social units (bottom right). Red lines indicate average within-group relatedness; histograms show the expected distribution of within-group relatedness values if groups were randomly organized but retained their original sample size.*
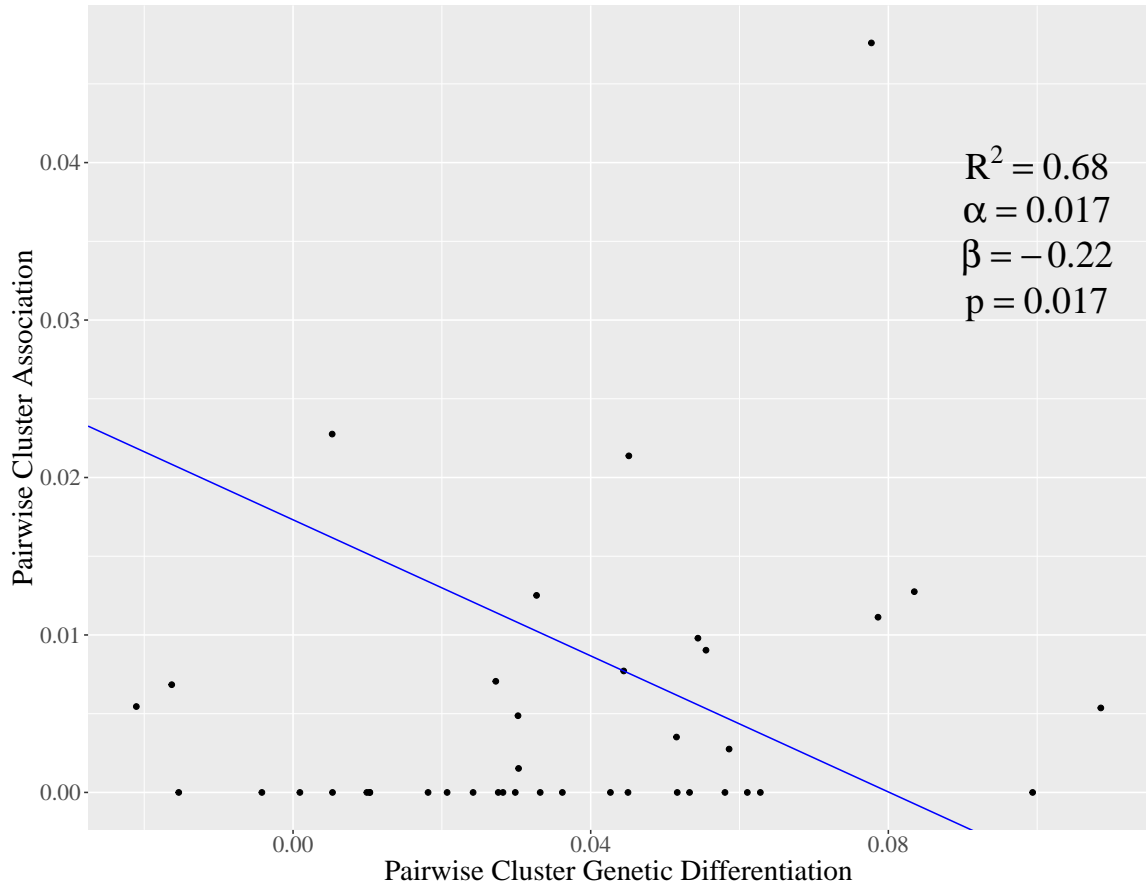
Figure 4.3: *Fixed effect linear regression comparing pairwise genetic differentiation (F_{ST}) and association in clusters.*

Table 4.1: *Molecular diversity indices for SNP and mtDNA datasets, using sub-sampled datasets so that diversity indices within strata were not biased by sample size. All regions includes samples pooled from the MHI, NWHI, and pelagic regions, listed individually below. N = sample size, H_o = observed heterozygosity, H_e = expected heterozygosity.*

	mtDNA N	θ_H	Haplotype diversity (h)		Nucleotide diversity (π)	SNP N	Ave. num. alleles	H_o	H_e
All regions	63	0.06	0.08	0.02	0.004	86	4	0.45	0.45
Regions									
MHI	204	0.007	0.01	0.01	0.004	63	3.9	0.46	0.46
Western MHI Community	–	–	–		–	21	3.5	0.49	0.47
Eastern MHI Community	–	–	–		–	42	3.7	0.45	0.45
NWHI	17	0.33	0.44	0.1	0.004	–	–	–	–
Pelagic	16	0.27	0.36	0.1	0.004	–	–	–	–

Table 4.2: *Mitochondrial haplotype distribution by stratum in the Hawaiian Islands.*

Stratum	MHI	NWHI	Pelagic
Haplotype			
J	203	12	16
C	1	0	0
K	0	0	2
12	0	5	0
11	0	0	1
2	0	0	1

Table 4.3: *Geographic population differentiation in Hawaiian Island short-finned pilot whales. For SNP data, only F_{ST} was calculated; for mtDNA data, both F_{ST} and ϕ_{ST} were calculated. Sample sizes for each stratum are shown in parentheses. Significant values are shown in bold.*

Stratum	F_{ST}	F_{ST} **P-value**	ϕ_{ST}	ϕ_{ST} **P-value**
mtDNA				
MHI (204) v. NWHI (17)	0.67	<0.001	0.58	<0.001
MHI (204) v. Pelagic (20)	0.39	<0.001	0.30	<0.001
NWHI (17) v. Pelagic (20)	0.08	0.07	0.01	0.28
SNP				
Eastern MHI Community (42) v. Western MHI Community (21)	0.01	0.009	NA	NA

Table 4.4: Genetic differentiation (F_{ST}) between five clusters with more than five sampled individuals (related individuals not included); sample sizes for each cluster are shown in parentheses. F_{ST} P-values are shown below F_{ST} values in parentheses; significant differentiation between clusters is shown in bold.

	Eastern Community Cluster 2 (8)	**Eastern Community Cluster 20 (10)**	**Eastern Community Cluster 22 (10)**	**Western Community Cluster 13 (9)**
Eastern Community Cluster 20 (10)	**0.05** **(<0.001)**			
Eastern Community Cluster 22 (10)	**0.06** **(<0.001)**	**0.04** **(0.002)**		
Western Community Cluster 13 (9)	**0.02** **(0.05)**	**0.02** **(0.04)**	0.01 (0.12)	
Western Community Cluster 24 (6)	**0.05** **(0.02)**	**0.03** **(0.03)**	**0.02** **(0.04)**	0.002 (0.39)

Chapter 5

Song of my people: Dialect differences among sympatric social groups of Hawaiian short-finned pilot whales

5.1   Abstract

In many social species, acoustic dialects are used to differentiate among social groups within a local population. These acoustic dialects, and their corresponding social groups, are often distinct in ecological behaviors such as foraging ecology and spatial movements, and it is possible that vocal repertoire variability is one of the proximate mechanisms driving or maintaining genetic and ecological diversity at a sub-species level in social species. Short-finned pilot whales (*Globicephala macrorynchus*) inhabiting Hawaiian waters have a stable hierarchical social structure, with familial social units associating in larger social clusters, within island-associated communities. We conducted ANOVA and support vector machine (SVM) learning analyses of the acoustic features of social calls collected from photographically-identified social clusters of short-finned pilot whales around the Main

Hawaiian Islands. Social clusters were significantly differentiated in their acoustic features, and the SVM classification accuracy was 67%. The results of this study indicate that vocal repertoire may be one of the mechanisms driving social segregation in short-finned pilot whales, thus contributing to genetic diversity within populations. The small sample size in this study decreases the ability to detect acoustic population structure; it is likely that additional sampling will improve our power to detect differences among social clusters of Hawaiian pilot whales and improve classification accuracy. The pattern described here highlights the importance of increasing the spatial and temporal resolution of conservation and management plans for this species, in order to conserve sub-population genetic and social structure, which may also be an indicator of ecological variability and resilience to environmental perturbations, as in other closely related social species (e.g. killer whales).

5.2 Introduction

Vocal dialects are used to differentiate among sympatric or allopatric groups at the population or sub-population level in many vocal taxa (e.g. birds (Baker and Cunningham, 1985; Wright and Wilkinson, 2001; Slabbekoorn and Smith, 2002; Podos, 2010), non-human primates (Green, 1975; Mitani et al., 1992; Fischer et al., 1998; Lemasson et al., 2003; Crockford et al., 2004; McComb and Semple, 2005; de la Torre and Snowdon, 2009), rock hyraxes (Kershenbaum et al., 2012), prairie dogs (Perla and Slobodchikoff, 2002), mouse lemurs (Kessler et al., 2014), bats (Esser and Schubert, 1998), and cetaceans (Winn et al., 1981; Ford, 1991; McDonald et al., 2006; Riesch et al., 2006; Papale et al., 2013; Balcazar et al., 2015; Cantor et al., 2015; Garland et al., 2015)). In the marine environment, where there are relatively few boundaries to individual or group dispersal, acoustic features may be especially important to identifying group membership in social species, since sound propagates much farther than light in water.

In some social species, differences in vocal dialects may be a proximate mechanism

driving or maintaining genetic differentiation among sympatric social groups. Correlations between genetic and acoustic structure have been identified in several taxa, including some birds (e.g. white-crowned sparrows (MacDougall-Shackleton and MacDougall-Shackleton, 2001; Soha et al., 2004)), bats (e.g. least horshoe bat (Yoshino et al., 2008)), and frogs (e.g. Tungara frogs (Prohl et al., 2006), Amazonian frogs (Amézquita et al., 2009)). Social cetaceans, such as sperm whales and killer whales, have been shown to use acoustic features to distinguish among social groups in an environment with few barriers to dispersal. Sperm whale clans, for example, remain vocally and genetically segregated although they are geographically and temporally sympatric in distribution (Rendell and Whitehead, 2003). Killer whales also form distinct vocal clans among genetically-distinct sympatric social groups (e.g. Yurk et al., 2002).

Vocal dialects are thought to be a culturally inherited trait, vertically or horizontally transmitted through vocal learning (Mundinger, 1980). Vocal learning has been demonstrated in birds (Baker and Cunningham 1985) as well as social cetaceans (Janik and Slater, 1997; Deecke et al., 2000; Crance et al., 2014), and may be maintained by gene-culture coevolution (Lachlan and Slater, 1999). Via the same coevolutionary process, some social cetaceans culturally inherit many ecological behaviors through learning, such as hunting strategies or habitat preferences (Whitehead, 2007; Cantor et al., 2015). Therefore, acoustic dialects may correspond with distinct, culturally-learned ecological behaviors. For example, ecologically and acoustically divergent groups of sympatric killer whales have been identified in several of the world's oceans, including the North Pacific Ocean and the Southern Ocean, and these groups may be undergoing a process of culturally-driven speciation (e.g. Riesch et al., 2012; Foote et al., 2016).

Short-finned pilot whales are a highly social species, known to form stable social groups of approximately 12 individuals for periods of a decade or more (Alves et al., 2013; Mahaffy et al., 2015). In the Main Hawaiian Islands (MHI) these small groups, defined as

social units, will often associate with a number of other social units in affiliations called clusters, with an average of 23 individuals (Mahaffy et al., 2015). Longitudinal observations and photo identification data collected since 2000 have revealed that social units, the most stable group in the social hierarchy, have a mean association index of 0.76. Clusters, the next hierarchical level, comprise one or more social units with mean association index of 0.48. Communities, the highest level of social organization, comprise multiple clusters that are generally resident to either Hawaii Island (eastern MHI community), Oahu/Kauai Islands (western MHI community), or Oahu/Lanai Islands (central MHI community) (Baird, 2016). Nine clusters have been identified in the eastern MHI community. Less is known of the central MHI community. Relatedness analyses indicate that social units are predominantly composed of immediate family members, while clusters likely represent extended family association (Chapter 4).

Social clusters are genetically distinct, indicating that they remain socially segregated over multiple generations (Chapter 4), yet the proximate mechanism for social segregation is unknown. It is possible that acoustic dialects among social groups are used to identify group membership, and therefore act as a driver maintaining social and genetic structure. In this study we will examine acoustic variability in Hawaiian pilot whales, specifically testing whether social clusters from the Hawaii Island community are acoustically distinct. Correlation between acoustic dialects and social cluster organization may indicate that vocal repertoire and acoustic features are a driving mechanism for maintaining social segregation in Hawaiian short-finned pilot whales.

5.3   Methods

5.3.1   Data collection

Data for this study were collected as in Van Cise et al. (2017). Recordings were collected from around Hawaii Island during Cascadia Research Collective field projects (R. W. Baird et al. 2013) from 2012-2013. Two recording instruments were used: a Biological Underwater Recording Package (BURP 3.2, developed at SWFSC), and a DMON Towfish. Table 5.1 displays specifications for both.

Recording packages were deployed during encounters with confirmed groups of short-finned pilot whales, and only if no other species were identified by trained observers during the encounter. Photographs were taken during each encounter, and used to identify the social unit(s) and cluster(s) present during each encounter, based on the hierarchical social structure described by Mahaffy et al. (2015). The BURP was attached to a surface buoy and deployed for periods of 15 minutes to 1 hour. The Towfish, containing a DMON acoustic recorder (e.g. Kaplan et al. 2014) developed at WHOI, in a custom-built towable body, was towed approximately 15 m behind an 8.2 m Boston Whaler with two 150 hp outboard motors.

To minimize the impact of noise and decrease the likelihood that animals pass through the recording area undetected, recordings were only used from conditions under 4 on the Beaufort scale. Recordings were only used for this study if pilot whales were the only species seen by trained observers within the horizon (approximately 4-5 km), and the social unit or cluster could be identified using photographs from the encounter. Encounters for which multiple clusters were identified were removed from all social structure analyses. Single-cluster encounters were assigned to their cluster (S. D. Mahaffy et al. 2015) using photographs from the encounter.

All calls were manually extracted using Raven 1.4. Spectrograms were created

using a DFT with a Hamming window (50% frame advance), and frame lengths were set to provide similar temporal and spectral resolution across recordings with different sampling rates (BURP NDFT = 2048, Towfish NDFT = 1280). Since pilot whales exhibit smooth transitions between pulsed calls and whistles (L. Sayigh et al. 2013), and some evidence indicates that these vocalizations may exist on the same continuous spectrum (Murray, Mercado, and Roitblat 1998), both pulsed calls and whistles are considered together in this study, and referred to as "calls".

Calls were visually classified and annotated as part of a previous study (Van Cise et al. 2017). Once extracted, calls were imported into PAMGUARD version 1.11.12 (Gillespie et al. 2009; 2013). The fundamental frequency of each whistle was traced using ROCCA for PAMGUARD (J. Oswald and Oswald 2013). For pulsed calls, the lowest band for which the entire call was visible was traced (i.e. the frequency band with the most power), representing the pulse repetition rate (Watkins 1968). Fundamental frequency and pulse repetition rate values were both analyzed as call frequency values. Up to 50 randomly selected calls were traced per encounter. Summary parameters were calculated for each call using the call trace exported from ROCCA (start frequency, min and max frequencies, mean frequency, frequency range, duration). Because the frequency parameters were all highly correlated, start frequency was used to represent this group of measurements.

5.3.2 Data analysis

The start frequency, frequency range and duration of each call was used to examine statistical differences among clusters, formed by one or more social units that spend the majority of their time in association (S. D. Mahaffy et al. 2015). We used a nested, non-parametric MANOVA, implemented using the BiodiversityR package (Kindt and Coe 2005), with encounters nested as a factor within cluster, to account for potential differences in acoustic behavior among encounters. We then used a post-hoc Tukey's test to determine

whether significant results were driven by a single encounter or cluster. ANOVA and Tukey's test analyses were performed in the R computing environment (R Core Team 2016).

We additionally used a support vector machine learning classification algorithm to test whether acoustic differences among clusters could be used to classify calls to the appropriate cluster. Support vector machine learning is a kernel substituion method that allows for binary, non-linear classification of multivariate data by finding the optimal hyperplane that separates two classes, which is achieved by maximizing the margins between each class' closest points. The algorithm is trained by quadratically optimizing a convex cost function between the closest points in the convex hulls of each distribution (Bennett and Campbell 2000). The package e1071 (Meyer et al. 2015), implemented in R, expands this concept to allow for classification of multiple groups using the same algorithm.

We then tested for differences in acoustic behavior between multi-cluster and single-cluster encounters, again using a nested, non-parametric ANOVA, with encounters nested as a factor within the single- and multi-cluster classes. A post-hoc Tukey's test was again used to determine whether significant results were driven by a single encounter or cluster.

5.4   Results

Between 2012 and 2015, acoustic recordings were collected during 26 encounters with short-finned pilot whales. Of these encounters, cluster membership was identified for 25 encounters. Multiple clusters were present during 8 encounters, and the remaining 17 encounters were with a single cluster. Recordings were made during single-cluster encounters with 9 clusters. However, vocalizations were not detected on some recordings, so not all encountered clusters were successfully recorded. Recordings were made, and vocalizations successfully extracted, from 10 encounters representing 6 clusters. Number of encounters per cluster, as well as number of extracted calls, can be found in Table 5.2. In some cases, the final per cluster sample size was too small to allow tests analyzing

differences among individual clusters; therefore, our analysis is focused on general trends of differentiation across all social clusters.

For some clusters, the small number of calls collected precluded our ability to directly test for differentiation from other clusters. We instead tested for a general pattern of differentiation among clusters using a nested MANOVA, with encounters nested within clusters, and tested significant results with a post-hoc Tukey's test. Both cluster and encounter were significantly associated with acoustic differentiation in start frequency, frequency range and duration (cluster p-value $<$0.0001, encounter p-value $<$0.0001). The Tukey's test of Honest Significant Difference for all pairwise tests of clusters showed that clusters with a larger sample size were more likely to be significantly differentiated (Figure 5.1).

Using an SVM learning algorithm and the three clusters with a sample size of at least 20 calls, we were able to successfully assign calls to their cluster with an accuracy of 63%, using a random 10% cross-validation method. When whistles were grouped by encounter for cross-validation rather than randomly, the classification accuracy was highly variable, with a mean classification accuracy of 18% and a range of 0-100% accuracy. Classification results are shown in Figure 5.2.

Finally, we found that single-cluster (n = 276) and multi-cluster (n = 264) encounters were significantly different in both the median and cumulative distribution of all three acoustic features analyzed, based on Kruskal-Wallis and Kolmogornov-Smirnov non-parametric differentiation tests (Table 5.3). Distributions and median values for each of the three acoustic figures are shown in Figure 5.3.

5.5   Discussion

Pilot whale social clusters show evidence of having distinct vocal dialects, as exhibited by the significant differentiation among clusters in the MANOVA analysis and post-hoc

Tukey's test, and the high accuracy with which the SVM learning algorithm classified calls to social clusters. It is important to note here that within-cluster sample sizes were small, which may decrease our power to detect differences in cluster means. Because of this, clusters with the smallest sample sizes were removed from the SVM learning algorithm. However, increased data collection from these social clusters, as well as additional clusters throughout the Hawaiian Islands, would likely improve our ability to differentiate among individual social clusters, based on results from the ad-hoc Tukey's test, which showed that tests of acoustic differentiation among clusters with larger sample sizes were more likely to be significant (Figure 5.1).

Vocal dialects may be one of the mechanisms pilot whales use to maintain group cohesion and social structure, which over multiple generations has led to genetic differentiation among clusters (Chapter 4). This could be caused by a combination of vertical transmissions along matrilines and horizontal transmission (social learning) within social clusters, with limited information transfer among clusters. Similar patterns of vertical (Yurk et al., 2002) and horizontal Filatova et al. (2013) transmission of vocal repertoires have been hypothesized to drive the acoustic population structure of killer whales.

As in other social cetaceans, such as killer whales, acoustically and genetically distinct social groups may also exhibit differences in their ecological behaviors, such as prey preference, foraging techniques, and temporal movements (Foote et al., 2009; Foote, 2012; Foote et al., 2016). These socially driven differences in ecological behaviors, as well as the increase in genetic diversity caused by social structure (Parreira and Chikhi, 2015), may increase a species' resilience to local environmental perturbations. Further studies comparing variability in ecological behaviors, such as diet, habitat use, or spatial movements, with genetic and acoustic variability among social clusters of Hawaiian pilot whales, could be used to examine the interaction of ecological, social and genetic factors in pilot whales, and may help further elucidate the nature of gene-culture evolution in social

species.

Pilot whales may also have vocal repertoires that differ in certain behavioral contexts, such as foraging versus socializing, or environmental contexts, for example depending on the ambient noise level. This is supported by the significant differentiation among encounters in the hierarchical ANOVA, and may have caused the poor performance of the SVM learning algorithm when samples were divided by encounter instead of randomly. Our comparison of multi-group vs. single-group encounters also found significant differences in acoustic features (Figure 5.3), which likely indicates a difference in acoustic behavior between these types of encounters. It is possible that specific calls are used to communicate information such as group identity in the presence of multiple groups. This variability in acoustic behavior could extend to other behavioral contexts, such as foraging, travel, or socialization. Short-finned pilot whales make social calls during foraging dives, possibly to maintain group cohesion (Jensen et al., 2011); the importance of social calls to pilot whales may be further indication of their likelihood to use different calls in different behavioral contexts. Additional data collection, and refinement of the classification methods presented in this study, would allow passive acoustic monitoring of social groups and their behaviors throughout the Hawaiian Islands.

Understanding acoustic population structure within a species, and its relationship with other aspects of the species, such as social structure, genetic structure, and ecological variability, allows a more nuanced approach to species conservation and management, one that conserves the diversity and ecological resilience of a species, rather than simply its abundance. If acoustic dialects are a proxy for genetic diversity and ecological resilience, acoustic research could be used as a non-invasive tool for the conservation management of a species. Passive monitoring of social groups, and their behaviorally-dependent vocalizations, would improve our understanding of local habitat use, providing a spatially and temporally explicit understanding of socially-driven spatial ecology at a subspecies level.

5.6   Acknowledgements

Chapter 5, in full, is currently being prepared for submission for publication of the material. Van Cise, Amy M., Mahaffy, Sabre D., Baird, Robin W., Mooney, T. Aran, Barlow, Jay. Song of my people: Dialect differences among sympatric social groups of Hawaiian short-finned pilot whales. The dissertation author was the primary investigator and author of this paper.

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Table 5.1: *Technical specifications for recording packages used in this study*

	BURP 3.2	DMON towfish
Sampling rate	192 kHz	512kHz
Functional bandwidth	2-60 kHz 5 dB	160 kHz
Recorder flat response rate	2-60 kHz	5-160 kHz
Pre-amplifier flat response rate	>2 kHz	NA
Recorder bit-depth	24-bit	16-bit
Hydrophone manufacturer and model	HTI, Inc.	Navy type II ceramics
Number of encounters	12	11
Recording period	2012	2012-2013

Table 5.2: *Number of encounters and sample size for social clusters included in this study.*

Cluster	Number of Encounters	Number of calls
H7	3	76
H20	2	160
H22	2	20
H27	1	4
W32	1	6
W16	1	10

Table 5.3: *Permutation test p-values for significance of KolmogorovSmirnov and Kruskal-Wallis measures of differentiation in the median and cumulative distributions of start frequency, frequency range and duration of calls recorded during single-cluster and multi-cluster encounters.*

Kolmogorov-Smirnov	Kruskal-Wallis
p <0.002	p <0.0001
p <0.004	p <0.0001
p <0.0002	p <0.0001
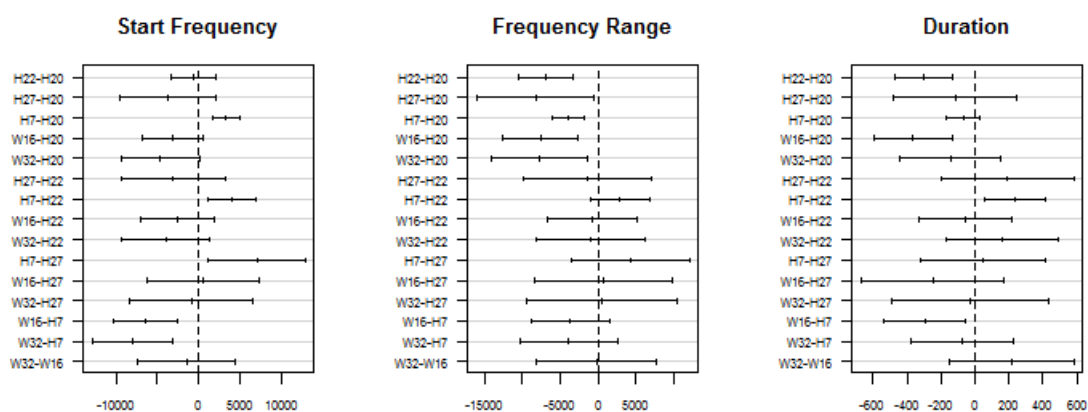
Figure 5.1: *Tukey's Honest Significant Difference test results for each of the three acoustic parameters included in this study. Mean and 95% confidence intervals of the difference between two clusters shown on each row; differences without a zero crossing are considered significant.*
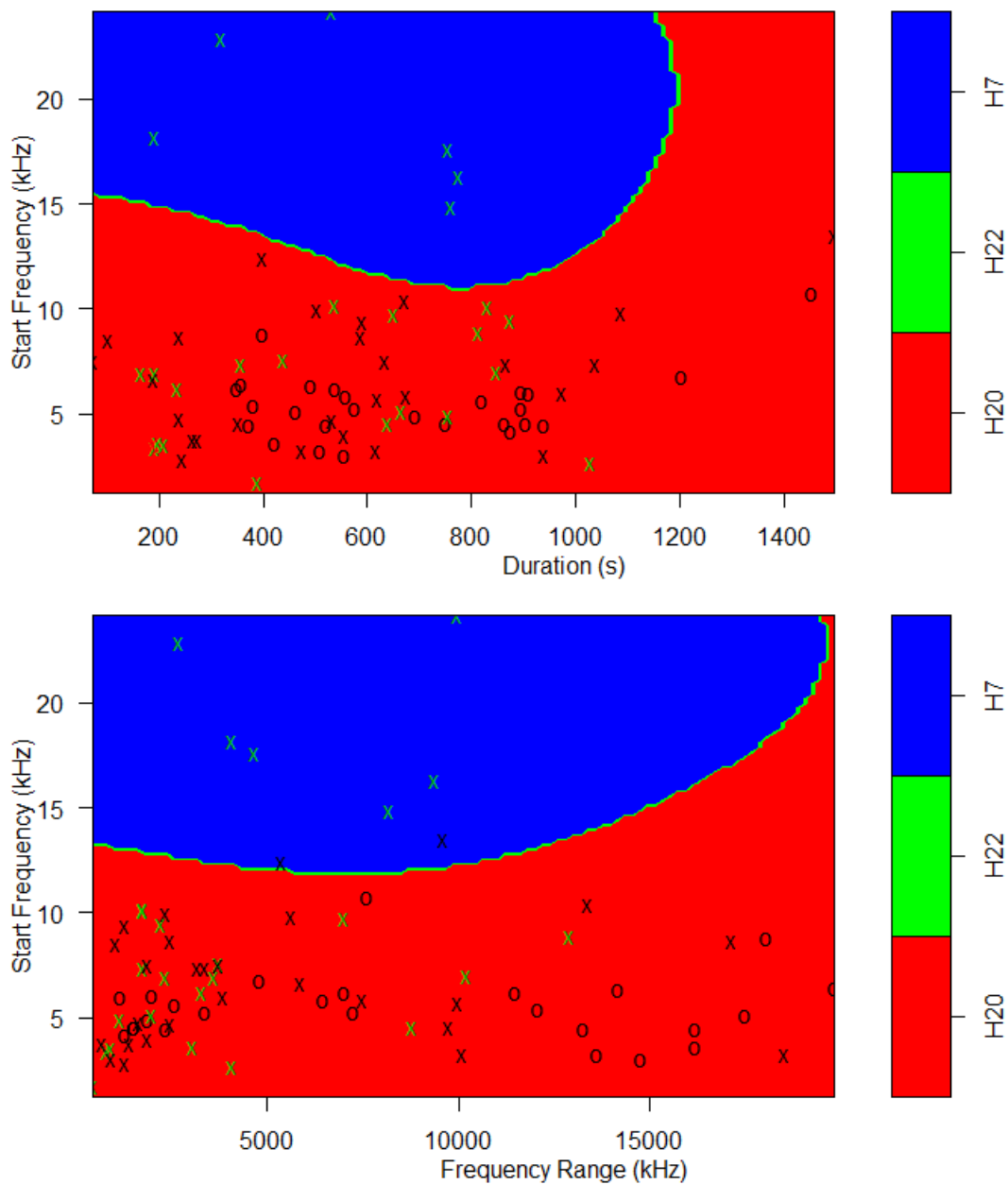
Figure 5.2: *Classification of calls by social cluster using a Support Vector Machine (SVM) learning algorithm. Start frequency, frequency range and duration are shown on the x and y axes. Support vectors are indicated by 'x', and data points are indicated by 'o'. Green 'x' represent additional support vectors for cluster H22.*
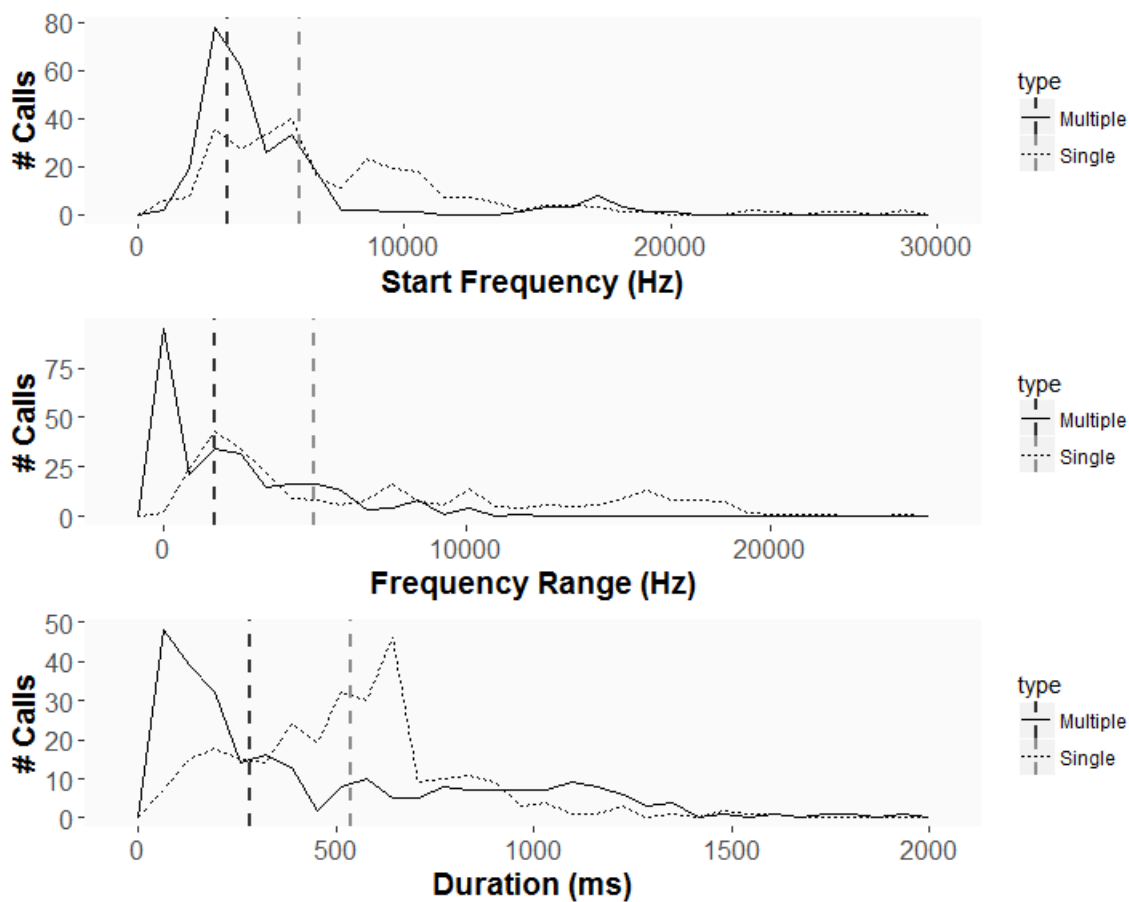
Figure 5.3: *Frequency distribution and median values for start frequency, frequency range, and duration of calls recorded during single-group and multi-group encounters.*

Chapter 6

Discussion

6.1   Pacific Ocean population structure

The results of this study support the hypothesis that there are at least two distinct sub-species or species of short-finned pilot whale in the Pacific Ocean. The Naisa- and Shiho-type short-finned pilot whales, first described off the coast of Japan in 1760 (Yamase, 1760), were re-discovered in the 1980s (Kasuya and Marsh, 1984; Kasuya, 1986; Kasuya et al., 1988). Here, I used mitochondrial markers and acoustic recordings to show that these genetically distinct types are also acoustically distinct (Chapter 3), and that they are distributed throughout the Pacific Ocean, with largely non-overlapping distributions (Chapter 2).

Though scientists had previously hypothesized that the distribution of Naisa- and Shiho-type short-finned pilot whales is correlated with sea surface temperature (Polisini, 1980; Kasuya et al., 1988), the results presented in Chapter 2 indicate an east-west division between the two types, rather than a tropical-subtropical division. It is possible that, instead, the two types are separated by the oligotrophic Pacific Ocean. Shiho-type individuals found in northern Japan may represent an ancestral link between the eastern and western Pacific Ocean, or may be descended from a founder group that followed the coastline west to Japan.

Diet may also be important to the distribution of the two types.

Acoustic differentiation between Shiho- and Naisa-type short-finned pilot whales may have been caused by acoustic drift following geographic isolation (Conner, 1982). However, some areas of the Pacific Ocean, such as the central North Pacific where the distributional boundaries of the two types remain unknown, are areas of potential overlap. In these areas, acoustic differentiation could be one factor maintaining separation between the two types. In this way, acoustic differentiation may be both a marker of passive drift and a driver acting to maintain, or possibly accelerate, isolation and divergence between the two types.

6.2   Local population structure

Comparing genetic and acoustic data with the known hierarchical structure in Hawaiian short-finned pilot whales revealed reciprocal links between social and genetic structure (Chapter 4), which may be maintained by differences in the vocal repertoire, or dialect differences, among clusters (Chapter 5). The coincidence of structure among these three data types suggests that genetic and cultural divergence are occurring simultaneously, and may be described by gene-culture coevolutionary theory (Feldman and Laland, 1996; Lachlan and Feldman, 2003; Laland et al., 1995). Genetics and cultural elements, such as social structure and vocal repertoire, may each be acting to stabilize the other in a manner that will accelerate overall divergence at a local level (Mayr, 1970; Laland, 1992), as has occurred in killer whales (Foote and Morin, 2016).

The hierarchical social structure of Hawaiian short-finned pilot whales (Mahaffy et al., 2015; Baird, 2016) is driven by genetic relatedness at multiple levels. The smallest units, called social units, comprise close relatives, including immediate family members, and are likely formed through natal group philopatry. Social units preferentially associate with a small number of other social units, forming clusters. Relatedness is also high among

social units within clusters, suggesting that clusters represent extended family groups, which may have formed through fission of large social units, for example when a matriarch dies. Fissioning has been demonstrated in several other socially organized or matrilineal species, such as elephants (Archie et al., 2006), macaques (Chepko-Sade and Sade, 1979), marmots (Armitage, 1984), and killer whales (Ford et al., 1984). Population genetic theory suggests that this type of linear fissioning can have a significant effect on genetic variance within a population (**?**); the genetic similarity exhibited within social units and clusters of short-finned pilot whales suggests that this population is also undergoing linear fission along matrilines.

Additionally, gene flow is limited between clusters, as well as between island communities, likely due to limited dispersal and/or mating between clusters. Clusters also have distinct vocal repertoires, and vocal behavior differs depending on whether one or multiple clusters are present. These differences in vocal behavior between clusters, and differences exhibited when a cluster is alone or with other clusters, suggest the possibility that vocal repertoire is used to maintain group cohesion. It is possible that vocal repertoire is linked with phenomena such as mate choice and dispersal, and ultimately with ecology and speciation, as is seen in many bird species (Kroodsma, 1974; Jenkins, 1978; Catchpole, 1987; Eens et al., 1991; Searcy, 1992, 2014; Lachlan and Slater, 1999; Slabbekoorn and Smith, 2002; Ellers and Slabbekoorn, 2003; Nowicki and Searcy, 2005; Byers and Kroodsma, 2009).

Finally, while two genetically distinct populations have been identified around the Hawaiian Islands, the lack of mitochondrial diversity in the eastern Pacific, including the California Current stock of short-finned pilot whales, indicates that a single population inhabits the entire eastern Pacific range, including coastal and pelagic habitats (Chapter 1). This difference may be an example of the importance of islands in creating heterogeneous habitats with a variety of niche spaces, and suggests the possibility that short-finned pilot

whales in the Hawaiian Islands have diverged in different oceanographic habitats.

6.3   Gene-culture coevolution and applications for the conservation of short-finned pilot whales

One of the primary objectives of this research was to test the hypothesis that the tenets of gene-culture coevolutionary theory can be used to shape our understanding of population structure and evolution in short-finned pilot whales. The results provide empirical support for the application of this theory. In many marine mammal species, understanding the links between social structure, cultural and ecological knowledge, and genetic structure will improve our understanding of overall population structure within a species, as well as the role that population structure plays in the species evolutionary trajectory. This has been demonstrated in a small number of marine species, such as killer whales (Riesch et al., 2012; Foote and Morin, 2016) and sperm whales (Whitehead, 2007; Rendell et al., 2012; Whitehead et al., 2017), but may also be true for a number of other marine mammals known to exhibit a variety of social behaviors (e.g. toothed whales such as beluga whales, false killer whales, common dolphins, spinner dolphins (Connor et al., 1998; Whitehead, 2007; Wade et al., 2012), and some baleen whales, such as humpback whales (Clapham, 1996; Ersts and Rosenbaum, 2003; Whitehead, 2007; Garland et al., 2013, 2015). For all of these social mammals, gene-culture coevolutionary theory may be applied to improve our understanding of the species evolutionary ecology.

In turn, an improved understanding of the evolutionary ecology of social marine mammals will improve management decisions for these species. Marine mammal management and conservation, mandated under the Marine Mammal Protection Act of 1972, is hampered by a lack of research, and research funding, for most species. According to the IUCN Red List, 51% of cetaceans are listed as data deficient, indicating that there is

not enough information available to determine whether these species are threatened by anthropogenic activities (IUCN, 2016).

The results of this research suggest that the California Current and Hawaiian stocks of short-finned pilot whales may represent two distinct sub-species or species, each containing multiple local populations. The presence of genetic, social and acoustic structure at a sub-population level further suggests that a variety of ecological strategies may exist within local populations. In the case of short-finned pilot whales, local diversity is not geographic or habitat-based, but rather socially and genetically driven among sympatric groups. This structure, therefore, requires high resolution data in order to elucidate ecological strategies at a subpopulation level, to allow the development of policy that protects the variety of ecological strategies.

Although social structure can increase diversity within populations (Parreira and Chikhi, 2015), it may decrease resilience of social species to anthropogenic threats (Wade et al., 2012). In many social species, social groups rely on a few key individuals to lead the group to prey resources or suitable habitat. Short-finned pilot whales are one of only three known species on the planet in which females undergo senescence (Marsh and Kasuya, 1986) - the other two are killer whales and humans. Because female short-finned pilot whales have long post-reproductive lifespans, they are thought to depend primarily on the decision-making of the eldest females in the group, similar to killer whales (Brent et al., 2015). Pilot whales are also known to strand in large groups, which is further indication of their reliance on group leaders (e.g. Perrin and Geraci, 2002; Hohn et al., 2006). Because of this social organization, Wade et al. (2012) suggest that the removal of a few individuals from a social group may precipitate the loss of the entire social group, unlike species that are not socially organized.

6.4 Continued work: quantifying acoustic population structure

This research provides the foundation for a quantitative comparison between acoustic and genetic differentiation in short-finned pilot whales, which could additionally be used to develop quantitative approaches for comparing acoustic and genetic data in other vocal species. To do this, it is necessary to develop quantitative metrics to measure acoustic divergence. For this purpose, Kullback-Liebler divergence, a measure of information divergence between two systems (originally developed to measure information divergence between a model and the system that model was built to mimic), can be employed as the basis of several analyses that are directly comparable to measures of population genetic structure.

For example, a KL-div distance matrix can be used to build a phylo-acoustic tree which, rooted in a sister species such as the long-finned pilot whale, can be compared with a phylogenetic tree to compare the divergence time between Naisa and Shiho types, or between local populations within each type, and to further determine whether genetic and acoustic intra-population divergence patterns are similar. Similarly, the magnitude of acoustic differentiation between types, or populations, can be quantified by creating a metric similar to an F-statistic using KL divergence:

$$K_{ST} = (K_{IT} K_{IS})/K_{IT} \qquad (6.1)$$

Where K_{ST}, similar to F_{ST}, is a measure of acoustic variance due to population structure, or the variance between subpopulations, and is calculated as the acoustic variance in the total population (K_{IT}) minus the acoustic variance within subpopulations (K_{IS}), divided by the acoustic variance in the total population (K_{IT}).

Metrics such as these may provide a framework to improve understanding of acoustic population structure, and represent a step toward calculating parameters affecting acoustic population structure, such as acoustic drift, or rates of acoustic learning between populations.

6.5 Continued work: global taxonomy of short-finned pilot whales

The results presented in the second and third chapters of this thesis support the hypothesis that the term short-finned pilot whale comprises multiple species or subspecies. In order to test this hypothesis, NOAAs Southwest Fisheries Science Center will complete a global analysis of the taxonomy of this species, using both mitochondrial and nuclear genomic data. In addition to resolving the divergence between the Naisa and Shiho types in the Pacific Ocean, this study aims to understand how short-finned pilot whales in the Atlantic and Pacific Oceans relate to these two types, and whether the distribution of either of these types extends farther than the Pacific Ocean basin. The results of this study may provide enough evidence to decide whether it is necessary to restructure the taxonomy of short-finned pilot whales.

6.6 Continued work: gene-culture coevolution in short-finned pilot whales

Gene-culture evolutionary theory provides a basis for understanding the links between social structure, genetic structure, and the transmission of cultural information (i.e. vocal repertoire) in short-finned pilot whales, both between populations at a regional level, and within local populations. As is seen in killer whales, it may be that social groups of short-finned pilot whales are ecologically distinct, and that the transfer of ecological informa-

tion follows the same patterns as the transfer of vocal repertoires. We can test the hypothesis that social structure drives ecological variability in short-finned pilot whales by examining differences in ecological parameters such as diet preference, movement, habitat use, or dive depth among groups using ecological data such as stable isotopes or satellite tag data. Studies examining the genetic basis of these cultural traits may also be warranted, given the correlation between genetic and cultural variability at the inter- and intra-populations levels. The applicability of gene-culture coevolutionary theory to understanding the evolutionary ecology of short-finned pilot whales is further proof that this theory is relevant outside humans, and merits the exploration of gene-culture coevolution models in social species across all taxa. The information gained by studies of this nature should improve our ability to manage anthropogenic threats to social species.

6.7   References

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Appendix A

Chapter 2 Supplemental Information

Table A.1: *Complete list of samples used, including short and long haplotye designations and GenBank accession numbers for sequences obtained from GenBank.*

SWFSC ID	Long (962 bp) Haplotype	Short (345 bp) Haplotype	GenBank Accesion #
34	J	J	KM624055
537	D1	D1	KM624040
1297	E3	E1	KM624047
1685	E3	E1	KM624047
1737	E3	E1	KM624047
1738	E3	E1	KM624047
1739	E3	E1	KM624047
1864	E3	E1	KM624047
2819	D2	D1	KM624041
3031	D1	D1	KM624040
4629	E3	E1	KM624047
4630	E3	E1	KM624047
4642	E3	E1	KM624047
4644	E3	E1	KM624047
4645	E3	E1	KM624047
4682	9	9	KM624056
4683	E3	E1	KM624047
4684	E3	E1	KM624047
4694	E3	E1	KM624047
4986	E3	E1	KM624047
4987	E3	E1	KM624047
4988	E3	E1	KM624047
5765	E3	E1	KM624047
5766	E3	E1	KM624047
5767	E3	E1	KM624047
7618	E3	E1	KM624047
8671	D2	D1	KM624041
8752	E3	E1	KM624047
9850	A1	A1	KM624042
9864	A1	A1	KM624042
9869	A1	A1	KM624042
9871	K	K	KM624054
9872	A1	A1	KM624042
9873	A1	A1	KM624042
11454	E3	E1	KM624047
11455	E3	E1	KM624047
11456	E3	E1	KM624047
11478	J	J	KM624055
11479	J	J	KM624055
11481	J	J	KM624055
11482	J	J	KM624055
11483	J	J	KM624055
11484	J	J	KM624055
11496	2	2	KM624043
11513	E3	E1	KM624047
11514	E3	E1	KM624047
11515	E3	E1	KM624047
11525	E3	E1	KM624047
11526	E3	E1	KM624047
11527	E3	E1	KM624047
11528	E3	E1	KM624047
11872	E3	E1	KM624047
11873	E3	E1	KM624047
11874	E3	E1	KM624047
11936	E3	E1	KM624047
11937	E3	E1	KM624047
11938	E3	E1	KM624047
11939	E3	E1	KM624047
11940	E3	E1	KM624047
11941	E3	E1	KM624047
11942	E3	E1	KM624047
11943	E3	E1	KM624047
11954	E3	E1	KM624047
11955	E3	E1	KM624047
11956	E3	E1	KM624047
11957	E3	E1	KM624047
11958	E3	E1	KM624047
11977	5	5	KM624050
11978	5	5	KM624050

SWFSC ID	Long (962 bp) Haplotype	Short (345 bp) Haplotype	GenBank Accesion #
11985	2	2	KM624043
12008	6	6	KM624051
12009	6	6	KM624051
12010	6	6	KM624051
12011	E3	E1	KM624047
12012	6	6	KM624051
12013	6	6	KM624051
12014	6	6	KM624051
12015	6	6	KM624051
12016	6	6	KM624051
12027	E3	E1	KM624047
12028	E3	E1	KM624047
12029	E3	E1	KM624047
12030	7	7	KM624052
12081	4	4	KM624045
12088	E3	E1	KM624047
12089	E3	E1	KM624047
12090	E3	E1	KM624047
12091	E3	E1	KM624047
12092	E3	E1	KM624047
12093	E3	E1	KM624047
12094	E3	E1	KM624047
12095	E3	E1	KM624047
12096	E3	E1	KM624047
12097	E3	E1	KM624047
12098	E3	E1	KM624047
13367	14	14	KM624060
16046	E3	E1	KM624047
16047	E3	E1	KM624047
16048	E3	E1	KM624047
16049	E3	E1	KM624047
16050	E3	E1	KM624047
16051	E3	E1	KM624047
16052	E3	E1	KM624047
16056	E3	E1	KM624047
16076	E3	E1	KM624047
16077	E3	E1	KM624047
16078	E3	E1	KM624047
16079	E3	E1	KM624047
16080	E3	E1	KM624047
16081	E3	E1	KM624047
16082	E3	E1	KM624047
16083	E3	E1	KM624047
16167	E3	E1	KM624047
16168	E3	E1	KM624047
17970	E2	E1	KM624048
17971	E3	E1	KM624047
17972	E2	E1	KM624048
17973	E3	E1	KM624047
17974	E2	E1	KM624048
17976	E2	E1	KM624048
17977	E3	E1	KM624047
17978	E3	E1	KM624047
17979	E3	E1	KM624047
17980	E2	E1	KM624048
17981	E2	E1	KM624048
17982	E3	E1	KM624047
18185	E3	E1	KM624047
18186	E3	E1	KM624047
18187	E3	E1	KM624047
18188	E3	E1	KM624047
18189	E3	E1	KM624047
18190	E3	E1	KM624047
18191	E3	E1	KM624047
18192	E3	E1	KM624047
18193	E3	E1	KM624047
18195	E3	E1	KM624047
18259	E3	E1	KM624047
18260	E3	E1	KM624047

SWFSC ID	Long (962 bp) Haplotype	Short (345 bp) Haplotype	GenBank Accesion #
18261	E3	E1	KM624047
18289	E3	E1	KM624047
18290	2	2	KM624043
18291	E3	E1	KM624047
18292	E3	E1	KM624047
18293	E3	E1	KM624047
18294	E3	E1	KM624047
18295	2	2	KM624043
18296	E3	E1	KM624047
18297	2	2	KM624043
18298	2	2	KM624043
18528	J	J	KM624055
18529	J	J	KM624055
18530	J	J	KM624055
18531	J	J	KM624055
18532	J	J	KM624055
18533	J	J	KM624055
18939	J	J	KM624055
18940	J	J	KM624055
18941	J	J	KM624055
18942	J	J	KM624055
18948	J	J	KM624055
18952	J	J	KM624055
18953	J	J	KM624055
23968	K	K	KM624054
25546	E3	E1	KM624047
27398	J	J	KM624055
27407	J	J	KM624055
27408	J	J	KM624055
27409	J	J	KM624055
27410	J	J	KM624055
27412	J	J	KM624055
27417	J	J	KM624055
30056	J	J	KM624055
30059	J	J	KM624055
30060	J	J	KM624055
30061	J	J	KM624055
30062	J	J	KM624055
30063	J	J	KM624055
30069	J	J	KM624055
30070	J	J	KM624055
30082	J	J	KM624055
30083	J	J	KM624055
30084	J	J	KM624055
30085	J	J	KM624055
30086	J	J	KM624055
30435	J	J	KM624055
30436	J	J	KM624055
30437	J	J	KM624055
30438	J	J	KM624055
30439	J	J	KM624055
30440	12	12	KM624059
30441	J	J	KM624055
30442	12	12	KM624059
30443	12	12	KM624059
30444	J	J	KM624055
30445	J	J	KM624055
30446	12	12	KM624059
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30456	J	J	KM624055
30457	J	J	KM624055
30458	J	J	KM624055
30459	J	J	KM624055
30460	J	J	KM624055
30461	J	J	KM624055
30462	J	J	KM624055
30463	J	J	KM624055

SWFSC ID	Long (962 bp) Haplotype	Short (345 bp) Haplotype	GenBank Accesion #
30464	J	J	KM624055
30465	J	J	KM624055
30508	J	J	KM624055
30511	J	J	KM624055
30518	J	J	KM624055
30519	J	J	KM624055
30520	J	J	KM624055
30521	J	J	KM624055
30527	J	J	KM624055
30528	J	J	KM624055
30529	C	C	KM624044
30530	J	J	KM624055
30531	J	J	KM624055
30532	J	J	KM624055
30533	J	J	KM624055
30535	11	11	KM624058
33294	A1	A1	KM624042
33295	C	C	KM624044
33296	C	C	KM624044
33297	C	C	KM624044
33298	A1	A1	KM624042
33299	A1	A1	KM624042
33791	J	J	KM624055
33795	J	J	KM624055
33796	J	J	KM624055
33797	J	J	KM624055
33798	J	J	KM624055
33806	J	J	KM624055
33807	J	J	KM624055
33808	J	J	KM624055
33809	J	J	KM624055
33810	J	J	KM624055
33811	J	J	KM624055
33812	J	J	KM624055
33813	J	J	KM624055
33814	J	J	KM624055
33815	J	J	KM624055
33851	J	J	KM624055
33860	J	J	KM624055
33861	J	J	KM624055
33862	J	J	KM624055
33878	J	J	KM624055
33879	J	J	KM624055
33880	J	J	KM624055
33881	J	J	KM624055
33882	J	J	KM624055
33883	J	J	KM624055
33911	J	J	KM624055
33912	J	J	KM624055
33913	K	K	KM624054
33914	J	J	KM624055
33915	J	J	KM624055
33916	J	J	KM624055
33917	J	J	KM624055
33939	J	J	KM624055
33940	J	J	KM624055
33948	J	J	KM624055
33949	J	J	KM624055
33980	J	J	KM624055
33981	J	J	KM624055
33982	J	J	KM624055
33983	J	J	KM624055
33984	J	J	KM624055
33985	J	J	KM624055
33990	J	J	KM624055
33991	J	J	KM624055
33992	J	J	KM624055
37746	E3	E1	KM624047
37747	E3	E1	KM624047

SWFSC ID	Long (962 bp) Haplotype	Short (345 bp) Haplotype	GenBank Accesion #
37748	E3	E1	KM624047
37749	E3	E1	KM624047
37750	E3	E1	KM624047
37752	E3	E1	KM624047
37753	E3	E1	KM624047
37764	10	10	KM624057
37765	10	10	KM624057
37766	10	10	KM624057
37767	2	2	KM624043
37768	2	2	KM624043
37769	2	2	KM624043
37770	2	2	KM624043
37771	2	2	KM624043
37772	2	2	KM624043
37773	2	2	KM624043
37774	2	2	KM624043
37781	E3	E1	KM624047
37782	E3	E1	KM624047
37783	8	8	KM624053
37784	E3	E1	KM624047
37785	E3	E1	KM624047
37786	8	8	KM624053
37787	E3	E1	KM624047
37788	E3	E1	KM624047
37789	E3	E1	KM624047
37790	8	8	KM624053
37791	E3	E1	KM624047
37876	E3	E1	KM624047
37877	E3	E1	KM624047
37878	E3	E1	KM624047
37879	E3	E1	KM624047
37881	E3	E1	KM624047
37882	E3	E1	KM624047
37883	E3	E1	KM624047
37884	E3	E1	KM624047
37885	E3	E1	KM624047
37896	3	3	KM624046
37897	2	2	KM624043
37907	E3	E1	KM624047
38312	E1	E1	KM624049
38313	E1	E1	KM624049
38314	2	2	KM624043
48090	15	15	KM624061
48103	A2	A1	KM624062
48104	A2	A1	KM624062
48105	A2	A1	KM624062
48112	A2	A1	KM624062
67152		10	KM624057
67165		10	KM624057
74708	K	K	KM624054
78787	K	K	KM624054
79766	C	C	KM624044
79793	D2	D1	KM624041
89564	D1	D1	KM624040
104026	A2	A1	KM624062
104027	A2	A1	KM624062
126092	D2	D1	KM624041
Genbank100		A1	FJ513328
Genbank101		A1	FJ513328
Genbank102		A1	FJ513328
Genbank103		A1	FJ513328
Genbank104		A1	FJ513328
Genbank105		A1	FJ513328
Genbank106		A1	FJ513328
Genbank107		A1	FJ513328
Genbank108		A1	FJ513328
Genbank109		A1	FJ513328
Genbank110		A1	FJ513328
Genbank111		A1	FJ513328

SWFSC ID	Long (962 bp) Haplotype	Short (345 bp) Haplotype	GenBank Accesion #
Genbank112		A1	FJ513328
Genbank113		A1	FJ513328
Genbank114		A1	FJ513328
Genbank115		A1	FJ513328
Genbank116		A1	FJ513328
Genbank117		A1	FJ513328
Genbank118		A1	FJ513328
Genbank119		A1	FJ513328
Genbank120		A1	FJ513328
Genbank122		C	FJ513330
Genbank123		C	FJ513330
Genbank124		C	FJ513330
Genbank125		C	FJ513330
Genbank126		C	FJ513330
Genbank127		C	FJ513330
Genbank128		C	FJ513330
Genbank129		C	FJ513330
Genbank130		C	FJ513330
Genbank131		C	FJ513330
Genbank132		C	FJ513330
Genbank133		C	FJ513330
Genbank134		C	FJ513330
Genbank135		C	FJ513330
Genbank136		C	FJ513330
Genbank137		C	FJ513330
Genbank138		C	FJ513330
Genbank139		C	FJ513330
Genbank140		C	FJ513330
Genbank141		C	FJ513330
Genbank142		C	FJ513330
Genbank143		C	FJ513330
Genbank144		C	FJ513330
Genbank145		C	FJ513330
Genbank146		C	FJ513330
Genbank147		C	FJ513330
Genbank148		C	FJ513330
Genbank149		D1	FJ513331
Genbank150		D1	FJ513331
Genbank151		D1	FJ513331
Genbank152		D1	FJ513331
Genbank153		D1	FJ513331
Genbank154		D1	FJ513331
Genbank155		D1	FJ513331
Genbank156		D1	FJ513331
Genbank157		D1	FJ513331
Genbank158		D1	FJ513331
Genbank159		E1	FJ513332
Genbank160		E1	FJ513332
Genbank161		E1	FJ513332
Genbank162		E1	FJ513332
Genbank163		E1	FJ513332
Genbank164		E1	FJ513332
Genbank165		E1	FJ513332
Genbank166		E1	FJ513332
Genbank167		E1	FJ513332
Genbank168		E1	FJ513332
Genbank169		E1	FJ513332
Genbank170		F	FJ513333
Genbank171		G	FJ513334
Genbank172		G	FJ513334
Genbank173		G	FJ513334
Genbank174		H	FJ513335
Genbank175		I	FJ513336
Genbank176		I	FJ513336
Genbank177		I	FJ513336
Genbank178		I	FJ513336
Genbank179		I	FJ513336
Genbank180		I	FJ513336
Genbank181		I	FJ513336

SWFSC ID	Long (962 bp) Haplotype	Short (345 bp) Haplotype	GenBank Accesion #
Genbank182		I	FJ513336
Genbank183		I	FJ513336
Genbank184		I	FJ513336
Genbank185		I	FJ513336
Genbank186		I	FJ513336
Genbank187		I	FJ513336
Genbank188		I	FJ513336
Genbank189		I	FJ513336
Genbank190		J	FJ513337
Genbank191		J	FJ513337
Genbank192		J	FJ513337
Genbank193		J	FJ513337
Genbank194		K	FJ513338
Genbank195		K	FJ513338
Genbank196		K	FJ513338
Genbank197		K	FJ513338
Genbank198		K	FJ513338
Genbank199		K	FJ513338
Genbank200		K	FJ513338
Genbank201		K	FJ513338
Genbank202		K	FJ513338
Genbank203		K	FJ513338
Genbank204		K	FJ513338
Genbank205		K	FJ513338
Genbank206		K	FJ513338
Genbank207		L	FJ513339
Genbank208		L	FJ513339
Genbank209		L	FJ513339
Genbank210		M	FJ513340
Genbank211		M	FJ513340
Genbank212		M	FJ513340
Genbank213		M	FJ513340
Genbank214		M	FJ513340
Genbank215		M	FJ513340
Genbank216		M	FJ513340
Genbank217		M	FJ513340
Genbank218		M	FJ513340
Genbank219		M	FJ513340
Genbank220		M	FJ513340
Genbank221		M	FJ513340
Genbank222		M	FJ513340
Genbank223		M	FJ513340
Genbank224		M	FJ513340
Genbank225		M	FJ513340
Genbank226		M	FJ513340
Genbank227		M	FJ513340
Genbank228		M	FJ513340
Genbank229		M	FJ513340
Genbank230		M	FJ513340
Genbank231		M	FJ513340
Genbank232		M	FJ513340
Genbank233		M	FJ513340
Genbank234		M	FJ513340
Genbank235		M	FJ513340
Genbank236		M	FJ513340
Genbank237		M	FJ513340
Genbank238		M	FJ513340
Genbank239		M	FJ513340
Genbank240		M	FJ513340
Genbank241		M	FJ513340
Genbank242		M	FJ513340
Genbank243		N	FJ513341
Genbank244		N	FJ513341
Genbank250		A1	DQ145030
Genbank251		13	DQ145032
Genbank252		C	DQ145031
Genbank253		C	DQ145033
Genbank254		A1	EU121124
Genbank256		B	FJ513329

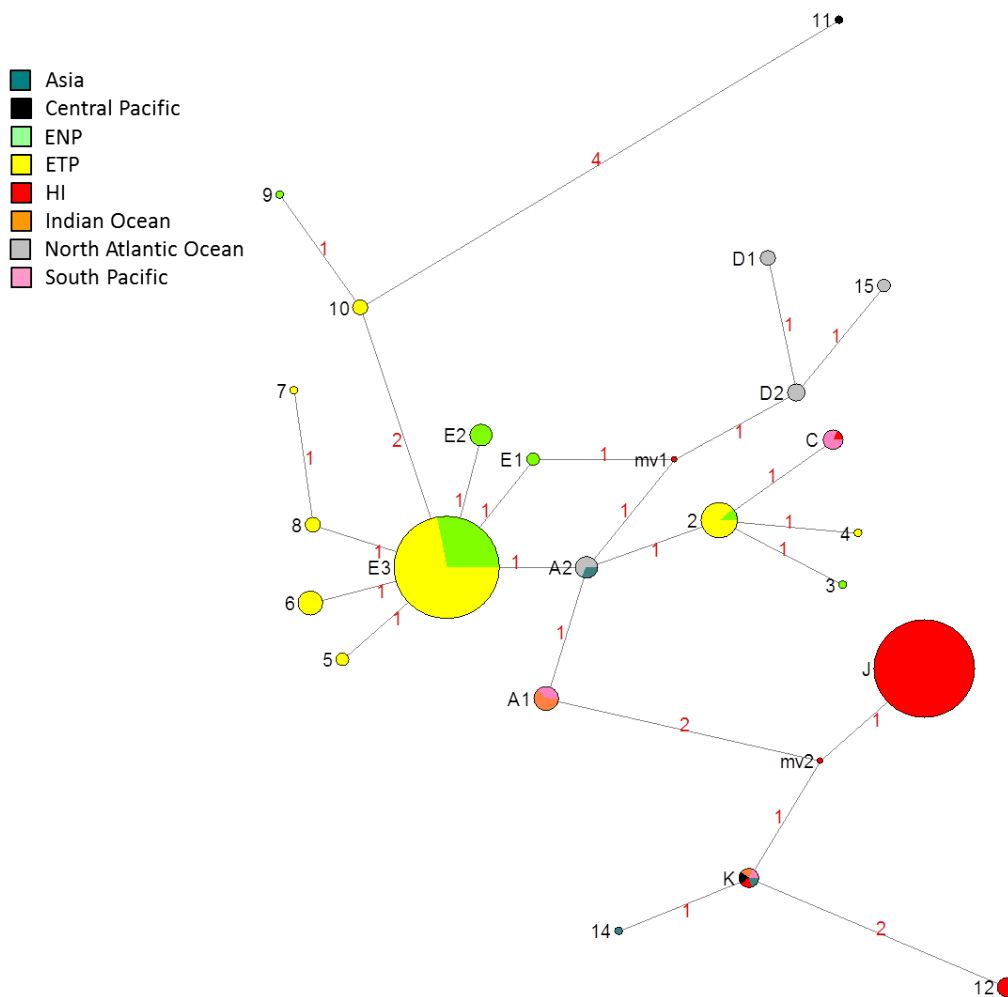| SWFSC ID	Long (962 bp) Haplotype	Short (345 bp) Haplotype	GenBank Accesion #
Genbank257		D1	FJ513331
Genbank258		M	FJ513340

Figure A.1: *Median joining network created using long (962 bp) sequences from SWFSC samples. Samples are segregated geographically; legend entries are: Asia = Southeast Asia and Guam, ENP = California Current, ETP = Eastern Tropical Pacific, HI = Hawaii. Red numbers indicate the number of basepair differences between each haplotype, black labels indicate haplotype.*

Table A.2: *Variance components of hierarchical AMOVA to test for regional differences among Pacific short-finned pilot whale populations, with Naisa type, Shiho type and the South Pacific each considered a separate region. The adjusted dataset was divided into strata as for the pairwise and diversity measurements, then grouped into regions.*

	Three Pacific Regions
Among regions	62.67
Among strata within regions	10.65
Within strata	26.68

Appendix B

Chapter 4 Supplemental Information

Table B.1: *Complete SNP genotypes for 106 samples included in this study.*

ID	ACTC_477_A	ACTC_477_B	Actin_560_A	Actin_560_B	ADH2_925_A	ADH2_925_B	AMBP_295_A	AMBP_295_B	AMBP_547_A	AMBP_547_B
30535	1	1	3	3	4	4	4	4	3	3
33813	1	3	3	3	4	4	3	3	3	3
33852	1	1	3	3			3	3	3	3
33860	1	1	3	3	3	3	4	4	3	4
33863	1	3	3	3	4	3	4	4		
33878	1	3	3	3	4	4	4	4	3	4
33879	1	3	3	2	4	3	4	3	3	3
33880	1	1	3		4	4	3	3		
33881	1	1	3	3	4	3	3	4		4
33882	1	3	3	3	4	4	4	4	3	3
33883	1	1	3	3	4	4	4	3	3	3
33940	1	1	3	3	4	4	4	4	3	3
33980	1	1					4	4	3	3
33982			3	3	4	3	3	3	3	3
33983	1	1	3	3	4	4	4	4	3	4
33984	1	1	3	3	4	4	4	4	3	3
33985	1	3							3	3
33990					4	4	4	4	3	3
33992			3	3	4	4			3	3
45934	1	3			4	4	4	3	3	3
51015	1	1	3	3	4	4	3	3	3	4
51025	1	1	3	3	4	3	3	3	3	3
51026	1	3	3	3			4	4	3	3
51028	1	1	3	3	3	3	4	3	3	3
51029	1	3	3	3	4	3	4	3	3	4
51031			3	3	4	4	4	3	3	3
51032	1	3	3	3	4	3	4	4	3	3
51033	1	1	3	3	4	3	4	4	3	3
55157	1	1			4	3	4	4	3	3
55160	1	3	3	3	4	3	4	4	3	4
55161	1	1	3	3	4	4	4	4	3	3
55165	1	3	3	3	4	4	4	4	3	4
55175	1	1	3	3	4	4	4	3	3	3
55226	1	1	3	3	4	3	4	3	3	3
55228	1	3	3	3	4	4	4	4	3	3
55229	1	3	3	3	4	4	3	3	3	3
55230	1	1	3	3	4	4	4	3	3	4
55234	1	1	3	3	4	4	4	4	3	3
55238	1	1	3	2	4	4	3	3	3	4
55239	1	3	3	2	4	3	3	3	3	3
55242	1	1	3	3	4	4	4	4	3	3
55243	1	1	3	3	4	4	4	3	3	4
55244			3	3	4	4	4	3	3	3
55248	1	1	3	3	4	3	3	3	3	3
55254	1	1	3	3	4	3	4	3	3	4

ID	ACTC_477_A	ACTC_477_B	Actin_560_A	Actin_560_B	ADH2_925_A	ADH2_925_B	AMBP_295_A	AMBP_295_B	AMBP_547_A	AMBP_547_B
61916	1	1	3	2	4	4	4	4	3	4
61918	1	3	3	3	4	3	4	4	4	4
61936	1	1	3	3	4	4	4	3	3	3
61939	1	3	3	3	4	4	4	4	3	3
73899	1	3	3	3	4	4	4	4	3	4
73901	1	1	3	3	4	4	4	3	4	4
74708	1	1	3	3	4	3	4	4	3	4
78810	1	3	3	3	4	4	4	3	3	3
78812	1	1	3	3	4	3	4	3	3	3
79976	1	1					4	3	3	4
79978	1	1	3	3	4	3	4	3	3	3
79992	1	1	3	3	4	4	3	3	3	3
80005	1	1	3	3	4	3	4	3	3	3
88591	1	1	3	3	4	4	4	4	3	3
88593									3	3
88594	1	3	3	3	4	4	4	4	3	3
94818	1	1					3	3	3	3
94820	1	1	3	3	4	4	4	4	4	4
102494	1	3	3		4	3	4	3	3	3
112632	1	3	3	3	4	4	4	3	3	3
112634	1	1					4	4	3	3
112635	1	1	3	3	4	4	4	4	3	4
112636	1	3					4	4	3	4
112637	1	1	3	3	4	3	4	3	3	4
112638	1	1	3	3	4	4	4	4	3	3
112639	1	1	3	3	4	4	4	3	3	3
112641	1	1	3	3	4	4	4	4	3	3
112642	1	3	3	3	4	4	4	3	3	4
112646	1	1	3	3	4	4	4	3	3	3
112647	1	1	3	3	4	3	4	3	3	3
112648	1	1	3	3			4		3	4
112649	1	3	3	3	4	3	3	3	3	3
112652	1	3	3	3	4	3	4	4	3	3
112653	1	1	3	3	4	4	4	3	3	3
112654	1	1	3	2			4	4	3	3
112655	1	1	3	3	4	4	4	4	4	4
112658	1	3	3	3	4	4	4	4	3	4
112660	1	3			4	4	4		3	4
113642	1	1	3	3			4		3	3
113647	1	1	3	3	4	4	4	4	3	4
114348	1	1	3	3	4	3	4	3	3	3
114352	1	3					4	4	3	3
114356	1	3	3	3	4	4	4	4	3	3
114564	1	1	3	3	4	4	4	4	3	3
114565	1	1	3	3	4	3	4	4	3	3

ID	ACTC_477_A	ACTC_477_B	Actin_560_A	Actin_560_B	ADH2_925_A	ADH2_925_B	AMBP_295_A	AMBP_295_B	AMBP_547_A	AMBP_547_B
114805	1	1	3	3	4	3	4	4	3	3
114806	1	1	3	3	4	3	4	3	3	3
114808	1	1							3	3
114809	1	3	3	3	4	4	4	3		
114813	1	3	3	2	4	3	4	4	3	3
114815	1	3	3	3	4	4	4	3		
114816	1	1	3	3	4	3	4	3	3	4
114817	1	3	3	3	4	4	4	3		
114818	1	1	3	3	4	4	4	4	3	3
114819	1	1	3	3	4	4	4	3	3	4
114820	1	1	3	3	4	4	4	3	3	4
114821			3	3	4	3	4	3	3	3
114822	1	1					4	3	3	3
114823	1	1							3	3
123340	1	1	3	3	4	4	4	3	3	3
123342	1	1	3	3	4	3	4	3	3	3

ID	AMBP_555_A	AMBP_555_B	AMBP_793_A	AMBP_793_B	AMBP_94_A	AMBP_94_B	BTN_181_A	BTN_181_B	BTN_822_A	BTN_822_B	CAT_267_A
30535	3		2	2	1	1	2	2	1	1	
33813	3	3	1	1	1	4	1	2	1	1	4
33852	4	4	1	1	4	4	2	2	1	1	
33860	3	3	2	1	1	1	2	2	1	1	4
33863			2	2	1	1	1	1	1	1	
33878	3	3	2	1	1	1	2	2	1	1	4
33879	3	4	2	1	1	4	1	1	2	2	4
33880			1	1	1	4	1	1	1	1	4
33881	3	3	2	1	1	1	2	2	1	1	4
33882	3	3	2	1	1	1	2	2	1	1	4
33883	3	4	2	1	1	4	1	1	1	1	4
33940	3	3	2	2	1	1	2	2	1	1	4
33980	3	3	2	2	1	1	1	1	1	1	4
33982	4	4	1	1	4	4	2	2	1	1	4
33983	3	3	1	1	1	1	2	2	1	1	
33984	3	3	2	2	1	1	2	2	2	2	4
33985	3	4	1	1	1	1	1	1	1	1	
33990	3	3	2	2	1	1	1	1	1	1	2
33992	3	3	2	2	1	1	1	1	1	1	4
45934	3	4	2	1	1	4	1	1	1	1	4
51015	3	4	1	1	1	4	2	2	1	1	4
51025	4	4	1	1	4	4	2	2	1	1	4
51026	3	3	2	2	1	1	2	2	1	1	4
51028	3	4	2	1	1	4	2	2	1	1	4
51029	3	3	1	1	1	4	1	1	1	1	4
51031	3	4	2	1	1	4	2	2	1	1	4
51032	3	3	1	1	1	1	2	2	1	1	4
51033	3	3	2	2	1	1	1	1	1	1	4
55157	3	3	2	1	1	1	1	1	1	1	
55160	3	3	1	1	1	1	2	2	1	1	4
55161	3	3	2	2	1	1	2	2	1	1	4
55165	3	3	2	1	1	1	1	2	1	1	4
55175	3	4	2	1	4	4	2	2	1	1	4
55226	3	4	2	1	4	4	1	1	1	1	4
55228	3	4	2	1	4	4	2	2	1	1	4
55229	4	4	1	1	4	4	2	2	1	1	4
55230	3	4	1	1	1	4	1	1	1	1	4
55234	3	3	2	2	1	1	2	2	1	1	4
55238	3	4	1	1	1	4	2	2	1	1	4
55239	3	4	2	1	1	4	2	2	1	1	4
55242	3	3	1	1	1	1	2	2	1	1	4
55243	3	3	1	1	1	1	2	2	1	1	4
55244	3	4	2	1	4	4	1	1	1	1	4
55248	3	4	2	1	4	4	2	2	1	1	4
55254	3	4	2	1	1	4	1	2	1	1	4

ID	AMBP_555_A	AMBP_555_B	AMBP_793_A	AMBP_793_B	AMBP_94_A	AMBP_94_B	BTN_181_A	BTN_181_B	BTN_822_A	BTN_822_B	CAT_267_A
61916	3	3	2	1	1	1	1	2	1	1	4
61918	3	3	2	1	1	1	2	2	1	1	4
61936	3	3	2	1	1	1	1	2	1	1	4
61939	3	3	2	1	1	1	2	2	1	1	4
73899	3	3	1	1	1	1	1	2	1	1	4
73901	3	3	1	1	1	1	1	2	1	1	4
74708	3	4	1	1	1	4	1	1	1	1	4
78810	3	3	2	2	1	1	2	2	1	1	4
78812	3	4	2	1	1	1	2	2	1	1	4
79976	3	4	1	1	1		1	1	1	1	4
79978	3	3	2	1	1	1	1	2	1	1	2
79992	3	4	1	1	1	4	1	2	1	1	4
80005	3	3	2	1	1	1	2	2	2	2	4
88591	3	3	2	1	1	1	2	2	1	1	4
88593			2	1	1	4	2	1	1	1	
88594	3	3	2	2	1	1	1	1	1	1	4
94818	3	4	2	1	1		1	2	1	1	4
94820	3	3	1	1	1	1	1	2	1	1	4
102494	3	4	1	1	1		1	1	1	1	4
112632	3	4	2	1	1		2	2	1	1	4
112634	3	3	2	1	1	1		2			4
112635	3	3	2	1	1	1	1	2		1	4
112636	3	3	2	1	1	1	1	2	1	1	4
112637	3	3	2	1	1	1	2	2	1	1	4
112638	3	4	2	1	1	4	2	2	1	1	4
112639	3	4	1	1	1	4	1	1	1	1	4
112641	3	3	2	1	1	1	2	2	1	1	4
112642	3	4	1	1	1	4	1	1	1	1	4
112646	3	4	2	1	1	4	1	2	1	1	2
112647	3	4	2	1	1	4	1	2	1	1	4
112648	3	4	1	1	1	4	1	2	1	1	4
112649	3	4	1	1	1	4	2	2	1	1	4
112652	3	3	1	1	1	1	1	2	2	2	4
112653	3	4	2	1	1	1	1	1	1	1	4
112654	3	3	2	2	1	1	1	2	1	1	4
112655	3	3	2	1	1	1	1	2	2	2	4
112658	3	3	2	1	1	1	1	1	1	1	4
112660	3	4	1	1	1	4	1	1	1	1	4
113642	3	3	2	2	1	1	2	2	1	1	
113647	3	3	2	1	1	1	1	1	2	2	4
114348	3		2	1	1	4	2	2	1	1	4
114352	3	3	2	1	1	1	2	2	1	1	
114356	3	3	2	2	1	1	2	2	1	1	4
114564	3	3	2	1	1	1	1	2	1	1	4
114565	3	3	2	1	1	1	2	2	1	1	4

ID	AMBP_555_A	AMBP_555_B	AMBP_793_A	AMBP_793_B	AMBP_94_A	AMBP_94_B	BTN_181_A	BTN_181_B	BTN_822_A	BTN_822_B	CAT_267_A
114805	3	3	2	2	1	1	1	2	1	1	4
114806	3	4	2	1	1	4	1	2	1	1	4
114808	3	4	2	1	1	4	2	2	1	1	
114809	3	4	1	1	4	4	2	1	1	1	4
114813	3	3	1	1	1	1	1	2	1	1	
114815			1	1	1	1	1	2	1	1	4
114816	3	4	1	1	1	4	1	2	1	1	4
114817			1	1	1	4	2	1	1	1	
114818	3	3	2	2	1	1	1	2	1	1	4
114819	3	3	1	1	1	1	1	2	1	1	
114820	3	4	1	1	1	4	1	2	1	1	4
114821	3	4	2	1	1	4	1	2	1	1	4
114822	3	4	2	1	1	4	1		1	1	4
114823	3	4	2	1	1	4			1	1	
123340	3	4	2	1	1	4	1	2	1	1	4
123342	3	3	2	1	1	1	2	2	1	1	2

ID	CAT_267_B	CAT_375_A	CAT_375_B	CAT_86_A	CAT_86_B	CGA_60_A	CGA_60_B	CHRNA1_293_A	CHRNA1_293_B	CHRNA1_606_A
30535		3	4	4	4			4	4	
33813	4	3	3	4	4	4	1	4	4	2
33852	4	4	4	4	4	4	4	4	4	2
33860	4	3	4	4	4	1	1	4	4	2
33863		3	4	4	4			4	4	2
33878	2	3	4	4	4	1	1	3	3	1
33879	2	3	4	4	4	1	1	3	3	1
33880	4	3	4	4	4	1	1	4	4	2
33881	4	3	4	4	4	1	1	4	3	2
33882	4	4	4	4	4	1	1	4	3	2
33883	4	3	4	4	4	1	1	4	4	2
33940	4	3	4	4	4	1	1	4	4	2
33980	4	4	4	4	4	4	1	4	4	2
33982	4	3	4	4	4	1	1	4	4	2
33983	4	3	3	4	4	1	1	4	4	2
33984		3	3	4	4			4	4	2
33985		3	4			1	1	4	3	2
33990	2	3	3	4	4	1	1	3	3	1
33992	4	3	3	4	3	1	1	4	3	2
45934	2	3	4	4	4	1	1	4	3	2
51015	2	3	3	4	4	4	1	3	3	1
51025	4	3	4	4	4	1	1	4	4	2
51026	4	3	4	4	4	1	1	4	4	2
51028	4	3	3	4	4	1	1	4	4	2
51029	2	3	3	4	4	1	1	4	3	2
51031	2	3	4	4	4	4	1	4	3	2
51032	2	3	3	4	4	1	1	4	4	2
51033	4	3	4	4	4	1	1	4	3	2
55157		3	3	4	3			4	4	2
55160	2	3	3	4	4	4	1	4	3	2
55161	4	3	3	4	4	1	1	4	4	2
55165	2	3	4	4	4	1	1	4	3	2
55175	4	3	3	4	3	4	1	4	4	2
55226	4	3	3	4	3	4	1	4	4	2
55228	4	3	4	4	4	4	1	4	4	2
55229	4	3	4	4	4	1	1	4	4	2
55230	4	3	3	4	4	1	1	4	4	2
55234	2	3	4	4	4	1	1	4	4	2
55238	4	3	3	3	3	1	1	4	4	2
55239	4	3	3	4	3			4	3	2
55242	4	3	3	4	3	1	1	4	4	2
55243	4	3	4	4	4	4	1	4	3	2
55244	4	3	4	4	4	1	1	4	4	2
55248	4	3	4	4	4	1	1	4	3	2
55254	4	3	3	4	3	4	1	4	4	2

ID	CAT_267_B	CAT_375_A	CAT_375_B	CAT_86_A	CAT_86_B	CGA_60_A	CGA_60_B	CHRNA1_293_A	CHRNA1_293_B	CHRNA1_606_A
61916	4	4	4	4	4	1	1	4	4	2
61918	4	3	3	4	3	4	1	4	4	2
61936	4	4	4	4	4	1	1	4	4	2
61939	4	3	3	3	3	1		4	3	2
73899	4	3	3	4	4	1	1	4	3	2
73901	2	3	3	4	3	4	1	4	4	2
74708	4	4	4	4	4	4	1	4	3	2
78810	4	3	3	4	3	4	1	4	4	2
78812	4	3	3	3	3	4	1	4	4	2
79976	4	4	4	4	4			4	3	2
79978	2	3	3	4	4	1	1	4	4	2
79992	4	4	4	4	4	4	1	4	4	2
80005	4	4	4	4	4	1	1	4	4	2
88591	4	4	4	4	4	1	1	4	4	2
88593		3	3	4	4	1	1	4	4	2
88594	4	3	3	4	4	4	1	4	3	2
94818	4	3	4	4		1	1	4	3	
94820	2	3	3	4	4	1	1	4	3	2
102494	4	3	3	4	4	1	1	4		1
112632	4	3	4	4	4	1	1	4	4	2
112634	4	3	3	4	4	1	1	4	3	2
112635	4	3	4	4	4	4	1	4	3	2
112636	4	3	4	4	3	1	1	4	3	
112637	4	3	4	4	4	4	1	4	4	2
112638	4	3	4	4	4	1	1	4	4	2
112639	4	4	4	4	4	1	1	4	4	2
112641	4	3	4	4	4	1		4	3	2
112642	4	3	4	4	4			4	4	2
112646	2	3	4	4	4			4		2
112647	4	3	3	4	4	1	1	4	4	2
112648	4	3	3	4	4	1	1	4	4	2
112649	4	4	4	4	4	1	1	4	4	2
112652	4	3	4	4	4	1	1	4	3	2
112653	4	3	4	4	3	1	1	4	4	2
112654	2	3	4	4	4			4	4	2
112655	2	3	3	4	4	1	1	4	4	2
112658	2	3	3	4	3	1	1	4	3	
112660	4	3	4	4				4	4	2
113642		4	4	4	4	1	1	4	4	
113647	2	3	4	4	4	1	1	4	4	2
114348	4	3	4	3	4	1	1	4	3	2
114352		3	3	4	3			4	3	2
114356	2	3	3	4	3	1		4	4	2
114564	4	3	4	4	4			4	4	2
114565	4	3	3	4	4	1	1	4	4	2

ID	CAT_267_B	CAT_375_A	CAT_375_B	CAT_86_A	CAT_86_B	CGA_60_A	CGA_60_B	CHRNA1_293_A	CHRNA1_293_B	CHRNA1_606_A
114805	4	3	3	4	3	1	1	4	4	2
114806	4	3	4	4	4	1	1	4	4	2
114808		3	4	4	4			4	3	2
114809	4	3	3	3	3	1	1	4	4	2
114813		3	4	4	4	4	1	4	4	2
114815	2	3	3	4	4	1	1	4	3	2
114816	2	3	3	4	4	1	1	4	3	2
114817		3	4	4	4	1	1	4	3	2
114818	2	3	3	4	4	1	1	4	4	2
114819		3	3	4	4	4	1	4	3	2
114820	4	3	4	4	4	1	1	4	4	2
114821	4	3	3	4	3	1	1	4	4	2
114822	4			4	3	4	4	4	4	2
114823				4	4					2
123340	4	3	3	3	3	1	1	4	4	2
123342	2	3	3	4	4	1	1	4	3	2

ID	CHRNA1_606_B	CHY_427_A	CHY_427_B	CHY_902_A	CHY_902_B	CK_394_A	CK_394_B	CKMM_239_A	CKMM_239_B	CKMM_546_A
30535						4	3	2	2	4
33813	2	2	2			4	3	2	2	4
33852	2	2	2		1	3	3	2	3	4
33860	2	2	2		1			2	2	4
33863	2				1	4	3	2	2	
33878	1	2	2		1	3	3	2	3	4
33879	1	2	2		1	4	4	2	2	4
33880	2	1	2		1			2	3	
33881	1	2	2		2	4	3	2	2	4
33882	2	2	2		2	3	3	2	3	
33883	2	2	2		1	3	3	2	3	4
33940	2	2	2		1	4	3	2	2	4
33980	2	2	2		1	4	3	2	2	4
33982	2	2	2		1	4	3	2	3	4
33983	2	2	2		2	4	3	2	2	
33984	2	2	2		1			2	2	4
33985	1	2	2			4	4	2		
33990	1	2	2		1	4	3	2		4
33992	1	2	2		1	4	3	2	3	4
45934	1	1	2		2	3	3	2	2	4
51015	1	2	2		1	4	3	2	2	4
51025	2	2	2		1	4	3	2	3	4
51026	2	2	2		1	4	4	2	2	4
51028	2	2	2		1	4	3	2	3	4
51029	1	2	2		1	4	3	2	2	4
51031	1	2	2		2	3	3	2	3	4
51032	2	2	2		2	4	3	2	2	4
51033	1	2	2		2	4	3	2	2	4
55157	2	2	2		1	3	3	2	2	4
55160	1	1	2		1	4	3	2	2	4
55161	2	2	2		2	3	3	2	3	4
55165	1	2	2		1	4	3	2	2	4
55175	2	2	2		1	4	3	2	2	4
55226	2	2	2		1	4	3	2	3	4
55228	2	2	2		2	3	3	2	2	4
55229	2	2	2		2	3	3	2	2	4
55230	2	2	2		2	4	3	2	2	4
55234	2	2	2		1	4	3	2	2	4
55238	2	2	2		1	4	3	2	3	4
55239	1	2	2		2	3	3	2	3	4
55242	2	2	2		2	4	3	2	2	4
55243	1	2	2		2	4	3	2	2	4
55244	2	2	2			3	3	2	2	4
55248	1	2	2		1	3	3	2	3	4
55254	2	2	2		2	4	3	2	3	4

ID	CHRNA1_606_B	CHY_427_A	CHY_427_B	CHY_902_A	CHY_902_B	CK_394_A	CK_394_B	CKMM_239_A	CKMM_239_B	CKMM_546_A
61916	2	2	2	1	2	3	3	2	3	4
61918	2	2	2	1	1	4	4	2	2	4
61936	2	1	2	1	2	4	3	2	2	4
61939	1	2	2	1	2	3	3	2	2	4
73899	1	2	2	1	1	4	3	2	2	4
73901	2	2	2	1	2	3	3	2	2	4
74708	1	2	2	1	1	4	3	2	2	4
78810	2	2	2	1	1	3	3	2	3	4
78812	2	2	2	1	2	3	3	2	2	4
79976	1	2	2	1		4	3	2	3	
79978	2	1	2	1	1	3	3	2	2	4
79992	2	2	2	1	1	4	3	2	3	4
80005	2	2	2	1	1	4	4	2	2	4
88591	2	2	2	1	1	4	3	2	2	4
88593	2							2	2	
88594	1	2	2	1	1	4	3	2	2	4
94818		2	2	1	1	4	3	2	2	
94820	1	1	2	1	1	4	3	2	2	4
102494	1			1	1			2	2	
112632	2	2	2	1	2	4	3	2	2	4
112634	2	2	2			3	3	2	3	4
112635	1	2	2	1	1	3	3	2	3	4
112636		1	2	1	1	3	3	2	2	4
112637	2	2	2	1	1	3	3	2	2	4
112638	2	1	2	1	1	3	3	2	2	4
112639	2	2	2	1	2	3	3	2	2	4
112641	1	2	2	1	2	3	3	2	3	4
112642	2	2	2	1	1	3	3	2	2	4
112646	1	2	2	1	1	3	3	2	2	4
112647	2	2	2	1	1	4	3	2	2	4
112648	2	2	2	1	1			2	2	4
112649	2	2	2	1	1	3	3	2	2	4
112652	1	1	2	1	1	4	3	2	2	
112653	2	1	2	1	1	3	3	2	2	4
112654	2	2	2	1		4	3	2	3	4
112655	2	2	2	1	1	4	3	2	2	4
112658		2	2	1	1	4	3	3	3	4
112660	2					3	3	2	2	4
113642		1	2	1	1	4	3	2	2	4
113647	2	2	2	1	1	3	3	2	3	4
114348	1	1	1	1	1	3	3	2	3	4
114352	1							2	3	
114356	2	1	2	1	1	3	3	2	2	4
114564	2	2	2	1	2			2	2	4
114565	2	2	2	1	1	4	4	2	2	4

ID	CHRNA1_606_B	CHY_427_A	CHY_427_B	CHY_902_A	CHY_902_B	CK_394_A	CK_394_B	CKMM_239_A	CKMM_239_B	CKMM_546_A
114805	2	2	2	1	1			2	3	4
114806	2	2	2	2	2			2	3	4
114808	1	1	2			3	3	2	3	4
114809	2	1	2	1	2	3	3	2	2	4
114813	1	2	2	1	1			2	2	4
114815	2	2	2	1	1			2	2	4
114816	1	2	2	1	1	4	3	2	3	4
114817	1	1	2			3	3	2	3	4
114818	2	1	2	1	1	3	3	2	3	3
114819	2	2	2			3	3	2	2	4
114820	1	2	2	1	1			2	2	4
114821	2	1	2	1	1	4	3	2	2	4
114822	2	2	2	1	1	3	3	3	3	
114823	1	1	2	1	1			2	2	4
123340	2	1	2	1	1	4	3	2	2	4
123342	1	2	2	2	2	4	3	2	3	4

ID	CKMM_546_B	COL10A1_221_A	COL10A1_221_B	COL10A1_572_A	COL10A1_572_B	COL10A1_883_A	COL10A1_883_B	COL3A1_104_A	COL3A1_104_B
30535	4	4		1		1	1	2	2
33813	4	4		1		1	1	2	2
33852	4	4		1		1	1	4	4
33860	4	3		1		1	4	2	2
33863		4		1		1	1	2	2
33878	4	3		1		1	4	2	2
33879	4	3		1		1	4	2	2
33880						1	4	2	2
33881	4	3		1		1	4	2	2
33882		4				1	1	2	2
33883	4	4		1		1	1	2	2
33940	4	4		2		1	4	2	4
33980	4	3		1		1	1	2	2
33982	4	4		1		1	1	2	2
33983		4				1	1	2	2
33984	4	4				1	1	2	2
33985		4				1			
33990	4	4				1	1	2	2
33992	4	4				1	1	2	2
45934	4	4				1	1	4	4
51015	4	4		1		1	1	2	2
51025	4	4		1		1	1	2	2
51026	4	4		1		1	1	2	2
51028	4	4		1		1	1	2	2
51029	4	4		1		1	1	2	2
51031	4	3		1		1	4	2	2
51032	4	3		1		1	4	2	2
51033	4	4		1		1	1	2	2
55157	4	4		1		1	1	2	2
55160	3	4		1		1	1	2	2
55161	4	4		1		1	1	2	2
55165	4	4		1		1	1	2	2
55175	4	4		1		1	1	2	2
55226	4	3		1		1	4	2	2
55228	3	3		1		1	4	2	2
55229	3	3		1		4	4	2	2
55230	3	3		1		1	4	2	2
55234	4	4		1		1	1	2	2
55238	4	4		1		1	1	2	2
55239	4	4		1		1	1	2	2
55242	4	4		1		1	1	2	2
55243	4	4		1		1	1	2	2
55244	4	4				1	1	2	2
55248	4	4		1		1	1	2	2
55254	4	4				1	1	2	2

ID	CKMM_546_B	COL10A1_221_A	COL10A1_221_B	COL10A1_572_A	COL10A1_572_B	COL10A1_883_A	COL10A1_883_B	COL3A1_104_A	COL3A1_104_B
61916	3	4	4	1	1	1	1	2	2
61918	4	4	4	2	1	1	1	2	2
61936	4	4	3	1	1	1	4	2	2
61939	4	4	3	1	1	1	4	2	2
73899	4	4	4	1	1	1	1	2	2
73901	4	4	3	2	1	1	4	2	2
74708	4	4	4	1	1	1	1	2	2
78810	4	4	4	1	1	1	1	2	2
78812	4	4	3	1	1	1	4	2	2
79976		4	4	1	1	1			
79978	3	4	4	1	1	1	1	2	2
79992	4	4	4	1	1	1	1	2	2
80005	4	4	4	1	1	1	1	2	2
88591	4	4	3	1	1	1	4	2	2
88593							1	2	2
88594	3	4	4	1	1	1	1	2	2
94818		4	4	1	1				
94820	4	4	4	1	1	1	1	2	2
102494		4	3	1	1			2	2
112632	4	4	4			4	4	2	2
112634	4	4	3	1	1	1	4	2	2
112635	4	4	3	1	1		1	2	2
112636	4	4	3						
112637	4	4	4	1	1	1	1	2	2
112638	4	4	4	1	1	1	1	2	2
112639	3	4	4	1	1	1	1	2	2
112641	4	4	4	1	1	1	1	2	2
112642	4	4	4	1	1	1	1	2	2
112646	3	4	3	1	1	1	4	2	2
112647	4	4	4	1	1	1	1	2	2
112648	4	4	4	1	1	1	1	2	2
112649	4	4	4	1	1	1	1	2	2
112652		4	4	1	1	1	1	2	2
112653	4	4	4	2	2	1	1	2	2
112654	4	4	4	1	1	1	1	2	2
112655	4	4	4	1	1	1	1	2	2
112658	4	4	4				1	2	2
112660	4							2	2
113642	4	4	4	1	1	1	1	2	2
113647	4	4	4	1	1	1	1	2	2
114348	4	4	4	1	1	1	1	2	2
114352		4	4				1	2	2
114356	4	4	4	1	1	1	1	2	4
114564	4	4	4			1	1	2	2
114565	4	4	3	1	1	1	4	2	2

ID	CKMM_546_B	COL10A1_221_A	COL10A1_221_B	COL10A1_572_A	COL10A1_572_B	COL10A1_883_A	COL10A1_883_B	COL3A1_104_A	COL3A1_104_B
114805	4	4	3	1	1	1	4	2	2
114806	3	4	4	1	1	1	1	2	2
114808	4	4	4	1	1	1	1	2	2
114809	4	4	4	2	1	1	1	2	2
114813	4	4	4	1	1	1	1	2	2
114815	4	4	3			1	4	2	2
114816	4	4	3	1	1	1	4	2	2
114817	4							2	2
114818	3	4	3			1	1	2	2
114819	3					1	1	2	2
114820	4	4	3	1	1	1	4	2	2
114821	4	4	3	1	1	1	4	2	2
114822		4	4					2	2
114823		4	3					2	2
123340	4	4	4	1	1	1	1	2	2
123342	4	4	3	1	1	1	4	2	2

ID	COL3A1_420_A	COL3A1_420_B	COL3A1_429_A	COL3A1_429_B	COL3A1_455_A	COL3A1_455_B	CYO19_363_A	CYO19_363_B	CYO19_593_A
30535	1		2	2	4	4	4	4	3
33813	1		2	2	4	4	4	3	3
33852	1	1	2	2	3	3	4	3	1
33860	1	2	2	1	4	4	4	4	
33863							4	4	1
33878	1	1	2	2	4	4	4	4	1
33879	1	1	2	1	4	4	4	4	1
33880	1	1	2	2	4	4	4	3	1
33881	1	1	2	2	4	4	4	4	1
33882	1	1	2	2	4	4	4	4	1
33883	1	1	2	1	4	4	4	3	1
33940	1	1	2	2	4	4	4	3	1
33980	1	1	2	2	4	3	4	4	3
33982	1	1	2	2	4	4	4	3	1
33983	1	1	2	1	4	4	4	3	1
33984	1	1	1	1	4	4	4	4	1
33985	1	1	2	1	4	4	4	4	3
33990	1	1	2	1	4	4	4	4	1
33992	1	1	2	1	4	4	4	4	1
45934	1	1	2	2	4	4	4	3	1
51015	1	1	2	1	4	4	4	4	3
51025	1	1	2	2	4	4	4	3	1
51026	1	1	2	2	4	4	4	4	1
51028	1	2	2	2	4	4	4	4	3
51029	1	1	2	1	4	4	4	4	1
51031	1	2	2	2	4	4	4	4	3
51032	1	1	1	1	4	4	4	4	1
51033	1	1	2	1	4	4	4	4	1
55157	1	1	2	2	4	4	4	4	1
55160	1	1	2	2	4	4	4	4	1
55161	1	1	2	2	4	4	4	4	3
55165	1	2	2	2	4	4	4	3	3
55175	1	1	2	2	4	4	4	4	1
55226	1	1	1	1	4	4	4	4	3
55228	1	1	2	2	4	4	4	4	3
55229	1	2	2	2	4	4	4	4	3
55230	1	2	2	2	4	4	4	3	1
55234	1	1	2	1	4	4	4	4	3
55238	1	1	2	1	4	4	4	4	1
55239	1	2	2	1	4	4	4	4	1
55242	1	1	2	2	4	4	4	4	3
55243	1	1	2	2	4	4	4	3	1
55244	1	1	2	2	4	4	4	3	1
55248	1	1	2	2	4	4	4	3	1
55254	1	1	2	2	4	4	4	4	1

ID	COL3A1_420_A	COL3A1_420_B	COL3A1_429_A	COL3A1_429_B	COL3A1_455_A	COL3A1_455_B	CYO19_363_A	CYO19_363_B	CYO19_593_A
61916	1	1	2	1	4	4	4	3	1
61918	1	1	2	2	4	4	4	4	1
61936	1	2	2	1	4	4	4	4	3
61939	1	1	2	2	4	4	4	3	1
73899	1	1	2	1	4	4	4	3	1
73901	1	1	2	2	4	4	4	4	3
74708	1	1	2	1	4	4	4	4	3
78810	1	1	2	2	4	4	4	4	1
78812	1	1	2	1	4	4	4	4	1
79976	2	2	2	2	4	4	4	4	3
79978	1	1	2	2	4	4	4	3	1
79992	1	1	2	2	4	4	4	4	1
80005	1	2	2	2	4	4	4	3	1
88591	1	1	1	1	4	4	4	4	1
88593	1	1	2	2	4	4	4	4	1
88594	1	1	2	2	4	4	4	4	3
94818	1	1	2	2	4	4	4	3	1
94820	1	1	2	2	4	4	4	4	1
102494	1	1	2	2	4	4	3	3	1
112632	1	1	2	2	4	4	4	4	1
112634	1	1	2	2	4	4	4	4	1
112635	1	2	2	1	4	4	4	4	1
112636	1	1	2	2	4	4	4	4	1
112637	1	1	2	2	4	4	4	4	1
112638	1	1	2	2	4	4	4	4	1
112639	1	1	2	2	4	4	4	3	1
112641	1	1	2	2	4	4	4	4	3
112642	1	1	2	2	4	4	4	4	3
112646	1	1	2	2	4	4	4	4	1
112647	1	1	1	1	4	4	4	4	1
112648	1	1	2	1	4	4	4	4	1
112649	1	1	2	1	4	4	4	4	1
112652	1	1	2	2	4	4	3	3	1
112653	1	1	2	2	4	4	4	4	3
112654	1	1	2	2	4	4	4	4	1
112655	1	1	2	2	4	4	4	4	3
112658					4	4	4	4	1
112660					4	4	4	4	1
113642	1	1	2	2	4	4	4		3
113647	1	1	2	1	4	4	4	3	1
114348	1	1	2	1	4	4	4	4	3
114352	1	1			4	4	4	4	3
114356	1	1	2	2	4	3	4	4	1
114564	1	1	2	1	4	4	4	4	3
114565	1	2	2	2	4	4	4	4	1

ID	COL3A1_420_A	COL3A1_420_B	COL3A1_429_A	COL3A1_429_B	COL3A1_455_A	COL3A1_455_B	CYO19_363_A	CYO19_363_B	CYO19_593_A
114805	1	1	2	1	4	4	4	3	1
114806	1	1	2	1	4	4	4	4	3
114808	1	1	2	2	4	3	4	4	3
114809	1	1	2	2	4	4	3	3	1
114813	1	1	2	2	4	4	4	4	3
114815	1	1	2	2	4	4	4	4	1
114816	1	1	2	2	4	4	4	4	3
114817	1	1	2	1	4	4	4	4	3
114818	1	1	2	2	4	4	4	4	1
114819	1	1	2	2	4	4	4	4	3
114820	1	2	2	1	4	4	4	4	3
114821	1	1	2	2	4	4	4	4	1
114822	1	1	2	2	4	4	4	4	3
114823	1	1	2	1	4	4	4	4	1
123340	1	1	2	1	4	4	4	4	1
123342	1	1	2	1	4	4			

ID	CYO19_593_B	CYO19_789_A	CYO19_789_B	CYP1A1_107_A	CYP1A1_107_B	CYP1A1_480_A	CYP1A1_480_B	DRD2_313_A	DRD2_313_B	DRD2_507_A
30535	3	4	4	3	3	4	3	1	2	
33813	3	4	4	3	3	4	4	1	1	1
33852	3	4	1	3	3	4	3	1	2	1
33860		4	1	3	3	4	3	2	2	1
33863	1	4	4			4	4	1	1	
33878	1	4	4	3	3	4	3	1	2	1
33879	3	4	4	3	4	4	4	1	1	1
33880	3	4	1	3	4	4	4	1	1	
33881	1	4	4	3	3	4	4	1	2	1
33882	3	4	4	3	3	4	4	1	1	4
33883	3	1	1	3	3			1	2	
33940	1	4	1	3	3	4	3	1	2	1
33980	3	4	4	3	3	4	3	1	1	
33982	1	4	1	3	3	4	4	2	2	1
33983	1	4	1	3	3	4	3	1	2	1
33984	3	4	4	3	3	4		1	1	4
33985	3	4	4	3	4		3	1	2	
33990	3	4	4	3	3			1	2	1
33992	1	4	4					1	1	
45934	3	4	1	3	3	4	3	1	1	4
51015	3	4	4	3	3	4	4	1	2	1
51025	1	4	1	3	3	4	3	2	2	1
51026	1	4	4	3	3	4	3	1	1	4
51028	3	4	4	3	3	4	3	2	2	1
51029	1	4	4	3	3	4	4	1	1	1
51031	3	4	4	3	4	4	4	1	1	1
51032	3	4	4	3	3	4	4	1	1	4
51033	3	4	4	3	3	4	4	1	1	4
55157	3	4	4	3	3	4	4	2	2	1
55160	3	4	4	3	3	4	4	1	2	1
55161	3	4	4	3	3	4	3	1	1	4
55165	3	4	1	3	3	4	3	2	2	1
55175	3	4	4	3	3	4	4	1	1	1
55226	3	4	4	3	3	4	4	1	1	4
55228	3	4	4	3	3	4	3	1	1	4
55229	3	4	4	3	3	4	4	1	1	4
55230	3	4	1	3	3	4	4	1	1	4
55234	3	4	4	3	3	4	3	1	1	4
55238	3	4	4	3	3	4	4	1	1	4
55239	3	4	4	3	3	4	4	1	1	1
55242	3	4	4	3	3	4	4	1	2	4
55243	3	4	1	3	3	4	4	1	1	4
55244	3	1	1	3	3	4	4	1	1	
55248	3	4	1	3	3	4	4	1	2	4
55254	3	4	4	3	3	4	3	1	1	4

ID	CYO19_593_B	CYO19_789_A	CYO19_789_B	CYP1A1_107_A	CYP1A1_107_B	CYP1A1_480_A	CYP1A1_480_B	DRD2_313_A	DRD2_313_B	DRD2_507_A
61916	3	4	1	3	3	4	4	1	1	1
61918	3	4	4	3	3	4	3	1	2	1
61936	3	4	4	3	3	4	3	1	1	4
61939	1	4	4	3	3	4	4	1	1	4
73899	3	4	1	3	3	4	4	2	2	1
73901	3	4	4	3	3	4	3	1	1	1
74708	3	4	4	3	3	4	3	1	2	1
78810	3	4	4	3	3	4	4	1	1	4
78812	3	4	4	3	3			1	2	1
79976				3	4			1	2	1
79978	1	4	1	3	4	3	3	1	1	4
79992	3	4	4	3	3	4	4	1	2	1
80005	3	4	1	3	3	3	3	1	2	1
88591	3	4	4	3	3	3	3	1	2	1
88593	3	4	4	3	3	4	4	1	1	4
88594	3	4	4	3	3	3	3	1	1	1
94818	1	4	1	3	3	4	4	1	1	
94820	1	4	4	3	3	4	4	1	1	4
102494	1	1	1			4	4		2	
112632	3	4	4	3	3	4	4	1	1	1
112634	3	4	4	3	3	4		1	1	4
112635	1	4	4	3	3	4	3	1	1	4
112636	3	4	4	4	4	4	4	1	1	4
112637	3	4	4	3	3	4	4	1	2	1
112638	3	4	4	3	3	4	3	1	1	4
112639	3	4	1	3	3	4	4	1	1	4
112641	3	4	4	3	3	4	3	1	1	4
112642	3	4	4	3	3	4	4	1	1	4
112646	3	4	4	3	3	4	3	1	1	4
112647	3	4	4	3	3	4	3	1	2	1
112648	3	4	4	3	3	4	4	1	2	1
112649	3	4	4	3	3	4	3	1	1	4
112652	3	4	1			4	4	1	2	1
112653	3	4	4	3	3	4	3	1	2	1
112654	3	4	4	3	3	4	4	1	2	1
112655	3	4	4	3	3	4	3	1	1	4
112658	3	4	4	3	3	4	3	1	1	4
112660	3	4	4	3	3	4	4	1	1	4
113642	3	4	4	3	3	4	4	1	1	1
113647	1	4	1	3	3	4	3	1	2	1
114348	3	4	4	3	3	4	4	1	1	4
114352	3	4	4	3	3	4	3	1	1	1
114356	3	4	4	3	4	4	4	1	1	1
114564	3	4	4	3	4			2	2	4
114565	3	4	4	3	3	4	4	1	1	4

ID	CYO19_593_B	CYO19_789_A	CYO19_789_B	CYP1A1_107_A	CYP1A1_107_B	CYP1A1_480_A	CYP1A1_480_B	DRD2_313_A	DRD2_313_B	DRD2_507_A
114805	3	4	1	3	3	4	4	1	1	
114806	3	4	4	3	3	4	4	1	2	1
114808	3	4	4	3	3	4	3	1	1	4
114809	1	1	1	3	3	4	4	1	2	1
114813	3	4	4	3	3	4	3	1	2	1
114815	3	4	4			4	4	1	1	
114816	3	4	4	3	4	4	4	1	2	1
114817	3	4	4	3	3	4	3	1	2	
114818	3	4	4	3	3	4	3	1	1	1
114819	3	4	4	3	3	4	3	1	2	1
114820	3	4	4	3	3	4	4	1	2	1
114821	3	4	4	3	3	4	4	1	1	4
114822	3	4	4	3	4	4	3	1	2	1
114823	3	4	4	3	3			1	1	
123340	1	4	4	3	3	4	4	1	2	1
123342	3	4	1	3	3	4	4	1	1	4

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ID	DRD2_507_B	DRD2_656_A	DRD2_656_B	DRD2_92_A	DRD2_92_B	ELN_614_A	ELN_614_B	ELN_756_A	ELN_756_B	ESD_537_A	ESD_537_B
30535						1	1			4	4
33813	4	4	4	3	3	1	1	1	1	4	4
33852	4	4	4	4	3	1	2	2	1	4	4
33860	1	1	1	4	4	1	1	2	2		
33863		1	4	3	3	1	2				
33878	4	1	4	3	3	2	2	2	1	3	3
33879	4	1	4	3	3	1	1	2	1	4	3
33880		4	4					2	1		
33881	1	1	1	3	3	1	1	1	1	4	3
33882	4	4	4	3	3			2	1		
33883		1	4	3	3			2	1	4	3
33940	4	1	4	4	3			2	1	4	4
33980		4	4	3	3			2	1		
33982	1	1	1	4	3	1	1	1	1	4	4
33983	1	1	1	4	3	1	1	2	2	4	4
33984	4	4	4	3	3						
33985		1	4	3	3						
33990	4	1	4	3	3					4	4
33992		4	4								
45934	4	4	4	3	3	1	1	2	2	4	4
51015	1	1	1	3	3	1	1	2	2	4	3
51025	1	1	1	4	3	1	1	1	1	4	4
51026	4	4	4	3	3	1	2	2	1	4	4
51028	1	1	1	4	3	1	1	2	2	4	4
51029	4	1	4	3	3	1	1	1	1	4	4
51031	4	1	4	3	3	1	2	2	1	4	4
51032	4	4	4	3	3	1	2	1	1	3	3
51033	4	4	4	3	3	1	1	2	2	4	3
55157	4	1	4	3	3	1	2	1	1	4	4
55160	1	1	1	3	3	1	2	1	1	4	4
55161	4	4	4	3	3	1	1	1	1	4	3
55165	4	1	1	4	3	1	1	2	1	4	3
55175	4	1	1	3	3	1	1	1	1		
55226	4	4	4	3	3	1	1	2	1	4	4
55228	4	4	4	3	3	2	2	1	1	4	3
55229	4	4	4	3	3	2	2	1	1	4	4
55230	4	4	4	3	3	2	2	2	1	4	4
55234	4	4	4	3	3	1	1	1	1	4	4
55238	4	4	4	3	3	1	2	2	1	4	4
55239	4	1	1	4	3	1	1	2	2	4	4
55242	4	4	4	3	3	2	2	1	1	4	4
55243	4	4	4	3	3	1	1	2	1	4	3
55244		1	4	4	3	1	2				
55248	4	4	4	3	3	1	2	1	1	4	4
55254	4	4	4	3	3					4	4

ID	DRD2_507_B	DRD2_656_A	DRD2_656_B	DRD2_92_A	DRD2_92_B	ELN_614_A	ELN_614_B	ELN_756_A	ELN_756_B	ESD_537_A	ESD_537_B
61916	4	1	4	3	3	1	1	2	1	4	3
61918	4	1	4	4	3	1	2	1	1	4	4
61936	4	4	4	3	3	1	1	2	1	3	3
61939	4	4	4	3	3	1	1	2	1		
73899	1	1	1	4	3	2	2	1	1	4	4
73901	4	1	4	3	3	1	2	2	2	4	3
74708	4	1	4	4	3	1	1	2	1	4	4
78810	4	4	4	3	3		2	1	1	4	3
78812	4	1	4	3	3	2	2	1	1		
79976	4	1	4	4	3	1	2	1	1		
79978	4	4	4	3	3	1	2	1	1	4	4
79992	4	1	4	3	3	1	1	2	1	4	4
80005	4	1	4	4	3	1	2	2	2	4	4
88591	4	1	4	4	3	1	2	1	1	4	4
88593	4	4	4							4	4
88594	1	1	1	3	3	2	2	1	1	4	3
94818				3	3						
94820	4	4	4	3	3	1	1	2	1	4	4
102494	4	1	4	4	3	1	1			4	4
112632	1	1	4	3	3	2	2	1	1		
112634	4	4	4	3	3			2	1	4	3
112635	4	4	4	3	3	1	2	1	1	4	3
112636	4	4	4	3	3						
112637	4	1	4	3	3	1	2	2	1	4	4
112638	4	4	4	3	3	1	2	1	1		
112639	4	4	4	3	3	1	1	2	1	3	3
112641	4	4	4	3	3	1		1	1	4	3
112642	4	4	4	3	3			1	1		
112646	4	4	4	3	3	1	1	2	1	4	3
112647	4	1	4	4	3	1	2	2	1	4	4
112648	4	1	4	4	3			2	1	3	3
112649	4	4	4	3	3	1	1	2	1	4	4
112652	4	1	4	4	3			2	1	4	4
112653	4	1	4	3	3	1	1	2	2	4	4
112654	1	1	4	4	3	1	2	2	1	4	3
112655	4	4	4	3	3	1	2	2	1	4	3
112658	4	4	4	3	3	1	2	1	1	4	4
112660	4	4	4	3	3	1	1	2	1		
113642	4	1	4	3	3	1	1	2	2		
113647	4	1	4	3	3	1	2	1	1	4	4
114348	4			3	3	1	1	2	1	4	4
114352		4	4			1	2	1	1	4	3
114356	4	4	4	3	3	1	1	2	1	4	4
114564		1	1	4	3	1	2	1	1		
114565	4	4	4	3	3	1	2	2	1	4	4

ID	DRD2_507_B	DRD2_656_A	DRD2_656_B	DRD2_92_A	DRD2_92_B	ELN_614_A	ELN_614_B	ELN_756_A	ELN_756_B	ESD_537_A	ESD_537_B
114805	4	1	4	3	3	1	1	2	1	3	3
114806	4	1	4	4	3	1	1	2	2	4	3
114808	4	4	4	3	3			2	1		
114809	4	1	4	4	3	1	2	1	1	4	4
114813	1	1	1	3	3	1	1	1	1	4	4
114815										4	3
114816	4	1	4	4	3	1	2	1	1	4	4
114817				4	3			2	1	3	3
114818	4	1	4	3	3	1	1	1	1	4	4
114819	4	1	4	4	3	1	2	2	1	3	3
114820	4	1	4	4	3	1	1	2	1	4	4
114821	4	4	4	3	3	1	2	2	1	4	4
114822	1	1	1	4	3			2	1	4	4
114823		1	1					1	1		
123340	4	1	4	3	3	1	2	1	1	4	4
123342	4	4	4	3	3	1	1	2	1	4	4

ID	FES_623_A	FES_623_B	Fibrinogen_474_A	Fibrinogen_474_B	FSHB_255_A	FSHB_255_B	FSHB_815_A	FSHB_815_B	GLB_177_A	GLB_177_B
30535	4	4	1	1	1	1	3	3	1	1
33813	4	3	2	2			3	3	1	2
33852	4	3	2	2	1	1		3	1	1
33860			2	1			3	3	1	1
33863	4	4	2	2	1	1	3	3	1	2
33878			2	1	1	1	3	3	1	1
33879	4	4	2	2	1	1	3	3	1	2
33880			2	2	1	1	3	1	1	1
33881	4	4	2	1	1	2	3		1	2
33882			2	1	2	2	1	3	1	1
33883			2	1	1	1	3	3	1	2
33940	4	3	2	2	1	1	3	3	1	2
33980	4	4	2	2	1	2	1	1	1	1
33982	4	4	2	1	1	2	3	1	1	1
33983			2	2	1	1	3	3	1	1
33984			2	1	1	1	3		1	1
33985	4	4	2	2	2	2	3	1	1	2
33990			2	2	1	2	3	1	1	1
33992			2	2			3	3	1	1
45934	3	3	2	1	1	1	3	3	1	2
51015	4	3	2	2	1	1	3	3	1	1
51025	4	4	2	1	1	2	3	1	1	1
51026	3	3	2	1	1	2	3	1	1	2
51028	4	3	2	1	1	1	3	1	1	1
51029			2	2	1	2	3	1	1	2
51031	4	3	2	2	1	1	3	1	1	2
51032	4	3	2	2	1	1	3	3	1	2
51033	4	4	2	2	1	2	3	1	1	1
55157	3	3	2	2	1	1	3	3	1	2
55160	4	3	2	2	1	2	3	1	1	1
55161	4	3	2	1	1	2	3	1	1	1
55165	4	4	2	2	1	2	3	1	1	1
55175			2	2	1	2	3	3	1	2
55226	4	3	1	1	1	1	3	1	1	2
55228	3	3	2	2	1	1	1	1	1	2
55229	4	3	2	2	1	2	3	3	1	2
55230	4	3	2	2	1	1	3	3	2	2
55234	4	4	2	1	1	1	3	3	1	2
55238	4	3	2	2	2	2	3	3	2	2
55239	3	3	2	2	1	1	3	1	1	1
55242	4	4	2	2	1	2	3	1	1	1
55243	4	4	2	1	1	1	3	3	1	1
55244			2	2	1	1	3	3	1	1
55248	3	3	2	2	1	1	3	3	2	2
55254	4	3	2	2	1	1	3	3	1	1

ID	FES_623_A	FES_623_B	Fibrinogen_474_A	Fibrinogen_474_B	FSHB_255_A	FSHB_255_B	FSHB_815_A	FSHB_815_B	GLB_177_A	GLB_177_B
61916	4	4	2	2	2	2	1	1	1	1
61918	4	4	2	1	2	2	1	1	1	1
61936	4	4	2	1	1	2	3	3	1	2
61939	4	3	2	2	1	1	3	1	1	1
73899	4	4	2	1	1	2	3	1	1	2
73901	4	3	2	2	1	2	3	1	1	1
74708	4	4	2	1	1	1	3	3	1	1
78810	4	3	2	2	1	1	3	3	1	2
78812	4	3	2	2	1	1	3	3	1	1
79976							3		1	1
79978			2	2	1	1	3	3	1	2
79992	3	3	2	2	1	1	3	3	1	2
80005	4	4	2	2	1	1	3	1	1	2
88591	4	4	2	2	1	1	3	3	1	2
88593	4	3	1	1	2	2			1	1
88594	4	3	2	1	1	1	3	3		2
94818			2	2			3	3	2	2
94820	4	3	2	2	1	1	3	3	1	1
102494	3	3	2	2	1	1			1	1
112632	4	4	2	1	1	1	3	3	1	2
112634	4	4	2	1	1	1	3	3	1	2
112635	4	4	2	1	2	1	3	3	1	1
112636	3	3	1	2	1	1	3	3	1	1
112637	4	3	2	2	1	1	3	3	1	2
112638	4	3	2	1	1	2	3	3	1	2
112639	4	3	2	2	1	2	3	1	1	1
112641			1	1	2	2	1	1	1	2
112642			2	2	1	2	3	1	1	1
112646	4	3	2	2	1	1	3	3	1	1
112647	4	3	2	2	1	1	3	3	1	1
112648			2	2	1	1	3	3	1	1
112649	4	3	2	1	1	2	3	1	1	2
112652	3	3	2	2			3	1	1	1
112653	4	4	2	1	1	1	3	1	1	1
112654	4	4	2	2	1	2	3	1	1	1
112655	4	3	2	2	1	2	3	1	1	1
112658	4	4	2	2	1	2	3	3	1	1
112660			2	2	1	1	3	3	1	
113642	4	4					3	3		
113647	3	3	2	1	1	2	3	3	2	2
114348	4	4	2	2	1	1	3	1	1	1
114352	4	3	1	1	2	2			1	1
114356	3	3	2	1	1	2	3	1	1	1
114564			2	1			3	1	1	1
114565	3	3	2	1	1	1	3	1	1	1

ID	FES_623_A	FES_623_B	Fibrinogen_474_A	Fibrinogen_474_B	FSHB_255_A	FSHB_255_B	FSHB_815_A	FSHB_815_B	GLB_177_A	GLB_177_B
114805	4	3	2	1	1	1	3	1	1	1
114806	4	4	2	1	1	1	3	1	1	2
114808	4	3	2	2	1	1	3	3	1	1
114809	4	3	2	2	1	1	3	3	1	1
114813	4	3	2	2	1	1	3	3	1	1
114815			2	2			3	1	1	1
114816	3	3	2	2	1	2	3	1	1	1
114817			2	2	1	1	3	3	1	1
114818	4	3	2	2	1	1	1	1	1	1
114819			2	2	1	1	3	3	1	1
114820	4	3	2	2	1	2	1	1	1	1
114821	4	3	2	1	2	2	3	1	1	1
114822	4	3	2	2	1	1	3	3	1	1
114823			2	2	2	2	1	1	1	2
123340	4	3	2	1	1	1	3	3	1	2
123342	4	3	2	2	1	1	3	3	1	1

ID	GLUT2_831_A	GLUT2_831_B	GRP_797_A	GRP_797_B	HAT1_701_A	HAT1_701_B	HGBA_548_A	HGBA_548_B	HGBA_572_A	HGBA_572_B
30535	3	4	2	2	1	1			1	1
33813			2	2			4	4	1	2
33852	3	3	2	1	1		4	4	1	2
33860	3	3	2	2	1	1	4	4	1	1
33863	3	3	2	1	1	1	4	3	1	1
33878	3	3	2	2	1	1	4	3	1	1
33879	3	3	2	2	1	1	4	4	1	2
33880	3	3	2	2	1	1	4	4	1	1
33881	3	3	2	2	2	1	4	4	1	2
33882	3	4	2	2	1	1	4	4	1	2
33883	3	3	2	1	2	1	4	4	1	
33940	3	3	2	2	1	1	4	4	2	2
33980	3	3	2	2	1	1	4	3	1	1
33982	3	3	2	2	1	1	4	4	1	1
33983			2		1	1	4	4	1	2
33984	3	3	2	2	1	1	4	4	1	
33985	3	3	2	2			4	4	1	1
33990	3	3	2	2	1	1				
33992			2	2	1	1				
45934	3	3	2	2	1	1	4	4	1	2
51015	3	3	2	2	1	1	4	4		
51025	3	3	2	2	1	1	4	3	1	1
51026	3	4	2	2	2	1	4	3	1	1
51028	3	3	2	2	1	1	4	4	1	1
51029	3	3	2	1	2	1	4	4	1	2
51031	3	3	2	2	1	1	4	4	1	1
51032	3	4	2	1	1	1	4	4	1	1
51033	3	3	2	2	1	1	4	3	1	2
55157			2	2	1	1	4	4	1	2
55160	3	3	2	2	1	1	4	4	1	2
55161	3	4	2	1	2	1	4	4	2	2
55165	3	3	2	2	1	1	4	4	1	2
55175	4	4	2	2	2	1	4	4		
55226	3	3	2	2	2	1	4	4	1	2
55228	3	3	2	1	2	1	4	4	1	2
55229	3	3	2	1	1	1	4	4	1	1
55230	3	3	2	2	2	1	4	4	1	2
55234	3	3	2	2	1	1	4	4	1	2
55238	3	3	2	2	1	1	4	4	1	2
55239	3	3	2	1	1	1	4	4	1	1
55242	3	3	2	2	2	1	4	4	1	2
55243	3	3	2	2	2	2	4	4	1	2
55244	4	4	2	2	2	1	4	4	1	
55248	3	3	2	2	1	1	4	4	1	2
55254	3	3	2	2	1	1	4	4	1	1

ID	GLUT2_831_A	GLUT2_831_B	GRP_797_A	GRP_797_B	HAT1_701_A	HAT1_701_B	HGBA_548_A	HGBA_548_B	HGBA_572_A	HGBA_572_B
61916	3	3	2	1	2	1	4	4	1	2
61918	3	3	2	2	1	1	4	4	1	2
61936	3	3	2	1	1	1	4	4		
61939			2	2	1	1	4	4	1	2
73899	3	3	2	2	1	1	4	4	1	1
73901	3	3	2	2	2	2	4	3	1	1
74708	3	4	2	2	1	1				1
78810	3	4	2	2	2	1	4	4	2	2
78812	3	3	2	2	1	1	4	4	1	2
79976	3	4	1	1	2	1				
79978	3	3	2	2	1	1	4	4	1	2
79992	3	3	2	2	1	1	4	4	1	1
80005	3	3	2	2	1	1	4	4	1	1
88591	3	3	2	2	1	1	4	4	1	2
88593	3	3	2	2	1	1				
88594	3	3	2	1	2	1	4	4	1	2
94818	3	3			2	2	4	3		
94820	3	3	2	2	1	1	4	4	1	2
102494	3	3			2	1	4	3	1	1
112632	3	3					4	4	1	2
112634	3	3			2	1	4	4	1	1
112635	3	3	2	2	1	1	4	4	1	1
112636	3	3	2	1	2	1	4	4		
112637	3	3	2	1	1	1	4	4		
112638	3	3	2	2	1	1	4	4	1	1
112639	3	3	2	2	1	1	4	4	1	2
112641	3	3	2	2	2	1	4	4	1	1
112642	3	3	2	2	1	1	4	4		
112646	3	3	2	2	1	1	4	4	1	1
112647	3	3	2	2	1	1	4	4	1	1
112648	3	3	2	2	1	1	4	4		
112649	3	3	2	2	1	1	4	3		
112652			2	2	1	1	4	4	1	1
112653	3	3	2	2	1	1	4	4	1	2
112654	3	3	2	2	1	1	4	3	1	1
112655	3	3	2	1	1	1	4	4	1	1
112658	3	3	2	2	1	1	4	4		
112660	4	4	2	1						
113642	4	4			1	1	4	4	1	2
113647	3	3	2	2	1	1	4	4	1	1
114348	3	3	2	2	1	1	4	4	1	2
114352	3	3	2	2			4	4	1	1
114356	3	3	2	1	2	1	4	4	1	2
114564	3	3	2	2	1	1	4	4	1	2
114565	3	3	2	2	2	1	4	4	1	2

ID	GLUT2_831_A	GLUT2_831_B	GRP_797_A	GRP_797_B	HAT1_701_A	HAT1_701_B	HGBA_548_A	HGBA_548_B	HGBA_572_A	HGBA_572_B
114805	3	3	2	2	1	1	4	4	1	2
114806	3	3	2	2	2	1	4	4	1	2
114808	3	3	2	2	2	1	4	3	1	1
114809	3	4	2	2	2	1	4	4	1	2
114813	3	3	2	2	2	1	4	4	1	2
114815	3	4	2	2	2	1	4	4	1	2
114816	3	3	2	2	2	1	4	4	1	2
114817	3	3	2	1	1	1				
114818	3	3	2	1	1	1	4	3	1	1
114819	3	4			1	1	4	4	1	1
114820	3	3	2	1	1	1	4	4	1	1
114821	3	3	2	1	2	1			1	1
114822	3	3	2	2	1	1	4	4	1	2
114823	3	4			1	1				
123340	3	3	2	2	2	1	4	3	1	1
123342	3	3	2	1	1	1			1	1

ID	HGBA_588_A	HGBA_588_B	HGBA_717_A	HGBA_717_B	HGBA_79_A	HGBA_79_B	HOXc8_173_A	HOXc8_173_B	HOXc8_348_A	HOXc8_348_B
30535	1		1	1			4	4	1	1
33813	2	2	1	1	4	4	4	4	1	1
33852	2	2	1	1	4	4	4	4	1	1
33860	1	2	1	1	4	1	4	3	1	1
33863	1	2	1	2					1	1
33878			1	1	4	1	4	3	1	1
33879	2	2	1	1	4	4	4	3	1	1
33880			1	1			4	4	1	1
33881	2	2	1	1	4	4	4	4	1	1
33882	2	2					4	4	1	1
33883							4	4	1	1
33940	1	2	1	1			4	3	1	1
33980			1	2					1	1
33982	1	2	1	1	1	1	3	3	1	1
33983	1	2	1	1	4	4	4	3	1	1
33984			1	1			4	4	1	1
33985	1	1					4	4	1	1
33990			1	1					1	1
33992									1	1
45934	2	2	1	1	4	4	4	4	1	1
51015			1	1	4	1	3	3	1	1
51025	1	2	1	1	4	1	3	3	1	1
51026	1	1	1	1	1	1	4	3	1	1
51028	1	2	1	1	4	1	4	4	1	1
51029	2	2	1	1	4	4	4	4	1	1
51031	1	2	1	1	4	1	4	3	1	1
51032	1	2	1	1	4	1	4	3	1	1
51033	1	2	1	1	4	1	4	4	1	1
55157	2	2	1	1	4	4	4	3	1	1
55160	2	2	1	1	4	4	4	4	1	1
55161	2	2	1	1	4	4	4	3	1	1
55165	1	2	1	1	4	4	4	3	1	1
55175			1	1	4	4	4	4	1	1
55226	2	2	1	1	4	4	4	3	1	1
55228	2	2	1	1	4	4	4	4	1	1
55229	1	2	1	2	4	1	4	4	1	1
55230	2	2	1	1	4	4	4	3	1	1
55234	2	2	1	1	4	4	3	4	1	1
55238	2	2	1	1	4	4	4	3	1	1
55239	2	2	1	1	4	4	4	4	1	1
55242	2	2	1	1	4	4	4	4	1	2
55243	1	2	1	1	4	1	4	4	1	2
55244					4	4	4	4	1	1
55248	2	2	1	1	4	4	4	3	1	1
55254	1	2	1	1	4		4	3	1	2

ID	HGBA_588_A	HGBA_588_B	HGBA_717_A	HGBA_717_B	HGBA_79_A	HGBA_79_B	HOXc8_173_A	HOXc8_173_B	HOXc8_348_A	HOXc8_348_B
61916	2	2	1	1	4	4	4	4	1	1
61918			1	1	4	1	4	4	1	1
61936	2	2	1	1	4	4	3	3	1	2
61939							3	3	1	1
73899	1	2	1	1			4	4		1
73901	1	1	2	1	1	1	4	4	1	1
74708	1	2	1	1	4	1	3	3	1	1
78810	2	2	1	1	4	4	3	3	1	1
78812	2	2	1	1	4	4	3	3	1	1
79976			1	1			4	4	1	1
79978			1	1	4	4	3	3	1	1
79992	1	2	1	1	4	1	4	4	1	1
80005	2	2	1	1	4	1	4	4	1	1
88591	2	2	1	1	4	4	4	4	1	1
88593			1	1			4	4	1	1
88594	2	2	1	1	4	4	4	4	1	2
94818			2	2	1	1	4	4	1	1
94820	2	2	1	1	4	4	4	3	1	1
102494	1	1	1	2	1	1			1	1
112632	2	2	1	1	4	4	4		1	1
112634	1	1	1	2			4	4	1	2
112635	2	2	1	1	4	4	4	4	1	1
112636	2	2	1	1	4	4	4	3	1	2
112637	1	2	1	1	4	4	4	4	1	2
112638	2	2	1	1	4	4	4	4	1	1
112639	2	2	1	1	4	4	4	3	1	1
112641	1	2	2	2	4	1	4	3	1	1
112642			1	1	4	4	4	3	1	1
112646	1	2	2	2	4	4	4	3	2	2
112647	2	2	1	1	4	4	4	3	1	2
112648			1	1			4	3	1	1
112649	1	1	2	2	1	1	4	4	1	1
112652	1	2	1	1	4	1	4	4	1	1
112653	1	2	2	2	4	1	4	3	1	1
112654	1	2	1	1	4	1	4	3	1	1
112655	1	2	1	1	4	4	4	4	1	1
112658			1	1	4	1	4	4	1	1
112660	1	2	1	1	4	4	4		1	1
113642	2	2	1	1	4	4	4	4	1	1
113647	1	2	1	1	4	1	4	4	1	1
114348	2	2	1	1	4	4	4	4	2	2
114352	1	2	1	1	4	1	4	3	1	1
114356	1	2	1	1		1	3	3	1	1
114564	1	2	1	1			3	3	1	1
114565	2	2	1	1	4	4	3	4	1	1

ID	HGBA_588_A	HGBA_588_B	HGBA_717_A	HGBA_717_B	HGBA_79_A	HGBA_79_B	HOXc8_173_A	HOXc8_173_B	HOXc8_348_A	HOXc8_348_B
114805	2	2	1	1	4	4	4	3	1	1
114806	2	2	1	1	4	4	4	3	1	1
114808			2	2					1	1
114809	2	2	1	1	4	4	4	3	1	1
114813			1	1	4	1	4	3	1	1
114815					4	1	3	3	1	1
114816	2	2	1	1	4	4	4	4	1	1
114817			1	1					1	1
114818	1	2	1	1	4	1	4	3	1	1
114819	2	2	1	1			4	4	1	1
114820	1	2	1	1	4	1	4	4	1	1
114821	1	2	1	1	4	1	4	3	1	2
114822	1	1	1	1	4	1	4	3	1	1
114823							4	4	1	1
123340	1	1	1	1	4	1	4	3	1	1
123342	1	2	1	1	4	1	4	4	1	1

ID	HOXc8_411_A	HOXc8_411_B	HOXc8_642_A	HOXc8_642_B	HOXc8_760_A	HOXc8_760_B	INT_575_A	INT_575_B	Lactalbumin_89_A	Lactalbumin_89_B
30535	3	3			2	2	4	3		
33813	4	3	2	2			4	3	1	1
33852	3	3	2	2	2	2	4	3	1	2
33860	4	3	2	1	2	2	4	3	1	1
33863	3	3					4	3	1	2
33878	4	4	2	1	2	2	4	4	1	1
33879	4	3	2	2	2	2	3	3	1	2
33880			2	2	2	2	4	3	1	1
33881	4	3	2	2	2	2	4	3	1	2
33882	4	3	2	2	2	4	4	4	1	2
33883			2	2			4	3	1	1
33940			2	1			4	3	2	2
33980							4	4	1	2
33982	4	4	1	1	2	2	4	3	1	2
33983	4	3	2	2			4	4	1	1
33984			2	2			3	3	1	2
33985			2	2			4	4	1	2
33990	4	4	2	1			4	3		
33992			2	1			3	3		
45934	3	3	2	2	2	2	3	3	1	2
51015	4	4	1	1	2	2	4	3		
51025	4	4	1	1	2	2	4	3	1	2
51026	4	3			2	2	4	3	1	2
51028	4	3	2	2	2	4	4	3	2	2
51029	3	3	2	2	2	2	4	3	2	2
51031	4	3	2	1	2	2	3	3	1	2
51032	4	4	2	2	2	4	4	4	2	2
51033	4	3	2	1	2	4	4	3	1	2
55157	4	3	2	2	2	2	4	4	1	2
55160	3	3	2	2	2	2	3	3	1	1
55161	4	3	2	2	2	2	4	3	1	2
55165	4	4	2	2	2	4	3	3	1	1
55175	3	3	2	2	2	2	3	3	1	1
55226	4	3	2	2	2	2	4	4	1	1
55228	3	3	2	2	2	2	3	3	1	1
55229	3	3	2	2	2	2	4	3	1	1
55230	3	3	2	2	2	2	3	3	1	2
55234	4	4	1	1	2	2	4	3	1	1
55238	3	3	2	2	2	4	4	3	1	1
55239	3	3	2	2	2	2	4	4	1	2
55242	4	3	2	2	2	4	4	4	1	1
55243	4	4	2	2	2	2	4	3	1	
55244	4	3	2	2	2	2	4	4	1	2
55248	4	4	2	2	2	4	4	3	1	1
55254	4		2	1	2	2	4	4	1	2

ID	HOXc8_411_A	HOXc8_411_B	HOXc8_642_A	HOXc8_642_B	HOXc8_760_A	HOXc8_760_B	INT_575_A	INT_575_B	Lactalbumin_89_A	Lactalbumin_89_B
61916	3	3	2	2	2	2	4	3	2	2
61918	3	3	2	2	2	2	4	3	1	2
61936	4	4	2	1	2	2	4	4	1	1
61939			2	1	2	2	4	3	1	1
73899	4	3	2	2	2	2	4	3	1	2
73901	4	3	2	2	2	2	4	3	2	2
74708	4	4	1	1	2	2	4	3	1	2
78810	4	4			2	2	4	4	1	1
78812	4	4	2	1	2	4	4	3	1	1
79976	3	3					4	3	1	2
79978	4	4	1	1	2	2	4	4	1	1
79992	4	3	2	2	2	4	3	3	1	2
80005	3	3	2	2	2	2	4	3	1	1
88591	4	3	2	2	2	4	4	4	1	2
88593	3	3	2	2			4	4	1	1
88594	4	3	2	2	2	2	4	4	1	1
94818	3	3			2	2	4	3		
94820	4	3	2	2	2	2	3	3	1	2
102494			2	1	2	2			2	2
112632	4	4	2	2			4	4	1	2
112634	4	4	2	2	2	2	4	3	1	2
112635	4	3	2	2	2	4	4	3	1	1
112636	4	4					3	3		
112637	4	3	2	2	2	2	4	3	1	2
112638	3	3	2	2	2	2	4	4	1	1
112639	4	3	2	2	2	2	4	3	2	2
112641	4	4	2	1	2	2	4	4	1	1
112642	4	4	1	1	2	2	4	4	2	2
112646	4	4	2	2	2	2	3	3	1	2
112647	4	4	2	1	2	2	4	4	1	2
112648	4	4	2	1	2	4	4	3	1	1
112649	3	3	2	2	2	2	3	3	1	2
112652	4	3	2	2	2	4	3	3	1	1
112653	4	3	2	1	2	2	4	3	1	2
112654	4	3	2	1	2	2	3	3	1	2
112655	4	3	2	2	2	4	3	3	1	2
112658	4	3	2	2			4	3		
112660	4	3	2	1			4	4		
113642	3	3	2	2	2	2	4	4		
113647	3	3	2	2	2	2	4	3	1	1
114348	4	3	2	2	2	2	4	4	1	2
114352	4	3	2	1	2	2	4	3		
114356	4	4	1	1	2	2	4	4	1	1
114564	4	4	2	2			4	3		
114565	4	3	2	1	2	2	4	3	1	2

ID	HOXc8_411_A	HOXc8_411_B	HOXc8_642_A	HOXc8_642_B	HOXc8_760_A	HOXc8_760_B	INT_575_A	INT_575_B	Lactalbumin_89_A	Lactalbumin_89_B
114805	4	4	2	1	2	2	4	4	2	2
114806	4	3	2	1	2	2	4	3	1	2
114808	4	3			2	4	4	4	1	1
114809	4	3	2	1	2	2	4	3	1	1
114813	4	3	2	1	2	2	4	4	1	2
114815	4	3	2	1	2	2	4	4	1	1
114816	3	3	2	2	2	2	4	3	1	1
114817	4	3	2	1			4	3	1	1
114818	4	4	2	2	2	2	4	3	1	1
114819	4	3	2	2	2	4	4		1	1
114820	3	3	2	2	2	2	4	3	2	2
114821	4	4	2	1	2	2	4	4	1	1
114822	3	3	2	2			3	3	1	1
114823			2	2			3	3	1	
123340	4	3	2	1	2	2	4	3	1	1
123342	3	3	2	2	2	2	4	3	2	2

ID	LAPTM4A_446_A	LAPTM4A_446_B	LAPTM4A_601_A	LAPTM4A_601_B	LAPTM4A_837_A	LAPTM4A_837_B	LHY_355_A	LHY_355_B	MATR3_219_A
30535	2	2	3		1	1			3
33813	2	2	3		1	1	1	1	3
33852	1	1	3		1	1	1	1	3
33860	1	2	3		1	1	1	1	3
33863	2	2	3		1	1	1	1	3
33878	1	2	3		1	1	1	2	3
33879	2	2	3		1	1	1	1	3
33880	2	2	3		1	1			3
33881	1	1	3		1	1	1	2	3
33882	1	2	3		1	1	1	2	3
33883	2	2	3		1	1	1	1	3
33940	1	2	4		2	1	1	1	3
33980	1	2	3		1	1	1	1	3
33982	2	2	3		1	1	1	1	3
33983	2	2	3		1	1	1	1	3
33984	1	2	3		1	1	1	2	3
33985	1	1	3		1	1	1		3
33990	2	2	3		1	1	1	2	3
33992	1	2	3		1	1	1	1	3
45934	2	2	3		1	1	1	1	3
51015	2	2	3		1	1	1	1	3
51025	2	2	3		1	1	1	1	3
51026	2	2	3		1	1	1	1	3
51028	2	2	3		1	1	1	1	3
51029	2	2	3		1	1	1	1	3
51031	2	2	3		1	1	1	1	3
51032	1	2	3		1	1	1	1	3
51033	1	2	4		2	1	1	1	3
55157	1	2	3		1	1	1	1	3
55160	1	1	3		1	1	1	1	3
55161	1	2	3		1	1	1	1	3
55165	2	2	3		1	1	1	1	3
55175	1	1	3		1	1	1	1	3
55226	2	2	3		1	1	1	2	3
55228	1	2	4		2	1	1	1	3
55229	1	2	4		2	1	1	1	3
55230	1	1	4		2	1	1	1	3
55234	1	2	3		1	1	1	1	3
55238	1	2	3		1	1	1	1	3
55239	2	2	3		1	1	1	2	3
55242	2	2	3		1	1	1	1	3
55243	2	2	3		1	1	1	1	3
55244	2	2	3		1	1	1	2	3
55248	2	2	3		1	1	1	1	3
55254	1	2	3		1	1	1	1	3

ID	LAPTM4A_446_A	LAPTM4A_446_B	LAPTM4A_601_A	LAPTM4A_601_B	LAPTM4A_837_A	LAPTM4A_837_B	LHY_355_A	LHY_355_B	MATR3_219_A
61916	1	2	3	3	1	1	1	1	3
61918	2	2	3	3	1	1	1	1	3
61936	1	2	4	3	1	2	1	1	3
61939	1	2	3	3	1	1	1	1	3
73899	2	2	3	3	1	1	1	2	3
73901	1	2	3	3	1	1	1	1	3
74708	1	2	3	3	1	1	1	1	3
78810	2	2	3	3	1	1	1	1	3
78812	2	2	3	3	1	1	1	1	3
79976	2	2	3	3	1	1	1	1	3
79978	1	2	3	3	1	1	1	1	3
79992	2	2	3	3	1	1	1	1	3
80005	1	2	3	3	1	1	1	1	3
88591	1	1	3	3	1	1	1	1	3
88593	1	2	3	3	1	1	1	1	3
88594	2	2	3	3	1	1	1	1	3
94818	1	1			1	1	1	1	3
94820	2	2	3	3	1	1	1	1	3
102494	2	2	3	3	1	1	1		3
112632	2	2	3	3	1	1	1	2	3
112634			3	3	1	1	1	1	3
112635	2	2	3	3	1	1	1	2	3
112636	1	1	4	3	2	1	1		3
112637	2	2	3	3	1	2	1	2	3
112638	1	2	3	3	1	1	1	2	3
112639	1	1	3	3	1	1	1	1	3
112641	2	2	3	3	1	1	1	1	3
112642	2	2	3	3	1	1	1	1	3
112646	2	2	3	3	1	1	1	1	3
112647	2	2	3	3	1	1	1	1	3
112648	1	1	3	3	1	1	1	1	3
112649	2	2	3	3	1	1	1	2	3
112652	1	2	3	3	1	1	1	1	3
112653	1	1	3	3	1	1	1	1	3
112654	1	1	3	3	1	1	1	1	3
112655	2	2	3	3	1	1	1	1	3
112658			3	3	1	1	1	2	3
112660	1	2	3	3	1		1		3
113642	2	2	3	3			1		3
113647	1	2	3	3	1	1	1	1	3
114348	2	2		3	1	1	1	1	3
114352	2	2		3	1	1	1	1	3
114356	2	2	3	3	1	1	1	1	3
114564	1	1	3	3	1	1	1	2	3
114565	2	2	3	3	1	1	1	2	3

ID	LAPTM4A_446_A	LAPTM4A_446_B	LAPTM4A_601_A	LAPTM4A_601_B	LAPTM4A_837_A	LAPTM4A_837_B	LHY_355_A	LHY_355_B	MATR3_219_A
114805	2	2	3	3	1	1	1	2	3
114806	2	2	3	3	1	1	1	1	3
114808	1	2	3	3	1	1	1	1	3
114809	1	2	3	3	1	1	1	1	3
114813	1	2	3	3	1	1	1	1	3
114815	1	2	3	3	1	1	1	1	3
114816	1	2	3	3	1	1	1	1	3
114817	1	2	3	3	1	1	1	1	3
114818	2	2	3	3	1	1	1	2	3
114819	1	1	3	3			1	1	3
114820	2	2	3	3	1	1	1	1	3
114821	1	2	3	3	1	1	1	1	3
114822	2	2	3	3	1	1	1	1	3
114823	1	2	3	3	1	1	1	1	3
123340	1	2	3	3	1	1	1	2	3
123342	1	2	4	3	1	2	1	1	3

ID	MATR3_219_B	MATR3_840_A	MATR3_840_B	MPO_628_A	MPO_628_B	MYH4_124_A	MYH4_124_B	MYH4_315_A	MYH4_315_B	MYH4_355_A
30535	3	3	3	4	3	2	2	1	1	4
33813	3	3	3	3	3	1	2	2	1	4
33852	3	3	3	3	3	1	2	1	1	4
33860	3	3	4	4	3	2	2	1	1	4
33863	3	3	4	3	3	2	2	1	1	4
33878	3	3	3	3	3	2	2	1	1	4
33879	3	3	3	3	3	2	2	1	1	4
33880	3	3	3			2	2	1	1	4
33881	3	3	3	3	3	2	2	2	1	4
33882	3	3	3	4	3	1	2	1	1	4
33883	3	3	4			1	2	2	1	4
33940	3	3	3	4	3	1	2	1	1	4
33980	3	3	3			1	2	1	1	4
33982	4	3	3	4	3	2	2	1	1	4
33983	3	3	3	3	3	2	2	1	1	4
33984	3	3	4			1	2	1	1	4
33985	3	3	3			2	2	2	1	4
33990	3	3	3	4	3	1	2	1	1	4
33992	3	3	3			1	2	1	1	4
45934	4			4	4	2	2	2	1	4
51015	3	3	3	3	3	1	2	1	1	4
51025	3	3	3	4	3	1	2	2	1	4
51026	3	3	3	3	3	2	2	1	1	4
51028	3	3	3	4	3	1	2	1	1	4
51029	3	3	3	3	3	2	2	1	1	4
51031	3	3	3	4	3	2	2		1	4
51032	3	3	3	3	3	2	2	1	1	4
51033	3	3	3	3	3	2	2	2	1	4
55157	3		4	3	3	1	2	1	1	4
55160	3	3	3	3	3	2	2	2	1	4
55161	3	3	3	4	3	1	2	1	1	4
55165	3	3	3	4	4	2	2	1	1	4
55175	3	3	3	3	3	1	2	1	1	4
55226	3	3	3	3	3	1	2	1	1	4
55228	3	3	3	3	3	1	2	1	1	4
55229	3	3	4	3	3	1	2	1	1	4
55230	4	3	4	3	3	2	2	2	1	4
55234	4	3	4	3	3	1	2	1	1	4
55238	3	3	4	3	3	1	2	1	1	4
55239	3	3	3	4	3	2	2	2	1	4
55242	3	3	3	3	3	1	2	1	1	4
55243	3	3	3	3	3	1	2	1	1	4
55244	3	3	3	3	3	2	2	1	1	4
55248	3	3	3	3	3	1	2	2	1	4
55254	3	3	3	4	3	2	2	1	1	4

ID	MATR3_219_B	MATR3_840_A	MATR3_840_B	MPO_628_A	MPO_628_B	MYH4_124_A	MYH4_124_B	MYH4_315_A	MYH4_315_B	MYH4_355_A
61916	3	3	3	4	3	2	2	2	1	4
61918	3	3	3	4	3	1	2	1	1	4
61936	3	3	3	4	4	2	2	2	1	4
61939	3	3	3	4	3	2	2	1	1	4
73899	3	3	3	3	3			2	1	4
73901	3	3	4	3	3	2	2	1	1	4
74708	3	3	4	4	3	2	2	2	1	4
78810	3	3	3	3	3	1	2	1	1	4
78812	3	3	3		3	1	2	1	1	4
79976	3			3	3	2	2	1	1	4
79978	3	3	3	4	3	1	2	1	1	4
79992	3	3	3	4	3	2	2	1	1	4
80005	4	3	4	4	4			2	1	4
88591	3	3	3	4		2	2	2	1	4
88593	3	3	4		3	1	2	1	1	4
88594	3	3	3	4	4	2	2	1	1	4
94818	3	3	3	4	3	2	2	2	1	4
94820	3	3	4	4	4	2	2	1	1	4
102494	3	3	3	4	3	2	2	2	1	4
112632	3			3	3	1	2	1	1	4
112634	4	3	3	3	3	2	2	1	1	4
112635	3	3	4	3	3	2	2	1	1	4
112636	3			4	3	1	2	1	1	4
112637	3	3	3	4	3	1	2	1	1	4
112638	3	3	3	4	3	1	2	1	1	4
112639	3	3	4	3	3	2	2	1	1	4
112641	3	3	3	3	3	1	2	1	1	4
112642	3			4	3	2	2	1	1	4
112646	3	3	3	4	3	1	2	1	1	4
112647	3	3	3	4	3	2	2	1	1	4
112648	3	3	3	4	4	2	2	1	1	4
112649	3	3	3	3	3	1	2	1	1	4
112652	3	3	3	4	4	2	2	1	1	4
112653	3	3	3	4	3	2	2	1	1	4
112654	3	4	4	4	4	2	2	1	1	4
112655	3	3	4	4	3	2	2	1	1	4
112658	3	3	3	3	3	2	2	1	1	4
112660	3					2	2	2	1	4
113642	3			3	3	2	2	2	1	4
113647	3	3	3	3	3	2	2	2	1	4
114348	3	3	4	3		2	2	2	1	4
114352	3					1	2	1	1	4
114356	3	3	3	4	3	2	2	1	1	4
114564	3	3	3	4	4	2	2	1	1	4
114565	3	4	4	4	3	1	2	1	1	4

ID	MATR3_219_B	MATR3_840_A	MATR3_840_B	MPO_628_A	MPO_628_B	MYH4_124_A	MYH4_124_B	MYH4_315_A	MYH4_315_B	MYH4_355_A
114805	3	3	3	4	3	2	2	2	1	4
114806	3	3	3	3	3	1	2	1	1	4
114808	3	3	4	3	3	1	2	1	1	4
114809	3	4	4	4	3	2	2	2	1	4
114813	3	3	3	4	3	2	2	2	1	4
114815	3					2	2	1	1	4
114816	3	3	3	4	4	2	2	1	1	4
114817	3					1	2	1	1	4
114818	3	3	3	3	3	2	2	1	1	4
114819	3	3	3	4	3	1	2	1	1	4
114820	3	3	3	3	3	2	2	1	1	4
114821	4	3	3	4	4	2	2	1	1	4
114822	3	3	3	3	3	1	2	1	1	4
114823	3	3	4	4	3	1	2	1	1	4
123340	3	3	3	4	3	2	2	1	1	4
123342	3	3	4	4	3	2	2	2	1	4

ID	MYH4_355_B	MYH4_424_A	MYH4_424_B	MYH4_543_A	MYH4_543_B	MYL4_110_A	MYL4_110_B	MYL4_394_A	MYL4_394_B	MYL4_413_A	MYL4_413_B
30535	4	1	1	3	4						3
33813	1	1	1	3	3	3	1	1	2	4	3
33852	4	1	1	3	3	3	3	2	2		
33860	1	1	1			3	1	1	2	4	3
33863	1	1	1	3	3	3	3				
33878	4	1	1			3	1	1	1	4	4
33879	1	1	1	3	3	3	1	1	2	4	3
33880	4	1	1	3	4			2	2		
33881	1	1	1	3	4	3	3	2	2	3	3
33882	4	1	1	3	4			2	2	3	3
33883	4	1	1			3	1	1	2	4	3
33940	1	1	1	3	4	3	1	1	2	4	3
33980	4	1	1	3	4	3	1				
33982	4	1	1	3	4	3	3	2	2	3	3
33983	4	1	1	3	4	3	3	2	2		
33984	1	1	1								
33985	1	1	1					1	2	3	3
33990	4	1	1			3	1	1	2	4	4
33992	4	1	1					1	2	4	3
45934	1	1	1	3	3	3	1	2	2	3	3
51015	1	1	1	3	3	3	1	1	2	4	3
51025	1	1	1	3	3	3	3	2	2	3	3
51026	1	1	1	3	4	3	1	1	2	4	3
51028	4	1	2	3	3	3	1	1	2	4	3
51029	1	1	1	3	3	3	3	2	2	3	3
51031		1	1	3	3	3	3	2	2	3	3
51032	1	1	1	3	4	3	3	2	2	3	3
51033	1	1	1	3	4	3	3	2	2	3	3
55157	4	1	1	3	3	3	3	2	2	3	3
55160	1	1	1	3	3	3	3	2	2	3	3
55161	1	1	1	3	4	3	3	2	2	3	3
55165	1	1	1	3	4	1	1	1	2	3	3
55175	4	1	2	3	4	3	3	2	2	4	3
55226	4	1	1	3	4	1	1	1	2	3	3
55228	4	1	2	3	3	3	1	1	2	4	3
55229	4	1	2	3	3	3	1	1	2	4	3
55230	1	1	1	3	3	3	1	1	2	4	3
55234	4	1	2	3	3	1	1	1	2	4	3
55238	4	1	2	3	3	3	1	1	2	4	3
55239	1	1	1	3	4	3	1	2	2	3	3
55242	4	1	1	3	3	3	1	1	2	4	3
55243	4	1	2	3	3	3	3	2	2	4	3
55244	4	1	1	3	3	3	3	1		3	3
55248	1	1	1	3	3	1	1	1	1	3	4
55254		1	1	3	3	3	1	2	2	3	3

ID	MYH4_355_B	MYH4_424_A	MYH4_424_B	MYH4_543_A	MYH4_543_B	MYL4_110_A	MYL4_110_B	MYL4_394_A	MYL4_394_B	MYL4_413_A	MYL4_413_B
61916	1	1	1	3	4	1	3	2	2	3	3
61918	4	1	1	3	4	3	3			3	3
61936	1	1	1	3	4	1	3	2	2	3	3
61939	1	1	1	3	3	3	3	2	2	3	3
73899	1	1	1	3	3	3	3	2	2	3	3
73901	1	1	1	3	3	3	3	2	2	3	3
74708	1	1	1	3	3	1	3	2	2	3	3
78810	1	1	1	3	3	3	3	2	2	3	3
78812	4	1	1	3	3	1	3	2	2	3	3
79976	1	1	1			3	3				
79978	1	1	1	3	3		3	2	2	3	3
79992	4	1	2	3	3	3	3	2	2	3	3
80005	4	1	1			3	3	2	2	3	3
88591	1	1	1	3	3	3	3	2	2	3	3
88593	4	1	2	3	3	3	3				
88594	1	1	1	3	3	1	3	2	2	3	3
94818	1	1	1	3	4						
94820	4	1	2			1	3	1	2	4	3
102494	1	1	1	3	4	3	3	2	2	3	3
112632	4	1	2	3	3	1	3	2	2	3	3
112634	1	1	1			3	3	2	2	3	3
112635	4	1	1	3	4	3	3	2	2	3	3
112636	4	1	2	3	4	3	3	2	2	3	3
112637	4	1	2	3	4	3	3	2	2	3	3
112638	4	1	2	3	3	3	3	2	2	3	3
112639	1	1	1	3	3	3	3	2	2	3	3
112641	4	1	1	3	4			2	2	3	3
112642	1	1	1	3	4	1	3	2	2	3	3
112646	4	1	1	3	4	3	3	2	2	3	3
112647	1	1	1	3	4	3	3	2	2	3	3
112648	1	1	1	3	4	1	3	2	2	3	3
112649	4	1		3	4	3	3	2	2	3	3
112652	4	1	2	3	4	1	1	1	1	4	4
112653	4	1	1	3	4	1	1	1	2	4	3
112654	1	1	1	3	4	1	3	2	2	3	3
112655	4	1	1	3	4	1	1	1	1	4	4
112658	4	1	1	3	4			2	2	3	3
112660	1	1	1	3	4						
113642	1	1	1	3	4	1	3	1	2	4	3
113647	1	1	1	3	4	3	3	2	2	3	3
114348	1	1	1	3	3	3	3	2	2	3	3
114352	4	1	2	3	4	3	3				
114356	4	1	1	3	4	3	3	2	2	3	3
114564	1	1	1	3	4	1	3	2	2	3	3
114565	4	1	1	3	3	3	3	2	2	3	3

ID	MYH4_355_B	MYH4_424_A	MYH4_424_B	MYH4_543_A	MYH4_543_B	MYL4_110_A	MYL4_110_B	MYL4_394_A	MYL4_394_B	MYL4_413_A	MYL4_413_B
114805	1	1	1	3	4	1	3	1	2	4	3
114806	4	1	2	3	4	1	3	2	2	3	3
114808	4	1	1	3	3	1	1	2	2	3	3
114809	1	1	1	3	4	1	3	1	2	4	3
114813	1	1	1	3	3	3	3	2	2	3	3
114815	4	1	1	3	4	1	3	2	2	3	3
114816	1	1	1	3	4	3	3	2	2	3	3
114817	4	1	1	3	4	1	1				3
114818	4	1	1	3	4	3	3	2	2	3	3
114819	4	1	1	3	3	3	3	2	2	3	3
114820	4	1	1	3	3	1	3	1	2	4	3
114821	4	1	1	3	4	3	3	2	2	3	3
114822	4	1	2	3	4		3	2	2	3	3
114823	4	1	2	3	3	1	3				
123340	4	1	1	3	4	3	3	2	2	3	3
123342	1	1	1	3	4	3	3	2	2	3	3

ID	MYL4_774_A	MYL4_774_B	PND_1002_A	PND_1002_B	PND_1020_A	PND_1020_B	PND_1680_A	PND_1680_B	PND_1741_A	PND_1741_B	ODC1_458_A
30535	4	4	1		4	3	3	3	4	4	1
33813	4	4	1	1	3	3	3	3	4	4	1
33852	4	4	1	1	4	4	3	3	4	4	1
33860	4	4	1	1	3	3	3	4	4		1
33863	4	4	1	1	3	3	3	3	4	4	1
33878	4	3	1	1	4	3	3	4	4	4	1
33879	4	4	1	1	3	3	3	4	4	4	1
33880	4	4	1	1	3	3	3	4	4	4	1
33881	4	4	1	1	3	3	3	3	4	4	1
33882	4	4	1	1	4	3	3	4	4	4	1
33883	4	3	1	1	4	3	3	3	4	4	1
33940	4	3	1	1	3	3	3	3	4	4	1
33980	4	4	1	1	4	3	3	3	4	4	1
33982	4	4	1	1	4	3	3	3	4	4	1
33983	4	4	1	1	3	3	3	3	4	4	1
33984	4	4	1	1	3	3	3	4	4	4	1
33985	4	3	1	1	3	3	3	4	4	4	1
33990	4	3	1	1	3	3	3	4	4	4	1
33992	4	3	1	1	3	3	3	3	4	4	1
45934	4	4	1	1	3	3	3	3	4	4	1
51015	4	3	1	1	3	3	3	3	4	4	1
51025	4	4	1	3	4	3	3	3	4	3	1
51026	4	3	1	3	4	3	3	3	4	4	1
51028	4	4	1	1	3	3	3	4	4	4	1
51029	4	4	1	1	4	3	3	3	4	4	1
51031	4	4	1	1	4	3	3	3	4	4	1
51032	4	4	1	3	4	4	3	3	4	3	1
51033	4	4	1	3	4	4	3	3	4	3	1
55157	4	4	1	3	4	3	3	3	4	4	1
55160	4	4	1	1	4	3	3	3	4	4	1
55161	4	4	1	1	3	3	3	3	4	4	1
55165	4	3	1	3	4	3	3	3	4	3	1
55175	4	4	1	1	4	3	3	3	4	4	1
55226	4	4	1	1	4	3	3	3	4	4	1
55228	4	4	1	1	4	3	3	4	4	4	1
55229	4	4	1	1	4	3	3	4	4	4	1
55230	4	4	1	1	4	3	3	3	4	4	1
55234	4	4	1	1	3	3	3	4	4	4	1
55238	4	4	1	1	3	3	4	4	4	4	1
55239	4	4	1	3	4	3	3	3	4	3	1
55242	4	4	1	1	4	3	3	3	4	4	1
55243	4	4	1	1	3	3	3	3	4	3	1
55244	4	4	1	3	4	4	3	3	4	4	1
55248	4	3	1	1	4	4	3	3	4	4	1
55254	4	4	1	1	3	3	3	4	4	4	1

ID	MYL4_774_A	MYL4_774_B	PND_1002_A	PND_1002_B	PND_1020_A	PND_1020_B	PND_1680_A	PND_1680_B	PND_1741_A	PND_1741_B	ODC1_458_A
61916	4	4	1		3	4	4	4	4	4	1
61918	4	4	1		4	3	3	3	4	4	1
61936	4	4	1		3	3	3	4	4	4	1
61939	4	4	1		3	3			4	4	1
73899	4	4	1		4	3	3	3	4	4	1
73901	4	4	1		3	3	4	4	4	3	1
74708	4	4	1	3	4	3	3	3	4	4	1
78810	4	4	1		4	4	3	3	4	4	1
78812	4	4	1		4	4	3	3	4	4	1
79976	4	4	1		3	3				4	1
79978	4	4	1		3	3	3	3	4	4	1
79992	4	4	1		3	3	3	4	4	4	1
80005	4	4	1		4	4	3	3	4	4	1
88591	4	4	1		3	3	3	4	4	4	1
88593	4	4	1				3	3	4	4	1
88594	4	4	1		4	3	3	3	4	4	1
94818	4	4	1		4	4	3	3	4	4	1
94820	4	3	1		3	3	3	4	4	4	1
102494	4		1		4	4			4	4	1
112632	4	4	1	3	4	4	3	3	3	3	1
112634	4	4	1		4	3			4	4	1
112635	4	4	1	3	4	3	3	3	3	3	1
112636	4	4	1		3	3			4	4	1
112637	4	4	1		3	3	3	4	4	4	1
112638	4	4	1		4	3	3	3	4	4	1
112639	4	4	1		4	3	3	4	4	4	1
112641	4	4	1		3	3	3	3	4	4	1
112642	4	4	1		3	3	3	3	4	4	1
112646	4	4	1		3	3	3		4	4	1
112647	4	4	1		4	3	3	3	4	4	1
112648	4	4	1		4	3	3	3	4	4	1
112649	4	4	1		3	4	4	4	4	4	1
112652	4	3	1	3	4	3	3	3	4	3	1
112653	4	3	1		4	3	3	3	4	4	1
112654	4	4	1	3	4	3	3	4	4	3	1
112655	4	3	1		3	3	3	4	4	4	1
112658	4	4	1	3	4	3	3	4	4	3	1
112660	4	4	1		4	3			4	4	1
113642	4	4	1		4	3			4	4	1
113647	4	4	1		4	3	3	3	4	4	1
114348	4	4	1		4	4	3	3	4	4	1
114352	4	4	1		4	3	3	4	4	4	1
114356	4	4	1		3	3	3	3		4	1
114564	4	4	1		4	3	3	3	4	4	1
114565	4	4	1		3	3	3	4	4	4	1

ID	MYL4_774_A	MYL4_774_B	PND_1002_A	PND_1002_B	PND_1020_A	PND_1020_B	PND_1680_A	PND_1680_B	PND_1741_A	PND_1741_B	ODC1_458_A
114805	4	3	1	1	4	3	3	4	4	4	1
114806	4	4	1	1	4	3	3	4	4	4	1
114808	4	4	1	1	4	3	3	3	4	4	1
114809	4	4	1	1	4	3	3	3	4	4	1
114813	4	4	1	1	4	3	3	3	4	4	1
114815	4	4	1	1	4	3	3	3	4	4	1
114816	4	4	1	1	3	3	3	4	4	4	1
114817	4	4	1	1	4	3	3	3	4	4	1
114818	4	4	1	3	4	3	3	3	4	3	1
114819	4	4	1	1	3	3	3	4	4	3	1
114820	4	3	1	3	4	4	3	3	4	3	1
114821	4	4	1	1	4	3	3	4	4	4	1
114822	4	4	1	1	4	3	3	3	4	4	1
114823	4	3	1	1	3	3	3	3	4		1
123340	4	4	1	1	4	3	3	4	4	4	1
123342	3	4	1	3	4	3	3	3	4	3	1

ID	ODC1_458_B	ODC1_907_A	ODC1_907_B	PGK1_115_A	PGK1_115_B	PGK1_452_A	PGK1_452_B	PGK1_504_A	PGK1_504_B	PGK1_652_A	PGK1_652_B
30535	1	1	1	4	4			4	3	1	1
33813	1	1	1				4	4	3	1	1
33852	1	1	1	4	3	3	4	4	3	1	1
33860	1	1	1	4	3	3	4	4	3	1	1
33863	1	1	1				3	4		1	1
33878	1	1	1	4	4	3	3	4	4	1	1
33879	1	1	1	4	4	4	4	4	3	1	1
33880	1	1	1	4	4	4	4	4	4	1	1
33881	1	1	1	4	3	3	4	4	4	1	1
33882	1	1	1			3	3	4	4	1	1
33883	3	3	1	4	4	4	4	4		1	1
33940	1	1	1			3	3	4	4	1	1
33980	1	1	1	4	3	3	3	4	4	1	1
33982	1	1	1	4	4	3	3	4	4	1	1
33983	1	1	1			3	4	4	3	1	1
33984	1	1	1	4	4	3	4	4	4	1	1
33985	1	1	1			3	4	4	4	1	2
33990	1	1	1	4	4	3	4	4	3	1	2
33992	3	3	1	4	3	3	3	4	4	1	2
45934	1	1	1	4	4	3	4	4	3	1	1
51015	1	1	1	4	4	3	4	4	3	1	1
51025	1	1	1	4	4	3	3	4	4	1	1
51026	3	3	1	4	4	3	4	4	3	1	1
51028	3	3	1	4	4	4	4	3	3	1	1
51029	1	1	1	3	3	3	3	4	4	1	1
51031	1	1	1	4	4	4	4	3	3	1	1
51032	1	1	1	4	4	4	4	3	3	1	1
51033	1	1	1	4	3	3	3	4	4	1	1
55157	1	1	1	4	4	3	4	4	4	1	1
55160	1	1	1	4	3	3	4	4	3	1	1
55161	3	3	1	4	3	3	4	4	4	1	1
55165	1	1	1	3	3	3	3	4	4	1	1
55175	1	1	1	4	3	3	3	4	4	1	1
55226	1	1	1	4	3	3	3	4	4	1	1
55228	1	1	1	4	4	4	4	3	3	1	1
55229	1	1	1	4	4	4	4	3	3	1	1
55230	1	1	1	4	3	3	4	4	4	1	1
55234	1	1	1	4	4	4	4	3	3	1	1
55238	1	1	1	4	3	3	3	4	4	1	1
55239	1	1	1	4	3	3	3	4	3	1	1
55242	3	3	1	4	3	3	3	4	4	1	1
55243	3	3	1	4	3	4	4	4	4	1	1
55244	1	1	1	4	4	4	4	3	3	1	1
55248	3	3	1	4	3	3	4	4	3	1	1
55254	1	3	1	4	4	3	4	4	3	1	2

ID	ODC1_458_B	ODC1_907_A	ODC1_907_B	PGK1_115_A	PGK1_115_B	PGK1_452_A	PGK1_452_B	PGK1_504_A	PGK1_504_B	PGK1_652_A	PGK1_652_B
61916	1	1	1	4	4	4	4	3	3	1	1
61918	3	3	1	4	4	3	4	4	3	1	2
61936	1	1	1	3	3	3	3	4	4	1	1
61939	1	1	1	4	4	3	4	4	4	1	1
73899	1	1	1	4	4	3	4	4	3	1	1
73901	1	1	1	4	4	3	4	3	3	1	2
74708	1	1	1	4	4	4	4	4	3	1	1
78810	1	1	1	4	4	3	4	3	3	1	1
78812	1	1	1	4	4	3	4	4	3	1	1
79976	1	1	1			4	4	4	4	1	1
79978	1	1	1	4	4	4	4	4	3	1	1
79992	1	1	1	4	4	3	4	4	4	1	1
80005	1	1	1	3	3	3	3	4	4	1	1
88591	1	1	1	4	4	4	4	3	3	1	1
88593	1	1	1			3	3	4	4	1	1
88594	1	1	1	4	3	3	3	4	4	1	1
94818	1	1				3	3	4	4	1	1
94820	1	1	1	4	3	3	4	4	4	1	1
102494	1	1	1			4	4	4	3	1	1
112632	1	1	1	4	4	4	4	4	3	1	1
112634	1	1	1			4	4	3	3	1	1
112635	1	1	1	4	4	3	4	4	3	1	1
112636	1	1	1			3	4	4	3	1	1
112637	1	1	1	4	4	3	3	4	4	1	1
112638	1	1	1	3	3	3	3	4	4	1	1
112639	1	1	1	4	4	4	4	3	3	1	1
112641	3	3	1	3	3	3	3	4	4	1	1
112642	1	1	1	4	4	3	4	4	4	1	1
112646	1	1		3	3	3	3	4	3	1	1
112647	1	1	1	4	4	4	4	3	3	1	1
112648	1	1		4	4	3	4	4	3	1	1
112649	1	1	1	4	3	3	3	4	3	1	1
112652	1	1		4	4	3	4	4		1	1
112653	1	1	1	4	3	3	3	4	4	1	1
112654	1	1	1	3	3	3	4	4	3	1	1
112655	1	1	1	4	4	4	4	4	3	1	1
112658	1	1	1	4	4	3	4	4	3	1	1
112660	1			4	3	4	4	4	4	1	1
113642	1					3	3	4	4	1	1
113647	1	1	1	4	3	3	4	4	3	1	1
114348	1	1	1	4	4	3	3	4	4	1	1
114352	1	1	1			3	4			1	1
114356	3	3	1	4	4	4	4	4	3	1	1
114564	1	1	1	4	3	3	3	4	4	1	1
114565	1	1	1	4	3	3	4	4	3	1	1

ID	ODC1_458_B	ODC1_907_A	ODC1_907_B	PGK1_115_A	PGK1_115_B	PGK1_452_A	PGK1_452_B	PGK1_504_A	PGK1_504_B	PGK1_652_A	PGK1_652_B
114805	1	1	1	4	4	4	4	4	4	1	1
114806	1	1	1	4	3	3	4	4	3	1	1
114808	1	1	1	4	4	3	4	4	4	1	1
114809	3	3	1	4	4	4	4	4	3	1	1
114813	1	1	1	4	4	4	4	4	3	1	1
114815	1	1	1	4	4	3	4	4	4	1	1
114816	1	1	1	4	3	3	4	4	4	1	1
114817	1	1	1	4	3	3	3	4	4	1	1
114818	1	1	1	4	3	3	4	4	3	1	1
114819	1	1	1		4	4	4	4	3	1	1
114820	1	1	1	4	4	3	4	4	3	1	1
114821	1	1	1	3	3	3	3	4	4	1	1
114822	1	1	1	4	3	3	3	4	4	1	1
114823	1	1	1	4	3	3		4	3	1	1
123340	1	1	1	3	3	3	3	4	4	1	1
123342	1	1	1	4	4	4	4	3	3	1	1

ID	PGK1_675_A	PGK1_675_B	PGK1_793_A	PGK1_793_B	PGK1_843_A	PGK1_843_B	PGK1_913_A	PGK1_913_B	PGK1_951_A	PGK1_951_B	PIM_549_A
30535	3	4	1	1	4	4	4	3	3	3	4
33813	3	3	1	1	4	4	4	4	3	4	4
33852	3	4	1	3	4	4	4	4	3	4	4
33860	3	4	1	1	4	4	4	4	3	4	4
33863	4	4	1	1		4	4	4	3	3	4
33878	3	3	1	1	4	4	4	3	3	4	4
33879	3	4	1	1	4	4	4	3	3	4	3
33880	3	3	1	1	4	4	4	3	3	3	4
33881	3	3	1	3	4	4	4		3	4	3
33882	3	3	1	1	4	4	4	3	3	4	4
33883	3	3	1	3	4	4	4	3	4	3	3
33940	3	3	1	3	4	4	4	3	3	4	4
33980	3	3	1	1	4	4	4	3	3	4	4
33982	3	3	1	1	3	4	3	3	3	3	4
33983	3	4	1	1	3	4	3	4	3	4	4
33984			1	1	4	4	4	3	3	3	
33985	3	3	1	1	3	4	4	3	3	4	
33990	3	4	1	1	4	4	4	4	3	3	4
33992	3	3	1	3	4	4	4	4	4	4	
45934	3	4	1	1	3	4		3	3	3	4
51015	3	4	1	1	3	4	4	4	4	4	3
51025	3	3	1	1	3	4	3	3	3	3	4
51026	3	4	1	1	3	4	4	3	3	3	4
51028	4	4	1	1	4	4	4	4	3	3	4
51029	3	3	1	1	4	4	4	4	4	4	4
51031	4	4	1	1	4	4	4	4	3	3	4
51032	4	4	1	1	4	4	4	4	3	3	4
51033	3	3	1	1	4	4	4	3	3	4	4
55157	3	3	1	1	4	4	3	3	3	3	3
55160	3	4	1	1	3	4	4	4	3	4	4
55161	3	3	1	3	3	4	3	3	3	4	3
55165	3	3	1	1	3	4	4	4	4	4	4
55175	3	3	1	1	3	4	3	3	3	3	4
55226	3	3	1	3	4	4	4	3	3	4	4
55228	4	4	1	1	3	4	3	4	3	4	4
55229	4	4	1	1	4	4	4	4	3	3	3
55230	3	3	1	1	4	4	4	4	3	4	4
55234	4	4	1	1	4	4	4	4	3	4	3
55238	3	3	1	1	3	4	3	3	3	3	3
55239	3	3	1	1	4	4	3	3	3	3	3
55242	3	3	1	3	4	4	3	3	3	4	4
55243	3	4	1	3	4	4	4	3	3	4	4
55244	4	4	1	1	4	4	4	4	3	3	4
55248	3	4	1	1	3	4	4	4	3	4	4
55254	3	4	1	1	3	4	4	4	3	4	4

ID	PGK1_675_A	PGK1_675_B	PGK1_793_A	PGK1_793_B	PGK1_843_A	PGK1_843_B	PGK1_913_A	PGK1_913_B	PGK1_951_A	PGK1_951_B	PIM_549_A
61916	4	4	1	1	4	4	4	4	3	3	4
61918	3	4	1	1	3	3	4	4	3	4	4
61936	3	3	1	1	3	3	4	4	4	4	3
61939	3	3	1	1	4	4	3	3	3	3	4
73899	3	3	1	1	4	4	3	3	3	3	4
73901	3	4	1	1	3	3	4	4	3	4	4
74708	4	4	1	1	4	4	4	4	3	3	4
78810	4	4	1	1	3	3	4	4	3	3	4
78812	3	4	1	1	3	3	3	3	3	3	4
79976	3	4	1	1	3	3	3	3	3	3	
79978	3	4	1	1	4	4	3	3	3	3	4
79992	3	3	1	3	4	4	3	3	3	4	4
80005	3	3			3	3	4	4	4	4	4
88591	4	4	1	1	3	3	4	4	3	3	4
88593	3	3	3	3	4	4	4	4	3	4	4
88594	3	3	1	1	4	4	3	3	4	4	4
94818	3	3	1	1	3	3	3	3	3	3	
94820	3	3	3	3	3	3	3	3	3	3	4
102494	3	3	1	1	4	4			3	3	4
112632	3	4	1	1			3	3	3	3	4
112634	4	4	1	1	4	4	4	4	3	3	4
112635	3	4	1	1	4	4	3	3	3	3	4
112636	3	4	1	1	3	3	4	4	3	3	4
112637	3	3	1	3	4	4	3	3	3	4	4
112638	3	3	3	3	4	4	3	3	4	4	4
112639	4	4	1	1	4	4	4	4	3	3	4
112641	3	3	1	3	3	3	4	4	4	4	
112642	3	4	1	1			3	3	3	3	4
112646	3	3			3	3	4	4	3	4	4
112647	4	4	1	1	3	3	4	4	3	3	4
112648	3	4	1	1	4	4	3	3	3	3	4
112649	3	3	3	3	4	4	3	3	3	3	4
112652	3	4	1	1	4	4	4	4	4		4
112653	3	3	1	1	3	3	4	4	3	4	4
112654	3	3	1	1	4	4	4	4	3	4	4
112655	3	4	1	1	3	3	4	4	3	3	4
112658	3	4	1	1	4	4	3	3	3	3	4
112660	3	3	3	3	4	4			3	4	
113642	3	3	1	1	4	4	3	3	3	3	4
113647	3	4	1	1	3	3	4	4	3	4	4
114348	3	3	1	1	4	4	3	3	3	3	4
114352	3	4	1	3	4	4	4	4	3	4	4
114356	3	3	1	1	4	4	3	3	3	3	4
114564	3	3			4	4	3	3	3	4	4
114565	3	4	1	3	4	4	4	4	3	4	4

ID	PGK1_675_A	PGK1_675_B	PGK1_793_A	PGK1_793_B	PGK1_843_A	PGK1_843_B	PGK1_913_A	PGK1_913_B	PGK1_951_A	PGK1_951_B	PIM_549_A
114805	3	3	1	4	4	3	3	3	3	3	4
114806	3	4	1	4	4	4	3	3	3	4	4
114808	3	3	1	3	4	3	3	3	3	3	4
114809	3	4	1	4	4	3	3	3	3	3	4
114813	3	4	1	3	4	4	3	3	3	3	4
114815	3	3	1	4	4	4	3	3	3	4	3
114816	3	3	1	3	4	3	3	3	3	4	4
114817	3	3	1	4	4	4	3	3	4	4	
114818	3	3	3	4	4	3	3	3	3	3	4
114819	3	4	1	4	4	4	3	3	3	3	4
114820	3	4	1	3	4	3	3	3	3	3	4
114821	3	3	1	4	4	4	4	4	4	4	4
114822	3	3		4	4	3	4	3	3	4	4
114823	3	4	1	3	4	4	4	4	3	3	4
123340	3	3	3			4	4	3	4	4	4
123342	4	4	1	4	4	4	4	4	3	3	4

ID	PIM_549_B	PIM_795_A	PIM_795_B	PIT1_210_A	PIT1_210_B	PIT1_376_A	PIT1_376_B	PKM_315_A	PKM_315_B	PKM_889_A	PKM_889_B	PLP_841_A
30535	4	1	2	1	1	2	2	3	3	3	3	2
33813	4	1	1	2	1	2	2	3	3	3	1	1
33852	4	1	1	1	1	2	2	4	3			
33860	3			2	1	2	2	3	3	3	3	1
33863	4	2	2	1	1	2	2	3				1
33878	4			2	1	2	2	3	3	3	3	1
33879	3	1	1	2	1	2	2	3	3	3	1	1
33880	4			1	1	2	2	3	3	3	3	1
33881	4	1	2	2	1	2	2	3	3	3	3	1
33882	3			2	1	2	2	3	3	3	3	1
33883	4			1	1	2	2	3	3	3	3	1
33940	4			2	1	2	2	3	3	3	1	1
33980	4			1	1	2	2	4	3	3	3	
33982	4	1	1	1	1	2	2	3	3	3	1	1
33983	3			2	1	2	1	4	3	3	3	1
33984				1	1	2	2	4	3	3	1	
33985				2	1	2	1	4	4	3	3	2
33990	4			1	1	2	2	3	3	3	3	1
33992				1	1	2	2	3	3	3	1	
45934	4	1	2	2	2	2	2	4	3	3	1	1
51015	3			2	1	2	2	4	3	3	3	1
51025	4	1	1	1	1	2	2	3	3	3	1	1
51026	3	1	1	2	1	2	2	3	3	3	3	1
51028	4	1	2	1	1	2	2	4	4	3	3	1
51029	4			1	1	2	2	3	3	3	1	1
51031	3	1	1	2	1	2	2	4	3	3	1	1
51032	4	1	2	2	1	2	2	3	3	3	1	1
51033	4	1	1	2	1	2	2	3	3	3	1	1
55157	4	1	2	2	1	2	2	3	3	3	1	1
55160	4	1	1	1	1	2	2	3	3	3	1	1
55161	3	2	2	2	1	2	2	3	3	3	3	1
55165	4	1	2	2	1	2	2	3	3	3	3	1
55175	3	1	2	2	1	2	1	3	3	3	3	1
55226	4	1	2	2	1	2	1	3	3	3	3	1
55228	3	1	2	1	1	2	1	3	3	1	1	1
55229	3	1	1	2	1	2	2	3	3	3	3	1
55230	3	1	1	1	1	2	2	3	3	3	3	1
55234	3	1	2	2	1	2	2	4	4	3	1	1
55238	3	1	2	2	1	2	2	3	3	3	3	1
55239	4	1	1	1	1	2	2	3	3	3	1	1
55242	4	1	1	1	1	2	2	3	3	3	1	1
55243	3	1	1	1	1	2	2	3	3	3	3	1
55244	3	2	2	1	1	2	2	3	3	3	3	1
55248	4	1	2	2	1	2	1	3	3	3	1	
55254	4	1	2	2	1	2	2	3	3	3	3	1

ID	PIM_549_B	PIM_795_A	PIM_795_B	PIT1_210_A	PIT1_210_B	PIT1_376_A	PIT1_376_B	PKM_315_A	PKM_315_B	PKM_889_A	PKM_889_B	PLP_841_A
61916	4	1	2	1	1	2	2	4	3	3	3	1
61918	4	1	2	1	1	2	2	3	3	1	1	1
61936	3	1	1	1	1	2	2	3	3	3	3	1
61939	4			2	2	2	2	4	3	3	3	1
73899	4	1	1	2	1	2	1	3	3	3	1	1
73901	4	1	2	2	2	2	1	3	3	1	1	1
74708	4	1	1	1	1	2	2	4	3	3	3	2
78810	4	1	1	1	1	2	2	4	3	3	3	1
78812	4	2	2	1	1	2	2	4	3	3	3	1
79976				1	1			3	3	1	1	1
79978	4			2	2	2	2	3	3	3	3	1
79992	3	1	1	2	1	2	2	3	3	1	1	1
80005	4			2	1	2	2	3	3	3	3	1
88591	3	1	1	2	1	2	2	3	3	1	1	1
88593	4		1	2	1	1	1	3	3	3	1	1
88594	4	1	2	1	2	2	2	3	3	3	1	2
94818				2	2	1	1	3	3	1	3	2
94820	3	1	1	1	1	2	2	4	3	3	3	1
102494	3	1	1	2	1	2	1	3	3	3	3	
112632	4	1	1	1	1	2	2	3	3	3	1	1
112634	3	1	2	1	1	2	2	3	3	3	3	2
112635	4	1	1	1	1	2	2	3	3	3	3	2
112636	3			1	1	2	2	3	3	3	1	1
112637	3	1	1	1	1	2	2	4	3	3	1	2
112638	4	1	1	2	1	2	1	3	3	3	1	
112639	4	1	2	2	1	2	2	3	3	3	1	1
112641		1	1	1	1	2	2	3	3	3	1	1
112642	4	1	2	2	2	2	1	4	3	3	1	2
112646	4			2	1	2	2	3	3	3	3	1
112647	4	2	2	1	1	2	2	4	4	3	3	1
112648	4	1	1	2	1	2	1	4	3	3	3	1
112649	4	1	1	1	1	2	2	4	3	3	3	1
112652	4	1	1	1	1	2	2	4	3	3	1	1
112653	4	1	1	2	2	2	2	3	3	3	1	1
112654	3	1	2	2	1	2	2	4	3	3	1	1
112655	3	1	2	1	1	2	2	4	3	3	3	1
112658	4	1	2	1	1	2	2	3	3	3	1	1
112660				2	1	2	2		3	3	3	
113642	3	1	1	1	1			3		3	3	1
113647	3	1	1	2	2	2	2	3	3	3	3	1
114348	4	1	1	1	1	2	2	3	3	3	3	1
114352	4	1	2	2	1	2	2	4	3	3	3	1
114356	4	1		1	2	2	2	3	3	3	3	1
114564	4			1	1	2	2	3	3	3	3	1
114565	4	1		2	1	2	2	3	3	3	3	1

ID	PIM_549_B	PIM_795_A	PIM_795_B	PIT1_210_A	PIT1_210_B	PIT1_376_A	PIT1_376_B	PKM_315_A	PKM_315_B	PKM_889_A	PKM_889_B	PLP_841_A
114805	3	1	1	1	1	2	2	3	3	3	3	1
114806	3	1	2	2	2	2	1	3	3	1	1	1
114808	3	1	2	1	1	2	2	4	3	3	1	1
114809	4	1	2	2	2	2	2	3	3	3	3	1
114813	4	1	1	2	2	2	1	4	3	3	3	1
114815	3			1	1	2	2	3	3	3	1	1
114816	3	1	1	1	1	2	2	4	3	3	1	1
114817		1	1	1	1	2	2	4	3	3	3	1
114818	4	1	2	1	1	2	2	3	3	3	3	1
114819	3	1	1	1	1	2	2	3	3	3	3	1
114820	4	2	2	2	1	2	2	3	3	3	1	1
114821	4	1	1	1	1	2	2	3	3	3	1	2
114822	4	1	1	2	1	2	2	3	3	3	1	1
114823	3			1	1	2	2		3	3		1
123340	4	1	2	1	1	2	2	3	3	3	1	2
123342	4	1	1	1	1	2	2	3	3	3	1	1

ID	PLP_841_B	PND_287_A	PND_287_B	PND_638_A	PND_638_B	PND_864_A	PND_864_B	RYR2_339_A	RYR2_339_B	RYR2_472_A	RYR2_472_B
30535	2	3	4	4	3	3	3			4	4
33813	2	3	4	4	4	3	3			4	4
33852	1	3	4	4	4	3	4	4	1	4	4
33860	1	4	4	4	4	3	3	1	1	4	4
33863	2	4	4	4	4	3		4	1	4	
33878	1					3	3			4	4
33879	1	4	4	4	4	3	3	4	1	4	3
33880	1					3	3	4	1	4	4
33881	1	4	4	4	4	3	3	4	1	4	3
33882	1	3	4		4	3	4	4	4	4	4
33883	1					3	3			4	4
33940	1			4	4	3	3			4	4
33980		3	4	4	4	3	4	4	4	4	4
33982	1	4	4	4	4	3	3	4	1	4	4
33983	1	4	4	4	4	3	3	4	4	4	3
33984		4	4	4		3	3	4	4	4	4
33985	2	4	4	4	4	3	3			3	3
33990	1							1	1	4	4
33992						3	3			4	3
45934	1	4	4	4	4	3	4	1	1	4	4
51015	1	4	4	4	4	3	3	4	1	4	3
51025	1	4	4	4	4	3	3	4	1	4	4
51026	2	3	4	4	4	3	3	4	4	4	3
51028	1	4	4	4	4	3	3	4	1	4	3
51029	1	4	4	4	4	3	3	1	1	4	4
51031	2	3	4	4	3	3	3	4	1	4	4
51032	2	3	3	4	4	3	4	1	1	4	4
51033	1	3	4	4	4	3	3	1	1	4	4
55157	1	3	4	4	4	3	3	1	1	4	4
55160	2	3	4	4	4	3	3	4	4	4	4
55161	1	4	4	4	4	3	3	4	1	4	4
55165	1	3	4	4	4	3	3	1	1	4	4
55175	1	4	4	4	4	3	3	4	1	4	3
55226	1	4	4	4	4	3	3	1	1	4	4
55228	1	4	4	4	4	3	3	4	1	4	4
55229	1	4	4	4	4	3	3	4	1	4	3
55230	1	4	4	4	4	3	3	4	4	4	3
55234	1	4	4	4	4	3	3	4	1	4	4
55238	1	4	4	4	4	3	3	1	1	4	4
55239	1	3	4	4	4	3	3	1	1	4	4
55242	1	3	4	4	4	3	3	4	4	4	4
55243	2	4	4	4	4	3	3	4	1	4	4
55244		3	3	4	4	3	3			4	3
55248	1	3	3	4	4	3	3	1	1	4	4
55254	2	4	4	4	4	3	3	4	1	4	3

ID	PLP_841_B	PND_287_A	PND_287_B	PND_638_A	PND_638_B	PND_864_A	PND_864_B	RYR2_339_A	RYR2_339_B	RYR2_472_A	RYR2_472_B
61916	1	4	4	4	4	3	3	4	1	4	4
61918	1	3	4	4	4	3	4	4	1	4	4
61936	2	4	4	4	4	3	3	4	1	4	4
61939	1	4	4	4	4	3	3			4	4
73899	1	3	3	4	4	3	4	4	4	4	4
73901	1	4	4	4	4	3	3	4	1	4	3
74708	2	3	4	4	4	3	3	1	1	4	4
78810	1	3	4	4	3	3	3	4	1	4	3
78812	1	3	4	4	4	3	4	4	1	4	3
79976	2	4	4	4	4	3	3			4	3
79978	1	4	4	4	4	3	3	1	1	4	4
79992	1	4	4	4	4	3	3	1	1	4	4
80005	2	3	4	4	4	3	4	4	1	4	3
88591	1	4	4	4	4	3	3	4	4	4	3
88593				4	4	3	3	4	4	4	4
88594	2	3	4	4	3	3	3	1	1	4	4
94818	2	3	4	4	4	3	4	1	1	4	4
94820	1	4	4	4	4	3	3	4	1	4	4
102494		4	4	4		3	3				
112632	1	3	3	4	4	3	4	1	1	4	4
112634	2	4	4	4	4	3	3	4	1	4	4
112635	2	3	4	4	4	3	3	4	1	4	4
112636	2	4	4	4	4	3	3	4	1	4	4
112637	2	4	4	4	4	3	3	4	1	4	4
112638		4	4	4	4	3	3	4	4	4	4
112639	1	3	4	4	4	3	3	4	4	4	3
112641	1	4	4	4	4	3	3			4	4
112642	2	4	4	4	4	3	3	1	1	4	4
112646	2	4	4	4	4	3	3	4	1	3	3
112647	2	4	4	4	4	3	3	4	1	4	3
112648	1	4	4	4	4	3	3			4	4
112649	1	4	4	4	4	3	3	4	1	4	
112652	1	3	4	4	4	3	3	4	1		
112653	1	3	4	4	4	3	4	1	1	4	4
112654	1	3	4	4	4	3	3			4	4
112655	1	4	4	4	4	3	3	1	1	4	4
112658	1	3	4	4	4	3	3	1	1	4	4
112660		3	4	4	3	3	3				
113642	1	3	4	4	4	3	4	4	1	4	4
113647	2	3	4	4	4	3	3	1	1	4	4
114348	1	4	4	4	4	3	3	4	1	4	4
114352	1	3	3	4	4	3	3	4	4		
114356	1	4	4	4	4	3	3	1	1	4	4
114564	1	3	4	4	4	3	3			4	3
114565	1	4	4	4	4	3	3	4	1	4	4

ID	PLP_841_B	PND_287_A	PND_287_B	PND_638_A	PND_638_B	PND_864_A	PND_864_B	RYR2_339_B	RYR2_339_A	RYR2_339_B	RYR2_472_A	RYR2_472_B
114805	1	3	4	4	4	3	4	1	1		4	4
114806	2	3	4	4	4	3	4	4	1		4	3
114808	1	3	4	4	4	3	4				4	4
114809	1	3	4	4	4	3	3	1	1		4	4
114813	1	3	4	4	4	3	3	4	1		4	3
114815	1	4	4	4	4	3	3				4	4
114816	2	4	4	4	4	3	3	4	1		4	3
114817	1					3	4	4	1		4	4
114818	1	3	4	4	4	3	3	1	1		4	4
114819	1	4	4	4	4	3	3	4	1		4	3
114820	1	3	3	4	4	3	4				4	4
114821	2	4	4	4	4	3	3				4	3
114822	2	4	4	4	4	3	3	4	1		4	4
114823	2	4	4			3	3				4	4
123340	2	4	4	4	4	3	3	4	1		4	3
123342	1	3	4	4	4	3	3	1	1		4	4

ID	RYR2_474_A	RYR2_474_B	RYR2_837_A	RYR2_837_B	RYR2_844_A	RYR2_844_B	SST_411_A	SST_411_B	SPTBN1_80_A	SPTBN1_80_B	SST_318_A
30535	3	1	3	1	1	1	2	2	1	1	2
33813	1	1	1	1	1	1			1	1	1
33852	3	1	3	1	1	1	2	2		1	1
33860	1	1	1	1	1	2		1	1		1
33863			3	1	1	1	2	1			1
33878	3	1	3	1	1	1	2	2		1	1
33879	3	1	3	1	1	1	1	1	1	1	1
33880	3	1	3	1	1	1	2	2			1
33881	3	1	1	1	1	1	2	2			1
33882	3	1	3	1	1	1	2	2			2
33883	3	1	1	1	1	1			1	1	1
33940	1	1	1	1	1	1	2	2	1	1	1
33980	3	1	3	1	1	2	2	1		1	2
33982	3	1	3	1	1	1	2	2	1	1	1
33983	3	3			1	1	1		1		
33984	3		3	3	1	1	1	1	1		1
33985	3	3	3	3	1	1	1	1	1		
33990	1	1	1		1	1			1	1	1
33992	3	1			1	1	2	2	1	1	1
45934	1	1	1	1	1	1	2	1	1	1	1
51015	3	1	3	1	1	1	2	1	1	1	1
51025	3	1	3	1	1	1	2	2	1	1	2
51026	3	3	3	3	1	1	2	2	1	1	1
51028	3	1	3	1	1	1	2	1	1	1	1
51029	1	1	1	1	1	1	2	2	2	1	1
51031	3	1	3	1	1	1	2	2	2	1	1
51032	1	1	1	1	1	1	2	2	2	1	1
51033	1	1	1	1	1	1	2	1		1	1
55157	1	1	3	1	1	1	2	1		1	1
55160	3	1	3	1	1	1	2	1	1	1	1
55161	3	1	3	1	1	1	2	2	1	1	1
55165	1	1	1	1	1	1	2	1	2	1	1
55175	3	1	3	1	1	1	2	2	2	1	1
55226	1	1	1	1	1	1	2	1	1	1	1
55228	3	1	3	1	1	1	2	2	1	1	1
55229	3	1	3	1	1	1	2	2	1	1	1
55230	3	3	3	3	1	1	2	2	1	1	1
55234	1	1	1	1	1	1	1	1		1	1
55238	1	1	1	1	1	1	2	1	1	1	1
55239	1	1	1	1	2	2	2	1	1	1	2
55242	3	1	3	1	1	1	2	1	1	1	1
55243	3	1	3	1	1	1	2	1	1	1	1
55244	3	1	3	1	1	1	2	2	1	1	1
55248	1	1	1	1	1	1	2	2	1	1	1
55254	3	1	3	1	1	1	2	2	1	1	1

ID	RYR2_474_A	RYR2_474_B	RYR2_837_A	RYR2_837_B	RYR2_844_A	RYR2_844_B	SST_411_A	SST_411_A	SST_411_B	SPTBN1_80_A	SPTBN1_80_B	SST_318_A
61916	3	1	3	1	1	1	2	1	1	1	1	1
61918	3	1	3	1	1	1	2	2	1	1	1	1
61936	3	1	3	1	1	1	2	2	1	1	1	1
61939	1	1	1	1	1	1	2	2	1	1	1	1
73899	3	3	3	3	1	1	2	2	2	1	1	2
73901	3	1	3	1	1	1	2	2	1	1	1	1
74708	1	1	1	1	1	1	2	2	1	1	1	1
78810	3	1	3	1	1	2	2	2	1	1	1	1
78812	3	1	3	1	1	1	2	2	1	1	1	1
79976	3	1	3	1	1	2	1	1	1	1	1	1
79978	1	1	1	1	1	2	2	2	2	2	1	1
79992	1	1	1	1	1	1	2	1	1	1	1	1
80005	3	1	3	1	1	1	2	2	2	1	1	1
88591	3	3	3	3	1	1	2	2	2	1	1	1
88593	3	3	3	3	1	1						
88594	1	1	1	1	1	1						1
94818	1	1					2	2	2	1		1
94820	3	1	3	1	2	2	1	1	1	1	1	1
102494			3	3	1	1	2	2	1	1		1
112632	1	1	1	1	1	2	2	2	1	1	1	1
112634	3	1	3	1	1	1	2	2	1	1	1	1
112635	3	1	3	1	1	1	2	2	1	1	1	1
112636	3	1			1	1	2	1	1	1		1
112637	3	1	3	1	1	2	2	2	1	1	1	1
112638	3	3	3	3	1	1	2	2	1	1	1	1
112639	3	1	3	1	1	1	2	2	1	1	1	1
112641	1	1	3	3	1	2	2	2	1	1	1	1
112642	1	1			1	1	2	2	1	1		1
112646	3	1	3	1	1	1	2	2	1	1	1	1
112647	3	1	3	1	1	1	2	2	1	1	1	1
112648	1	1	1	1	1	1	2	2	1	1	1	1
112649	3	1	3	1	1	1	2	2	2	1		2
112652			3	3	1	2	2	2	1	1		1
112653	1	1	1	1	1	1	2	2	1	1	1	1
112654	1	1	1	1	1	1	1	1	1	1	1	1
112655	1	1	1	1	1	2	1	1	2	1	1	1
112658	1	1	1	1	1	1	2	2	1	1		1
112660					1	1	2	2	1	1		1
113642	3	1	3	1	1	1	2	2	1	1	1	
113647	1	1	1	1	1	1	2	2	1	1	1	1
114348	3	1	3	1	1	1	2	1	1	1	1	1
114352			3	3	1	1	1	1	1	1		2
114356	1	1	1	1	1	2	2	1	1	2	1	1
114564	3	1	3	1	1	1	2	2	2	1	1	1
114565	3	1	3	1	1	1	2	1	1	1	1	1

ID	RYR2_474_A	RYR2_474_B	RYR2_837_A	RYR2_837_B	RYR2_844_A	RYR2_844_B	SST_411_A	SST_411_B	SPTBN1_80_A	SPTBN1_80_B	SST_318_A
114805	1	1		1	1	2	2	2	1	1	1
114806	3	1	3	1	1	1	2	2	1	1	1
114808	1	1	1	1	1	1	2	2	1	1	1
114809	1	1	1	1	1	1	2	2	1	1	1
114813	3	1	3	1	1	1	2	2	1	1	1
114815	1	1	1	1	1	1	2	2	1	1	1
114816	3	1	3	1	1	2	2	2	1		1
114817	3	1	3	1	1	1	2	2			1
114818	1	1	1	1	1	1	1	1	1	1	1
114819	3	1	3	1	1	1	2	1	1	1	1
114820	1	1	1	1	1	1	2	1	1	1	1
114821	3	1	3	1	1	1	2	1	1	1	1
114822	3	1	3	1	1	2	1	1			
114823	1	1	1	1	1	1	2	2	1		
123340	3	1	3	1	1	1	2	1	2	1	1
123342	1	1	1	1	1	2	2	1	1	1	1

ID	SST_318_B	TCRA1_422_A	TCRA1_422_B	TCRB_446_A	TCRB_446_B	TCRB_530_A	TCRB_530_B	TCRB_551_A	TCRB_551_B	TCRB_90_A
30535	2	2	2	1	1	1	1	2	2	
33813	1	2	2	1	1	1	1	2	2	1
33852	1	2	2	1	2	1	3	2	2	2
33860	2	4	4	1	2	1	3	2	2	2
33863	1	2	2	1	1	1	1	2	2	
33878	2	2	2	1	1	1	3	2	2	2
33879	1	2	4	1	1	1	1	2	2	1
33880	2	2	2	1	2	1	1	2	2	2
33881	2	2	4	1	2	1	1	2	2	2
33882	2	2	2	1	2	1	3	2	2	2
33883	1	2	4	1	1	1	3	2	2	1
33940	1	2	4	1	2	1	1	2	2	2
33980	2	2	4	1	1	1	1	2	2	2
33982	2	2	4	1	2	1	3	2	2	2
33983	2	2	2	1	2	1	3	2	2	2
33984		2	2	1	1	1		2	2	2
33985	1	2	4	1	1	1	1	2	2	2
33990	1	4	4	1	2	1	3	2	2	2
33992	2			1	1	1	1	2	2	2
45934	1	2	2	1	2	1	3	2	2	2
51015	1	2	4	1	2	1	1	2	2	2
51025	2	2	4	1	2	1	3	2	2	2
51026	1	2	2	1	1	1	3	2	2	2
51028	2	2	2	1	1	1	3	2	2	2
51029	1	4	4	1	1	1	3	2	2	2
51031	2	2	4	1	1	1	1	2	2	2
51032	1	2	2	1	2	1	3	2	2	2
51033	2	2	2	1	1	1	3	2	2	1
55157	1	2	4	1	1	1	1	2	2	2
55160	1	2	2	1	1	1	1	2	2	1
55161	1	2	2	1	1	1	1	2	2	1
55165	1	2	4	1	2	1	3	2	2	2
55175	1	2	2	1	1	1	1	2	2	1
55226	1	2	4	1	1	1	1	2	2	1
55228	2	2	2	1	1	1		2	2	2
55229	2	2	2	1	1	1	1	2	2	2
55230	2	2	2	1	1	1	1	2	2	2
55234	1	2	4	1	1	1	1	2	2	1
55238	2	2	4	1	2	1	3	2	2	2
55239	2	2	4	1	2	1	1	2	2	2
55242	1	2	2	1	1	1		2	2	1
55243	2	2	2	1	1	1	3	2	2	1
55244	1	2	4	1	2	1	1	2	2	1
55248	1	2	2	1	2	1	1	2	2	1
55254	1	2	4	1	1	1	1	2	2	1

ID	SST_318_B	TCRA1_422_A	TCRA1_422_B	TCRB_446_A	TCRB_446_B	TCRB_530_A	TCRB_530_B	TCRB_551_A	TCRB_551_B	TCRB_90_A
61916	1	2	2	1	2	1	3	2	2	2
61918	1	2	4	1	2	1	3	2	2	1
61936	2	2	4	1	1	1	1	2	2	2
61939	1	4	4	1	1	1	1	2	2	2
73899	1	4	4	1	2	1	1	2	2	2
73901	2	2	4	1	1	1	3	2	2	2
74708	1	2	2	1	2	1	3	2	2	2
78810	1	2	4	1	1	1	1	2	2	2
78812	1	4	4	1	2	1	1	2	2	2
79976	1	4	4	1	1	1	1	2	2	2
79978	1	2	4	1	1	1	1	2	2	1
79992	2	2	2	1	1	1	1	2	2	2
80005	2	2	2	1	1	1	1	2	2	2
88591	2	2	2	1	1	1	1	2	2	1
88593	2	2		1	2	1	3	2	2	2
88594	1	2	2	1	1	1	1	2	2	1
94818		2	2	1	1	1	1	2	2	1
94820	1	2	4	1	2	1	3	2	2	2
102494	2	2	2	1	1	1	1	2	2	2
112632	1	2	4	1	2	1	3	2	2	2
112634	2	2	2	1	1	1	3	2	2	1
112635	2	2	2	1	1	1	3	2	2	2
112636	1	2	2	1	1	1	1	2	2	2
112637	1	2	2	1	1	1	1	2	2	1
112638	1	2	2	1	1	1	3	2	2	2
112639	2	2	2	1	1	1	3	2	2	2
112641	2	2	2	1	1	1	1	2	2	1
112642	1	2	2	1	1	1	3	2	2	1
112646	2	2	2	1	1	1	3	2	2	2
112647	1	2	2	1	1	1	1	2	2	2
112648	1	2	4	1	1	1	1	2	2	1
112649	2	2	2	1	1	1	1	2	2	2
112652	1	2	2	1	1	1	3	2	2	2
112653	2	2	2	1	1	1	1	2	2	1
112654	1	2	2	1	1	1	1	2	2	2
112655	1	2	2	1	1	1	3	2	2	2
112658	2	2	2	1	1	1	1	2	2	2
112660	1	2	4	2	1	1	3	2	2	2
113642		2	4	1	1	1	3	2	2	1
113647	2	2	2	1	1	1	1	2	2	2
114348	1	2	4	1	1	1	3	2	2	2
114352	2	2	2	1	2	1	3	2	2	1
114356	1	2	2	1	1	1	3	2	2	2
114564	2	2	4	1	2	1	3	2	2	2
114565	1	2	2	1		1	3	2	2	2

ID	SST_318_B	TCRA1_422_A	TCRA1_422_B	TCRB_446_A	TCRB_446_B	TCRB_530_A	TCRB_530_B	TCRB_551_A	TCRB_551_B	TCRB_90_A
114805	1	2	2	1	2	1	3	2	2	2
114806	1	2	2	1	1	1	1	2	2	2
114808		2	2	1	1	1	1	2	3	1
114809	1	2	2	1	1	1	1	2	2	2
114813	1	2	4	1	1	1	1	2	2	2
114815	1	2	2	1	2	1	3	2	2	1
114816	1	2	4	1	1	1	1	2	2	2
114817	2	2	4	1	1	1	3	2	2	1
114818	1	2	2	1	1	1	3	2	2	2
114819	1	2	4	1	1	1	3	2	2	1
114820	1	4	4	1	1	1	1	2	2	1
114821	1	2	4	1	1	1	1	2	3	1
114822	1	2	2	1	1	1	1	2	3	1
114823		2	4	1	1	1	1	2	2	1
123340	1	4	4	1	1	1	1	2	2	2
123342	1	2	2	1	2	1	3	2	2	2

ID	TCRB_90_B	TOP1_404_A	TOP1_404_B	TOP1_442_A	TOP1_442_B	TOP1_839_A	TOP1_839_B	TPI1_613_A	TPI1_613_B	TPI1_678_A	TPI1_678_B
30535		1	1		4	1	1	4	4	1	1
33813	2	1	2	1	4	1	2	4	3	1	4
33852	2		2	1	4	1	2	4	4	1	1
33860		1	2	1	4	1	2	4	3	1	1
33863		1	2	1	4	1	2	4	3	1	4
33878	2	1	1	4	4	1	1	4	4	1	4
33879	2	1	1	4	4	1	1	4	3	1	4
33880	2	1	1	4	4	1	1	4	4	1	1
33881	2	1	2	1	4	1	2	4	4	1	1
33882	2	1	1			1	1	4	4	1	1
33883	2	1	1	4	4	1	1	4	1	1	4
33940	2	1	1	1	4	1	2	4	4	1	1
33980	2	1	1	4	4	1	1	4	4	1	4
33982	2	1	2	1	4	1	2	4	3	1	1
33983	2	1	1	4	4	1	1	4	4	1	4
33984	2	1	2	1	4	1	2	4	4	1	4
33985	2	1	1	4	4	1	1	4	4	1	4
33990	2	1	1	4	4	1	1	4	4	1	4
33992	2	1	1	4	4	1	1		4	1	4
45934	2	1	2	1	4	1	2	4	3	1	1
51015	2	1	1	4	4	1	1	4	4	1	1
51025	2	1	2	1	4	1	2	4	3	1	1
51026	2	1	1	4	4	1	1	4	4	1	1
51028	2	2	2	1	4	1	2	4	3	1	1
51029	2	2	2	1	1	2	2	4	4	1	1
51031	2	1	1	4	4	1	1	4	4	1	1
51032	2	1	2	1	4	1	2	4	3	1	1
51033	2	1	1	4	4	1	1	4	4	1	1
55157	1	1	2	1	4	1	2	4	3	1	1
55160	2	2	2	1	4	2	2	4	3	1	1
55161	1	1	1	4	4	1	1	4	3	1	1
55165	2	1	1	4	4	1	1	4	4	1	1
55175	1	1	1	4	4	1	1	4	4	1	1
55226	2	1	1	4	4	1	1	4	4	1	1
55228	2	1	1	4	4	1	1	4	4	1	1
55229	2	1	2	1	4	1	2	4	3	1	1
55230	2	1	2	1	4	1	2	4	3	1	1
55234	2	2	2	1	1	2	2	4	4	1	1
55238	2	1	2	1	4	1	2	4	4	1	1
55239	2	1	2	1	4	1	2	4	4	1	1
55242	1	1	1	4	4	1	1	4	3	1	1
55243	2	1	1	4	4	1	1	3	3	1	1
55244	2	1	1	4	4	1	1	4	4	1	4
55248	2	1	1	4	4	1	1	4	4	1	4
55254	2	1	1	4	4	1	1	4	4	1	1

ID	TCRB_90_B	TOP1_404_A	TOP1_404_B	TOP1_442_A	TOP1_442_B	TOP1_839_A	TOP1_839_B	TPI1_613_A	TPI1_613_B	TPI1_678_A	TPI1_678_B
61916	2	1	2	1	4	1	2	4	3	1	1
61918	2	1	2	1	4	1	2	4	3	1	4
61936	2	1	1	4	4	1	1	4	4	1	4
61939	2	1	2	1	4	1	1	4	4	1	4
73899	2	1	2	1	4	1	2	4	3	1	1
73901	2	1	2	4	4	1	2	4	4	1	4
74708	2	1	1	4	4	1	1	4	4	1	4
78810	2	1	1	1	4	1	2	4	4	1	4
78812	2	1	2	1	4	1	1	4	4	1	4
79976	2	1	1	4	4	1	1	4	4	1	4
79978	2	1	1	4	4	1	1	4	3	1	4
79992	2	1	2	1	4	1	2	4	4	1	1
80005	2	1	2	1	4	1	2	4	4	1	1
88591	1	1	2	1	4	1	2	4	4	1	1
88593	2	1		1	4	1	2	4	3	1	4
88594	2	1	2	4	4	1	2	4	3	1	1
94818	2	1	1	4	4	1	1	4	4	1	4
94820	2	1	1	4	4	1	1	4	4	1	1
102494	2	1	1	4	4	1	1	4	3	1	4
112632	2	1	2	4	4	1	2	4	3	1	4
112634	2	1	1	4	4	1	1	4		1	
112635	2	1	1	4	4	1	1	4	4	1	4
112636	2	1	1	4	4	1	1	4	4		
112637	2	1	2	1	4	1	2	4	3	1	4
112638	2	1	2	4	4	1		4	4		
112639	2	1	1	4	4	1	1	4	3	1	1
112641	2	1	1	4	4	1	1	3	3	1	4
112642	2	1	1	4	4	1	1	4	4	1	1
112646	2	1	1	4	4	1	1	4	3	1	1
112647	2	1	1	4	4	1	1	4	4	1	
112648	2	1	1	4	4	1	1	4	4	1	4
112649	2	1	1	4	4	1	1	4	4	1	4
112652	2	1	1	4	4	1	1	4	3	1	
112653	1	1	1	4	4	1	1	4	4	1	1
112654	2	1	2	1	4	1	2	4	3	1	1
112655	2	1	1	4	4	1	1	3	3	1	1
112658	2	1	1	4	4	1	1	4	4	1	4
112660	2	1	1	4	4	1	1	4	4	1	
113642	2	1	2	1	4	1	2	4	4	1	
113647	2	1	1	4	4	1	1	4	4	1	
114348	2	1	2	1	4	1	2	4	4	1	4
114352	2	1	1	4	4	1	1	4	3	1	4
114356	2	1	2	1	4	1	2	3	3	1	1
114564	2	1	1	4	4	1	1	4	4		
114565	2	1	1	4	4	1	1	4	4	1	4

ID	TCRB_90_B	TOP1_404_A	TOP1_404_B	TOP1_442_A	TOP1_442_B	TOP1_839_A	TOP1_839_B	TPI1_613_A	TPI1_613_B	TPI1_678_A	TPI1_678_B
114805	2	1	1	4	4	1	1	4	3	1	1
114806	2	1	2	1	4	1	2	4	3	1	1
114808	1	1	1	4	4	1	1	4	3	1	1
114809	2	1	1	4	4	1	1	3	3	1	4
114813	2	1	2	1	4	1	1	4	4	1	1
114815	2	1	2	1	4	2	2	4	4	1	4
114816	2	1	2	1	4			4	4	1	4
114817	2	2	2	4	4	1	2	3	3		
114818	2	1	1	1	4	1	1	4	4	1	4
114819	2	1	2	4	4	1	2			1	4
114820	1	1	1	4	4	1	1	4	4	1	1
114821	2	1	2	1	4	1	2	4	3	1	4
114822	2	2	2	1	1	2	2	4	4	1	4
114823	1	2	2	1	4	1	2	4	4		
123340	2	1	1	4	4	1	1	4	4	1	1
123342	2	1	2	1	4	1	2	4	3	1	1

Table B.2: Summary metrics for 119 SNP loci included in this study.

Locus	No. genotyped	Prop. genotyped	No. Alleles	Allelic richness	Prop. Unique Alleles	H_E	H_O
ACTC_477	99	0.93	2	0.02	0	0.29	0.34
Actin_560	89	0.84	2	0.022	0	0.07	0.07
ADH2_925	89	0.84	2	0.022	0	0.32	0.36
AMBP_295	99	0.93	2	0.02	0	0.41	0.41
AMBP_547	101	0.95	2	0.02	0	0.29	0.3
AMBP_555	100	0.94	2	0.02	0	0.38	0.43
AMBP_793	106	1	2	0.019	0	0.49	0.48
AMBP_94	101	0.95	2	0.02	0	0.37	0.4
BTN_181	103	0.97	2	0.019	0	0.5	0.4
BTN_822	103	0.97	2	0.019	0	0.06	0.06
CAT_267	93	0.88	2	0.022	0	0.26	0.22
CAT_375	104	0.98	2	0.019	0	0.44	0.41
CAT_86	101	0.95	2	0.02	0	0.24	0.18
CGA_60	90	0.85	2	0.022	0	0.23	0.22
CHRNA1_293	103	0.97	2	0.019	0	0.33	0.33

Table B.2 – continued from previous page

Locus	No. genotyped	Prop. genotyped	No. Alleles	Allelic richness	Prop. Unique Alleles	H_E	H_O
CHRNA1_606	101	0.95	2	0.02	0	0.33	0.32
CHY_427	101	0.95	2	0.02	0	0.2	0.2
CHY_902	90	0.85	2	0.022	0	0.28	0.27
CK_394	92	0.87	2	0.022	0	0.43	0.5
CKMM_239	104	0.98	2	0.019	0	0.3	0.33
CKMM_546	93	0.88	2	0.022	0	0.13	0.12
COL10A1_221	101	0.95	2	0.02	0	0.26	0.29
COL10A1_572	84	0.79	2	0.024	0	0.07	0.05
COL10A1_883	95	0.9	2	0.021	0	0.26	0.26
COL3A1_104	102	0.96	2	0.02	0	0.05	0.03
COL3A1_420	103	0.97	2	0.019	0	0.13	0.12
COL3A1_429	102	0.96	2	0.02	0	0.32	0.29
COL3A1_455	103	0.97	2	0.019	0	0.06	0.04
CYO19_363	104	0.98	2	0.019	0	0.23	0.23
CYO19_593	104	0.98	2	0.019	0	0.49	0.49
CYO19_789	105	0.99	2	0.019	0	0.25	0.21

Table B.2 – continued from previous page

Locus	No. genotyped	Prop. genotyped	No. Alleles	Allelic richness	Prop. Unique Alleles	H_E	H_O
CYP1A1_107	101	0.95	2	0.02	0	0.09	0.1
CYP1A1_480	96	0.91	2	0.021	0	0.34	0.43
DRD2_313	106	1	2	0.019	0	0.37	0.37
DRD2_507	90	0.85	2	0.022	0	0.46	0.39
DRD2_656	101	0.95	2	0.02	0	0.45	0.41
DRD2_92	99	0.93	2	0.02	0	0.26	0.28
ELN_614	83	0.78	2	0.024	0	0.41	0.43
ELN_756	93	0.88	2	0.022	0	0.46	0.46
ESD_537	81	0.76	2	0.025	0	0.36	0.27
FES_623	82	0.77	2	0.024	0	0.49	0.48
Fibrinogen_474	104	0.98	2	0.019	0	0.34	0.31
FSHB_255	97	0.92	2	0.021	0	0.36	0.3
FSHB_815	102	0.96	2	0.02	0	0.42	0.42
GLB_177	105	0.99	2	0.019	0	0.32	0.3
GLUT2_831	100	0.94	2	0.02	0	0.18	0.12
GRP_797	98	0.92	2	0.02	0	0.21	0.21

Table B.2 – continued from previous page

Locus	No. genotyped	Prop. genotyped	No. Alleles	Allelic richness	Prop. Unique Alleles	H_E	H_O
HAT1_701	101	0.95	2	0.02	0	0.29	0.29
HGBA_548	94	0.89	2	0.021	0	0.14	0.15
HGBA_572	88	0.83	2	0.023	0	0.41	0.5
HGBA_588	82	0.77	2	0.024	0	0.43	0.43
HGBA_717	98	0.92	2	0.02	0	0.12	0.11
HGBA_79	83	0.78	2	0.024	0	0.39	0.39
HOXc8_173	97	0.92	2	0.021	0	0.44	0.39
HOXc8_348	106	1	2	0.019	0	0.12	0.1
HOXc8_411	95	0.9	2	0.021	0	0.5	0.44
HOXc8_642	97	0.92	2	0.021	0	0.35	0.29
HOXc8_760	86	0.81	2	0.023	0	0.18	0.2
INT_575	104	0.98	2	0.019	0	0.49	0.5
Lactalbumin_89	94	0.89	2	0.021	0	0.45	0.43
LAPTM4A_446	104	0.98	2	0.019	0	0.42	0.41
LAPTM4A_601	103	0.97	2	0.019	0	0.08	0.08
LAPTM4A_837	104	0.98	2	0.019	0	0.07	0.08

Table B.2 – continued from previous page

Locus	No. genotyped	Prop. genotyped	No. Alleles	Allelic richness	Prop. Unique Alleles	H_E	H_O
LHY_355	101	0.95	2	0.02	0	0.18	0.2
MATR3_219	106	1	2	0.019	0	0.06	0.07
MATR3_840	95	0.9	2	0.021	0	0.25	0.23
MPO_628	95	0.9	2	0.021	0	0.45	0.41
MYH4_124	104	0.98	2	0.019	0	0.33	0.41
MYH4_315	105	0.99	2	0.019	0	0.23	0.26
MYH4_355	104	0.98	2	0.019	0	0.37	0.48
MYH4_424	105	0.99	2	0.019	0	0.17	0.18
MYH4_543	95	0.9	2	0.021	0	0.4	0.55
MYL4_110	94	0.89	2	0.021	0	0.41	0.39
MYL4_394	92	0.87	2	0.022	0	0.3	0.27
MYL4_413	92	0.87	2	0.022	0	0.3	0.25
MYL4_774	105	0.99	2	0.019	0	0.15	0.16
PND_1002	106	1	2	0.019	0	0.14	0.15
PND_1020	105	0.99	2	0.019	0	0.47	0.49
PND_1680	96	0.91	2	0.021	0	0.32	0.31

Table B.2 – continued from previous page

Locus	No. genotyped	Prop. genotyped	No. Alleles	Allelic richness	Prop. Unique Alleles	H_E	H_O
PND_1741	101	0.95	2	0.02	0	0.14	0.15
ODC1_458	106	1	2	0.019	0	0.11	0.11
ODC1_907	100	0.94	2	0.02	0	0.12	0.13
PGK1_115	91	0.86	2	0.022	0	0.4	0.33
PGK1_452	103	0.97	2	0.019	0	0.5	0.43
PGK1_504	102	0.96	2	0.02	0	0.44	0.36
PGK1_652	106	1	2	0.019	0	0.06	0.06
PGK1_675	105	0.99	2	0.019	0	0.45	0.37
PGK1_793	102	0.96	2	0.02	0	0.19	0.18
PGK1_843	102	0.96	2	0.02	0	0.3	0.37
PGK1_913	102	0.96	2	0.02	0	0.43	0.45
PGK1_951	104	0.98	2	0.019	0	0.45	0.42
PIM_549	98	0.92	2	0.02	0	0.34	0.28
PIM_795	79	0.75	2	0.025	0	0.37	0.33
PIT1_210	106	1	2	0.019	0	0.41	0.41
PIT1_376	104	0.98	2	0.019	0	0.13	0.13

Table B.2 – continued from previous page

Locus	No. genotyped	Prop. genotyped	No. Alleles	Allelic richness	Prop. Unique Alleles	H_E	H_O
PKM_315	101	0.95	2	0.02	0	0.27	0.24
PKM_889	102	0.96	2	0.02	0	0.39	0.43
PLP_841	98	0.92	2	0.02	0	0.33	0.19
PND_287	98	0.92	2	0.02	0	0.39	0.38
PND_638	94	0.89	2	0.021	0	0.05	0.05
PND_864	104	0.98	2	0.019	0	0.15	0.16
RYR2_339	85	0.8	2	0.024	0	0.48	0.52
RYR2_472	101	0.95	2	0.02	0	0.25	0.28
RYR2_474	101	0.95	2	0.02	0	0.46	0.53
RYR2_837	100	0.94	2	0.02	0	0.47	0.52
RYR2_844	102	0.96	2	0.02	0	0.16	0.16
SST_411	99	0.93	2	0.02	0	0.38	0.29
SPTBN1_80	91	0.86	2	0.022	0	0.08	0.09
SST_318	100	0.94	2	0.02	0	0.35	0.29
TCRA1_422	104	0.98	2	0.019	0	0.39	0.35
TCRB_446	105	0.99	2	0.019	0	0.25	0.3

Table B.2 – continued from previous page

Locus	No. genotyped	Prop. genotyped	No. Alleles	Allelic richness	Prop. Unique Alleles	H_E	H_O
TCRB_530	103	0.97	2	0.019	0	0.34	0.44
TCRB_551	106	1	2	0.019	0	0.03	0.03
TCRB_90	103	0.97	2	0.019	0	0.35	0.28
TOP1_404	105	0.99	2	0.019	0	0.37	0.35
TOP1_442	103	0.97	2	0.019	0	0.35	0.38
TOP1_839	104	0.98	2	0.019	0	0.36	0.38
TPI1_613	101	0.95	2	0.02	0	0.35	0.34
TPI1_678	94	0.89	2	0.021	0	0.34	0.44

Table B.3: *Sample stratification levels used for statistical analyses in this study.*

Animal ID	mtDNA?	SNP?	mtDNA Haplotype	mtDNA strata	Island Community	Cluster	Social Unit
33852	Y	Y	J	MHI	OAKAMC	W6	
33860	Y	Y	J	MHI	OAKAMC	W6	
33863	N	Y			OAKAMC	W2,W8	
33878	Y	Y	J	MHI	OAKAMC	W24	
33879	Y	Y	J	MHI	OAKAMC	W24	
33880	Y	Y	J	MHI	OAKAMC	W24	
33881	Y	Y	J	MHI	OAKAMC	W24	
33882	Y	Y	J	MHI	OAKAMC	W24	
33883	Y	Y	J	MHI	OAKAMC	W24	
33940	Y	Y	J	MHI	OAKAMC	W11	
33980	Y	Y	J	MHI	OAKAMC	W13	
33982	Y	Y	J	MHI	OAKAMC	W13	
33984	Y	Y	J	MHI	OAKAMC	W13	
33985	Y	Y	J	MHI	OAKAMC	W6	
33990	Y	Y	J	MHI	OAKAMC	W13	

Table B.3 – continued from previous page

Animal ID	mtDNA?	SNP?	mtDNA Haplotype	mtDNA strata	Island Community	Cluster	Social Unit
33992	Y	Y	J	MHI	OAKAMC	W6	
45934	Y	Y	J	MHI	HMC	H26	F
51015	Y	Y	J	MHI	OAKAMC	W13	
51031	Y	Y	J	MHI	OAKAMC	W13	
51032	Y	Y	J	MHI	OAKAMC	W13	
51033	Y	Y	J	MHI	OAKAMC	W13	
55157	Y	Y	J	MHI	HMC	H2	G
55160	Y	Y	J	MHI	HMC	H19	
55161	Y	Y	J	MHI	HMC	H22	B1
55165	Y	Y	J	MHI	HMC	H7	
55175	Y	Y	J	MHI	HMC	H19	
55228	Y	Y	J	MHI	HMC	H18	
55230	Y	Y	J	MHI	HMC	H18	E
55234	Y	Y	J	MHI	HMC	H18	E
55244	Y	Y	J	MHI	HMC	H21	
55254	Y	Y	J	MHI	HMC	H21	

Table B.3 – continued from previous page

Animal ID	mtDNA?	SNP?	mtDNA Haplotype	mtDNA strata	Island Community	Cluster	Social Unit
61916	N	Y			HMC	H20	H
61918	Y	Y	J	MHI	HMC	H19	
61936	Y	Y	J	MHI	HMC	H11	
61939	Y	Y	J	MHI	HMC	H11	
73899	Y	Y	J	MHI	HMC	H26	
73901	Y	Y	J	MHI	HMC	H7	
79976	Y	Y	J	MHI	HMC	H26	
79978	Y	Y	J	MHI	HMC	H2	G
80005	Y	Y	J	MHI	HMC	H5	
88594	Y	Y	J	MHI	HMC	H21	A
94818	Y	Y	J	MHI	HMC	H8	
94820	Y	Y	J	MHI	HMC	H20	H
112642	Y	Y	J	MHI	HMC	H11	
112647	Y	Y	J	MHI	HMC	H2	
112648	Y	Y	J	MHI	HMC	H2	
112649	N	Y			HMC	H22	

Table B.3 – continued from previous page

Animal ID	mtDNA?	SNP?	mtDNA Haplotype	mtDNA strata	Island Community	Cluster	Social Unit
112658	Y	Y	J	MHI	HMC	H11	
114352	Y	Y	J	MHI	HMC	H22	B1
114356	Y	Y	J	MHI	HMC	H22	B2
114805	Y	Y	J	MHI	OAKAMC	W8	
114806	Y	Y	J	MHI	OAKAMC	W8	
114808	N	Y			HMC	H7	
114809	Y	Y	J	MHI	HMC	H7	
114813	Y	Y	J	MHI	HMC	H7	
114815	Y	Y	J	MHI	HMC	H13	
114816	Y	Y	J	MHI	HMC	H13	
114817	Y	Y	J	MHI	HMC	H13	
114818	Y	Y	J	MHI	HMC	H20	C1
114819	Y	Y	J	MHI	HMC	H20	C2
114820	Y	Y	J	MHI	HMC	H20	C2
114822	Y	Y	J	MHI	HMC	H19	
114823	Y	Y	J	MHI	HMC	H19	

Table B.4: *Genetic differentiation (F_{ST}) between five clusters with more than five sampled individuals (related individuals not included); sample sizes for each cluster are shown in parentheses. F_{ST} p-values are shown below F_{ST} values in parentheses; significant differentiation between clusters is shown in bold.*

Cluster 1	Cluster 2	Cluster 1 n	Cluster 2 n	F_{ST}	p-value
H2	H20	9	10	0.055	<**0.001**
H2	H22	9	13	0.059	<**0.001**
H2	W13	9	11	0.033	**0.009**
H2	W24	9	6	0.053	**0.002**
H20	H22	10	13	0.045	**0.001**
H20	W13	10	11	0.024	**0.011**
H20	W24	10	6	0.03	**0.018**
H22	W13	13	11	0.028	**0.004**
H22	W24	13	6	0.028	**0.03**
W13	W24	11	6	0.01	0.285