Seascape Genomics of Australian and New Zealand common dolphins

(*Delphinus delphis*)

By

ANDREA BARCELÓ CELIS

B.V.Sc. (Veterinary Science) | M.Sc. (Marine Biology)

Thesis
Submitted to Flinders University
for the degree of

Doctor of Philosophy

College of Science and Engineering

9th August 2021

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

The common dolphin (*Delphius delphis*) is a wide-ranging near top marine predator that inhabits a variety of environments in temperate and subtropical waters around the world. The movements of common dolphins are generally associated to those of their prey, which are mostly small-pelagic fishes targeted by commercial fisheries. This occasionally leads to common dolphin-fishery interactions, including mortalities due to by-catch. Although common dolphins are relatively abundant in Australasia, limited information is available for this species about population differentiation, connectivity and adaptation, making it difficult to develop conservation and management plans. Coastal waters in Australasia are characterised by highly heterogeneous and dynamic environments that are expected to influence eco-evolutionary processes in marine populations, including in predatory species with vast distributions. This thesis utilised genome-wide markers, population genomics and seascape genomics to elucidate population differentiation, connectivity, and environmental drivers of adaptive divergence in Australasian common dolphins.

The first aim of this work was to investigate neutral genomic diversity and clarify population structure and connectivity of common dolphins at different spatial scales across Australasia. A double digest restriction-site associated DNA sequencing (ddRADseq) method was used to obtain over 14,700 filtered and putatively neutral Single Nucleotide Polymorphisms (SNPs) for 478 Australasian common dolphins. To date, this represents one of the largest population genomic datasets reported for a small cetacean. This section included samples from both strandings and free-living dolphins from across the species range in Australasia: southern and eastern Australia, and the west and east coasts of New Zealand. In addition, population genetic analyses were carried out using novel and published mitochondrial DNA (mtDNA) control region sequences (173 haplotypes), which suggested differentiation between Pacific and Indian Ocean common dolphins. Analyses of the more resolving genome-wide SNP dataset pointed to a hierarchical metapopulation structure, with three main regional common dolphin populations: southern Australia, eastern Australia, and Tasmania/New Zealand combined. Additional sub-substructure was disclosed within regional populations, with a signal of isolation by distance along coastlines. Nonetheless, connectivity was still observed over thousands of kilometres and across multiple jurisdictions, with considerable genetic exchange across the Tasman Sea. These findings indicate that state and international collaborations are needed for the management of common dolphin populations and fishery-dolphin interactions in the region.

The second aim of the thesis was to implement a seascape genomics framework to identify signals of selection due to environmental heterogeneity and putatively adaptive genomic variation in common dolphins from across southern Australia. This section focused on Indian Ocean common dolphins because this heterogeneous region sustains one of the main regional populations of the species in Australasia and is well represented in our sampling. For this part of the study, only samples from free-ranging individuals for which an associated geolocation was available were used. From an initial dataset of 17,327 filtered SNPs, a putatively adaptive dataset of 806 SNPs was identified based on a multivariate Genotype Environment-Association (GEA) analysis and a Bayesian method. The results of multiple statistical tests point to five adaptively divergent populations of common dolphins in southern Australia. The GEA analysis suggested that adaptive diversity in these populations is mainly influenced by variation in four environmental variables: current velocity, sea surface temperature, primary productivity, and salinity. In turn, these variables appear to be broadly governed by differences in ocean circulation, and by the presence of upwellings and semi-enclose coastal habitats. Both coding and non-coding regions in the candidate adaptive loci appear to have responded to environmental selection. The results of this study of the southern Australian segment of the metapopulation, highlight the impact of environmental heterogeneity on common dolphin connectivity and adaptive divergence.

The third section of the thesis includes free-ranging samples from both southern Australia (Indian Ocean) and the Australian east coast (Pacific Ocean) to carry out a seascape genomics study of adaptation across the Australian-wide common dolphin metapopulation. A combination of analytical tests of selection produced two putatively adaptive SNP datasets. At the broad-scale, over 1,000 candidate adaptive SNPs were identified for the Australian-wide metapopulation. At a fine-scale, 200 candidate adaptive SNPs were found for the eastern Australia segment of the metapopulation. This two-scale strategy allowed determining associations between adaptive genomic variation and environmental variables, after accounting for the effects of spatial distance within the two Australian coasts. At the metapopulation scale, two regional populations were identified, consistent with the previous results based on putatively neutral markers. Genomic variation in these populations appeared strongly associated with variation in sea surface temperature, current velocity, salinity, bathymetry and primary productivity. Lower adaptive divergence was detected along the east coast population segment, which appeared associated mainly to variation in primary productivity. It appears that both broad- and fine-scale adaptive divergence in Australian common dolphins is influenced by three oceanographic and coastal features: (i) ocean circulation patterns at range edges, (ii) areas of eddies and upwellings, and (iii) semi-enclosed coastal habitats. We also detected preliminary evidence for repetitive selection in some regions of the genome, which is speculated in the context of parallel evolution of dolphins on separate coastlines. These results provide environmentally-influenced perspectives for conservation management of multiple segments of the Australian common dolphin metapopulation.

By analytically integrating neutral and adaptive genomic variation and information from key ecological predictors, this thesis generated novel baseline information for the conservation and management of Australasian common dolphins in the context of a rapidly changing and heterogeneous marine environment. The outcomes of this work also call for new collaborative efforts across state and international jurisdictions to ensure that management goals for the species, including those related to maximum by-catch levels in fisheries, are achieved. It also provides an initial first step towards our understanding of adaptive resilience of local and regional populations of a small cetacean, to naturally- and anthropogenically-driven environmental changes.

DECLARATION

I, Andrea Barceló Celis, certify that this thesis:

1. Does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and
2. to the best of my knowledge and belief, does not contain any material previously published or written by another person except where due reference is made in the text.

Signed

Andrea Barceló Celis

ACKNOWLEDGMENTS

First of all, I am really grateful with my supervisors Luciana, Luciano and Kerstin, for the confidence placed in me, and to let me do this project with samples that had been collected since many years ago, it has been a real treasure. Since my multiple emails wanted to do a PhD, reaching Luciana and on some occasions Luciano, to the full completion of the thesis only a few hours ago, you both had always share your knowledge, past experiences and even lots of writing tips, always guiding me in the right direction.

Additionally, I would like to thank Guido Parra and Mike Gardner for the feedback provided during my Milestones, and the international collaborators Karen Stockin and Krista Humpan, for their comments in the Chapter 2 and samples provided, without them it would had been a narrow overview of the Australasian common dolphins metapopulation system.

This project will not have been possible without my two Flinders families MELFU that always make me think and challenge every aspect of my project and personal life. Yuma, thanks all your support and knowledge. Chris, thanks for your sarcasm and knowledge. Katie, you had taught me so much about life in general thanks for that. Andrea, I hope to continue the spanish lessons. Sean, thanks for my first Australian wedding experience. Cat my hybrid sis always welling to help. As well as my second family CEBEL which made me realise that the power of girls in science, Kim thanks for being very quiet and teach me about your real passion netball, "the other office" Elly and Bec, getting to know you better at the conference was a real pleasure. Rodrigo, nice to share your quick year around the lab and of course I will never forget the rising star Isabella (I expect greater things from you), and all the previous and current members of the lab, and to all those volunteers in the field that I will probably will never know all your names.

Erika my sister, thank you for being you and also to my brother from another mother Rene that always got my back, and listen to me.

A mi mamá, "gracias" por tu apoyo incondicional y porque siempre estas a solo una llamada, espero que la culminacion de mis estudios pueda brindarte algo de paz. Aunque papá ya no pudo leer mis tesis (licenciatura, meastria y ahora doctorado) se que siempre esta desde lejos cuidandome y apoyandome, como siempre lo hizo. De igual manera, quiero agradecer a una o mejor dicho la persona mas importante y lista que he conocido, Orlando, gracias por seguirme hasta el otro lado del mundo en esta aventura de la vida, sin tu apoyo este camino hubiera sido mucho mas sinuoso.

I also thank everyone that has been involve in some part in my professional development, since my first memories of going into my dad's work and look into a microscope, into the full competition of this PhD. I had learnt so much from you even if you did not noticed, the good and bad things, it has been an amazing journey. Lastly but clearly not less important, I would like to thank my study species, the common dolphins, you inspire me to understand you in every step of the way.

This study was supported by CONACYT (the Mexican National Council for Science and Technology) Scholarship (Grant No. 440689) and sponsorship from Flinders University.

ETHICS STATEMENT

Samples for this study were collected under the ethics approval of the Flinders University Macquarie University, and Massey University animal ethics committees, and under research permits from Flinders University and South Australia Health Service Animal Welfare Committee (E326); DENR,SA (E25889); DEC,WA (SF008961); DSE,VIC (FF383247); DECCW, NSW (A2126); DEWHA (2008-001), SA State water a Ministerial Exemption PIRSA (9902404); KAS and ELB New Zealand Department of Conservation (RNW/HO/2008/03); GTP New Zealand Department of Conservation (DOCDM-13171418); GTP and KS New Zealand (AEC/17 14/25).

THESIS RATIONALE

Genetic variation in marine species with a wide spatial distribution may be influenced by environmental heterogeneity, which facilitates or restrict spatial movements of individuals, and the impacts of natural selection. This thesis advances the knowledge about population divergence and potential local adaptation of fisheries at-risk common dolphins (*Delphinus delphis*) in Australia and New Zealand using genome-wide markers. Previous studies utilised a handful of genetic markers (microsatellites and mitochondrial DNA) to investigate population structure in different parts of the species' range in Australasia (Möller et al., 2011; Amaral et al., 2012; Bilgmann et al., 2014; Stockin et al., 2014). In this thesis, I explore the degree of gene flow and potential selective pressures occurring at multiple spatial scales in the populations of common dolphins in the Australasian region. I first clarify population structure and connectivity of common dolphins based on a neutral genomic variation across Australia and New Zealand. Then, I investigate adaptive genomic variation based on samples from live animals collected along the southern and eastern Australian distribution of common dolphins. This is done using a genotype-environment association and an outlier methodology, which provides insights into the potential adaptive resilience of populations to local environments. This thesis provides ecologically valuable information for the conservation and management of the species in the Australasian region.

"Like members of the Australian Arunta (Arrernte) tribe, population ecologists tend to count one, two, and (infinitely) many. The extreme cases of only two local populations and very many local populations, turn out to be easier to deal with than more realistic case of tens of local populations"-Ilkka Hansaki

CHAPTER 1. GENERAL INTRODUCTION

Neutral and adaptive genetic variation

Genetic variation is the result of ecological and evolutionary long-term processes with cumulative hereditable changes in morphological and behavioural traits of individuals, populations and species (Fisher, 1930; Wright, 1931; Halden, 1957). In natural systems, the most advantageous genetic variation will be favoured for the survival of the species and populations (Wright, 1931). In an ideal environment with no drastic changes, natural selection will depend on the rate of the fitness of a population at a specific moment (Fisher, 1930). However, in real life environments, natural conditions will continuously create changes in the genetic variation among and within species, and populations, due to intrinsic (e.g. behaviour, learning-culture) and extrinsic (e.g. heterogeneity of the environment) factors (Wright, 1931; 1968). These factors can occur either by natural selection or stochastic events, leading to fixed or nearly fixed alleles that will impact on the fitness of a populations or species (Wright, 1931; 1968; Crow and Kimura, 1970). Thus, genetic variation across individuals will provide the capacity to evolve and adapt, enhancing the chances of survival to individuals, populations and/or species that are best suitable for an environment. These changes in genetic variation can be described by four evolutionary forces: i) genetic drift, ii) gene flow, iii) mutation and iv) selection.

Genetic drift is the process in which allele frequencies in a population are modified through generations due to random mating (Whitlock and Barton, 1997; Whitlock and McCauley, 1999). In small populations, random mating may contribute to the loss of alleles with low frequency (Fisher, 1930; Wright, 1931), in which case the population could become mainly composed of homozygous individuals (Hanski and Saccheri, 2006; Allendorf, 2017). Thus, in small populations adaptive potential may be reduced and in turn increase the risk of decline or extinction (Wright, 1931; 1968; Hanski and Saccheri, 2006). In contrast, in large populations or inter-connected populations, genetic drift may be negligible or reduced by gene flow (Wright, 1968; Hanski, 1999; Hanski and Saccheri, 2006).

Species that exhibit the ability to migrate and reproduce over large spatial scales, will tend to maintain higher levels of genomic diversity within large populations or inter-connected populations (Slatkin, 1987; Whitlock and McCauley, 1999). This higher genetic variation may lead to potential "beneficial" alleles to persist or be introduced into a population, and in turn enhance adaptive capacity for those individuals to respond and survive to selective pressures

(Slatkin, 1987; Hanski and Saccheri, 2006). Yet, genetic variation within and among populations can also be driven by mutations (Kimura, 1968; Wright, 1968).

Mutations are the result of variation in genomic sequences and are believed to be responsible for the long-term evolution of populations and species by providing hetero-allelism into the genetic pool (Kimura, 1968; Wright, 1968; Wellenreuther and Bernatchez, 2018). These variations are changes in the amino acid chain that can be created by duplications, substitutions, insertions, deletion, inversion, and/or translocations (Wellenreuther and Bernatchez, 2018). However, ecological adaptations can also lead to modifications in the gene expression of an individual, without involving changes in the DNA sequence that may be heritable, also known as epigenetics (Funk et al., 2019; Rajora, 2019). In the cases of variations in the genomic sequences, most of the mutations are neutral, and will not have an impact on the fitness of an individual (Kimura, 1968; Wright, 1968). If a mutation occurs on genes that are under selection, it may lead to an impact on the fitness of an individual (Kimura, 1968; Wright, 1968; Barrett and Hoekstra, 2011).

Natural selection occurs when some individuals are favoured in an environment. This occurs when advantageous alleles or genotypes of a population are more likely to favour the survival and reproduction of individuals that disperse (Wright, 1931; Halden, 1957). Thus, natural selection can ensure long-term viability of populations or species by passing their “beneficial” alleles to the next generation, which can be triggered either by a *de novo* mutation or high standing genetic variation maintained and acting upon an adaptive gene (Barrett and Hoekstra, 2011; Lotterhos and Whitlock, 2014; Basener and Sanford, 2018). For example, fitness in small populations where standing genetic variation is generally lower, could be severely impacted if a mutation or adaptive process occur in a detrimental allele, whereas in large populations high standing genetic variation may allow them to cope and adapt to different selective pressures (Whitlock and McCauley, 1999; Barrett and Schluter, 2008).

Ecological factors play a critical role in determining the number of individuals that survive and reproduce, and in most cases they would be a reflection of the heterogeneity in the environment (Hanski and Saccheri, 2006). In the cases of large populations or metapopulation systems exhibited by several marine taxa, ecological factors such as food availability, environmental gradients or density of individuals in a given space, could be impacting life history traits (e.g. size, longevity, sexual maturity) (Rajora, 2019; Oleksiak and Rajora, 2020). It is expected that these ecological factors, which may differ between different environments, will shape population structure and connectivity across a metapopulation (Saccheri and Hanski, 2006).

Implications of evolutionary forces to marine ecosystems

In marine species, evolutionary and ecological processes are a topical issue among molecular ecologists who aim to obtain a better understanding of the past, current and future adaptive capacity of species and populations of a species (Palumbi, 1994; Grummer et al., 2019). Traditionally, studies in marine ecosystems used to characterise species as "genetically homogenous" due to the general high dispersal capability of marine species and lack of obvious hard physical barriers in marine environments (Selkoe et al., 2010) compared to terrestrial environments (e.g. mountains, rivers, lakes, roads) (Manel et al., 2003; Balkenhol et al., 2016). After almost two decades of studies, researchers demonstrated that marine species are generally genetically differentiated when inhabiting heterogeneous environments (Manel and Holderegger, 2013; Riginos et al., 2016). In these cases, genetic structure was generally impacted by topographic, oceanographic and environmental gradients (e.g. canyons, strait, currents, water masses), which may have restricted or facilitated the dispersal of marine organisms (Manel and Holderegger, 2013; Riginos et al., 2016; Xuereb et al., 2018a). Hence, genomic variation between marine species and their populations is in part a reflection of their environment (Selkoe et al., 2008; Manel and Holderegger, 2013; Grummer et al., 2019). Understanding the degree of genetic differentiation and gene flow among populations is essential for making decisions as part of management and conservation plans (Funk et al., 2012; Riginos et al., 2016; Grummer et al., 2019).

Marine species coexist under different spatial and temporal environmental scales, and understanding these can provide information for the management and conservation of their populations (Rodriguez-Zarate et al., 2018; Dunn et al., 2019). Worldwide marine ecosystems have been categorised based on their environmental and geological differences (e.g. Kämpf and Chapman, 2016; Costello et al., 2017). Some species can only survive in specific environments (i.e. endemic species) (Costello et al., 2017). However, most marine species exhibit dispersal at some stage of their life, presenting in many cases a metapopulation system (Hanski and Saccheri, 2006; Allendorf et al., 2010), which leads to higher genomic diversity due to gene flow persistence within and among their populations (Kritzer and Sale, 2004; Riginos et al., 2016; Selkoe et al., 2016).

The research field of population structure and dynamics has evolved since the development of the Island Biogeography theory and Metapopulation Dynamics by MacArthur and Wilson (1967) and Levins (1969). Today it has diversified into multiple research fields, one of them, seascape and landscape genetics integrates oceanographic, geological and ecological drivers that may impact on connectivity and selection of a species between habitat patches under different temporal and spatial scales (Manel and Holderegger, 2013; Grummer et al., 2019; Manel et al., 2019). Several ongoing and past definitions of the term "population" and "metapopulations" have been proposed, ranging from typical theoretical definitions to marine related definitions (Table 1.1). The majority of these definitions underline characteristics about the heterogeneity and dynamics of habitat patches, whereas other differ based on the species analysed and its application. This highlights that there are no unanimous definitions for what a population and metapopulation are. For this thesis, I define a population as "a group of individuals that have the same probability of mating with each other and produce offspring, being restricted to a delimited geographic area over one generation time", whereas a metapopulation is a "a group of local populations that maintain connectivity, but the majority of individuals in each population are restricted to a specific spatial space".

Table 1.1 Definitions used across studies for the terms 'population' and 'metapopulation'.

Definition	Reference
Theoretical ecology of a Metapopulation (restriction of movements): "Metapopulation is the ecological term for assemblage of species within larger areas of space, with long-term survival of the species depending on a shifting balance between local extinctions and recolonizations in the patchwork of a fragmented landscape".	Hanski (1998; 1999)
Metapopulations: "A metapopulation is a collection of populations if a species found in differing geographic locations and with a restricted gene flow (exchange of genes) between the populations".	Allendorf et al. (2010)
Review on "What is a population?" "Ecological paradigm: A group of individuals of the same species that co-occur in space and time and have an opportunity to interact with each other". "Evolutionary paradigm: A group of individuals of the same species living in close enough proximity that any member of the group can potentially mate with any other member."	Waples and Gaggiotti (2006)

Marine population genetics: "A Population can be closed or open based on their genetic variation and dispersal".	Palumbi (2003)
Population genetics: "A population is a group of individuals in sufficiently close proximity that any member of the group can potentially reproduce with any member of the other sex".	Frankham et al. (2017)
Conservation unit: "A population of organisms that is considered distinct for conservation purposes, such as management unit, evolutionary significant unit and/or discrete population segments."	Funk et al. (2012)

Population structure and dynamics as a research field, has evolved and allowed to characterise how specific ecological factors may shape genomic differentiation across populations and species. However, large marine predators that can disperse at any stage of their life, will exhibit complex interactions between spatial and environmental features that influence multiple life-history traits, that can result in metapopulations systems (e.g. Louis et al., 2014a; Castro-Tavares et al., 2019; Sandoval-Castillo and Beheregaray, 2020). Moreover, large marine predators, such as cetaceans, exhibit different evolutionary and ecological process that shape their species and populations over time, which can vary depending on the environment they inhabit. In such cases, assessments of contemporary population differentiation and connectivity in response to the environment will often involve multiple ecological variables (e.g. Pratt, 2020; Andrews et al., 2021), and these results may provide meaningful information for their conservation and management.

Macroevolutionary and microevolutionary adaptations in Cetaceans

The field of populations genetics focuses on the ecological and evolutionary processes that affect species and their populations based on analyses of macroevolutionary and microevolutionary processes (Rajora, 2019). For cetacean species, macroevolutionary studies are one of the best examples of documented adaptations from terrestrial to aquatic habitats, focusing on the origin, evolutionary history and long-term distribution of species (Steeman et al., 2009; McGowen et al., 2014). However, studies about the microevolution of cetaceans, which focus on ecological and biological interactions of populations or closely related species, are still scarce (but see Foote et al., 2016; Zhou et al., 2018a; Pratt, 2020).

Cetaceans have adapted to different environments since their transition from terrestrial to marine environments, which led to their speciation and colonisation of the world's oceans (Steeman et al., 2009; Gatesy et al., 2013; McGowen et al., 2014). These macroevolutionary adaptations began approximately 53 million years ago (Ma), with the transition to an early amphibious aquatic life, represented by the Packicetidae (Thewissen and Williams, 2002; Steeman et al., 2009; McGowen et al., 2014). Most of the macroevolutionary processes occurred from the Eocene to Oligocene (60 to 20 Ma), with three main phases that led to the early modern cetaceans: early aquatic specialisation, evolution of filter feeding, and origin of echolocation (Arnason et al., 2004; Gatesy et al., 2013; McGowen et al., 2014). These environmental transitions of expansion and contractions of niches during glacial cycles (12,000 to 120,000 ybp) (Amaral et al., 2016) allowed them to disperse and adapt across oceans and river systems (McGowen et al., 2009). Some of these macroevolutionary adaptations led to the extinction or nearly extinction of lineages and clades such as Physeteroidea, Ziphiidae, and Platanistidae (e.g. Steeman et al., 2009; McGowen et al., 2014). In contrast, others enabled cetaceans to specialise in a range of traits, including morphological, ecological and behavioural (Gatesy et al., 2013; McGowen et al., 2014; Cammen et al., 2016). Examples of these can be seen across multiple cetacean genera (e.g. *Orcinus, Tursiops, Balanoptera, Kogia*) showing inactivation/activation of genes involved with the aquatic eye, olfactory bulb, taste, hearing, vision, and echolocation, which allowed them to dive to great depths, and likely influenced their feeding and hunting behaviours (Foote et al., 2016; Hindle, 2020; McGowen et al., 2020). To date, there are 92 recognised species of cetaceans (Perrin, 2021), 76 of them belonging to the toothed whales (parvorder Odontoceti) (Committee on Taxonomy, 2017), but adaptations between closely related species and within species are still poorly understood.

Microevolutionary processes led to diversification into subspecies, ecotypes and populations of toothed whales (e.g. Arnason et al., 2004; Slater et al., 2010; McGowen et al., 2020). Studies of species such as killer whales (*Orcinus orca*), bottlenose dolphins (*Tursiops* spp.), spinner dolphin *(Stenella longirostris)*, and finless porpoises (*Neophocaena* spp.) have demonstrated genetic divergence at subspecies and/or ecotype levels (e.g. Foote et al., 2016; Zhou et al., 2018a; Pratt, 2020). These studies have focused on assessing selection at genes associated with ecological adaptations between habitats, revealing that different selective pressures can lead to fixation or near fixation of alleles (Moura et al., 2013b; Foote et al., 2016).

The first studies on microevolution in cetaceans were undertaken on the killer whale, a cosmopolitan species that exhibits genetic differentiation and adaptation among , different ecotypes that may share the same or similar geographical regions (e.g. Morin et al., 2015; Foote et al., 2016; Foote et al., 2019). These genetic differentiations were possibly driven by highly evolved cultures, resulting in strong social structure and feeding specialisations (Foote et al., 2016). For this species, differences in their genetic variation were found in genes associated with digestion, adipogenesis, growth, metabolism, reproduction, biological development, and functions of the heart and muscles (e.g. Foote et al., 2016; Foote et al., 2019). Another study on microevolutionary processes in toothed whales revealed genetic divergence between populations of Yangtzen finless porpoises inhabiting freshwater and ocean environments by osmoregulation adaptations (Ruan et al., 2015; Zhou et al., 2018a).

Two studies in bottlenose dolphins have also assessed microevolutionary processes. The first between subspecies of the southern Hemisphere (*T. truncatus truncatus* and *T. t. gephyreus.*), and the second at population level on Indo-Pacific bottlenose dolphins (*T. aduncus)* (Pratt, 2020). The first study demonstrated differentiation between ecotypes using SNPs from a ddRAD dataset, which were associated to adaptive responses in select genes involved in the circulatory system, hypoxia tolerance, osteogenesis, adipogenesis, echolocation, osmoregulation, and the nervous system (Pratt, 2020). The second study found variants nearing fixation between local populations in genes involved in osmoregulation, circulatory and skeletal systems, which were associated with environmental variables such as salinity, bathymetry and sea surface temperature (Pratt, 2020). A more recent microevolutionary study in toothed whales was on East Pacific spinner dolphins (*S. longirostris*) found divergence between ecotypes, with genes involved in social behaviours and associated with temperature and water depth (Andrews et al., 2021).

These studies provide baseline information about microevolution in toothed whales. However, they also underpin the need for more studies to better understand adaptations in modern species and their populations, which are currently vulnerable to various environmental stressors such as ongoing climate change, fisheries interactions, overfishing of their prey and pollution. Microevolutionary processes can impact marine species and its populations over broad and fine spatial scales (Manel et al., 2003; Balkenhol et al., 2016). Species of conservation and management concern, such as many delphinids, need to be protected in a way that can enable sufficient standing genetic variation for them to adapt by promoting gene flow among known populations, however this cannot be achieved without a general understanding of their population structure and dispersal.

Population structure in Delphinidae

Population structure within species of the family Delphinidae is not well understood given the narrow divergence, lack of monophyly in some lineages (Cassens et al., 2005; Segura-Garcia et al., 2016), and in some cases limited information on their genetic differentiation from some regions. Most delphinids exhibit a fluid social structure and high potential for dispersal, and therefore are generally expected to present some level of gene flow between populations (e.g. Quérouil et al., 2007; Rosel et al., 2009). However, delphinids are in many cases subdivided into small populations/sub-population entities, each with specific ecological and/or behaviour traits (e.g. Natoli et al., 2006; Louis et al., 2014a; Hoelzel et al., 2019). It has been suggested that differentiation between populations of delphinids is influenced by extrinsic (e.g. climatic, oceanographic circulation) and intrinsic (e.g. habitat preferences, site fidelity, complex social behaviours) factors (e.g. Hoelzel et al., 2007; Möller et al., 2007; Leslie and Morin, 2016). Furthermore, the range of group sizes, and limited knowledge on the population ecology and life history of some of the species has made it difficult to define populations and their boundaries (Cassens et al., 2005; Natoli et al., 2005; Mirimin et al., 2009). There are currently 37 species of delphinids recognised (Committee on Taxonomy, 2017), which includes eight closely related small species that are part of the *Stenella-Tursiops-Delphinus* (STD) complex.

Genetics studies on the STD complex have identified differentiation and connectivity among populations (e.g. Natoli et al., 2005; Mirimin et al., 2009; Leslie and Morin, 2016), with most carried out at regional and fine-scales, with the exception of a few global studies (e.g. Natoli et al., 2006; Tezanos-Pinto et al., 2009; Amaral et al., 2012a). The information obtained from these studies has disclosed population structure of these species mostly in relatively small areas,, with a few exceptions where larger areas were assessed and metapopulations identified. These include spinner dolphins (*S. longirostris)* distributed around several Pacific Islands (Oremus et al., 2007), and bottlenose dolphins (*Tursiops* spp.) in the North Atlantic Ocean, Mediterranean Sea and Indo-Pacific region (Louis et al., 2014b; Gaspari et al., 2015a; Pratt et al., 2018).

In the case of common dolphins (*Delphinus delphis*), two genetic studies were conducted at a global scale, which mainly characterised the genomic differentiation between dolphins from different ocean basins (Natoli et al., 2006; Amaral et al., 2012a). Studies in the Northern Hemisphere, specifically in the North Atlantic-Mediterranean Sea, had suggested little genetic differentiation between dolphins of this region (e.g. Mirimin et al., 2009; Moura et al., 2013a; Ball et al., 2017). In contrast, a few studies performed in the Southern Hemisphere, specifically in the Indian and Pacific Ocean, have investigated regional genetic differentiation and identified populations at relatively fine spatial scales (100 to 1,500 km) (e.g. Bilgmann et al., 2008; Möller et al., 2011; Stockin et al., 2014). These studies have suggested that genetic differentiation in common dolphins may be influenced by environmental patterns and potential feeding specialization to local food resources (e.g. Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014). Nevertheless, to the date only one study has investigated associations between populations and environmental variables. This was done using traditional genetic markers (e.g. mtDNA and microsatellites) between oceanic basins, disclosing the importance of chlorophyll *a* and sea surface temperature in differentiation of dolphins inhabiting different oceans (Amaral et al., 2012a). Yet, there is still a gap in knowledge about the impact of connectivity and various environmental variables on the genetic variation of *Delphinus* populations.

Common dolphins (*Delphinus delphis*)

The first description of the common dolphin was made by Linnaeus (1758). The world cetacean database and the Society of Marine Mammalogy currently recognises *Delphinus delphis,* referred herein as the common dolphin, as the only species of this genus (Committee on Taxonomy, 2017). Common dolphins are distinguished from other dolphins species by their criss-crossed pigmentation pattern of white, yellow and grey (Perrin, 2021). Besides its unique colorations pattern, they also exhibit morphological variation between subspecies, represented by beak length, number of teeth, and body size across their distribution (Hoelzel, 1994; Möller et al., 2011; Segura-Garcia et al., 2016). *D. delphis* is characterised by a short-beak due to the length of their rostrum, and has a worldwide distribution. However, some controversy remains about the number of species or subspecies in this genus (Committee of Taxonomy, 2017). For example, *D. capensis,* which is characterised by a long-beak and was previously believed to be a sister species, is now considered as a subspecies of *D. delphis* (Committee of Taxonomy, 2017).Thus, the current classification of this specie and subspecies was made based on genetics (Cunha et al., 2015; Rosel et al., 2017), and some known morphological and skeletal variation, such as coloration, body size and cranial differences (Cunha et al., 2015; Jordan et al., 2015; Perrin, 2021).

The common dolphin is a widely distributed species and is thought to be one of the most abundant small cetaceans (Committee on Taxonomy 2017; Perrin, 2021). Despite this, it is perhaps one of the less studies species of the STD complex. After their divergence during last glacial cycles of the Pleistocene (12,000 to 120,000 ybp) (Segura et al., 2006; Amaral et al., 2012b), common dolphins colonised temperate, subtropical, and some tropical waters in coastal and pelagic environments, being only absent from polar zones (Natoli et al., 2008; Whitehead et al., 2008; Möller, 2011) (Figure 1.1).

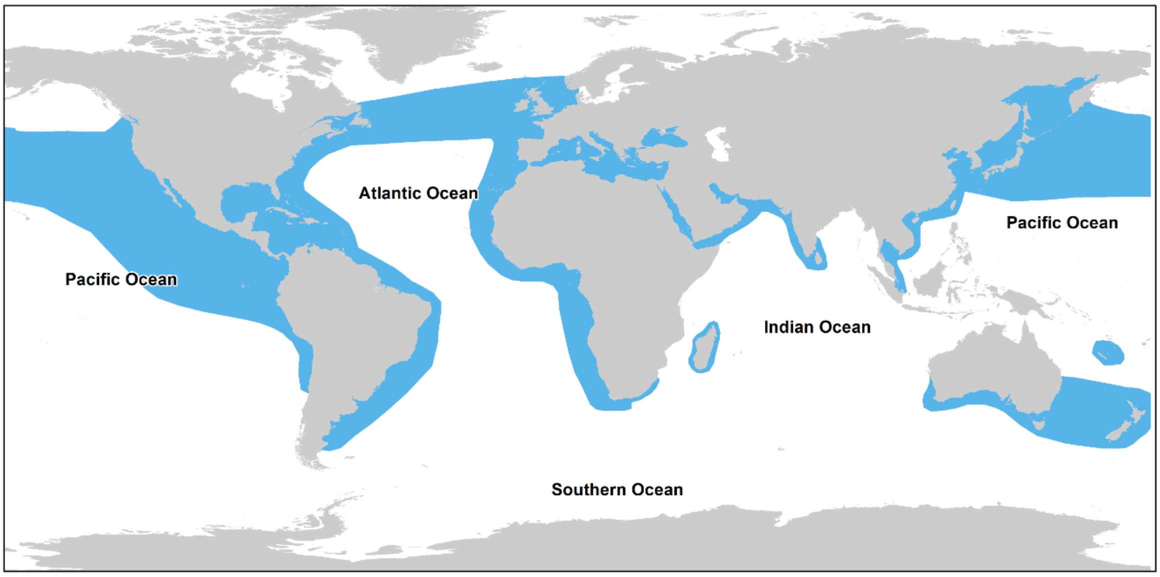


Figure 1.1 Worldwide distribution of the common dolphin (*Delphinus delphis*) (Modified from *Delphinus* sp. IUCN-Hammond et al. (2008)).

The vast distribution of common dolphins in the world's oceans has led them to be classified as a migratory species (CMS, 2020), and a listing of "least concern" by the International Union for Conservation of Nature - IUCN (Hammond et al., 2008). However, their distribution and abundance is still uncertain in many regions and may differ widely depending on the region analysed, and the population threats may also differ among regions (e.g. Bilgmann et al., 2018; Hupman et al., 2018; Murphy et al., 2019). It has been suggested that the world's abundance of common dolphins is in the millions of individuals (Hammond et al., 2008), but in many areas no abundances estimates are available, and in some places data is mainly based on incidental by-catch or stranding events (e.g. Hamer et al., 2008; Thompson et al., 2013). Furthermore, uncertainty about population structure and complex life history and behavioural interactions make it challenging to obtain robust and meaningful abundance estimates for their populations, which could provide essential information for the conservation status of populations.

Common dolphins are highly gregarious and form dynamic fission-fusion societies, where segregation in groups may occur by either sex or age (Stockin, 2008; Zanardo et al., 2016; Murphy et al., 2019). Group sizes can vary greatly according to their habitat, with reports of less than 20 individuals in shallow coastal waters, and in some cases high site fidelity to an area (<200 km^2) (Mason et al., 2016; Bilgmann et al., 2018; Pietroluongo et al., 2020). By contrast, in oceanic waters group sizes can reach hundreds or thousands of individuals (Bilgmann et al., 2019; Murphy et al., 2019), with photo-ID recorded long-distance movements greater that 1,000 km (e.g. Genov et al., 2012).

Although detailed information on common dolphin life history remains scarce for most regions and populations around the world, common dolphin sexual maturity has been estimated to be between 7-9 years of age, with a generation time of about 14.8 years, and interbirth interval of 1 to 3 years (Taylor et al., 2007; Murphy et al., 2019). The life span of a common dolphin is believed to be over 25 years of age, with a gestation period of less than 12 months (Mirimin et al., 2009; Möller, 2011).

Common dolphin movements are mainly driven by the distribution and density of their prey (e.g. Neumann, 2001; Meynier et al., 2008; Spitz et al., 2012). Their highly dynamic social structure and wide distribution allows them to utilise different feeding strategies depending on their environment and the targeted prey species (Natoli et al., 2008; Möller, 2011; Zanardo et al., 2016). These may include different strategies used in shallow waters, where some individuals may present high speed pursuits (Neumann and Orams, 2003; Meynier et al., 2008; Stockin and Orams, 2009), as compared to oceanic waters where they may prefer feeding cooperatively (e.g. Neumann and Orams, 2003; Stockin and Orams, 2009; Hupman, 2016). In some regions, common dolphins have been documented to perform seasonal migrations in relatively large areas, moving to large upwelling centres to feed in aggregation areas with other large marine predators (e.g. Natoli et al., 2008; Möller et al., 2011; Bilgmann et al., 2014).

However, in some areas where they seem to remain year-round, they may target different prey species depending on seasonal availability (e.g. Filby et al., 2013; Mason et al., 2016; Peters et al., 2020).

Common dolphins prefer to target small mesopelagic fish schools with high energy density, including but not limited to species such as sardines (*Sardinops sagax*), anchovies (*Engraulis australis*), mackerel (*Trachurus declivis, T.s. murphyi, T. novaezelandiae* and *Scomber australasicus*), herring (*Clupea harengus*) and blue withing (*Micromeristius poutassou*) (Murphy et al., 2013; Goldsworthy et al., 2019b; Peters et al., 2020).

Status of Australasian common dolphins

Common dolphins are distributed across Australasia in temperate and subtropical waters (e.g. Möller et al., 2011; Bilgmann et al., 2018; Peters and Stockin, 2021) (Figure 1.1). In Australia, common dolphins can be found from coastal to pelagic environments along the southern and eastern coasts, where they appear to concentrate over the continental shelf (Möller, 2011; Bilgmann et al., 2014; Bilgmann et al., 2018). In New Zealand, common dolphins can be found in coastal and pelagic environments around both North and South Islands, although they seem to mainly concentrate around the North Island (Stockin and Orams, 2009; Dwyer et al., 2020; Peters and Stockin, 2021). Overall, common dolphins inhabit a wide variety of environments in Australasia. Some groups inhabit protected shallow waters in embayment environments, which have been described as potential year-round habitat for the species (e.g. Filby et al., 2010; Mason et al., 2016; Dwyer et al., 2020). Other groups of common dolphins inhabit waters of the continental shelf, with seasonal migration to aggregations in areas of high biological productivity, such upwelling centres and eddies (e.g. Möller et al., 2011; Bilgmann et al., 2014).

Information on the total abundance of Australasian common dolphins is lacking, with only a few estimates available for some regions (Abraham et al., 2017; Bilgmann et al., 2018; Hupman et al., 2018). For New Zealand, the largest estimation was based on a model for the Northern Island, which provided a total of 18,145 common dolphins (CV =0.33, 95% CI = 9,669-33,726) (Abraham et al., 2017). Seasonal abundance estimates based on photo-ID and mark-recapture models in the Hauraki Gulf yielded an estimate of 732 dolphins (CI= 460-1,177) during autumn, and 5,034 (CI=4,745-5,930) during spring of 2010 (Hupman et al., 2018). For

Australia, two estimates were done based on aerial surveys, both in southern Australia. One covering over 40,000 km^2 of the two South Australian Gulfs and adjacent shelf waters, which led to an estimate of 21,733 common dolphins (CV = 0.25; 95% CI = 13,809-34,203) (Parra et al., in review), while the other over the continental shelf in the waters off the western Eyre Peninsula in the Great Australian Bight estimated between 20,000 to 22,000 common dolphins (CV = 0.28-0.31; 95% CI = 11,067-38,003) (Bilgmann et al., 2018). Despite the limited information on population sizes and dispersal patterns of the species across Australasia, there are additional photo-ID studies that provided information of abundance and structure (Stockin, 2008; Mason et al., 2016; Hupman et al., 2018). These photo-ID studies have showed that common dolphins groups can vary from less than 10 individuals in shallow protected waters (e.g. Filby et al., 2010; Mason et al., 2016; Dwyer et al., 2020), to over 100 individuals in some pelagic areas (e.g. Bilgmann et al., 2018; Hupman et al., 2018; Parra et al., in review).

Genetic markers, such as mitochondrial DNA (mtDNA) and microsatellites, have been used to investigate the population structure of Australasian common dolphins (e.g. Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014). A world-wide study that analysed some common dolphins from Australasia suggested a degree of genetic differentiation between Pacific and Indian Ocean dolphins (>1,500 km) (Amaral et al., 2012a). This genetic differentiation was also shown in further studies with traditional markers looking at finer spatial scales (<1,000 km) (Bilgmann et al., 2014). In the case of southern Australia, the presence of at least five common dolphin populations was suggested (Bilgmann et al., 2014), while for eastern Australian three populations were disclosed (Möller et al., 2011). In New Zealand, a study suggested at least two separate populations, one close to shore and the other in oceanic waters (Stockin et al., 2014). However, studies based on a few molecular markers may not be accurate for determining spatial population structure (e.g. Teske et al., 2018; Rajora, 2019). In addition, there is no detailed information about connectivity of common dolphins on a larger scale across southern Australia, eastern Australia and New Zealand. This limited information about population boundaries and connectivity between and among Australasian common dolphin populations has hindered conservation and management programs for the species in this region since they are essential to set sustainable limits for spatial fisheries by-catch.

Threats to Australasian common dolphins

The rapid anthropogenic and climatic events that are currently impacting common dolphins in Australasia could potentially change ecosystem services that this species provide to the marine environment (Castro-Tavares et al., 2019; Sousa et al., 2019). Studies about the potential impacts of climate change on Australasian common dolphins are scarce, and mainly focus on specific areas with human threats across different species (e.g. Robbins et al., 2017). Some studies of other small cetacean species that share Australian waters have suggested that future climate may compromise their populations (e.g. Watson et al., 2013) leading to declines or habitat displacement (e.g. Bilgmann et al., 2019; Reed et al., 2020), potential negative impacts on reproduction and health, and occasionally lead to large morbidity and/or mortality events (e.g. Kemper et al., 2016; Reed et al., 2020; Batley et al., 2021). For Australasian common dolphins, a previous epizootic event of cetacean morbillivirus, which coincided with a marine heatwave and algae bloom caused the mortality of at least eight individuals of this species (Kemper et al., 2016).

Historically, common dolphins are considered one of the most impacted cetacean species by commercial fisheries (Thompson et al., 2013; Abraham et al., 2017; Tulloch et al., 2020). Commercial fishery interactions occur mainly due to the close association of common dolphins to small pelagic fish schools while fishing practices are taking place (Bilgmann et al., 2008; Abraham et al., 2017). Thus, these interactions often result in incidental encirclements or capture depending on the type of fishery, and occasionally lead to by-catch of individuals (Abraham et al., 2017; Goldsworthy et al., 2019b; Tulloch et al., 2020). In Australia, common dolphin incidental by-catch has occurred in trawl, purse-seine, gillnet and long-line fisheries, which catches mainly for mackerel (*T. declivis, T.s. murphyi, T. novaezelandiae* and *S. australasicus*), sardines (*E. australis*), and gummy sharks (*Mustelus antarticus*) (Australian Goverment, 2019b). In New Zealand, the incidental by-catch of common dolphins occurs mainly in mid-water trawl and long-line fisheries, which target various mackerel species (*T. declivis, T.s. murphyi, T. novaezelandiae and S. australasicus*) (Thompson et al., 2013; Abraham et al., 2017).

In at least two of these fisheries, incidental by-catch has resulted in large mortalities of common dolphins. In Australia, during a period of seven months in 2004-2005, more than 1,700 encirclements and over 370 mortalities of common dolphins occurred in the South Australian Sardine Fishery (SASF) (Hamer et al., 2008). In New Zealand, between 2002-2003, over 200 common dolphins mortalities were registered in the trawl fishery (Thompson et al., 2013). As a response, fishery codes of practices were soon implemented in both countries, which led to a general reduction of dolphin mortalities (Goldsworthy et al., 2019b; Fisheries of New Zealand, 2020). However, recent studies in New Zealand found that common dolphins are still one of the main marine mammal species accidentally caught by commercial fisheries (Abraham et al., 2017). Furthermore, in 2018-2019 the SASF reported a discrepancy between the data recorded by commercial fishers and independent observers on board vessels (with a current observer coverage of around 10% of the fishery) (AFMA, 2019b; Goldsworthy et al., 2019b; AFMA, 2020b), suggesting that mortalities of common dolphins may be underreported. In addition, the cumulative impacts on dolphin populations of mortalities occurring in different fisheries is currently unknown (Mackay and Goldsworthy, 2017). This is exacerbated by the limited information about population boundaries, connectivity and abundance.

Seascape genomics of Australasian common dolphins

To assist management and conservation strategies, it is essential to understand eco-evolutionary processes that shape the population structure and connectivity of marine species (Grummer et al., 2019). Genetic variation is expected to provide marine species with adaptive resilience to rapid environmental changes (Grummer et al., 2019; Manel et al., 2019). Past genetic studies of common dolphins in Australasia have suggested that population differentiation may be driven by environmental variables, including oceanographic currents that may restrict the dispersal of the species (e.g. Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014). However, only one study has explicitly tested for associations of genetic variation and environmental variation, revealing that the genetic differentiation between ocean basins is associated with differences in sea surface temperature and chlorophyll *a* (e.g. Amaral et al., 2012a). However, to the best of my knowledge, the association between connectivity and environmental features shaping genomic differentiation has not been assessed for common dolphins in a metapopulation context.

The recent implementation of genomic frameworks using thousands of genomic markers, has the potential to answer questions in conservation genetics that were, in most cases, intractable using a handful of traditional genetic molecular markers (Allendorf et al., 2010; Stapley et al., 2010; Funk et al., 2012). This includes, but is not limited to, what loci are likely to be associated with selective pressures, or which genomic variants are involved in specific adaptations. Genomic studies can provide these answers by increasing the power and accuracy of parameter estimation for species and populations of conservation and management concern (Luikart et al., 2003; Stapley et al., 2010; Funk et al., 2012). In the case of common dolphins, such studies would provide greater resolution to delineate population structure and potential boundaries of dispersal, levels of connectivity, and to evaluate environmental factors shaping their populations in particular regions and local areas.

For other members of the STD complex, for example the spinner (*S. longirostris*) and pantropical spotted (*S. attenuata*) dolphins from the eastern tropical Pacific Ocean, the use of genomic markers (SNPs) led to the proposal of biologically meaningful management units for fishery-impacted populations of these species, which previously could not be genetically differentiated based on traditional genetic markers (Leslie and Morin, 2016). More recently adaptive divergence between ecotypes was also suggested (Andrews et al., 2021). For Indo-Pacific bottlenose dolphins *(T. aduncus*)*,* putative adaptive genomic markers allowed to differentiate populations and ecotypes based on adaptive divergence, which was not previously disclosed with traditional genetic markers (e.g. Pratt et al., 2018; Pratt, 2020). For Lahille's bottlenose dolphins (*T. t. gephyreus*), recent used of neutral genomic markers distinguished populations with strong social behaviour at a very fine-scale (<50 km) (Genoves et al., 2020). These studies suggest that efforts should focus on both neutral and adaptive genomic variation to provide a better understanding of patterns and processes that may impact the genomic structure of dolphins and adaptive divergence among their populations. This is essential for species such as common dolphins that inhabit continuous environments over large geographic areas, to ensure appropriate conservation and management actions that could in turn provide long-term, high standing genomic variation of populations. It is proposed that these assessments will provide additional information about populations capacity for long-term persistence and potential for adaptive resilience given ongoing and future anthropogenic impacts and environmental changes.

THESIS STATEMENT

This thesis aims to assess neutral and adaptive genomic variation of Australian and New Zealand common dolphins (*Delphinus delphis*). It uses a seascape genomics framework to integrate genomic variation and environmental data to investigate adaptive divergence and to provide information for conservation and management of populations. Particular focus was given to the following objectives: (1) Clarify population genomic diversity, structure and connectivity among Australasian common dolphins; (2) assess common dolphin adaptive divergence at different population segments; and (3) evaluate the association between common dolphin genomic differentiation and environmental variables to identify oceanographic phenomena that may be impacting on the populations. Overall, the outcomes of this project provide information about neutral population structure, connectivity and adaptive divergence, as well as preliminary evidence of parallel selection in some regions of the common dolphin genome. It also emphasises the benefits of using neutral and adaptive genomic markers when studying metapopulation systems, and assists with information for the conservation and management of common dolphins in Australasia.

Thesis Structure

This thesis consists of five chapters. The first chapter (I) is a general introduction, followed by three data chapters (II, III and IV) that are currently written as stand-alone papers. The last chapter (V) is a general discussion of the thesis.

Chapter I. This chapter provides a general introduction detailing general concepts relevant to the thesis, including evolutionary theory, adaptation in cetaceans, population structure in delphinids, general knowledge about common dolphins, current status of the species in Australasia, and the importance of seascape genomic studies for conservation and management of marine species.

Chapter II. This chapter expands from past studies that used neutral genetic markers (microsatellites and mtDNA) to investigate population structure of Australian and New Zealand common dolphins (Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014). The main aim was to clarify neutral population structure and connectivity of common dolphins and compare it, for the first-time, across its main distribution in Australasia. To achieve this objective, a small representation of the genome was obtained using a double digest restriction-site associated DNA sequencing (ddRADseq) method, which provided genomic markers that could be distinguished into putatively neutral and adaptive single nucleotide polymorphisms (SNPs). For this chapter, the putatively neutral SNP dataset was analysed, and compared to novel and previous genetic data (mtDNA control-region haplotypes). The sampling design covered the known distribution of the species across Australia and New Zealand, representing one of the largest datasets for small cetaceans utilised for a population genomics study. This chapter is published in *Frontiers and Marine Science* journal, special issue *Small Cetacean Conservation: Current Challenges and Opportunities*. (**Barceló A**, Sandoval-Castillo J, Stockin KA, Bilgmann K, Attard CM, Zanardo N, Parra GJ, Hupman K, Reeves IM, Betty EL, Tezanos-Pinto G, Beheregaray LB and Möller LM (2021) *A Matter of Scale: Population Genomic Structure and Connectivity of Fisheries At-Risk Common Dolphins (Delphinus delphis) From Australasia*. Front. Mar. Sci. 8:616673. doi: 10.3389/fmars.2021.616673). Co-author contributions are stated at the beginning of this chapter.

Chapter III. This research expands from chapter II, where only putatively neutral genomic markers were used, into a comparative analysis of putatively neutral and adaptive variation for the southern Australian regional population. This builds on the main results of the previous chapter that characterised neutral metapopulation structure across Australasia, and focuses on the environmental heterogeneity in southern Australia (i.e. Indian Ocean). This chapter assesses the association between genomic variation and environmental variables to identify signals of selection that might be leading to adaptive divergence between populations. For this, southern Australian common dolphins were extracted from the full metapopulation dataset (Australia and New Zealand) to implement a Bayesian and a Genotype-Environment Association approach, and to assess whether a range of environmental, oceanographic and topographic variables were associated with their genomic variation in different habitats across the region. To the best of my knowledge, this is the first study of common dolphins using a seascape genomics framework.

Chapter IV. In this chapter, the entire Australian metapopulation was assessed, with samples collected from southern and eastern Australia common dolphins. The main objective was to determine if environmental variables were associated with the genomic divergence observed between Australian common dolphin regional populations. To characterise this, putatively adaptive makers were identified based on a seascape genomics and on a Bayesian method. This study expands from the previous chapters of the Australasian metapopulation and on availability of free-ranging samples, focusing on describing the influence of environmental gradients and discontinuities at the Australian-wide metapopulation level (broad-scale), as well and in the eastern Australia segment (fine-scale). The outcomes of this chapter intend to inform managers and policy makers of the potential adaptive capacity of common dolphins, as well as the relevance of connectivity at metapopulation level for appropriate conservation and management of the species in the region.

Chapter V. This chapter is a general discussion about the three data chapters, including neutral and adaptive genomic variation of common dolphins across the hierarchical Australasian metapopulation. Here, I focus on contrasting the results with other species, particularly cetacean species and other large predators. I also discuss the management and conservation implications of the thesis' findings, mostly in relation to common dolphin connectivity within the hierarchical metapopulation structure, which includes putative evidence of localised adaptive divergence disclosed by the seascape genomic analyses. I integrated this discussion with some of the benefits of including both neutral and adaptive genomic datasets for investigating population structure and connectivity in marine species and populations of conservation and management concern.

During my candidature, I also contributed to the laboratory, analytical and written components of a report related to this project, as well as with the laboratory and some analytical components of a population genomic study of another Australasian cetacean species, the killer whale, *Orcinus orca*. These are listed below, and for the report already published, the cover was added to Appendix A.

1) Möller L., **Barceló A.**, Sandoval-Castillo J., Beheregaray L., Hupman K., Betty E., Stockin K.A. *Population structure and size of New Zealand common dolphins*. New Zealand Aquatic Environment and Biodiversity Report, Ministry of Primary Industries, New Zealand. 54pp.

2) Reeves, I. M., J. Totterdell, **A. Barceló**, J. Sandoval-Castillo, K. Batley, K. Stockin, E. Betty, D. Donnelly, R. Wellard, L. B. Beheregaray and L. B. Möller. *Population genomic structure of killer whales (Orcinus orca) in Australian and New Zealand waters*. In review, Marine Mammal Science.

CHAPTER 2. A MATTER OF SCALE: POPULATION GENOMIC STRUCTURE AND CONNECTIVITY OF FISHERIES AT-RISK COMMON DOLPHINS (*DELPHINUS DELPHIS*) FROM AUSTRALASIA

This chapter is published in *Frontiers and Marine Science* journal, special issue *Small Cetacean Conservation: Current Challenges and Opportunities*. (**Barceló A**, Sandoval-Castillo J, Stockin KA, Bilgmann K, Attard CM, Zanardo N, Parra GJ, Hupman K, Reeves IM, Betty EL, Tezanos-Pinto G, Beheregaray LB and Möller LM (2021) *A Matter of Scale: Population Genomic Structure and Connectivity of Fisheries At-Risk Common Dolphins (Delphinus delphis) From Australasia*. Front. Mar. Sci. 8:616673. doi: 10.3389/fmars.2021.616673). A copy of the manuscript in the journal format can be found as part of the Appendix A.

Author contributions

Andrea Barceló Celis - Conceptualization and design of the study, DNA extractions, ddRAD library preparation, mtDNA sequencing, bioinformatics, data analyses, writing of the chapter and corresponding author.

Luciana Möller - primary supervisor - Conceptualization and design of the study, guidance on data analysis and interpretation, collection of samples, and drafting manuscript.

Luciano Beheregaray - associate supervisor- Guidance on data analysis and interpretation, and drafting manuscript.

Kerstin Bilgman - adjunct supervisor - Collection of samples and drafting manuscript.

Jonathan Sandoval-Castillo - Guidance on laboratory methods, bioinformatics, interpretation of analyses and drafting final manuscript.

Karen Stockin - Collection of samples and drafting final manuscript

Catherine Attard - Drafting final manuscript.

Nikki Zanardo - Collection of samples and drafting final manuscript.

Guido Parra - Collection of samples and drafting final manuscript.

Kirsta Hupman - Drafting final manuscript.

Isabella Reeves – Drafting final manuscript.

Emma Betty - Collection of samples.

Gaby Tezanos-Pinto - Collection of samples.

Abstract

An understanding of population structure and connectivity at multiple spatial scales is required to assist wildlife conservation and management. This is particularly critical for widely distributed and highly mobile marine mammals subject to fisheries by-catch. Here, we present a population genomic assessment of a near-top predator, the common dolphin (*Delphinus delphis*), which is incidentally caught in multiple fisheries across the Australasian region. The study was carried out using 14,799 ddRAD sequenced genome-wide markers genotyped for 478 individuals sampled at multiple spatial scales across Australasia. A complex hierarchical metapopulation structure was identified, with three highly distinct and genetically diverse regional populations at large spatial scales (>1,500 km). The populations inhabit the southern coast of Australia, the eastern coast of Australia, and New Zealand and Tasmania, with the latter also showing a considerable level of admixture to Australia's east coast. Each of these regional populations contained two to four nested local populations (i.e. subpopulations) at finer spatial scales, with most of the gene flow occurring within distances of 50 to 400 km. Estimates of contemporary migration rates between adjacent subpopulations ranged from 6 to 25%. Overall, our findings identified complex common dolphin population structure and connectivity across state and international jurisdictions, including migration and gene flow across the Tasman Sea. The results indicate that inter-jurisdictional collaboration is required to implement conservation management strategies and mitigate fisheries interactions of common dolphins across multiple spatial scales in the Australasian region.

Keywords: Delphinids, fisheries genomics, isolation-by-distance, migration, gene flow, metapopulation, conservation genomics.

Introduction

Genetic connectivity and the delineation of populations, including their boundaries, are fundamental issues in conservation biology, because such information can advise on the scale of which to conserve and manage wildlife species (Leslie and Morin, 2016; Taylor et al., 2017; Dunn et al., 2019; Pierre, 2019; Sousa et al., 2019; Taft et al., 2020; Tulloch et al., 2020). Studies using molecular markers can inform on the number and distribution of populations, their genetic diversity, their resilience to environmental change, as well as their vulnerability to anthropogenic impacts and disease outbreaks (DiBattista et al., 2017; Holland et al., 2017; Bradburd et al., 2018; Batley et al., 2019; Breed et al., 2019; Grummer et al., 2019; Jasper et al., 2019; Perry and Lee, 2019; Leitwein et al., 2020). However, incorporating genetic data into conservation policy and management remains a challenge, and enhanced collaboration between conservation geneticists and wildlife managers is needed (Funk et al., 2012; Hendricks et al., 2018; Gardner et al., 2020; Holderegger et al., 2020; Taft et al., 2020).

Studies of population structure and dynamics emerged with the theories of island biogeography and metapopulation dynamics (MacArthur and Wilson, 1967; Levins, 1969; Hanski, 1998), and have evolved since then into characterising connectivity of species among habitat patches in heterogeneous environments under different spatial and temporal scales (Waples and Gaggiotti, 2006; Compton et al., 2007; Manel et al., 2019). In marine environments, there is still limited information about how geographic barriers and spatial scales impact on population genetic structure (Riginos et al., 2016). Population structure and the dispersal of marine species may be associated with a range of factors such as spatial distance, oceanographic features (e.g. currents, upwellings, environmental gradients) and ecological traits (e.g. feeding ecology and life history), making it difficult to disentangle these factors (Selkoe et al., 2016; Bernatchez et al., 2018) and establishing policies for conservation and management.

The movement of marine species with active dispersal, such as delphinids, can occur at any life stage. Despite this, dolphins can exhibit population genetic structure at relatively small spatial scales (e.g. Hoelzel, 1998; Natoli et al., 2006; Möller et al., 2007; Quérouil et al., 2007) and are often subdivided into local populations (e.g. Natoli et al., 2005; Hoelzel et al., 2007; Mendez et al., 2008; Möller, 2011; Caballero et al., 2012; Nykanen et al., 2018; Parra et al., 2018; Pratt et al., 2018). When these populations are interconnected, but exhibit specific ecological and/or behavioural traits in a geographic area, a complex metapopulation system may arise (Riginos et al., 2016; Selkoe et al., 2016; Perry and Lee, 2019).

At large scales, the dispersal and population structure of dolphins is influenced by oceanographic or environmental variables such as depth, currents, upwellings, salinity gradients, sea surface temperatures and primary productivity (Fullard et al., 2000; Natoli et al., 2005; Quérouil et al., 2007; Mirimin et al., 2009; Möller et al., 2011; Amaral et al., 2012a; Bilgmann et al., 2014; Fruet et al., 2014; Gaspari et al., 2015a; Pratt et al., 2018). At smaller scales, localised site fidelity, complex social behaviour and feeding specialisations may result in adaptations to local environments, which leads to further population subdivision (Hoelzel et al., 2007; Möller et al., 2007; Ansmann et al., 2012; Fruet et al., 2014; Cammen et al., 2016; Foote et al., 2016; Zanardo et al., 2017; Pratt et al., 2018).

Common dolphins (*Delphinus delphis*) have a high dispersal potential and inhabit coastal and pelagic environments in temperate and subtropical waters of both southern and northern hemispheres (Natoli et al., 2008; Whitehead et al., 2008; Möller, 2011). In Australasia, common dolphin distribution ranges from embayment and gulf waters, to coastal and shelf waters of Australia and New Zealand (Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014; Mason et al., 2016; Zanardo et al., 2016; Dwyer et al., 2020; Peters and Stockin, 2021). At its most extreme, common dolphins in some semi-enclosed, relatively shallow embayments, show moderate to high site fidelity, such as in Port Phillip Bay (Victoria, Australia), Gulf St Vincent (South Australia) (Filby et al., 2010; Mason et al., 2016), and in the Hauraki Gulf (New Zealand) (Stockin et al., 2008; Hupman, 2016; Hupman et al., 2018; Pawley et al., 2018).

Differences in prey abundance, distribution and diversity can lead to feeding specialisations in common dolphins (Neumann and Orams, 2003), which may shape their population structure at fine and medium spatial scales (Möller et al., 2007; Tezanos-Pinto et al., 2009; Möller et al., 2011). Movements of common dolphins are known to generally associated with the movement of their prey, which includes schooling fish such as jack mackerel (*Trachurus declivis, T. symmetricus, T. murphyi* and *T. novaezelandiae*), blue mackerel (*Scomber australasicus*), sardines (*Sardina sagax*), southern calamari (*Sepioteuthis australis*) and anchovies (*Engraulis australis*) (e.g. Meynier et al., 2008; Goldsworthy et al., 2019a). In turn, most of these prey species are heavily targeted by fisheries, both for human consumption and to feed fish held in aquaculture farms, making common dolphins particularly susceptible to interactions with fisheries and to incidental mortalities (Kemper et al., 2003; Bilgmann et al., 2008; Stockin et al., 2009b).

Indeed, common dolphins in Australasia suffer mortalities as by-catch in multiple fisheries (Hamer et al., 2008; Thompson et al., 2013; Abraham et al., 2017; Tulloch et al., 2020). In Australia, common dolphins are incidentally by-caught in purse-seine, trawl, and gillnet fisheries (e.g. Hamer et al., 2008; AFMA, 2019b), with approximately 380 mortalities recorded in purse-seine nets in 2004-2005 (Hamer et al., 2008), and more than 100 mortalities during 2011-2019 in gillnets (AFMA, 2019a; 2020b). In New Zealand, common dolphins are mainly threatened by trawl and surface long-line fisheries (Abraham et al., 2017; Pierre, 2019), with at least 200 captures occurring from 2002 to 2017 in the trawl fishery (MPI, 2019). While mitigation of common dolphin by-catch in these countries has led to a general reduction in mortalities over time (Rowe, 2007; Ward and Grammer, 2018; Goldsworthy et al., 2019b), by-catch incidents have continued and occasionally spike in numbers (Abraham et al., 2017; Goldsworthy et al., 2019b). Notably, the cumulative impacts of dolphin-fishery interactions are currently unknown (Mackay et al., 2016), and by-catch is still managed separately by each fishery and based on fishing management zones, not based on dolphins' stock structure. These issues are exacerbated by limited information about dolphin abundance in Australasia, and how many dolphins can be caught without compromising the long-term viability of the populations. These estimates of potential biological removal (PBR), have been estimated based on aerial surveys and fisheries surveys. For South Australia, an aerial assessment done over 40,000km^2 led to an estimation of 21,733 common dolphins (CV = 0.25; 95% CI = 13,809-34,203) (Parra et al., in review), while in New Zealand an estimation for the Northern Island was of 18,145 common dolphins (CV =0.33, 95% CI = 9,669-33,726) (Abraham et al., 2017).

In Australasia, common dolphins are known from previous studies to exhibit a degree of population genetic structure (Bilgmann et al., 2007b; Möller et al., 2011; Amaral et al., 2012a; Bilgmann et al., 2014; Zanardo et al., 2016). These studies utilised traditional genetic markers such as mitochondrial DNA (mtDNA) and microsatellites and have identified population genetic differentiation at broad spatial scales (>1,500 km) between common dolphins of the Pacific and Indian Oceans (Amaral et al., 2012a; Bilgmann et al., 2014), as well as over finer spatial scales (<1,000 km; in southern (Bilgmann et al., 2014) and eastern Australia (Möller et al., 2011), and New Zealand (Stockin et al., 2014). However, studies based on a few molecular markers may not be accurate for determining spatial population structure (e.g. Teske et al., 2018; Rajora, 2019). The use of thousands of genome-wide markers circumvents this issue by providing powerful data to clarify spatially complex population structure (Frankham et al., 2010; Funk et al., 2012; Cammen et al., 2016; Teske et al., 2018; Manel et al., 2019).

Here, we assess the population genomic structure of common dolphins using a multi-scale approach across its distribution in Australasia. Our primary aims are to elucidate patterns of genomic diversity, population structure and connectivity using a novel and powerful genome-wide dataset for common dolphins based on single nucleotide polymorphisms (SNPs). We complement this population genomic assessment with analyses of novel and previously published mtDNA sequences. Our study combines broad and fine-scale approaches to resolve structure and connectivity and provides detailed information to enhance the conservation management of common dolphins in Australasia.

Methods

Study area and sampling

The study area encompasses two major oceanic regions, the southern Indian Ocean (Australia's southern coast) and the south-western Pacific Ocean (Australia's eastern coast, Tasmania and New Zealand). Skin samples were collected from live animals (i.e. biopsied) and carcasses (i.e. stranded and by-caught animals) over 17 years (2000-2017) at 16 localities across the species range in Australia and New Zealand (Figure 2.1). Samples from live individuals were obtained using a hand held biopsy pole (Bilgmann et al., 2007a) or a remote biopsy system (PAXARMS) (Krutzen et al., 2002). A total of 510 samples were analysed for population genomics, including 310 biopsy samples and 200 stranding and by-catch samples, with the GPS location allocated to where an individual was found/caught (Figure 2.1).

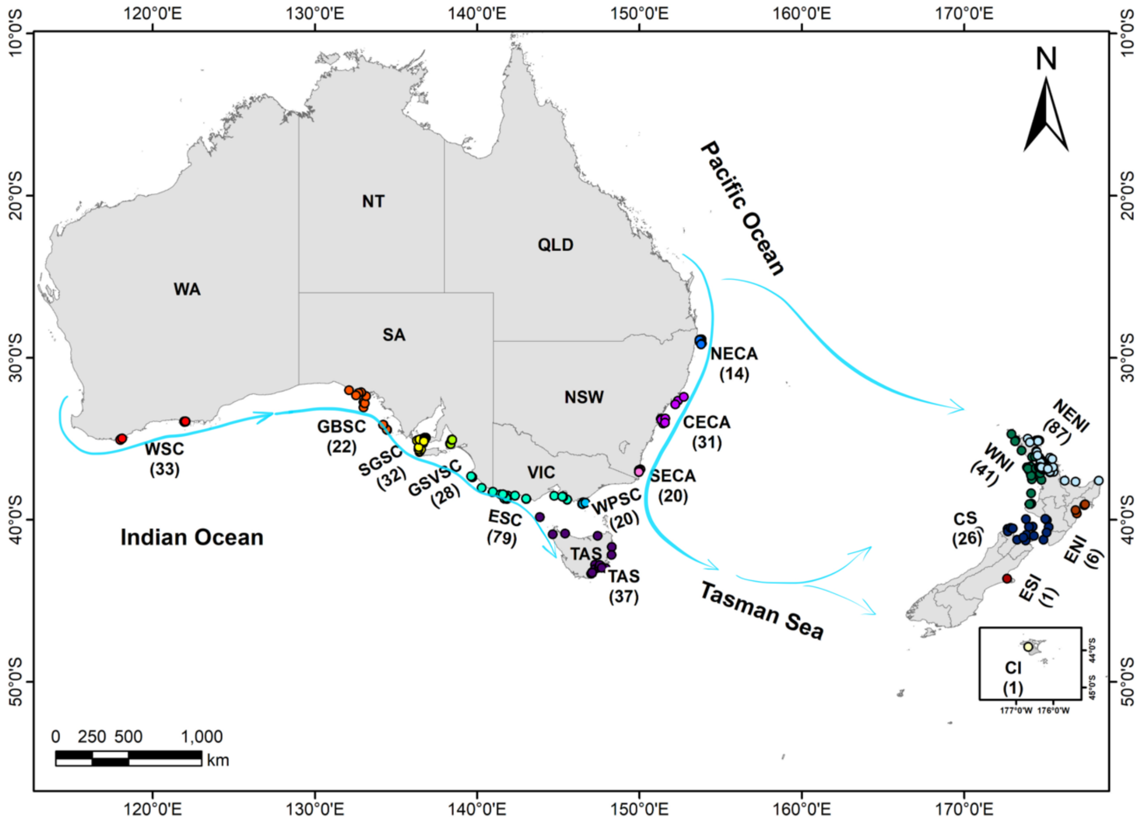


Figure 2.1 Study area in the Australasian region showing the geolocations for 478 common dolphin (*D. delphis*) samples used for the genome-wide analyses. Blue lines correspond to main current systems in Australasia. Acronyms: *West, Southern coast of Australia (WSC); Great Australian Bight, Southern coast of Australia (GBSC); shelf waters in Spencer Gulf, Southern coast of Australia (SGSC); Gulf St Vincent, Southern coast of Australia (GSVSC); East, Southern coast of Australia (ESC); Wilson Promontory, Southern coast of Australia (WPSC); North, Eastern coast of Australia (NECA); Central, Eastern coast of Australia (CECA); South, Eastern coast of Australia (SECA); Cook Strait, New Zealand (CS); West North Island, New Zealand (WNI); North East Island, New Zealand (NENI), East, North Island, New Zealand (ENI); Chatman Island, New Zealand (CI); East, South Island, New Zealand (ESI).

DNA extraction and sex determination

Genomic DNA was extracted from samples using a modified salting out protocol (Sunnucks and Hales, 1996). Extraction quality was then assessed using a NanoDrop-2000 (Thermo scientific) spectrophotometer, quantity estimated by a Qubit 2.0 fluorometer (Life Technologies), and integrity evaluated with agarose gels. If degradation was observed, DNA fragments >5 Kbp were selected using AMPure XP magnetic beads (Beckman Coulter Genomics), using a ratio of 0.8:1 (beads: DNA). The sex was genetically determined by the amplification of fragments of the *ZFX* and *ZFY* genes for all DNA samples, following Banks et al. (1995).

Mitochondrial DNA control region (mtDNA CR) sequencing and data analysis

A fragment of the mtDNA CR of approximately 450 base pairs (bp) was amplified by the polymerase chain reaction (PCR) with primers DLP1.5 and DLP5, as modified by Möller and Beheregaray (2001), and sequenced in an Applied Biosystems 3730XL Sequencer. MtDNA CR sequences were then trimmed and aligned using Geneious v.6.0.4 (Kearse et al., 2012). ARLEQUIN v3.5.2.2 (Excoffier and Lischer, 2010) was used to estimate nucleotide and haplotype diversities overall and for each locality. To assess genetic differentiation between localities, pairwise ϕ_{ST} (Weir and Cockerham, 1984) was estimated with significance assessed using 10,000 permutations False Discovery Rate (FDR = 10%) and corrected for multiple tests by the B-Y method (Benjamini and Yekutieli, 2001). Heatmap plots of pairwise ϕ_{ST} values were then constructed in the language R (R Development Core Team, 2018), with the package ggplot2 (Wickham, 2016). A haplotype network was built in PopART 1.7, using the ancestral parsimony and 95% cut-off (Clement et al., 2002). The latter was carried out to assess evolutionary relationships of the inferred maternal lineages (i.e. mtDNA CR haplotypes). Together with estimates of nucleotide diversity, this provides an indication of long-term evolutionary divergence (or similarity) of common dolphin lineages. A total of 197 samples were sequenced and retained for analysis after filtering out poor quality peaks, and trimming to 440 bp to match the sequence fragments of Möller et al. (2011) (N = 63), Stockin et al. (2014) (N = 24), and Bilgmann et al. (2014) (N = 110). Altogether a total of 394 individual sequences were available for analyses based on mtDNA CR.

Genomic library preparation and ddRAD sequencing

Double digest restriction-site associated DNA (ddRAD) libraries were prepared following Peterson et al. (2012), with modifications. Each sample was digested with two restriction enzymes *SbfI* and *MseI,* and then ligated with one of 96 individual barcodes designed in-house. Samples were then pooled into a multiplex of 12 individuals. Libraries were size selected for 250-800 bp fragments with a Pippin prep electrophoresis gel (Sage Science). The samples were amplified by PCR, and after this removal of PCR by-products was done using AMPure XP magnetic beads (ratio of 0.8:1). Real-time PCR was used to determine the DNA concentration to accurately pool eight libraries of 12 samples together in equal concentrations, creating one multiplex library of 96 uniquely barcoded samples sent for sequencing. The multiplex libraries were then single-end, 100 bp sequenced using multiple lanes in an Illumina HiSeq 2500 at the South Australian Health & Medical Research Institute (SAHMRI).

Sequences and SNP filtering

Sequence quality checks were performed on the raw reads, followed by demultiplexing, trimming of barcodes and RAD tags (only one error allowed) and sorting into individual samples using process_radtags with STACKS v1.48 (Catchen et al., 2013). Next, filtered sequences were processed to generate a final SNP dataset using the dDocent2.2.19 pipeline (Puritz et al., 2014). The resulted variant calling file (VCF), with sequence variation across all samples (raw SNP catalogue), was then filtered using VCFtools (Danecek et al., 2011) (for details see Appendix B). To further assess the quality of the SNP dataset and to exclude exogenous sequences, the quality-filtered reads were mapped against two genomes from closely related dolphin species: the *Tursiops truncatus* genome (Tur_tru_Illumina_phased_v1, GenBank Assembly ID: GCA_003435595.3) and the southern Australian bottlenose dolphin (SABD), *Tursiops aduncus* genome (Batley et al., unpublished). This was done using Bowtie2, following suggested standard procedures from Langmead and Salzberg (2012), allowing no mismatches in seed alignment and up to 20 consecutive seed fails. A linkage disequilibrium (LD) filter was implemented to obtain a dataset with the most likely number of independent markers (for details see Appendix B).

Detecting neutral SNPs

SNPs putatively under selection were identified and removed from the dataset so that population structure analyses were based on markers conforming to neutral expectations (Luikart et al., 2003). This was done using an outlier test in BayeScan v2.1 (Foll and Gaggiotti, 2008) run with 100,000 iterations and prior odds of 10,000. Loci with a false discovery rate <10% were considered as not behaving as neutral and removed from the population analyses.

Relatedness estimates for excluding potential duplicate samples

Relatedness between pairs of individuals was estimated using the triadic likelihood estimator (TrioML) in Coancestry v1.0.1.9 (Wang, 2011) to exclude potential re-sampled individuals (set at $r > 0.7$) from the population analyses. This method estimates pairwise relatedness (r) by using a third individual as a control, thus decreasing the chance of genes identical in state being mistakenly inferred as identical by descent (Wang, 2007).

Genomic Data Analyses

Genomic diversity, population structure and genomic differentiation

Genomic diversity was estimated for each locality sample as expected heterozygosity (H_E), observed heterozygosity (H_O), the inbreeding coefficient (F_{IS}), and percentage of polymorphic loci (P) using Genodive 2.0b27 (Meirmans and Van Tienderen, 2004). Population genetic structure was assessed using a Principal Component Analysis (PCA) and Discriminant Analysis of Principal Components (DAPC) with the R package Adegenet (Jombart and Ahmed, 2011) using an annealing simulation of 50,000 steps, and an optimal number of PCs to be retained, as suggested in Adegenet (Jombart and Collins, 2015). Both PCA and DAPC are model-free approaches for investigating population structure. The Bayesian information criterion (BIC) and Akaike information criterion (AIC) were then used to determine the best-supported number of clusters in the dataset, using the snapclust.chooseK function in the R package Adegenet (Beugin et al., 2018). Bayesian clustering was used to infer population stratification based on estimated individual ancestries using Admixture v1.3.0 (Alexander et al., 2009). This was done by performing a maximum likelihood estimates, using the ancestry portion and the population allele frequency to assign the most likely number of K (e.g. populations) in the dataset, testing for K1-16, and to model the probability of observed genotypes. The maximum likelihood of K and the fast-sequential quadratic algorithm were subsequently used as a cross validation with ten replicates for each K value, using K1-8 (Alexander et al., 2009; Alexander and Lange, 2011). Genetic differentiation among localities was estimated as pairwise F_{ST} (Weir and Cockerham, 1984) using Genodive 2.0b27. Significance levels were assessed using 10,000 permutations (FDR = 10%), and then corrected by the B-Y method. Heatmap plots of F_{ST} were constructed with the R package ggplot2. A Mantel test (Mantel, 1967) was used to test for isolation by distance (IBD) using the shortest waterway distance matrix calculated in ArcMap v10.4 (Esri Inc., Redlands, CA) and a linearised pairwise F_{ST} matrix (F_{ST} /1- F_{ST}) as genetic distance. Scatterplots were then generated with the R package Adegenet.

Contemporary migration rates and first-generation migrants

Contemporary migration rates were estimated with BayesAss v3.0.4 (Wilson and Rannala, 2003) using the putatively neutral, unlinked SNPs. The method applies a Bayesian Markov chain Monte Carlo approach to estimate asymmetrical rates of recent migration (m), which represents the proportion of each population having migrant ancestry over the last generations. Common dolphins exhibit a long generation time ~15 years, with interbirth intervals from 1-3 years (Taylor et al., 2007; Möller, 2011). The analysis was run with 10 million iterations and 1 million iterations as burn-in, and mixing parameters (allele frequencies, inbreeding coefficients and migration rates) were adjusted to achieve recommended acceptance rates (Wilson and Rannala, 2003). Convergence was then inspected by plotting the cumulative log likelihoods of the iterations using TRACER 1.7 (Rambaut et al., 2018), with three runs used to verify consistency across runs.

First generation migrants were identified by performing a population assignment test in GeneClass2 (Piry et al., 2004), using the criteria of Rannala and Mountain (1997). This uses the multilocus genotypes and 1,000 simulations to provide a probability of an individual belonging to a population (Paetkau et al., 2004). An exclusion rate of 0.01 was applied. Only 800 SNPs were used due to the limitations of the software which only allowed successful runs to this maximum number of SNPs. The SNP subset was chosen using a random generator in R studio, and extracted from the full dataset of filtered putatively neutral SNPs.

Results

Diversity and differentiation based on mtDNA CR

In the 440 bp of the mtDNA CR sequences of 394 Australasian common dolphins, three indels and 94 substitutions were observed. This resulted in 173 unique mtDNA haplotypes, 66 of which were not previously described for common dolphins in this region (Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014). Most haplotypes were represented by only one individual in the dataset. The overall haplotype diversity was high (*h* = 0.860), while the nucleotide diversity was low ($\pi = 0.0160$) (Appendix B, Table B.4). The haplotype diversity observed was similar to that previously reported for the eastern and southern Australia and for New Zealand (e.g. Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014). Fixation indices based on mtDNA CR indicated low to moderate differentiation between samples from the Pacific and the Indian Ocean (0.029 - 0.620) (Appendix B, Figure B.2; Table B.7). The haplotype network indicated very shallow phylogeographic structure (Appendix B, Figure B.3).

Genome-wide SNP data and filtering for putatively neutral loci

A total of 1,601,109,786 raw sequence reads were obtained, and a raw SNP catalogue of 339,932 SNPs (Appendix B, Table B.1). The alignment rates with the *Tursiops* genomes were very high, attesting to the high quality of the SNP dataset: 97% aligned with the *T. truncatus* genome and 99% with the SABD *T. aduncus* genome (retaining 26,199 SNPs, Appendix B, Table B.1). Filtering with stringent criteria resulted in a high-resolution dataset of 17,875 SNPs (Appendix B, Table B.1). The outlier test detected 3,076 SNPs likely not behaving as neutral, and these were excluded from the total dataset. This final dataset included 14,799 unlinked, putatively neutral SNPs (Appendix B, Table B.1; Figure B.1) that were used for the population structure analyses and to estimate migration rates.

Exclusion of duplicate samples

Thirty-two sample pairs were estimated as likely originating from duplicate individuals ($r \geq 0.7$), including twenty-four pairs of biopsies and eight pairs of stranding or by-caught individuals. One sample from each of the pairs was excluded, resulting in a final dataset of 478 individuals (Figure 2.1).

Genomic diversity, population structure and genomic differentiation

Genome-wide diversity was relatively high for all localities (Table 2.1) and there was no indication of population-level inbreeding (Table 2.1). When analysing all samples combined, PCA and DAPC analyses suggested three distinct regional populations: (1) southern coast of

Australia; (2) eastern coast of Australia; and (3) New Zealand and Tasmania, although the latter shows a degree of admixture to Australia's eastern coast (Appendix B, Figures B.5; B.6). Admixture analysis suggested a hierarchical metapopulation structure in Australasia, with moderate levels of admixture within the regional populations (Figures 2.2, Appendix B, Figure B.7). At a metapopulation level, three clusters (K=3), corresponding to geographical regional populations, were considered most likely (Figure 2.2). The membership probability of an individual belonging to a population varied according to the geographic position of the locality, with individuals from localities close to the interface between the Indian and Pacific Oceans (i.e. Wilsons Promontory in Victoria and southern localities in New South Wales, Australia), and between Tasmania and Australia's eastern coast being more admixed (Appendix B, Figure B.7a).

Further subdivision was disclosed within each regional population, when analysing the three datasets separately, with two additional clusters (K=2) within each region (Figures 2.2; Appendix B, Figure7b-d) best supported, but three and four clusters also highly supported for eastern and southern Australia (Figures 2.2, Appendix B, Figure B.7b-d), respectively. In the southern coast of Australia, the strongest separation was disclosed between individuals from Gulf St Vincent and the other localities, followed by Wilsons Promontory compare to the west coast individuals. In the case of Australia's eastern coast, the northern localities were most distinct from the central-south localities, with a greater proportion of admixed individuals in the central localities, possibly representing a further sub-population. For New Zealand and Tasmania, differentiation was disclosed mainly between localities in the east coast and west coast of New Zealand, with Tasmanian individuals considerable admixed. However, most of the Tasmanian common dolphins showed higher probability of assignment to the New Zealand population (~57%) based on Admixture's Q-values (>0.8), and DAPC results (Appendix B, Figures B.6; B.7), and were therefore considered primarily part of the New Zealand regional population.

Table 2.1 Measures of genomic diversity based on 14,799 SNPs for Australasian common dolphins (*D. delphis*) by locality*. Observed heterozygosity (H_O), expected heterozygosity (H_E), inbreeding coefficient (F_{IS}), percentage of polymorphic loci (P%). NA: not applicable (due to only one sample available).

Population	**Locality**	**N**	**H_o**	**H_E**	**F_{IS}**	**P%**
SC	WSC	33	0.169	0.172	0.015	73.295
	GBSC	22	0.170	0.176	0.032	74.816
	SGSC	32	0.172	0.172	0.000	81.053
	GSVSC	28	0.154	0.160	0.037	59.862
	ESC	79	0.170	0.176	0.033	91.155
	WPSC	20	0.175	0.181	0.033	71.005
EC	NECA	14	0.189	0.189	-0.001	58.862
	CECA	31	0.209	0.209	-0.003	80.587
	SECA	20	0.201	0.209	0.037	67.126
NZTAS	TAS	37	0.209	0.209	0.002	93.614
	CS	26	0.207	0.208	0.004	82.215
	WNI	41	0.204	0.206	0.013	87.209
	NENI	87	0.194	0.200	0.031	85.134
	ENI	6	0.179	0.190	0.061	52.760
	CI	1	NA	NA	NA	NA
	ESI	1	NA	NA	NA	NA
Total average		*29.875*	*0.186*	*0.190*	*0.021*	*75.621*
Total SD			*0.018*	*0.017*	*0.019*	*12.523*

*Southern coast of Australia (SC), Eastern coast of Australia (EC), Tasmania (TAS) and New Zealand (NZ). West, Southern coast of Australia (WSC); Great Australian Bight, Southern coast of Australia (GBSC); shelf waters in Spencer Gulf, Southern coast of Australia (SGSC); Gulf St Vincent, Southern coast of Australia (GSVSC); East, Southern coast of Australia (ESC); Wilson Promontory, Southern coast of Australia (WPSC); North, Eastern coast of Australia (NECA); Central, Eastern coast of Australia (CECA); South, Eastern coast of Australia (SECA); Cook Strait, New Zealand (CS); West North Island, New Zealand (WNI); North East Island, New Zealand (NENI), East, North Island, New Zealand (ENI); Chatman Island, New Zealand (CI); East, South Island, New Zealand (ESI).

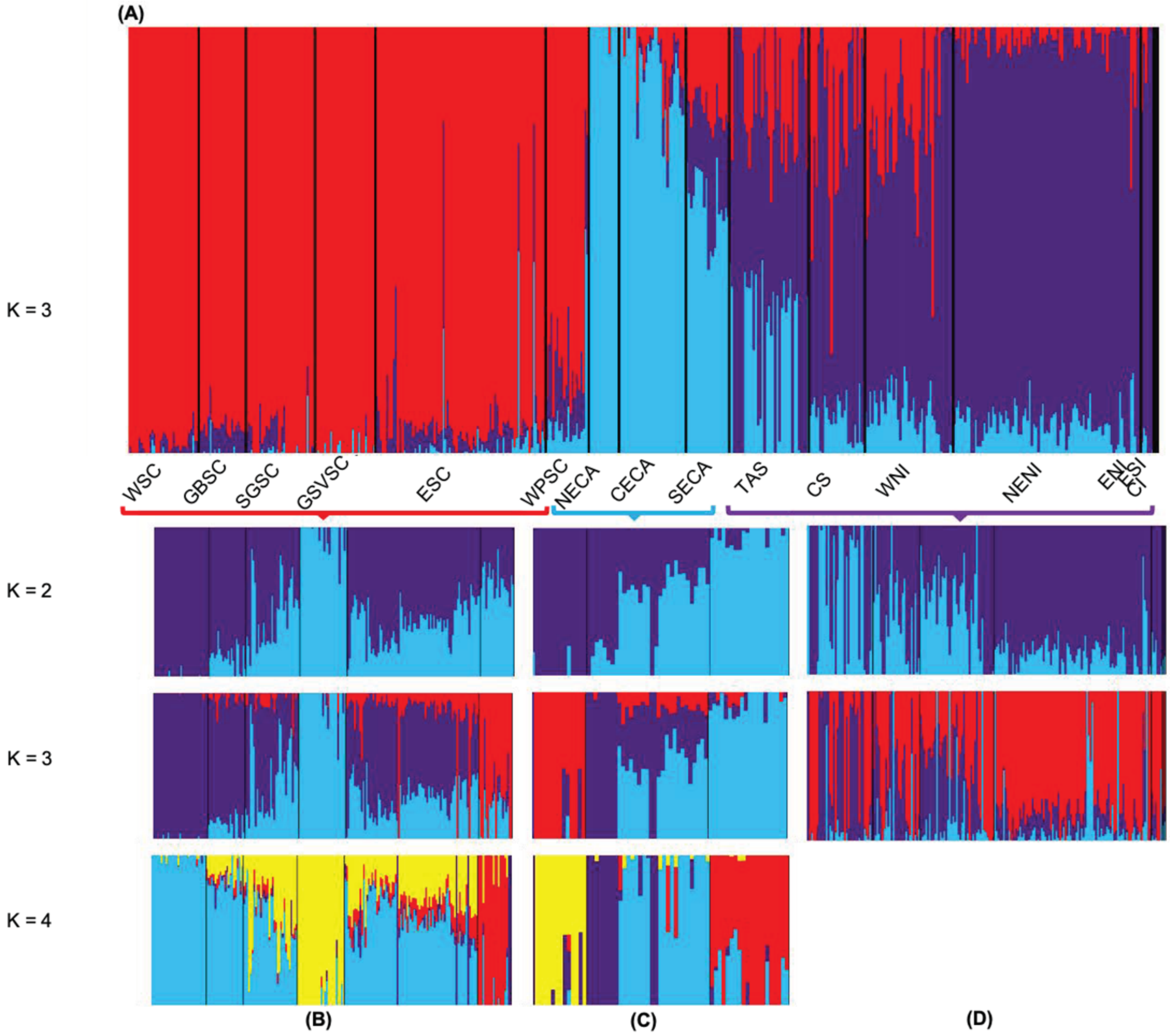


Figure 2.2 Population genomic structure analysis using Admixture based on 14,799 SNPs for Australasian common dolphins (*D. delphis*). The results depict levels of admixture for each individual sample and grouping into two and/or three genomic clusters. Each sample (labelled by geographic sample groups in the x axis) is represented by one vertical line and is colour-coded by the membership probability to **(A)** one of the three regional populations in Australia and New Zealand or **(B-D)** one of the potential local populations of the: **(B)** Southern coast of Australia; **(C)** Eastern coast of Australia; or **(D)** New Zealand and Tasmania. *Acronyms used as in Figure 2.1.

Fixation indices indicated moderate genetic differentiation between the southern coast of Australia (SCA), eastern coast of Australia (ECA) and the New Zealand/Tasmania (NZT) regional populations (SCA vs ECA = 0.060-0.213; SCA vs NZT = 0.045-0.142; ECA vs NZT = 0.018-0.142) (Figure 2.3a, Appendix B, Table B.6). In contrast, low genetic differentiation was observed between common dolphin subpopulations (Figure 2.3b-d). In the southern coast of Australia, the highest differences of F_{ST} were between Gulf St Vincent, Wilsons Promontory, and west southern coast versus the other localities; whereas for the eastern coast of Australia, the northern localities showed the highest differentiation compared to the southern localities, followed by the central localities versus the northern and southern localities. For New Zealand/Tasmania, the differentiation occurred between West coast of New Zealand/Tasmania versus the localities from the east coast of New Zealand (Figure 2.3; Appendix B, Figure B.8).

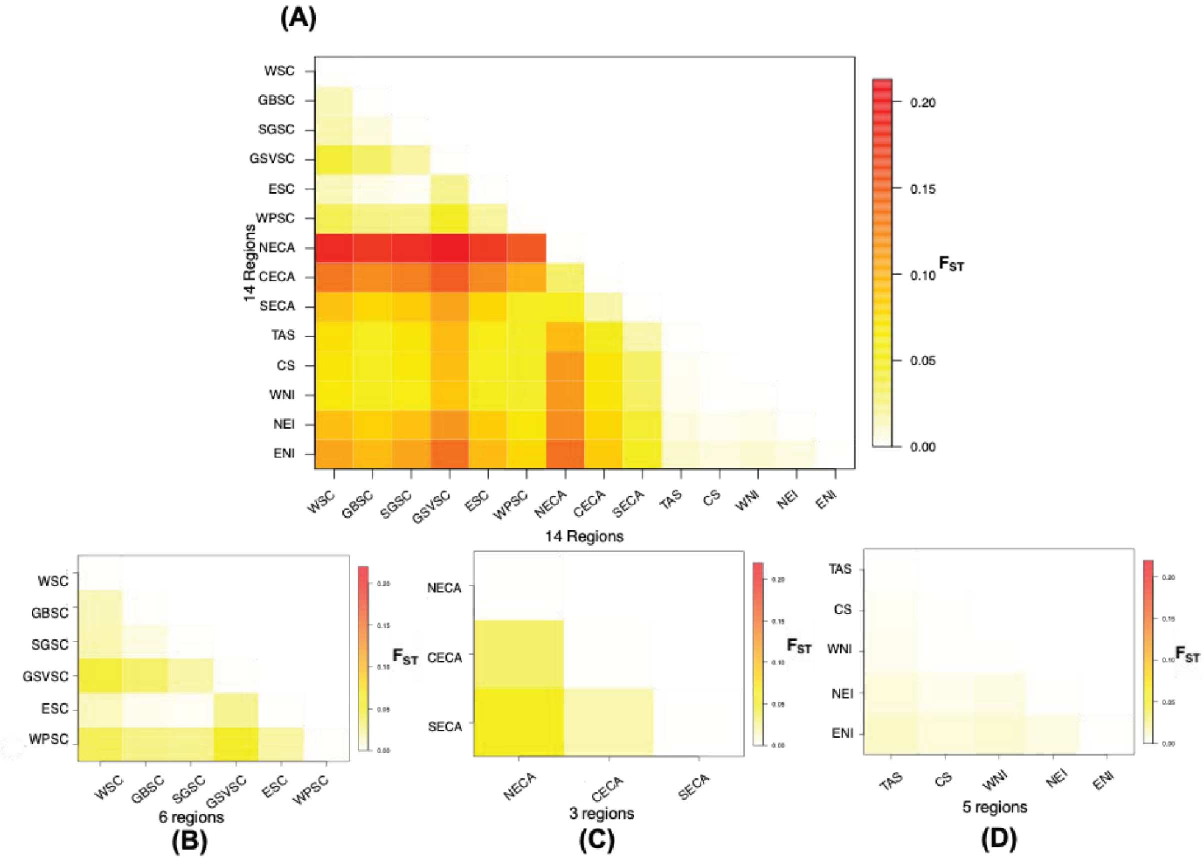


Figure 2.3 Heatmap of pairwise F_{ST} values between localities based on 14,799 SNPs for Australasian common dolphins (*D. delphis*); (A) Australia and New Zealand; (B) Southern coast of Australia; (C) Eastern coast of Australia; and (D) New Zealand and Tasmania. *Acronyms used as in Figure 2.1.

A significant signal of IBD was observed at the metapopulation level ($r^2 = 0.084$, $p = 0.003$) (Figure 2.4a), and for the populations from the southern and eastern Australia ($r^2 = 0.346$, $p = 0.001$; $r^2 = 0.742$, $p = 0.03$, respectively). In contrast, there was no evidence of IBD in the New Zealand and Tasmania regional population ($r^2 = 0.005$, $p = 0.615$) (Figure 2.4b-d).

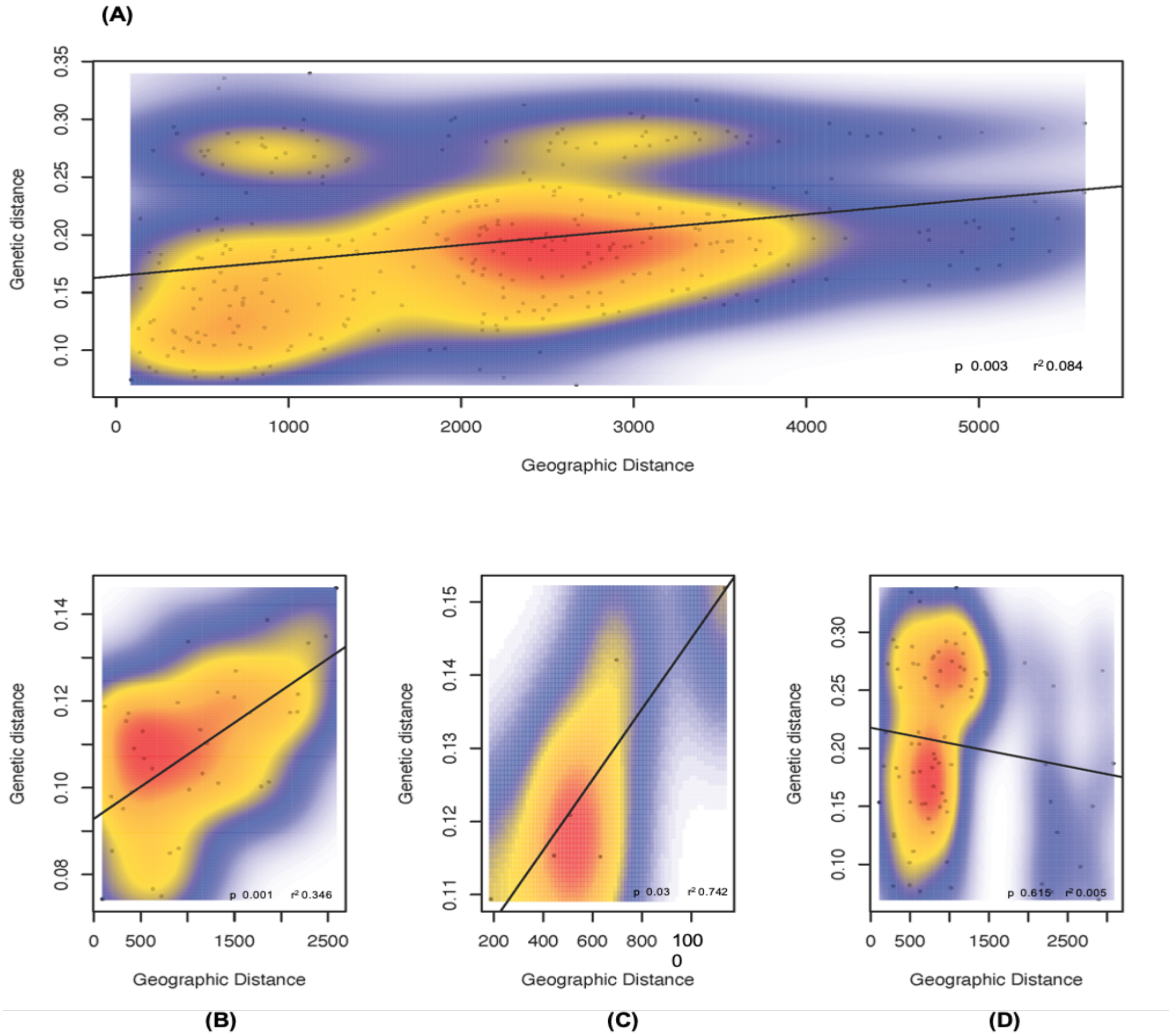


Figure 2.4 Isolation by distance between F_{ST} values and the shortest waterway distance based on 14,799 SNPs for Australasian common dolphins (*D. delphis*). (A) Australia and New Zealand metapopulation; and regional populations, (B) Southern coast of Australia, (C) Eastern coast of Australia, and (D) New Zealand and Tasmania.

Contemporary migration rates and first-generation migrants

Estimates of contemporary migration rates based on BayesAss, that provide inferred rates of the portion of recent immigration over the last generations, indicated asymmetric migration between population pairs (Figure 2.5; Appendix B, Table B.2). There were relatively low estimates of migration (2-9%) between pairs of the three main regional populations, and moderate estimates of migration (6-25%) between pairs of the two subpopulations (Figure 2.5). First-generation migrants were detected in GeneClass between the three main regional populations, with 14 individuals rejected ($p < 0.01$) from the population they were sampled in

(Appendix B, Table B.3). These individuals were retained in all the population analyses to provide a representative picture of the metapopulation dynamics (Appendix B, Table B.3).

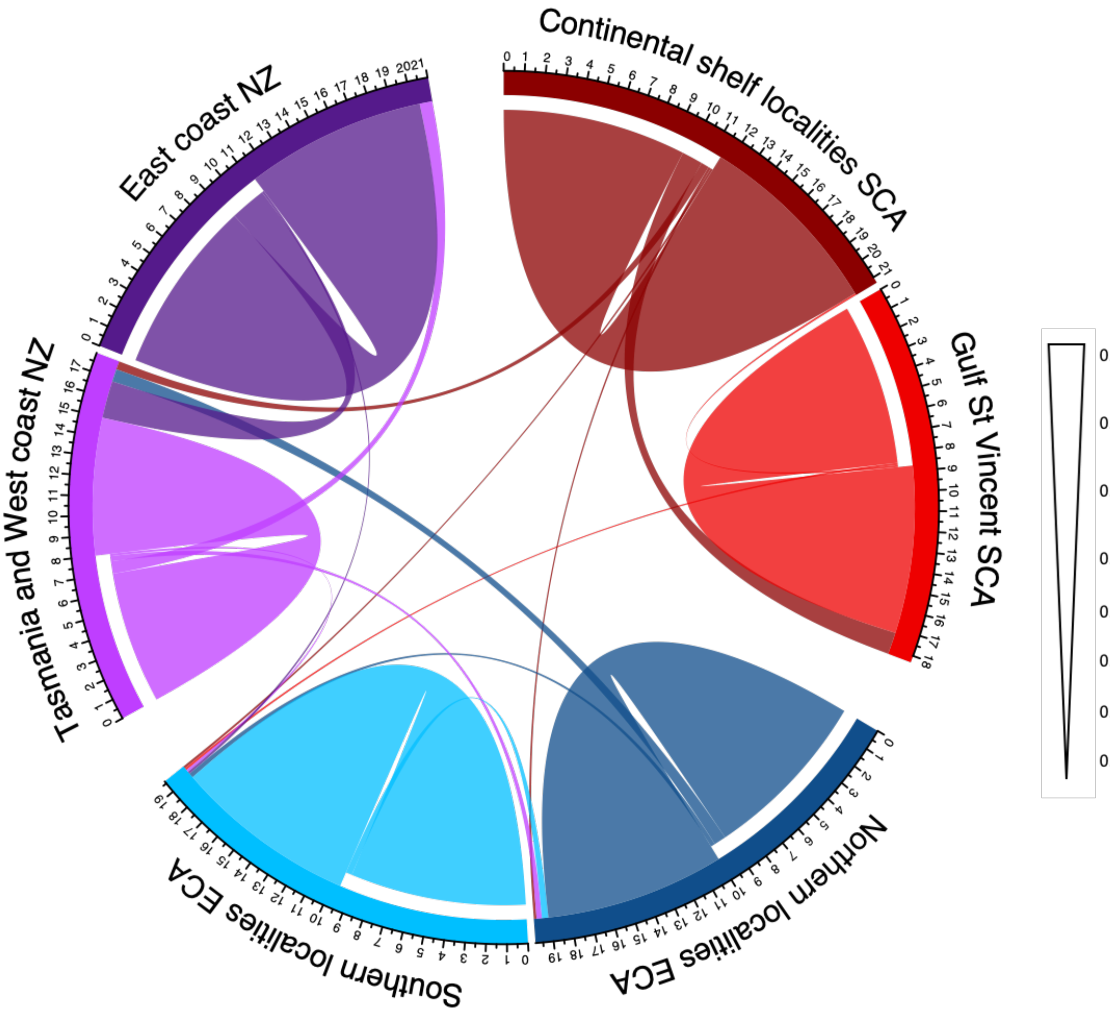


Figure 2.5 Circos plot of inferred contemporary migration rates (per last generations) between local populations of Australasian common dolphins (*Delphinus delphis*) based on 14,799 SNPs. Plot corresponds to the migration directionally (full values from BayesAss are provided in Appendix B, Table B.2). Width of the curves indicates the amount of migration according to the scale going from one subpopulation into another one. Scale bar is in units of the proportion of migrations. Ticks represent the gross number of migrants per 100s. Migration rate < 0.01 is not shown. *Southern coast of Australia (SCA), Eastern coast of Australia (ECA), New Zealand (NZ).

Discussion

The delineation of populations and their respective geographic boundaries, as well as estimation of the degree of connectivity between populations are crucial for the conservation management of small cetaceans (Rosel et al., 2017; Taylor et al., 2017; Dunn et al., 2019; Pierre, 2019; Sousa et al., 2019; Taft et al., 2020). Integrating genomic technology for answering these questions can inform about the dolphin populations and scale at which anthropogenic activities may impact upon them (e.g. Leslie and Morin, 2016). Genomic analyses also provide baseline information for design of further studies and the monitoring of populations; for example, the area at which to estimate population abundance and trends, data on parameters for modelling population persistence, and for estimating sustainable by-catch rates (Waples and Gaggiotti, 2006; Allendorf et al., 2010; Frankham et al., 2010; Grummer et al., 2019; Manel et al., 2019).

This study revealed a hierarchical metapopulation structure for Australasian common dolphins, with high levels of genome-wide diversity and negligible inbreeding among them. At a broad scale, the southern Indian Ocean was represented by a single regional population inhabiting the southern coast of Australia. The south-west Pacific Ocean was represented by two regional populations, one along the eastern coast of Australia and the other in New Zealand/Tasmania, which suggests substantial connectivity across the Tasman Sea. Further subdivision was disclosed at finer scales, with evidence for at least two subpopulations within each regional population, but perhaps more. The varying levels of population connectivity identified across inter-state and international jurisdictions, have substantial implications for the conservation and management of common dolphins, which are subject to interactions and mortalities in multiple fisheries in the region.

Population structure of Australasian common dolphins

Studies investigating genetic partitioning at fine spatial scales in the sea usually provide evidence for distinct subpopulations, whereas metapopulations are generally disclosed when broader spatial scales are explored (Pitt and Kingsford, 2000; Dawson et al., 2014; Calò et al., 2016; Almany et al., 2017; Jasper et al., 2019). Nonetheless, sampling effort often makes it difficult to assess marine systems over broad scales, and as a consequence metapopulations may remain largely undisclosed (Manel et al., 2019). We assessed the population structure of common dolphins over a broad geographical area and revealed a hierarchical metapopulation structure across Australasia. Metapopulations have also been described for other dolphin species, such as spinner dolphins (*Stenella longirostris*) among Pacific Islands (Oremus et al., 2007), Hector's dolphins (*Cephalorhynchus hectori hectori*) between the west and east coasts of New Zealand (Heimeier et al., 2018), bottlenose dolphins (*Tursiops truncatus*) in the North Atlantic Ocean and Mediterranean Sea (Louis et al., 2014b; Gaspari et al., 2015b), and Indo-Pacific bottlenose dolphins (*T. cf. australis*) in southern Australia (Pratt et al., 2018). Although our sampling took place over 17 years, we believe there was little impact on the population genetic structure disclosed given than common dolphins exhibit a long generation time (~15 years; Taylor et al., 2007). In addition, we found similar patterns of genomic diversity for sites sampled in multiple years, and similar levels of genomic differentiation between sites sampled in same and different years (data not shown).

At a broad scale, Australasian common dolphins showed moderate genomic differentiation at the level of the two ocean basins investigated, the Indian and Pacific Oceans. The mtDNA dataset provided enough resolution to distinguish historical population structure between the two oceans basins, as previously demonstrated in other genetic studies of common dolphins (e.g. Amaral et al., 2012a; Amaral et al., 2012b), bottlenose dolphins (*T.* spp.) (e.g. Tezanos-Pinto et al., 2009; Charlton-Robb et al., 2011), and killer whales (*Orcinus orca*) (e.g. Reeves et al., in review). This regional distinction was also clear based on analyses of the SNP dataset. In Australia, we found pronounced genomic divergence between common dolphins of the southern coast, the eastern coast, and Tasmania. This split was evident along the Wilsons Promontory, which was once a land-bridge (the Bassian Isthmus, ~14,000 ybp), which connected mainland Australia with Tasmania (Waters, 2008; Condie et al., 2011). The Wilsons Promontory region has been described as a prominent biogeographic boundary for many marine species (e.g. invertebrates, algae, small pelagic fish), accounting for many of the genetic discontinuities observed today along these coastlines (York et al., 2008; Teske et al., 2015; Costello et al., 2017; Teske et al., 2017).

An oceanographic perspective can also assist the interpretation of the pattern of regional genomic differentiation inferred in this study. The East Australian current (EAC) flows from the western boundary current into a southward direction, bringing warm and productive waters along the coast. The EAC is dominated by anticyclonic eddies, that creates three different water masses, and gradients of oceanographic variables along the coast, represented by northern, central and southern areas (Suthers et al., 2011). It then becomes weaker as it enters Tasmania and diverges eastward into New Zealand via the Tasman Front, where upwelling occurs mainly on the west coast (York et al., 2008; Flynn et al., 2018). These may impact on common dolphin movements along the eastern Australian region, leading to the pattern of local differentiation (Möller et al., 2011) and Tasman Sea regional separation.

The warm Leeuwin current runs south from western Australia into the southern coast of Australia. It then becomes the Great Australian Bight current, and later the Zeehan current, which extends from western Victoria into western Tasmanian waters, excluding the Bass Strait where currents in shallow waters tend to follow an eastward direction (York et al., 2008; Kämpf, 2015). Likewise, these currents may impact on common dolphin movements along the southern Australian region, leading to the proposed differentiation at finer scales. The Zeehan current is weaker, and during the summer it is replaced by the cold Flinders current that enters from the west coast of Tasmania into the southern coast of Australia, bringing productive waters towards the continental shelf and leading to upwelling events (York et al., 2008; Lynch et al., 2014; Kämpf, 2015; Flynn et al., 2018). These complex oceanographic features cause variations in primary and secondary productivities along the two Australian coasts and in Tasmania, and may act as contemporary barriers that maintain historical divisions between marine organisms (Waters, 2008; Condie et al., 2011; Teske et al., 2017). While common dolphins have a high dispersal capability, their distributions are known to associate closely with that of their prey movements (e.g. Bilgmann et al., 2008; Meynier et al., 2008; Natoli et al., 2008; Zanardo et al., 2016; Peters et al., 2020), which may coincide with areas of high primary productivity along the two Australian coasts, as well as in New Zealand and Tasmania.

Previous population genetic studies of common dolphins based on microsatellite DNA markers suggested five subpopulations along the southern coast of Australia, including Tasmania (Bilgmann et al., 2014), three in the eastern coast of Australia (Möller et al., 2011), and three in New Zealand (Stockin et al., 2014), with the last two studies not including samples from Tasmania. At finer spatial scales, the genetic differences disclosed in our study suggested further subdivision within the identified Australasian regional populations. Two additional sub-populations were disclosed for New Zealand/Tasmania, two to four in southern Australia, and two to three in eastern Australia. These could potentially be explained by geological and oceanographic features (as mentioned above) reflecting on the contemporary population and feeding ecology of common dolphins. In the Australasian region, common dolphins are mainly found along continental shelf waters between the 20 and 200 m isobaths (Stockin et al., 2008; Möller et al., 2011; Stockin et al., 2014; Meissner et al., 2015; Bilgmann et al., 2018; Peters and Stockin, 2021). By contrast, in the Gulf St Vincent, common dolphins are present in relatively shallow, protected waters (~20 m) of the inner gulf (Appendix B, Figure B.4), with seasonal circulation year-round and may represent a resident population (Filby et al., 2010; Kämpf and Bell, 2014). The geological formation during the Cenozoic, established the Gulf St Vincent and Spencer Gulf as inverse estuaries (Bourman et al., 2016). These unique formations provide highly productive ecosystems, offering shelter for common dolphin prey species, such as sardines (*S. sagax*) and anchovies (*E. australis*) (Filby et al., 2010; Kämpf and Bell, 2014). These characteristics may have impacted on site fidelity of dolphins to this area and over time leading to genetic differentiation of Gulf St Vincent animals to those outside the gulf.

In the case of the eastern Australia, the northern localities are oceanographically and biologically differentiated due to the presence of a distinct water mass (Keane and Neira, 2008; Suthers et al., 2011). This could affect the distribution of common dolphins if they feed upon particular fish assemblages (Möller et al., 2011), and in turn lead to restricted movement and genetic differentiation between subpopulations. Common dolphins along the continental shelf of southern and eastern Australia presented a strong signal of IBD, a finding consistent with other common dolphin studies carried out across different ocean basins (Amaral et al., 2012a; Bilgmann et al., 2014). With the use of genomic markers, the pattern of IBD was also disclosed in this study at smaller spatial scales.

In the New Zealand and Tasmania regional population, genetic subdivision was found between the west and east coasts of New Zealand. This pattern between west and east coast subdivision has also been reported for Hector's dolphins that inhabit the southern island of New Zealand (Heimeier et al., 2018). Common dolphins from the west coast of New Zealand and Tasmania appear to comprise a subpopulation exhibiting moderate gene flow to dolphins on New Zealand's east coast and, to a lesser extent, with populations in Australia's eastern coast. The latter could also be due to historical factors. After the last glacial cycle (12,000-120,000 ybp) (Ashe and Wilson, 2019), subpopulation differentiation of dolphins across the Tasman Sea could have occurred due to habitat preferences and changes in prey availability. In New Zealand, differences in major currents, such as the east and the west Auckland current in the North Island, and the D'Urville current in the Cook Strait (Ayers and Waters, 2005; Ross et al., 2009; Chiswell et al., 2015), may influence fish distribution (Papa et al., 2020), and could have also led to restrictions on dolphin movement, and subsequent genetic differentiation.

Contemporary migration within and between ocean basins

In an idealised population, individuals that are closer to each other, are genetically more similar than individuals that are further apart (Hanski, 1998). This may lead to a pattern of IBD, which was a common finding of the study across both broad and fine spatial scales. Migration of individuals between populations can also be shaped by intrinsic and extrinsic factors, promoting genetic discontinuities across heterogeneous environments (Armansin et al., 2019; Grummer et al., 2019; Rajora, 2019). For example, individuals may be unable or unlikely to disperse across physical or environmental barriers, and thus gene flow between populations may become compromised (Armansin et al., 2019). The estimated migration rates were relatively small between ocean basins (i.e. Pacific and Indian Oceans) and the regional populations (i.e. Southern Australia, Eastern Australia and New Zealand/Tasmania, as described above) (<6%), separated by strong oceanographic discontinuities (i.e. unique biogeographic region in the Bassian Isthmus (Waters et al., 2010; Teske et al., 2017) (Figure 2.5). By contrast, estimated migration rates between subpopulations within ocean basins and between more homogeneous environments were higher (<18%). The migration rates and the number of first-generation migrants identified support the idea that genetic connectivity mainly occurs between subpopulations nested within regional populations. This suggests that if an extinction event was to occur, by either natural or anthropogenic causes, a subpopulation's home range will more likely be recolonised by individuals from within that region (e.g. Sandoval-Castillo et al., 2018; Riginos et al., 2019; Waters et al., 2020). However, if such events are strong enough to prevent gene flow and change the availability of prey resources, the subpopulation could decline without replacement. These types of events have been recorded for common dolphin populations from the Mediterranean Sea, which suffered dramatic declines due to combined impacts from by-catch mortalities, reduction of prey availability, and habitat degradation (Genov et al., 2020).

It appears that, in addition to spatial distance, heterogeneous marine environments found across the distribution of Australasian common dolphins have led to low and moderate connectivity between and within regional populations, respectively. In southern Australia, gene flow is restricted from continental shelf waters to Gulf St Vincent (~5%). This protected environment allows common dolphin prey species to be locally available throughout the year (Filby et al., 2013; Ward et al., 2017; Goldsworthy et al., 2019a). The year-round availability of food resources could influence the feeding behaviour of the common dolphins, maximising their energy efficiency due to a lesser need for long-range movements, and perhaps increase reproductive success and lifetime fitness. All of these could lead to high site fidelity and residency by common dolphins to Gulf St Vincent, which while rare for the species, has been suggested for other semi-enclosed embayments in Australia, such as Port Philip Bay (Mason et al., 2016), and the Hauraki Gulf in New Zealand (Peters et al.2020; Stockin et al., 2008; Stockin et al., 2009a; Hupman, 2016). These characteristics, which may have led to genetic divergence of the Gulf St Vincent dolphins, also make them particularly at risk of decline due to interactions with fisheries in Gulf St Vincent and Investigator Strait (Hamer et al., 2008; Goldsworthy et al., 2019b).

In eastern Australia, stronger differentiation of common dolphins from the northern and southern localities translated in the lowest estimated migration rates (~3%) between any two subpopulations in Australasia. In this area, the EAC creates eddies, which act as barriers for eggs and larval fish (Condie et al., 2011; Suthers et al., 2011). Thus, given the close association of common dolphins' distribution to that of their prey, these circulation patterns and differences in water masses could potentially act as oceanographic barriers for dolphin movements and gene flow (Möller et al., 2011).

Within the New Zealand and Tasmania population, moderate migration rates were estimated between the two subpopulations (~18%). Migration here was strongly asymmetric, occurring mostly from the east into the west coast of New Zealand. Along the east coast of New Zealand there are several habitats (e.g. Hauraki Gulf), which have been proposed as breeding and calving grounds for groups of common dolphins (Stockin et al., 2008; Dwyer et al., 2020). In this regional population, New Zealand's east coast appears to be acting as a genetic source, while the west coast, which presents higher rates of dolphin mortality due to fisheries (Thompson et al., 2013; Abraham et al., 2017), may be acting as a sink, similar to source-sink dynamics observed in other marine species (e.g. Benestan et al., 2016a; DiBattista et al., 2017; Lal et al., 2017; Manel et al., 2019). Interestingly, Tasmania in Australia and the west coast of New Zealand displayed high connectivity over more than 1,000 km across the Tasman Sea, and genetic signatures show that individuals from western New Zealand are also found in Tasmanian waters. However, to the best of our knowledge, movements of common dolphins over long distances (~1,000 km) have only been document across the Mediterranean Sea through photo-ID (Genov et al., 2012). Similar patterns of connectivity across the Tasman Sea have been disclosed for other marine species, such as teleosts and invertebrates (e.g. *Hippocampus abdominalis, Hoplosthethus atlanticus, Nerita melanogastrus*) (Cumming et al., 2016; Flynn et al., 2018; Ashe and Wilson, 2019; Gardner et.al. unpublished). Historically, dispersal of marine species across the Tasman Sea seems to have occurred during the last glacial cycle (12,000-120,00 ybp), leading to the colonization of multiple areas by marine species in both countries (Ashe and Wilson, 2019). However, contemporary genetic connectivity seems to have been retained by oceanographic currents (Flynn et al., 2018). Further sampling and assessment of common dolphins from Tasmania may clarify whether this represents a contact area, and if they should be considered as a separate or combined unit for management with New Zealand. The latter would involve cross jurisdictional cooperation between policy makers.

Implications for conservation and management of Australasian common dolphins

Common dolphins in Australasia are mainly threatened due to by-catch in commercial fisheries (Abraham et al., 2017; Tulloch et al., 2020), and potentially by anthropogenic-associated competition for food resources. In Australia, incidental by-catch has occurred mainly in trawl fisheries and purse-seine fisheries that catch mackerel (*T. declivis, T. s. murphyi, T. novaezelandiae* and *S. australasicus*) and sardines (*S. sagax)*, as well as in gillnet fisheries targeting gummy sharks (*Mustelus* sp.) (Australian Goverment, 2019b). In New Zealand, the observed incidental by-catch of common dolphins occurs mainly in mid-water trawl fisheries that catch the same mackerel species (Thompson et al., 2013; Abraham et al., 2017). However, by-catch within recreational set nets has also been documented as a threat to these dolphins (Stockin et al., 2009b). These incidental catches are known to have resulted in mortalities of hundreds of common dolphins in at least two of these fisheries (Abraham et al., 2017; Goldsworthy et al., 2019b). High mortalities were disclosed in 2004-2005 in the South Australian Sardine Fishery (SASF) (Hamer et al., 2008), likely exceeding the potential biological removal of individuals for one of the population's segment (Parra et. al., in review). For New Zealand, an increase of common dolphin mortalities was reported between 2002-2003 in the trawl fishery (Thompson et al., 2013; MPI, 2019). After these periods, codes of practices were implemented in both fisheries, leading to a reduction in mortality rates (Hamer et al., 2008; Goldsworthy et al., 2019b; Pierre, 2019). More recently the Small Pelagic and Gillnet fisheries of Australia also implemented a by-catch trigger limit of six dolphins per operator, leading to a temporally exclusion of the vessel for six months from the fishing management zone if that occurs (Mackay et al., 2016; AFMA, 2019a; b). A recent study in New Zealand also reported that common dolphins are still one of the main marine mammal species accidentally caught by commercial fisheries (Abraham et al., 2017), although use of mitigation measures in the jack mackerel trawl fisheries has reduced mortalities to negligible levels in 2016-18 (Fisheries New Zealand, 2020). In Australia's SASF, an upsurge in mortalities has been recorded between 2018-19, with discrepancy in the data recorded by fishermen and independent observers (Goldsworthy et al., 2019b). These issues suggest that information about common dolphin population structure, connectivity and abundance are critical to evaluate the risk of by-catch to particular dolphin populations, and to establish strategies to mitigate the combined interactions and mortalities within the multiple fisheries.

In the Australasian region, fisheries that threaten common dolphins operate under different jurisdictions based on geographic delimitation and stock delineation for each prey targeted (Abraham and Thompson, 2015c; b; a; Patterson et al., 2019). The delineation of fish stocks represents different management zones (e.g. Appendix B, Table B.5) and often it does not consider the population structure of the targeted fish species (Papa et al., 2020). In addition, these management zones are not only used to manage the targeted species, but also to manage interactions and mortalities of by-caught species, such as common dolphins (Abraham and Thompson, 2015c; b; a; Mackay et al., 2016; AFMA, 2019a; b; Goldsworthy et al., 2019b; Patterson et al., 2019). Our findings suggest that regional populations and subpopulations of Australasian common dolphins are currently allocated across and within different fishing management zones. This suggests that the use of the management zones as presently implemented (Appendix B, Table B.5) could differentially impact populations of common dolphins.

Marine species that present connectivity over large spatial scales, such as common dolphins, need planning and implementation of conservation and management strategies over broad spatial scales that can guarantee the long-term persistence of populations (Rosel et al., 2017; Taylor et al., 2017; Dunn et al., 2019; Grummer et al., 2019; Manel et al., 2019; Sousa et al., 2019; Taft et al., 2020; Tulloch et al., 2020). Some of the dolphin subpopulations identified here are potentially at higher risk of negative impacts from the fisheries. For example, the Gulf St Vincent subpopulation, which is possibly resident and relatively small (Filby et al., 2010), suffers by-catch induced mortalities by the SASF (Goldsworthy et al., 2019b), and these could potentially impact their long-term viability. In the West coast of New Zealand-Tasmania subpopulation, interactions with common dolphins and other top predators occur mainly with the mid-water trawl fisheries (Kemper et al., 2003; Thompson et al., 2013; Hamilton and Baker, 2019). Both of these fisheries have implemented codes of practice to reduce the number of entanglements and mortalities, including not setting nets when a cetacean sighting occurs, reporting cetacean interactions, modifying the fishery's gear (FAO, 1995; Rowe, 2007; Hamer et al., 2008; Goldsworthy et al., 2019b), and/or implementing an annual assessment with independent observers (Hamer et al., 2008; Goldsworthy et al., 2019b). Nevertheless, the management zones used to mitigate common dolphin interactions with these fisheries (Appendix B, Table B.5) are not in concordance with the population genomic structure of common dolphin disclosed here (Figure 2.2).

In Australasia, small cetacean populations have been generally managed in zones or units that do not reflect their genetic structure (e.g. Möller et al., 2001; Krutzen and Sherwin, 2004; Möller and Beheregaray, 2004; Bilgmann et al., 2007b; Bilgmann et al., 2008; Wiszniewski et al., 2009; Möller et al., 2011; Amaral et al., 2012a; Bilgmann et al., 2014; Stockin et al., 2014; Zanardo et al., 2016; Zanardo et al., 2017; Bilgmann et al., 2018; Pratt et al., 2018). These could potentially make dolphin populations more vulnerable to decline due to anthropogenic impacts, as exemplified for common dolphins in the Mediterranean Sea (e.g. Natoli et al., 2008; Moura et al., 2013a; Genov et al., 2020). These challenges highlight the need of using genetics and genomics markers as a tool for delineating population and estimating connectivity for biological meaningful management zones to be implemented (Funk et al., 2012; Leslie and Morin, 2016; Rosel et al., 2017; Taylor et al., 2017; Dunn et al., 2019). In particular, genetic and genomic analyses provide an opportunity to identify populations or subpopulations that require prioritisation or additional conservation policies.

In this study, we found that Australasian common dolphins present a complex hierarchical metapopulation, with nested subpopulations within regional populations. The estimated contemporary migration rates between most of these subpopulations suggest that they are not entirely genetically or demographically independent, and therefore common dolphins in the Australasian region should be managed on both meso-scale (regional population level) and fine-scale (subpopulation level). Each population and subpopulation are relevant to conserve for the maintenance of the complex metapopulation system. Subpopulations with potentially high-risk of anthropogenic impacts due to fisheries may act as sink population as previously reported for other marine species with sink-source dynamics (e.g. Benestan et al., 2016a; Lal et al., 2017; Manel et al., 2019; Rajora, 2019). However, the levels of contemporary migration suggest that the subpopulations identified cannot be managed entirely separately. Thus, we suggest that assessment and management of by-catch interactions and mortalities of common dolphins needs to be considered across multiple fisheries, management zones and jurisdictions for adequate conservation management to occur. For example, interactions and mortalities in the West coast of New Zealand need to be perhaps considered in conjunction with impacts on common dolphins in Tasmania, as they (provisionally) appear to belong to the same subpopulation, albeit with moderate connectivity to other southeastern Australian localities. The equivalent level of management should be applied within southern Australian states (southern Western Australia, South Australia, Victoria) and within eastern Australia states (New South Wales and southern Queensland). Therefore, potential management zones for mitigation and assessments of common dolphin by-catch in Australasia need to be based on populations' boundaries and connectivity, and through collaboration between inter-state and international jurisdictions.

Our findings integrating genetics and genomics markers provide reliable estimates of population structure and connectivity at broad and fine spatial scales for common dolphins of Australasia. Future risk assessments of by-catch and potential biological removal will require an application of the population structure and connectivity information presented here. Genomic analyses are also essential in additional studies addressing adaptation in marine ecosystems, in which selection can potentially further clarify substructure within regional populations (e.g. Shafer et al., 2015; Bernatchez et al., 2018; Hendricks et al., 2018; Sandoval-Castillo et al., 2018; Xuereb et al., 2018a; Rajora, 2019). This is a topical issue that needs to be considered in future conservation policies of marine ecosystems given the increase in anthropogenic impacts and ongoing changes of Earth's climate.

CHAPTER 3. GENOME-WIDE DATA REVEAL ENVIRONMENTAL ADAPTATION IN COMMON DOLPHINS (*DELPHINUS DELPHIS*) FROM SOUTHERN AUSTRALIA

Author contributions

Andrea Barceló Celis - Conceptualization and design of the study, DNA extractions, ddRAD library preparation, bioinformatics, data analyses, writing of the chapter and corresponding author.

Luciana Möller - primary supervisor - Conceptualization and design of the study, guidance on data analyses and interpretation, collection of samples and drafting manuscripts.

Luciano Beheregaray - associate supervisor- Guidance on data analyses and interpretation, and drafting manuscripts.

Kerstin Bilgmann - adjunct supervisor - Collection of samples and drafting manuscript.

Jonathan Sandoval-Castillo - Guidance on laboratory methods, bioinformatics and data analyses.

Chris Brauer – Guidance with data analyses.

Abstract

Genomic variation of marine species can be driven by spatial configurations, as well as by the influence of oceanographic and geomorphological features upon the dispersal of organisms, potentially leading to local adaptation. For wide-ranging marine species, such as most marine mammals, recent advances in sequencing techniques using small representation of the genome (i.e. ddRADseq) have helped to elucidate the influences of space and environmental variables on local adaptation. In this study, using a combination of genotype-environment association analysis (GEA) and Bayesian outlier methods, 806 of a 17,327 SNPs were found to be putatively under selection. Multiple analyses suggested the presence of five locally adapted populations of common dolphins (*Delphinus delphis*) along southern Australia. GEA results showed genomic variation of these populations seems to be associated with current velocity, sea surface temperature, salinity, and primary productivity. Each of these environmental variables are related to three main oceanographic phenomena, which are likely affecting the dispersal of common dolphins: i) oceanic circulation, ii) presence of seasonal upwelling, and iii) seasonal circulations in protected coastal habitats. Moreover, results showed putative signal of selection at exonic regions, suggesting that local adaptation could be mainly related to metabolic traits. This study provides initial information about adaptive divergence of common dolphins in southern Australia. The association between populations with their environment can be used to inform and assist population management in forecasting the potential capacity of the species to cope with future climate change scenarios and ongoing anthropogenic impacts.

Introduction

Microevolutionary processes are the result of selective pressures in the environment that create adaptive divergence among populations (Manel and Holderegger, 2013; Balkenhol et al., 2016; Grummer et al., 2019). Marine ecosystems have been historically considered as largely homogenous environments due to a general absence of hard physical barriers (Rajora, 2019). However, several marine ecosystems are in fact environmentally heterogeneous, with coastal and pelagic species being differently impacted by contrasting selective pressures that can lead to local adaptation (e.g. Benestan et al., 2016a; Grummer et al., 2019; Sandoval-Castillo and Beheregaray, 2020). Understanding selective pressures created by environmental features and how they impact genomic variation enhances our ability for refining knowledge about population structure of widespread species with high dispersal potential, such as many marine mammals (Cammen et al., 2016; Manel et al., 2019).

Natural selection acts over both new mutations and standing genetic variation, with the majority of adaptations occurring without alleles reaching fixation (Pritchard et al., 2010; Manel et al., 2016). In most cases where adaptation occurs, it involves multiple loci at different traits, creating either a beneficial or detrimental impact on the fitness of an individual (Riginos and Liggins, 2013; Razgour et al., 2018). Local adaptation occurs when an individual or group of individuals display higher fitness in a distinct spatial and temporal environment due to specific genetic variants (Savolainen et al., 2013; Lotterhos and Whitlock, 2015; Hoban et al., 2016). In marine environments, differences in geomorphological and oceanographic features can potentially shape species connectivity, physiology and population structure, leading to local adaptation (e.g. Bernatchez et al., 2018; Sandoval-Castillo et al., 2018; Teske et al., 2019).

Genomic data has improved our understanding of macro and microevolutionary processes, providing power and accuracy to detect large scale molecular adaptations, as well as population structure, gene flow and adaptive divergence between populations (Therkildsen et al., 2013; Cammen et al., 2016; Kelley et al., 2016). In toothed whales (Odontoceti), most studies of adaptations using genomic markers have so far focused on a macroevolutionary perspective. Genomic studies investigating ecological specialisation from a microevolutionary perspective have been documented in a few species of this group (e.g. Foote et al., 2016; Pratt, 2020; Andrews et al., 2021). In killer whale (*Orcinus orca)* ecotypes*,* adaptations to different water temperature regimes and feeding specialisations were suggested to have a genomic basis (Foote et al., 2016). For the finless porpoises (*Neophocaena phocaenoide*), microevolutionary adaptations were demonstrated between populations inhabiting marine and freshwater environments, with variation at putative genes involved in osmoregulation (Ruan et al., 2015; Zhou et al., 2018a). In Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), salinity and bathymetry were found to correlate with genomic differentiation between local populations, with variation also in genes putatively involved in osmoregulation (Pratt, 2020). For spinner dolphin ecotypes, it was shown that different mixed depth layers and temperature regimes were associated with genes involved in social behaviours (Andrews et al., 2021). Despite these examples, population-level studies of microevolutionary processes remain highly under documented in small cetaceans. In particular, there are still uncertainties about the adaptive resilience of small cetaceans to local or regional environmental changes and to future climatic scenarios. Such studies are expected to provide information for refining conservation and management strategies and to clarify important aspects of species biology.

The common dolphin (*Delphinus delphis*) is a widespread small cetacean that inhabits temperate, subtropical and some tropical waters around the world (Natoli et al., 2008; Möller, 2011; Perrin, 2021). Their broad distribution suggests that several habitats are suitable for this species (e.g. Bilgmann et al., 2018; Becker et al., 2020). In Australia, common dolphins range from embayments and gulf waters to coastal, shelf and pelagic waters (Bilgmann et al., 2008; Möller et al., 2011; Bilgmann et al., 2018). From a neutral genomic perspective, the species in Australasia displays a hierarchical metapopulation structure and fine-scale sub-structuring (Barceló et al., 2021, Chapter 2). Although common dolphins exhibit high potential for dispersal, prey distribution has been suggested as a main driver for their movements (Möller et al., 2011; Bilgmann et al., 2014; Peters et al., 2020). In Australasian waters, they mainly hunt and feed upon schooling fish such as jack mackerel (*Trachurus declivis, T.s. murphyi* and *T. novaezelandiae*), blue mackerel (*Scomber australasicus*), sardines (*Sardina sagax*) and anchovies (*Engraulis australis*) (Meynier et al., 2008; Goldsworthy et al., 2019b). The ranges of common dolphin populations seem to be influenced by the distribution and abundance of their prey and often coincides with oceanographic circulation, areas of high primary productivity, and regions of salinity and sea surface temperature interfaces (Möller et al., 2011; Amaral et al., 2012a; Bilgmann et al., 2014). This suggests that oceanographic features and circulation could be shaping dispersal of common dolphins, as described for other Australian marine taxa (e.g. DiBattista et al., 2017; Sandoval-Castillo et al., 2018; Vu et al., 2020). The widespread distribution of common dolphins in southern Australia, where environmental gradients and discontinuities are observed, provides a good opportunity to investigate microevolutionary processes and adaptive divergence in this species.

The temperate waters of southern Australia harbour productive habitats for common dolphins (e.g. Filby et al., 2010; Bilgmann et al., 2014; Bilgmann et al., 2018). The southern Australia's zonal coastal boundary stretches for >3,000 km, with important species endemism (Costello et al., 2017). The geographic discontinuity along the large extent of the southern coastal and shelf waters is mainly characterised by: i) geological features such as presence of canyons, embayments, bights, gulfs, slope, islands, straits; and ii) oceanographic features such as bathymetry, currents, presence of seasonal upwellings, and gradients in current velocity, salinity and temperature (Ridgway, 2004; Condie et al., 2005; Kämpf and Chapman, 2016). These different geological and oceanographic features from west to east have been reported to impact on historical genetic and genomic subdivision of invertebrate and fish species (e.g. York et al., 2008; Waters et al., 2010; Teske et al., 2017). Oceanographic and geological characteristics also impact on different plankton biomasses (e.g. Eriksen et al., 2019), that small pelagic fish feed upon, which through restriction in distributions may indirectly impact on the genetic variation and adaptive potential of large marine predators across the region, such as common dolphins.

Methodologies that combine genotype and environment associations in the marine systems, known as seascape genetics/genomics, have the potential to clarify the relative influences of environment and space on the genomic variation of a species (Manel et al., 2003; Dalongeville et al., 2018; Grummer et al., 2019). Studies of population genetic structure of common dolphins in southern Australia based on neutral markers (e.g. mtDNA, microsatellites) (Bilgmann et al., 2008; Bilgmann et al., 2014), and SNPs under putative neutrality (Barceló et al., 2021, Chapter 2), have hypothesised that common dolphin populations are associated with environmental gradients. For other marine species, seascape genomic/genetic analyses have suggested that adaptive population structure may be driven by environmental gradients of bathymetry, temperature, oxygen, and salinity (e.g. Dalongeville et al., 2018; Oleksiak and Rajora, 2020), while for common dolphins on broad oceanic basins associations with temperature and chlorophyll have been proposed (Amaral et al., 2012a). For this study, genome-wide and environmental data was used to distinguish loci under selection and assess adaptive population structure and diversity along southern Australia within a seascape genomics context. The continuous distribution of common dolphins in the highly heterogeneous waters of southern

Australia allowed the investigation of the influence of environmental variables in the genomic variation, which may lead to adaptive divergence among populations. This information can in turn provide more accurate information about the number and distribution of common dolphin populations to assist with the conservation and management of the species across the region, where they are subject to fishery interactions, and other anthropogenic impacts such as pollution and possible prey overfishing, as well as future climate variations.

Methods

Sample collection and study area

Common dolphins were sampled at nine sites across southern Australia between 2000 and 2017, with locations allocated based on the GPS information about where an individual was sampled, providing a total of 234 biopsies for the genomic analyses (Figure 3.1). These sites encompass the distribution of this species along the oceanographic, environmental, and geological discontinuities of southern Australia. Samples of this study are analogous to a previous study that grouped common dolphins into six localities (Barceló et al., 2021, Chapter 2) due to the lack of high population differentiation based on genomic neutral markers. However, geographical distances between samples separated them into the nine sampling sites used here, which provided a similar number of samples per site to compare the influence of environmental variables on the genomic variation of common dolphins. Biopsy samples were collected from live individuals using a hand held biopsy pole (Bilgmann et al., 2007a) or remote biopsy gun (PAXARMS) (Krutzen et al., 2002). Dependent calves were not sampled to avoid the inclusion of closely related individuals. Biopsy samples were preserved in 90% ethanol or in a 20% salt-saturated solution of dimethyl sulphoxide (DMSO) and kept in a -80°C freezer until laboratory analyses took place.

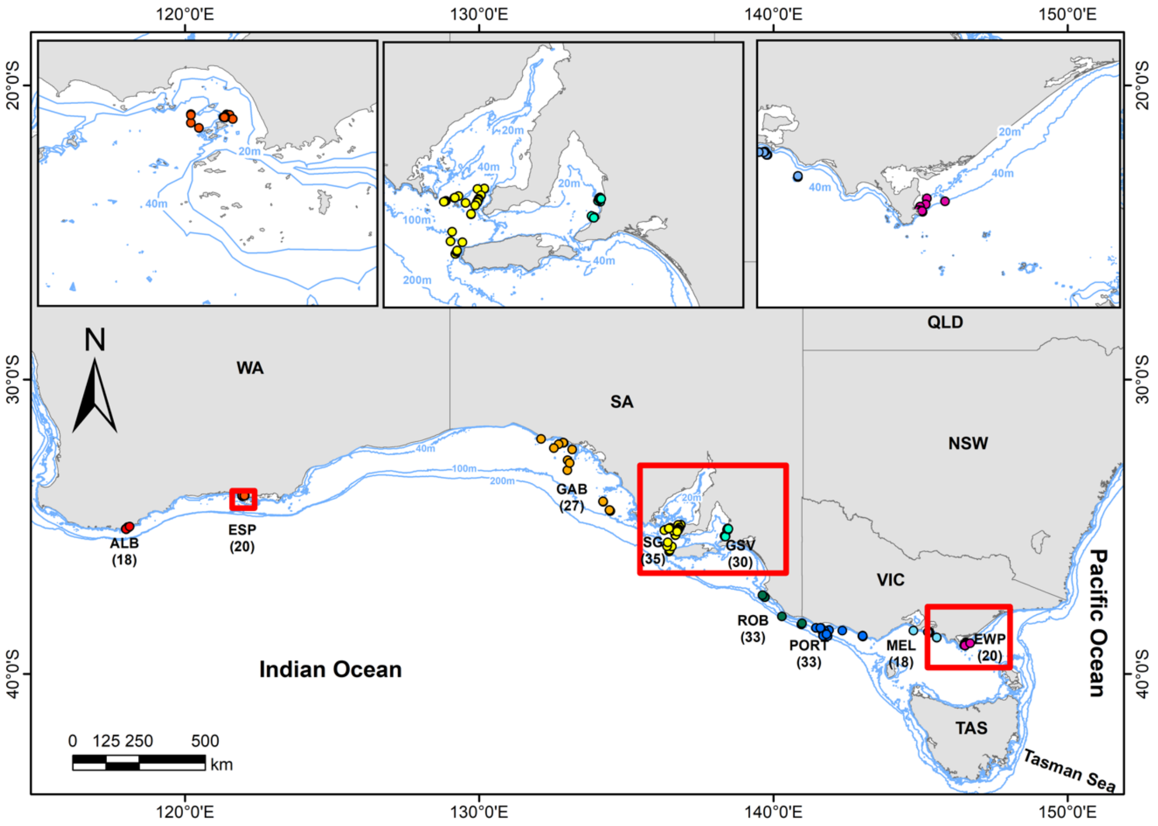


Figure 3.1 Study area in southern Australia showing the geolocations of 234 common dolphins (*D. delphis*) used for the genomic analyses. *Acronyms: Albany (ALB); Esperance (ESP); Great Australian Bight (GAB); shelf waters, Spencer Gulf (SG); Gulf St Vincent (GSV); Robe (ROB); Portland (PORT); Melbourne (MEL); and East, Wilson Promontory (EWP).

Laboratory analyses and bioinformatics

DNA extraction from biopsy samples were performed using a salting-out protocol (Sunnucks and Hales, 1996). Quantity and quality controls were determined using a Qubit 2.0 fluorometer (Life 178 Technologies), and a Nanodrop spectrophotometer (Thermo Scientific).

Library preparation for the double digest restriction-site associated (ddRAD) was performed following a modified protocol from Peterson et al. (2012), and later sequenced in an Illumina HiSeq 2500 platform at the South Australian Health & Medical Research Institute (SAHMRI).

Raw data quality was assessed, and demultiplexed using process_radtags, with STACKS v1.48 (Catchen et al., 2011; Catchen et al., 2013) and the dDocent2.2.19 pipeline 219 (Puritz et al., 2014). The resulting sequences were filtered using a modified protocol in VCFtools. The quality-filtered reads were then mapped against the genome of a closely related dolphin species, the Indo-Pacific bottlenose dolphin (*T. aduncus*) from southern Australia (Batley et al., unpublished), due to the absence of a high-quality *D. delphis* genome. Further details about the laboratory and bioinformatics can be found elsewhere (Barceló et al., 2021, Chapter 2). Genotype errors were considered and filtered by the incorporation of known replicas. To exclude potential duplicates in the dataset, relatedness between pairs of individuals was calculated by the triadic likelihood estimator (TrioML) in Coancestryv1.0.1.9 (Wang, 2011), and set as R <0.7 to be considered as a non-duplicate.

Genotype-environment association

Loci putatively under selection were detected using a seascape genomic approach within a genotype-environment association (GEA) framework. This methodology allowed the identification of associations between genetic and environmental variation across individuals using a multivariate analysis, the Redundancy Canonical Analysis (RDA) (below). RDA was chosen because it usually performs better than other GEA methodologies, such as univariate analyses (e.g. Latent Factor Mixed Models) for detecting genomic markers associated with environmental variables, and provides a lower number of false-positive and high true-positive candidates (e.g. Capblancq et al., 2018; Forester et al., 2018; Grummer et al., 2019).

Selection of environmental variables

This study used six available and ecologically relevant environmental variables to test for associations to genomic variation, based on previous suggestions (Möller et al., 2011; Bilgmann et al., 2014) about the heterogeneity of the southern coast and shelf waters, as well as data availability. The variables selected were 1) bathymetry 2) sea surface temperature, 3) chlorophyll *a*, 4) current velocity, 5) primary productivity, and 6) salinity. The annual maximum, mean, minimum, and range values of these variables between 2000 to 2014 were downloaded from the database BioOracle at a resolution of ~9.2 km, using the R package 'sdmpredictors' (Tyberghein et al., 2012; Assis et al., 2018) (see Appendix E for details), resulting in a total of 24 variables. The range of bathymetry was not available from the BioOracle database, therefore it was calculated from the recoded GPS location of each individual sample, based on the range of the minimum and the maximum values of the bathymetry.

To control for spatial autocorrelation, pairwise genetic distances were calculated with the GPS coordinates of each individual and the R function *viamaris* from the 'MELFU' package (MELFU/pigmyperch Github), using a resolution of 5000 pixels, which accounts for complex coastlines, and avoids land crossing. Pairwise geographic distances were then transformed to a Moran's eigenvector map (MEM) using the package 'memgene' (Galpern et al., 2014). The explanatory MEM axes were then used as spatial variables. To determine which environmental variables where significantly driving the population genomic differentiation, standardisation of the 24 variables was initially done in R (RCoreTeam 2017) using the function rescale with the package 'pysch' (Blanchet et al., 2008). To avoid overfitting the model, multicollinearity tests were implemented to exclude highly correlated variables, using a cut-off of $|r| > 0.7$ (Dormann et al., 2013; Prunier et al., 2015; 2017), and a maximum variance inflation factor (VIF) of 3 (O'brien, 2007). All the variables included in the models had to explain a significant ($p < 0.05$) portion of the genomic variation, and were identified using forward selection criteria (Blanchet et al., 2008; Legendre et al., 2011).

Redundancy Canonical Analysis (RDA)

A multivariate Redundancy Canonical Analysis (RDA) was applied to compare the association between the selected environment variables and the genomic variation among sampling sites, using the R package 'vegan' (Oksanen et al., 2019). Each environmental variable and axis were calculated through 1,000 permutations using an analysis of variance. Loci that scored greater than three standard deviations (± 3SD) from the mean locus scores were selected as candidates for each of the significant RDA axis. A selected axis had to explain a significant ($p < 0.05$) portion of the genomic variation to be considered for selection, as previously suggested (Legendre et al., 2011; Forester et al., 2018). Spearman's correlations were then calculated between each of the selected candidate loci and the retained environmental variables to determine which had a greater association per locus.

Test for outlier selection (F_{ST} outlier)

The results of the RDA multivariate analysis using a GEA approach, were compared to those of a popular outlier test implemented in Bayescan v2.1. (Foll and Gaggiotti, 2008). Although this approach does not test for associations with environmental variables, it has proved robust and conservative to identify loci potentially under selection, with a reduced number of false-positives, especially in scenarios of moderate to weak population differentiation (e.g. Rellstab et al., 2015; Brauer et al., 2018; Sandoval-Castillo et al., 2018). This method identifies outlier loci through a logistic regression model, considers the demographic population component, and decomposes F_{ST} values into locus-specific components (Foll and Gaggiotti, 2008). The outlier test was performed using a multinomial Dirichlet model with 100,000 iterations, 10 prior odds, and a burn-in of 50,000. Loci were considered candidate loci if their q-value was <0.1 (false discovery rate (FDR) <10%).

Adaptive population diversity and structure

Loci identified as potentially under selection by both methodologies, RDA and Bayescan, were extracted from the full SNP dataset to obtain a putative adaptive SNP dataset. Adaptive genomic diversity of the extracted subset of SNPs was assessed for each site and putative population using Genodive 2.0b27 (Meirmans and Van Tienderen, 2004). Measures of adaptive genomic diversity per site were also calculated, including expected heterozygosity (H_E) and observed heterozygosity (H_O).

Principal Component Analysis (PCA), a model-free approach, was used to investigate population structure using the R package 'Adegenet' (Jombart, 2008; Jombart and Ahmed, 2011), with annealing simulation of 50,000 steps. The Bayesian Information Criterion (BIC) and Akaike Information Criterion (AIC) were then used to determine the best-supported number of clusters in the dataset, using the snapclust.chooseK function, also in 'Adegenet' (Beugin et al., 2018).

Population structure was further investigated using a Bayesian clustering approach that infers population stratification based on estimated individual ancestries in Admixture v1.3.0 (Alexander et al., 2009). Although the putative adaptive dataset violates Hardy-Weinberg assumptions of equilibrium (Funk et al., 2012), this analysis was used as a comparison to the results based on the putatively neutral dataset (Barceló et al., 2021, Chapter 2). The maximum likelihood estimates were calculated by using the ancestry portion and the population allele frequency to assign the most likely number of K (i.e. populations) in the dataset, testing for K 1-9 and to model the probability of observed genotypes (Alexander and Lange, 2011). This was followed by cross validation with ten replicates for each of the K values performed.

Adaptive genomic differentiation among sites was estimated as pairwise F_{ST} (Weir and Cockerham, 1984) using Genodive 2.0b27. Significance levels were assessed using 10,000 permutations, corrected by the B-Y method (FDR <10%; Benjamini and Yekutieli, 2001). Heatmap plots of F_{ST} were constructed with the R package 'ggplot2' (Wickham, 2016).

Functional Enrichment Analysis and Annotation

A functional enrichment analysis was performed using the candidate adaptive loci detected with the RDA. The full dataset and adaptative dataset were first matched to all the available cetacean nucleotides and non-redundant proteins within the NCBI database (Wadi et al., 2016; Nam et al., 2017; Dalongeville et al., 2018; NCBI, 2020). Each SNP from the full dataset (neutral and adaptive, 17,327 SNPs) was flanked to sequences of 300 bp either side of it, and extracted based on the results of linkage disequilibrium (details in Barceló et al., 2021, Chapter 2), resulting in 601 bp sequences in length. Annotation was then performed using the alignment tool (BLAST) in the NCBI nucleotide and non-redundant protein databases, with an expectation e-value threshold of $1X10^{-3}$. After that, an enrichment Gene Ontology (GO) term analysis was performed for the putative candidate loci identified by the RDA, compared to the 601 bp sequences of the 17,327 SNPs, this was done using a Fisher's exact test and a FDR < 5% (Gene Ontology, 2015). Resulting GO terms were then related to a specific candidate, in which each SNP with a variant in a candidate gene was further examined for its sequence position using snpEFF (Cingolani et al., 2012). Each SNP found in a coding and non-coding region was further linked to a pathway and function using the Reactome and UnitProtKB, respectively (The UnitProt Consortium, 2018).

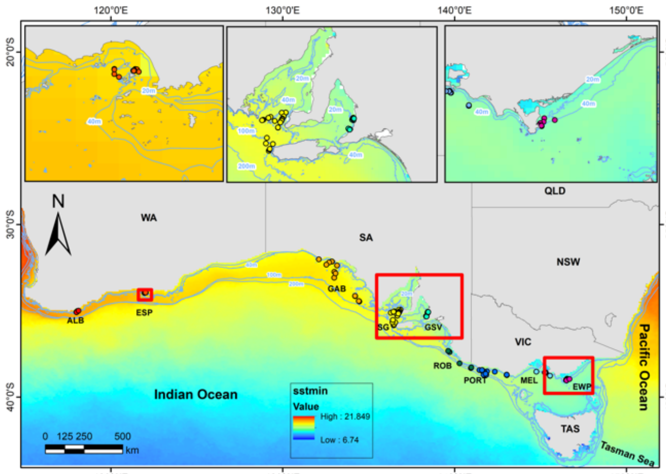
Results

Population genomic dataset

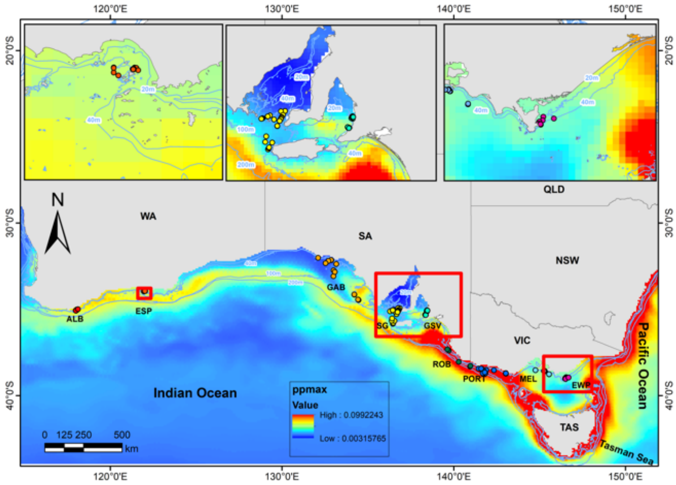
A total of 234 biopsy samples of common dolphins were sequenced across four Illumina HiSeq 2500 lanes, producing a total of 400 million filtered sequence reads. After filtering using stringent criteria (detailed in Appendix C, Table C.1), we obtained a high-resolution dataset of 17,875 filtered SNPs with 1% average missing data per locus. Low-quality individuals and close relatives ($R \geq 0.7$) were removed, resulting in a dataset of 214 individual samples for analyses. This dataset was then filtered for Minor Allele Count (MAC) <0.01, resulting in a final dataset of 17,327 SNPs.

Genotype-Environment Associations

A total of 24 environmental variables were initially available for analyses. Five environmental variables were retained after testing for multicollinearity (|*r*| >0.7 and VIF ≤3) (Appendix C, Figure C.1; Appendix E). The selected variables were salinity maximum, sea surface temperature minimum, primary productivity maximum, and current velocity maximum and range, with each environmental variable showing a marked gradient along southern Australia's coast and shelf waters (Figure 3.2a-e).



(A)



(B)

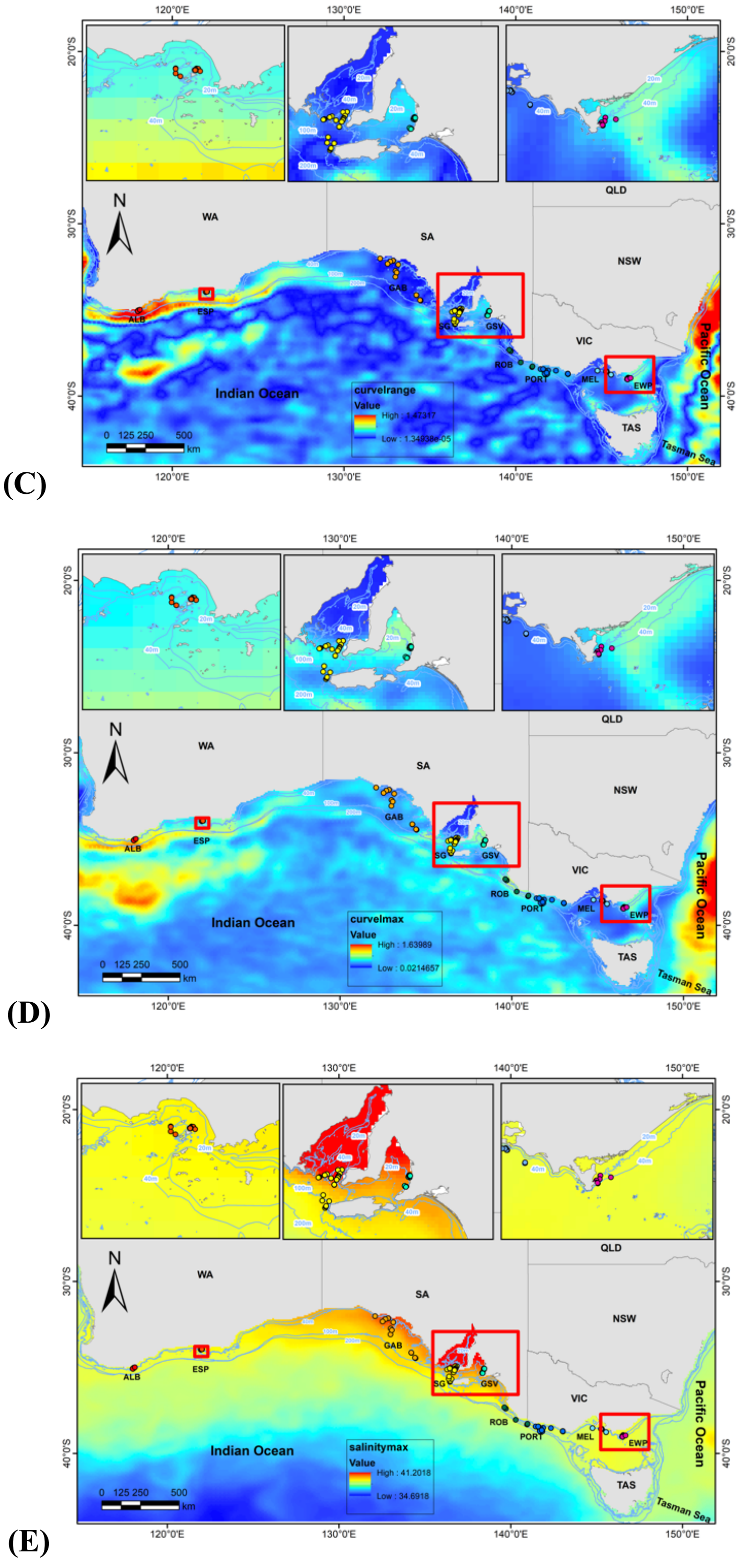


Figure 3.2 Environmental variables that were retained as significant for the Genotype-Environment and Redundancy Canonical Analyses for southern Australian common dolphins (*D. delphis*). (A) Sea surface temperature minimum, (B) Primary productivity maximum, (C) Current velocity range (D), Current velocity maximum, and (E) Salinity maximum. *Acronyms: Albany (ALB); Esperance (ESP); Great Australian Bight (GAB); shelf waters, Spencer Gulf (SG); Gulf St Vincent (GSV); Robe (ROB); Portland (PORT); Melbourne (MEL); and East, Wilson Promontory (EWP).

The overall model of the RDA was significant (p = 0.001), with the spatial variables explaining 3.5% of the variation of the full model, while the genotype dataset and the environmental variables explained 4.9% of the variation of the full model. The five environmental variables retained were significant for the constrained component of the RDA model (p = 0.001) (Table 3.1; Appendix C, Table C.2). A total of 747 SNPs was retained as candidate adaptive markers. The first component explained 0.7% of the full model and 32% of the constrained variance, while the second component explained 0.11% of the full model and 20% of the constrained variance (Appendix C, Table C.2). The visualisation of the first and second components demonstrated heterogeneity between the five environmental variables and the sample sites analysed (Figure 3.3). Changes in current velocity were strongly associated with the genomic differentiation of common dolphins between geographically close sites of Albany and Esperance, Western Australia. By contrast, primary productivity and sea surface temperature explained most of the genomic divergence of common dolphins from the Great Australian Bight, Spencer Gulf, Robe, Portland and Melbourne, to other sites in southern Australia. Finally, salinity was the variable that explained most of the genomic variation of common dolphins from Wilson Promontory and Gulf St Vincent to the other sites.

Table 3.1 Significance of the environmental variables in the MEM axis selection and Redundancy Canonical Analysis model for southern Australian common dolphins (*D. delphis*). Portion of the constrained variance explained by each environmental variable and the number of putative candidate loci is also presented.

Environmental variable	**p- value**	**Percentage explained by the model**	**No. of candidate loci**
Sea surface temperature minimum	0.001 ***	0.7111437	215
Primary productivity maximum	0.001 ***	0.61671554	88
Current velocity range	0.001 ***	0.6085044	152
Salinity maximum	0.001 ***	0.60087977	182
Current velocity maximum	0.001 ***	0.51730205	110

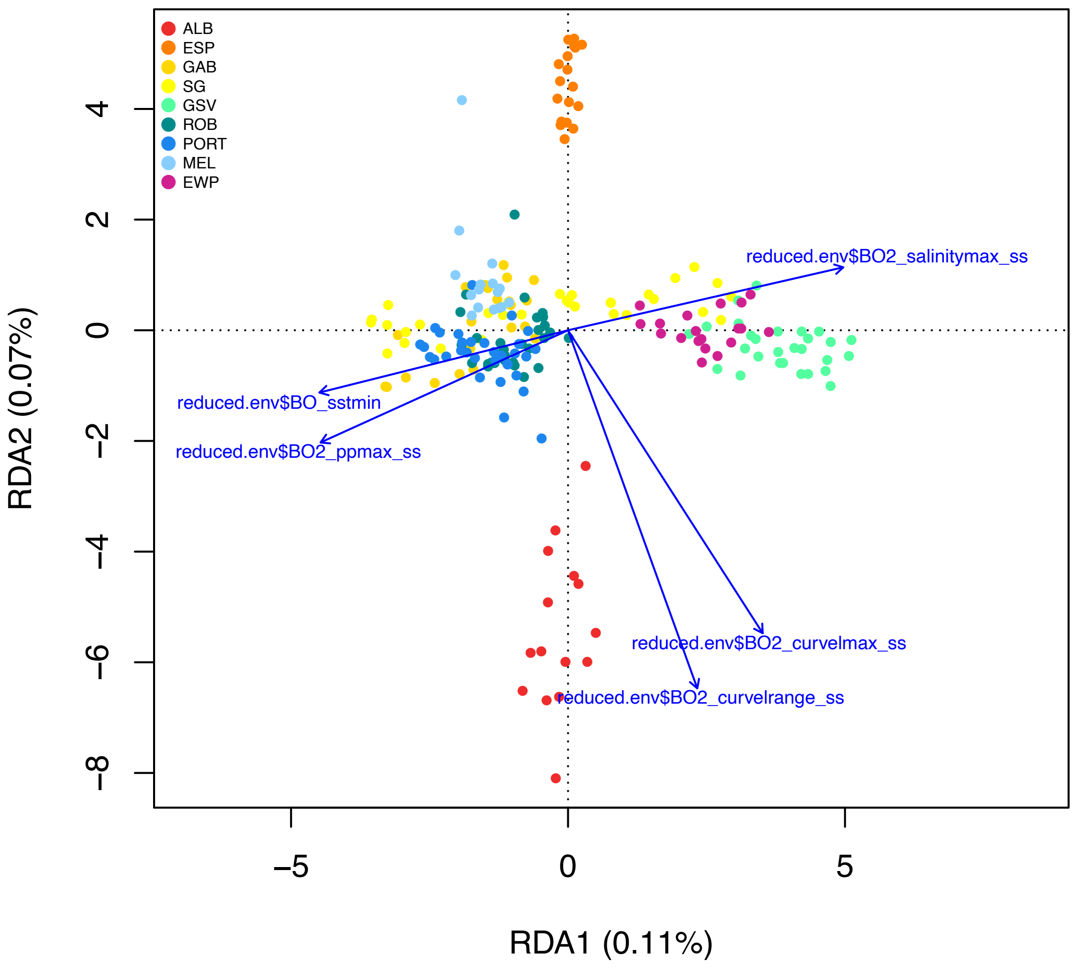


Figure 3.3 Redundancy Canonical Analyses (RDA) displaying the influence of five environmental variables on individual genomic variation of common dolphins (*D. delphis*) from southern Australia. The overall variance of the model explained was 3410 (p = 0.001) (see Table 3.2; Appendix C, Figure C.1 for more details). Legend displays sampling sites from west to east, and colours correspond to where common dolphins were sampled. *Acronyms: Albany (ALB); Esperance (ESP); Great Australian Bight (GAB); shelf waters, Spencer Gulf (SG); Gulf St Vincent (GSV); Robe (ROB); Portland (PORT); Melbourne (MEL); and East, Wilson Promontory (EWP).

Test for outlier loci under selection

The Bayescan outlier test identified 75 SNPs potentially under selection (Figure 3.4). Subsequent analyses of adaptive population structure were performed using a combined SNP dataset based on those identified by the RDA as candidate loci and the Bayescan analyses, which resulted in a dataset of 806 putatively adaptive SNPs (Appendix C, Figure C.3).

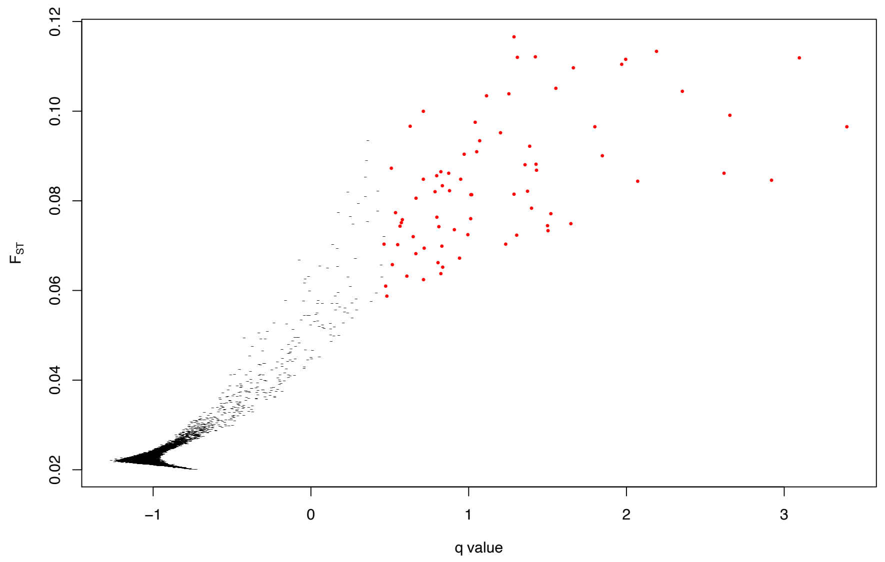


Figure 3.4 Outlier loci detected by the Bayescan analyses of common dolphins (*D. delphis*) from southern Australia. This is illustrated by locus specific F_{ST} plotted against the q values, with a False Discovery Rate (FDR) of <10%. Outlier loci are represented by the red dots.

Adaptive population genomic structure and diversity

The 806 SNPs were extracted from the full dataset (17,327 SNPs) to obtain a putatively adaptive dataset. The inferred levels of putatively adaptive genome-wide diversity were relatively high for all sites (H_E 0.369 to 0.405; H_O 0.361 to 0.402) compared to the neutral genomic diversity (H_E 0.160 to 0.181; H_O 0.154 to 0.175 (Table 3.2) (detailed in Barceló et al., 2021, Chapter 2).

Multiple analyses (described below) using the adaptive dataset indicated the presence of four to five putatively local populations supported by BIC and AIC tests (Appendix C, Figures C.4; C.5): (1) Albany (ALB), (2) Esperance (ESP), (3) Continental shelf sites (GAB, SG, ROB, PORT and MEL), (4) Gulf St Vincent (GSV), and (5) Wilsons Promontory (EWP) (Figure 3.5). Specifically, Admixture analysis revealed up to five adaptive putatively populations, with a separation between ALB and ESP, , GSV, and EWP, compared to considerable admixture among the other sites (Figures 3.5; Appendix C, Figure C.4; C.5). By contrast, PCA results mostly supported four populations, showing only a subtle separation between EWP, GSV sites and ALB, with admixed individuals from ESP and the continental shelf sites clustering in the middle of the two axes (Appendix C, Figure C.6).

Table 3.2 Measures of genomic diversity based on 806 putatively adaptive, and 14,799 putatively neutral SNP datasets by sampling site for southern Australian common dolphins (*Delphinus delphis*). Observed heterozygosity (H_O), expected heterozygosity (H_E) and number of samples used after filtering (N). *Acronyms: Albany (ALB); Esperance (ESP); Great Australian Bight (GAB); shelf waters, Spencer Gulf (SG); Gulf St Vincent (GSV); Robe (ROB); Portland (PORT); Melbourne (MEL); and East, Wilson Promontory (EWP).

		neutral		**adaptive**	
Site	**N**	**H_o**	**H_E**	**H_o**	**H_E**
ALB	15	0.167	0.166	0.381	0.382
ESP	18	0.171	0.172	0.382	0.386
GAB	22	0.170	0.176	0.386	0.405
SG	32	0.172	0.172	0.402	0.402
GSV	28	0.154	0.160	0.361	0.369
PORT	31	0.172	0.175	0.391	0.399
ROB	32	0.169	0.175	0.389	0.402
MEL	16	0.169	0.177	0.381	0.399
EWP	20	0.175	0.181	0.377	0.395
Total average		*0.169*	*0.173*	*0.383*	*0.393*
Total SD		*0.006*	*0.006*	*0.011*	*0.012*

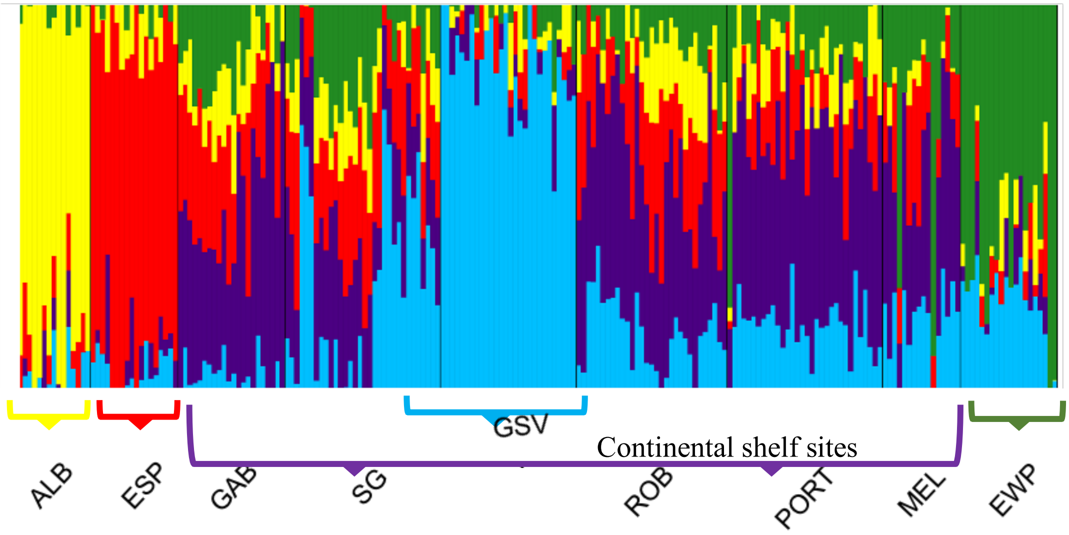


Figure 3.5 Population genomic structure analysis using Admixture based on 806 putatively adaptive SNPs for southern Australian common dolphins (*Delphinus delphis*), labelled by sampling site. The results depict levels of admixture for each individual sample, grouping them into up to five adaptive genomic clusters (K = 5). Each sample is represented by one vertical

line and is colour-coded based on the membership probability to one of the identified locally adapted populations.

Fixation indices indicated low to moderate (F_{ST} 0.001 to 0.120) genomic differentiation between dolphins based on the putatively adaptive dataset, with the majority of them significant and with higher F_{ST} than with the putatively neutral dataset (Appendix C, Figure C.2; Table C.3). The greater F_{ST} differentiation was between Gulf St Vincent (GSV) and East Wilsons Promontory (EWP) compared to the western sites [Albany (ALB) and Esperance (ESP)], with the lowest F_{ST} values creating a gradient along southern Australian sites on the continental shelf.

Functional enrichment and annotation

Of the full dataset (17,327 SNPs), a total of 1,871 SNPs (>10%) scored BLAST hits that annotated to publically available cetacean nucleotides and non-redundant proteins. Of the 747 SNPs retained as potentially under selection by the RDA, 148 were annotated (~19%). Functional enrichment analysis identified 22 GO terms over-represented when comparing the SNPs from the full dataset to the SNPs identified as potentially under selection (Appendix C, Table C.4). These over-represented GO terms belong mostly to biological processes, but some were also related to molecular functions and cellular components, with 26 SNPs related to adaptive candidate genes in both coding and non-coding regions in multiple pathways. These SNPs were further investigated, with three notable ones showing variants in exonic regions (Appendix C, Table C.5). These SNPs correspond to candidate genes MAN2B1 (related to breaking complex sugar molecules) and ZFP57 (related to early embryonic methylation), which were associated with primary productivity variation in the RDA, and NR2F6 (related to regulation of adipogenesis and energy metabolism), which was associated with the salinity gradient also in the RDA. Although the correlations between the candidate genes and the environmental variables were low ($r^2 < 0.5$), the correlations were still significant (Fisher's p-value <0.05), and considerable changes in the allele frequencies of these candidate genes were observed across the seascape (Appendix C, Figure C.7; C.8).

Discussion

Species and populations exhibiting high genomic variation have enhanced prospects of long-term persistence (Wright, 1968; Allendorf et al., 2010; Frankham et al., 2010). Biodiversity inhabiting multiple environments may be subject to disparate selective pressures, which in turn could result in adaptation to particular habitats (Manel and Holderegger, 2013; Riginos et al., 2016; Grummer et al., 2019). In this study, a seascape genomics approach was used to assess the influence of environmental heterogeneity in shaping adaptive divergence in common dolphin populations from southern Australia. Our analyses identified around 800 SNPs putatively under selection that delineated up to five putatively-adaptive divergent populations across the region. The seascape genomics component of the analyses revealed four key environmental variables in the region (sea surface temperature, primary productivity, current velocity, and salinity), which could explain most of the genomic variation between local common dolphin populations. This genomic signal may be associated with three different described oceanographic and geological phenomena along southern Australian coastal and shelf waters. These include (i) the oceanographic circulation in the western region and associated differences in current velocity; (ii) upwellings across the central shelf region associated with fluctuations of primary productivity and sea surface temperatures; and (iii) protected coastal environments in central and eastern regions characterised by marked variations in salinity and seasonal circulation patterns. To the best of our knowledge, this study represents the first genomic assessment of putatively-adaptive divergence among common dolphin populations.

Putatively-adaptive genomic variation in southern Australian common dolphins

Genomic variation within populations can be impacted by demographic history, but also through ongoing selective pressures that will promote or restrict the dispersal of individuals (Frankham et al., 2017; Rajora, 2019; Wilder et al., 2019). Estimates of genomic variation and fixation indices were, as expected, higher for the adaptive markers (this study) than for the neutral markers (see Table 3.2; and Appendix C, Figure C.2 and Table C.3 for comparisons). Furthermore, the population structure analyses revealed a dissimilar number of populations inferred via adaptive and neutral markers; four to five with the adaptive dataset (Figures 3.5; Appendix C, Figure C.5) and at least two with the neutral dataset (Barceló et al., 2021, Chapter 2). While neutral and adaptive genetic signals provide useful information about population structure, they arise through different evolutionary forces (Wright, 1968; Crow and Kimura, 1970), and as discussed below, are both relevant for conservation and management (Shafer et al., 2015; Sunnucks and Balkenhol, 2015; Funk et al., 2019).

Understanding the pressures that impact marine populations is critical for guiding their management (Oleksiak and Rajora, 2020). Common dolphins are a widespread species thought to have colonised different coasts and pelagic habitats off Australia during the Pleistocene (Amaral et al., 2012b). During that period, fluctuations in primary productivity may have opened new niches and promoted colonisation of the region by this species (Steeman et al., 2009; Amaral et al., 2012c; Amaral et al., 2016). However, current environmental pressures could also be influencing local adaptation of marine populations (Allendorf et al., 2010; Manel et al., 2010). This is relevant for common dolphins in southern Australia, which suffer ongoing impacts from anthropogenic activities, particularly by-catch in fisheries (e.g. Bilgmann et al., 2008; Hamer et al., 2008; Tulloch et al., 2020). In this region, common dolphins exhibit genetic connectivity over relatively long distances that was mainly disclosed by putatively neutral SNPs (Barceló et al., 2021, Chapter 2), when considering signals from genomic regions mostly shaped by genetic drift and migration (Wright, 1968; Crow and Kimura, 1970). They also appear to show site fidelity to embayment environments (Filby et al., 2010; Mason et al., 2016), with signatures of selection in adaptive markers disclosed here supporting the hypothesis of year-round site fidelity. Neutral and adaptive loci can provide different number of populations for management and conservation (Funk et al., 2012; Funk et al., 2019). For common dolphins in southern Australia, neutral loci may explain the interconnected pattern disclosed here, with migration occurring at the metapopulation level (Barceló et al., 2021, Chapter 2), while adaptive loci support the idea of putative adaptation to local environments or bioregions, despite the occurrence of gene flow. Each local habitat or bioregion exhibit different environmental gradients, such as temperature, oxygen and salinity which have been described to impact upon other marine taxa from southern Australia (e.g. *Haliotis*, Sandoval-Castillo et al., 2018; *Nerita*, Teske et al., 2015), and in another delphinid (*Tursiops* sp. Pratt, 2020). These environmental variables may be also impacting on common dolphins and their prey distribution in southern Australia, and in turn creating differentiation between putative locally adapted populations, despite the gene flow which occurs across the metapopulation. Effects of climate change may differ between adaptive populations, with local populations exhibiting low adaptive genomic diversity, such as those in coastal protected environments or embayments, perhaps more vulnerable to such effects (e.g. Bilgmann et al., 2019; Pratt, 2020; Reed et al., 2020). Thus, neutral and adaptive variation are both relevant to conserve for maintaining high standing genetic variation across the common dolphin metapopulation.

Environmental drivers of adaptive differentiation in southern Australian common dolphins

Adaptive differentiation can be driven by various selective pressures. In marine systems, oceanographic features, such as bathymetry, currents, primary productivity, salinity, and temperature may exert selective pressures (Benestan et al., 2016a; Bernatchez et al., 2018; Oleksiak and Rajora, 2020). These environmental gradients and discontinuities could be creating soft barriers, and in turn, lead to adaptive divergence among marine populations (e.g. Benestan et al., 2016a; Sandoval-Castillo et al., 2018; Xuereb et al., 2018a). Population differentiation in Australasian common dolphins, and their varied use of habitats, have been generally associated with the abundance and movements of their prey (e.g. Stockin et al., 2009a; Möller et al., 2011; Bilgmann et al., 2014), which mainly exhibit passive dispersal during their larvae stage (e.g. Ward et al., 2006; Kool et al., 2015; Ward et al., 2017). Although using a small representation of the genome led to a significant, albeit small, association between genomic variation with the key available environmental variables, it does not necessary fully elucidate the complex scenarios occurring in the marine system. The assessment of common dolphin populations in southern Australia, thus may require a general ecological understanding of this heterogeneous marine system.

At a global, coarse scale, an assessment of the seascape genetics of common dolphins has been previously made based on neutral microsatellite markers. This study correlated genetic variation in oceanic populations of common dolphins with environmental variables, finding evidence for the effect of chlorophyll *a* and sea surface temperature in delineating major population boundaries (Amaral et al., 2012a). Robust analyses in our study based on a large SNP panel disclosed that common dolphin genomic variation at fine-scale in southern Australia was associated with several environmental variables, including sea surface temperature, but also current velocity, primary productivity (which is generally positively correlated with chlorophyll), and salinity (Figure 3.3). Our findings suggest that different variables may be acting at different spatial scales, playing major roles in the differentiation of populations. The ocean circulation in the region, influenced by differences in environmental gradients, mainly seasonal differences in primary productivity and sea surface temperature, is likely to result in different levels of plankton biomass (e.g. Eriksen et al., 2019), that in turn mediate the abundance and distribution of the dolphins' prey. The genomic differentiation observed may be associated with three possible oceanographic phenomena discussed below.

Ocean circulation off southern Western Australia

The western and southern coasts of western Australia are characterised by the Leeuwin current, which originates in the warm Indo-Pacific Ocean, moving south along the western coast of Australia, and into the southern coast off Cape Leeuwin (Bird, 2005; Ridgway and Godfrey, 2015; Short, 2020). The warm waters that enter southern Australia, flowing from west to east, create distinct patterns of temperature, primary productivity and current velocity along the continental shelf (Middleton and Bye, 2007; Koslow et al., 2008). In southern Western Australia, common dolphins between the two geographically close sites of Albany and Esperance (~300 km apart) were found to be slightly differentiated based on the adaptive SNP dataset, and this distinction seems to be mainly driven by oceanographic currents, particularly changes in current velocity in this area (Figures 3.3 and 3.5). A previous microsatellite study suggested differentiation between dolphins of these two sites (Bilgmann et al., 2014), although this separation was not disclosed when analysing the putatively neutral SNP dataset (Barceló et al., 2021, Chapter 2).

At the western region of southern Australia, the Leeuwin current velocity rapidly declines due to geomorphological formations at the ocean floor, such as the presence of canyons and the Recherche archipelago (Bird, 2005; Currie et al., 2012; Kool et al., 2015). Models of larval dispersal in some fish species have shown that individuals move along the Leeuwin current, but separate fish aggregations from between Albany and Esperance (Lourey et al., 2006). Circulation and geomorphological differences characterise each site; Albany with strong mixing waters outside the embayment, whereas off Esperance it is more protected because of the archipelago (Brooke et al., 2017; Kent et al., 2020). Common dolphins are known to optimise their energy requirements by having different hunting strategies, and preferences for targeting diverse prey species between different sites and seasons (Spitz et al., 2010; Mason et al., 2016; Peters et al., 2020). Thus, common dolphins that inhabit Albany and Esperance could be targeting different fish aggregations, which may lead to differential habitat use. Adaptive genomic variation of common dolphins between these two sites was evident in the Minor Allele Frequency (MAF), especially in SNPs of the candidate genes EBF2, CHIA and KCTD16

(Appendix C, Figure C.8). These genes are involved in digestion, absorption of carbohydrates and energy conversion, as well as in the differentiation of brown adipocytes (e.g. Havird et al., 2016; Tabata et al., 2018; Angueira et al., 2020). Brown adipocytes, or white fat, are known to be the main source of energy storage that can be altered by food intake (Shao et al., 2016; Angueira et al., 2020). Moreover, differences in MAF in SNPs of the gene LEF1 was also disclosed between common dolphins of these two sites (Appendix C, Figure C.8). This gene is associated with anti-apoptotic signals in hypoxic conditions (Boso et al., 2019), a coping mechanism during episodes of hypoxia due to low oxygen availability (Larson et al., 2014). Thus, these genes may be involved in regulating energy and oxygen availability for common dolphins in western southern Australia, which sites are differentially impacted by current velocity.

Southern Australia's continental shelf and its upwellings

The Leeuwin current continues into southern Australia as the Great Australian Bight current, which is characterised by slower flow in an eastward direction following the break of the continental shelf (Middleton and Bye, 2007; Kämpf, 2015; Ridgway and Godfrey, 2015). The sea floor formation of the southern continental shelf of Australia creates a basin known as the Great Australian Bight, which extends several nautical miles from the coast into the continental shelf break (McClatchie et al., 2006; Richardson et al., 2009; Kämpf, 2010). While the warm currents tend to follow the continental shelf, there is also a counter-current of cold water, known as the Flinders current, which remains below the continental shelf break (Middleton and Bye, 2007). During the austral summer, anticyclonic weather favours the replacement of the warm currents by the cold and productive Flinders current, forming coastal upwellings over the continental shelf (Condie et al., 2005; Ridgway and Godfrey, 2015; Kämpf and Chapman, 2016). The GEA analysis in our study highlighted the influence of maximum primary productivity and minimum sea surface temperature, which are major characteristics of upwelling formations, on the adaptive genomic differentiation of common dolphins. This was detected in samples from regions of the Great Australian Bight, mouth of Spencer Gulf, Robe, Portland, and Melbourne (Figure 3.3). In the GEA analysis samples from these sites clustered together, and this was also disclosed in the PCA and Admixture analyses (Figure 3.5; Appendix C, Figure C.5; C.6).

Differences in primary productivity and sea surface temperatures have been characterised as the main forces that may drive seasonal upwellings in southern Australia (Lourey et al., 2006; Kämpf, 2010; Kämpf and Chapman, 2016). There are two types of upwelling centres along southern Australia. Large upwellings are represented by the Bonney upwelling located from about Robe, South Australia, to Portland, Victoria, and the Tasmania upwelling located off western Tasmania. There are additional, smaller upwelling centres that do not follow the classical Eckman model formation, such as the Eyre Peninsula and the Kangaroo Island upwellings (Kämpf, 2010; Currie et al., 2012; Kämpf, 2015). While the smaller upwellings could mainly have an impact upon spawning of fish species, such as sardines and anchovies (Ward et al., 2006), the larger upwelling centres are likely to attract higher density of predators, such as dolphins, whales, seals and sharks feeding upon large biomasses of krill and pelagic fish, and using these large upwelling centres as feeding grounds (e.g. Foo et al., 2020; Mackay et al., 2020; Möller et al., 2020). Common dolphins in open and unprotected continental shelf waters (i.e. Great Australian Bight, mouth of Spencer Gulf, Robe, Portland and Melbourne), presented similar MAFs in SNPs of candidate genes ERC2, MAN2B and ZFP57, compared to other sites along southern Australia (Appendix C, Figure C.8). The ERC2 gene has been associated with heat stress metabolism in other species (Emami et al., 2020); the MAN2B1 gene is known to play an important role in breaking complex sugar molecules (Lazzarotto, 2016; Tivey et al., 2020); and the ZFP57 gene is involved in the regulation of fatty acids (Cirillo et al., 2014). These genes could be involved in regulating energy intake and body mass index (e.g. Turcot et al., 2018; Boonanuntanasarn et al., 2019), with differences between common dolphins that feed upon schooling fish with higher energy density (Sptiz et al., 2010), from productive upwelling systems to those that do feed on these types of fish.

Protected coastal habitats

The geomorphology of southern Australia exhibits several embayments and protected areas (Bird, 2005; Short, 2020). Some of these protected embayments, such as Gulf St Vincent, South Australia, and Port Philip Bay, Victoria, have been previously described as important year-round habitats for common dolphins (Filby et al., 2010; Mason et al., 2016). The neutral dataset provided some differentiation between dolphins from the Gulf of St Vincent and other areas (Barceló et al. 2021, Chapter 2). However, this result was amplified by the GEA analysis which disclosed that the genomic variation of common dolphins in Gulf St Vincent and sheltered waters off Wilsons Promontory were apparently mainly driven by salinity, and correlated with primary productivity and sea surface temperature (Figure 3.3). The Gulf St Vincent is an hypersaline inverse estuary with seasonal circulations that create differences in primary productivity and temperature (Bird, 2005; Kämpf and Bell, 2014; Bourman et al., 2016). Similarly, Wilsons Promontory is a protected area described as a unique biogeographic region between the southern and eastern Australian currents, with seasonal circulation associated with differences in temperature that promotes the formation of seasonal fish assemblages (Waters, 2008; Colton and Swearer, 2012; Teske et al., 2017).

Common dolphins tend to target prey species with high energy density (Neumann and Orams, 2003; Spitz et al., 2010). In southern Australia, common dolphins mainly feed upon sardines (*S. sagax*), anchovies (*E. australis*), and mackerel (*Trachurus* spp.) (Mackay and Goldsworthy, 2017; Goldsworthy et al., 2019b). However, for some presumably resident populations in Port Phillip Bay and Hauraki Gulf, New Zealand, it has been suggested that common dolphins may change their target species based on their seasonal availability (Mason et al., 2016; Peters et al., 2020). Bottlenose dolphins that exhibit strong residency in embayment habitats in southern Australia have also showed genomic differentiation associated with salinity and temperature, suggesting that environmental variables could create indirect discontinuities in food availability (Pratt, 2020). For southern Australian common dolphins from coastal protected habitats, genomic variants showed differences in the MAF of SNPs in candidate genes STX7 and IGFBP7 (Appendix C, Figure C.8). While STX7 is associated with osmoregulation (Niedergang and Chavrier, 2004; Roca-Agujetas et al., 2019), IGFBP7 is related to physiological adaptation of species inhabiting freshwater and marine environments (e.g. Yau et al., 2015; Breves et al., 2017; Strobel et al., 2020). Moreover, members of the STX family genes were found to be positively selected in the macroevolution of marine mammals (e.g. Yim et al., 2014; Foote et al., 2016; McGowen et al., 2020). In southern Australian embayments, seasonal changes in salinity and temperature are associated with changes in the composition of fish assemblages (e.g. Colton and Swearer, 2012; Whitmarsh et al., 2020). Thus, it is possible that observed differences in genomic variation in common dolphins inhabiting Gulf St Vincent and Wilsons Promontory are related to mechanisms for coping with high salinities and allowing them to remain local year-round by alternating feeding upon different prey species.

Gene ontology

Interpretation of functional implications between candidate genes and their environment need to be made with caution, and this is, especially the case in marine systems as it is difficult to elucidate all possible oceanographic and demographic scenarios, and the ones inferred do not necessarily imply causality (Manel et al., 2016; Xuereb et al., 2018b, Sandoval-Castillo et al., 2018). Candidate genes previously identified for other species, however, can be generally implied in adaptive responses of non-model species (e.g. Vincent et al., 2013; Dalongeville et al., 2018; Oleksiak and Rajora, 2020). Macroevolutionary studies of odontocetes have suggested that adaptations between species mostly occurred during cycles of high productivity (Steeman et al., 2009; Amaral et al., 2012c; Amaral et al., 2016). In this study, positively selected variants in exonic gene regions of MAN2B1, ZFP57 and NR2F6 were associated with primary productivity and salinity (Figure 3.3; Appendix C, Figure C.7), which could be influencing physiological adaptation of common dolphins to different habitats.

The MAN2B1 is associated with the break of complex sugar molecules involved in carbohydrate metabolism (Lazzarotto, 2016; Sproles et al., 2019; Tivey et al., 2020), and it has been linked to metabolic processes in adaptation to ocean acidification in other taxa (Dineshram et al., 2015). The NR2F6 (also known as CoupTFII) is related to the regulation of adipogenesis, glucose, homeostasis and metabolism energy (Li et al., 2009; Jeong et al., 2014; Baldwin et al., 2017). The ZFP57 is associated with regulation in early embryonic imprinting methylation, which may be altered by nutrients in the diet (Amarasekera et al., 2014; Zglejc and Franczak, 2017; Irwin et al., 2019). Moreover, a gene of the family of ZFP is positively selected in killer whales, with genomic differences evident for one of the Antarctic ecotypes (Foote et al., 2016), which is known to show differences in its feeding specialisations (Pitman and Durban, 2012; Foote et al., 2019).

The three positively selected SNPs found in exonic regions were all associated with metabolic pathways. This could suggest that the optimization of nutrients and energy during cell cycle processes are important for common dolphins. However, there were also other positively selected variants located in promoters (LZTS1, KRBA1), intronic regions (PKD1L2, P3H2, SYT6, ERC2, LEF1, ABCB8, RTEL1, TLN2, MTCL1, STX7 and CFAP54), and intergenic parts of putative genes (LZTS1, EBF2, ELL, IGFBP7, KRBA1, NKD2, TAS1R2, MTCL1 and KCTD16). Although little is known about the importance of non-coding regions, there is strong evidence that they also play a role in adaptation (Andolfatto, 2005; Jones et al., 2012;

Charlesworth et al., 2017). Some of these non-coding genes are involved with the regulation of homeostasis (e.g. STX7, NKD2, RTEL2) (Zhang et al., 2007; Youds et al., 2010; Roca-Agujetas et al., 2019), osmoregulation (e.g. IGFBP7, KRBA1, KCTD16) (Fuentes et al., 2010; Havird et al., 2016; Breves et al., 2017), adipogenesis (e.g. LZTS1, EBF2, NR2F6) (Qiu et al., 2007; Li et al., 2009; Angueira et al., 2020), thermogenesis (e.g ERC2) (Turcot et al., 2018), and in regulating pathways of the sensory system, such as photoreceptors (e.g. ABCB8) (Allikmets et al., 1997), or inhibition of taste receptors (e.g. TAS1R2, PKDL1) (Horio et al., 2011; Pang et al., 2014). The evidence reported here is based on a small representation of the genome (less than 2% of the dolphin genome). Thus, it is highly expected that future studies using whole genome datasets will expand and report on many other gene regions and pathways likely to be under selection in these common dolphin populations.

Implications for conservation under future climatic scenarios

This study helps to elucidate how the environment may be influencing fine-scale, adaptive population differentiation of common dolphins across southern Australia. With the rapid climatic and anthropogenic pressures impacting upon marine species (Grummer et al., 2019; Manel et al., 2019; Razgour et al., 2019), it is essential to understand which environmental factors may shape genomic variation to identify locally adapted populations relevant for conservation and management. Models predicting the impact of climate change in marine systems have provided evidence that differences in circulation patterns will likely lead to warmer environments (Banks et al., 2010; Suthers et al., 2011; Antao et al., 2020). For cetaceans, two possible scenarios have been proposed so far. One scenario suggests that changes in ocean circulation, wind patterns and currents could enhance upwelling areas, with large predators such as common dolphins likely benefiting from these changes (e.g. Whitehead et al., 2008; Palacios et al., 2013; Schumann et al., 2013). By contrast, another scenario suggests that warmer sea surface temperatures would alter community dynamics and increase exposure of populations to various pathogens (e.g. Bossart, 2011; Schumann et al., 2013; Reed et al., 2020). In this second scenario, prey abundance and distribution could be greatly impacted by affecting plankton biomasses (e.g. Wernberg et al., 2011; Roberts et al., 2017), which could lead to outbreaks, prey depletion and population declines for cetaceans and other large marine predators.

Both types of scenarios could potentially impact on southern Australian common dolphins. The first scenario is perhaps most likely for common dolphins inhabiting sites where connectivity persists over thousands of kilometres due to seasonal aggregations in upwelling centres, as previously suggested for other marine predators (e.g. Palacios et al., 2013; Schumann et al., 2013). In this scenario, southern Australian common dolphins could enhance the movement of nutrients to different habitats and trophic levels (e.g. Castro-Tavares et al., 2019; Sousa et al., 2019). This movement of nutrients could affect on the timing and magnitude of the upwellings (e.g. Wernberg et al., 2011), impacting common dolphins and other cetaceans species that feed upon high density prey biomasses (Roberts et al., 2017; Sousa et al., 2019; Bestley et al., 2020). In contrast, the second scenario could perhaps be particularly relevant for common dolphins that live in protected habitats in which extreme climatic events, such as marine heatwaves, could lead to high mortalities of prey species (e.g. Wild et al., 2019) and alteration of spawning times (e.g. Ward et al., 2017; Richardson et al., 2020). Moreover, changes in temperature and nutrients of waters masses could lead to low abundance and redistribution of prey species (e.g. Watson et al., 2013; Foo et al., 2020). For dolphin species that inhabit protected environments, epizootic events often coincide with this type of extreme climatic stressors, leading to negative impacts on population health and reproduction, and occasionally large morbidity and mortality rates (e.g. Kemper et al., 2016; Batley et al., 2019; Reed et al., 2020). Moreover, common dolphins in embayment areas such as Gulf St Vincent and Spencer Gulf have been subjected to fisheries interactions for long periods of time (Bilgmann et al., 2008; Robbins et al., 2017), and extreme climatic events may compound impacts due to less food availability (e.g. Kemper et al., 2016; Bestley et al., 2020; Reed et al., 2020). Thus, these scenarios could compromise common dolphin populations, leading to a decline of local populations or habitat displacement (e.g. Reed et al., 2020), or extreme events of prey depletion, as seen in other common dolphins populations around the world (e.g. Murphy et al., 2019; Genov et al., 2020). The dynamics of marine ecosystems are extremely complex, and future climatic changes may present non-linear alterations that need to be contemplated in future conservation plans (Watson et al., 2013; Kämpf and Chapman, 2016).

As a near top predator, common dolphins provide important ecosystem services to the marine environment (Castro-Tavares et al., 2019; Sousa et al., 2019), and if anthropogenic or climatic impacts were to occur, these could lead to changes in food-webs and eutrophication of ecosystems (e.g. Daskalov, 2002; Reed et al., 2020; Ulman et al., 2020). Adaptation to heterogeneous environments in species with high genomic diversity can promote population resilience to climatic changes (Wilder et al., 2019). When making policies and management decisions, it is important to incorporate information from both neutral and adaptive markers to ensure the persistence of high standing genomic variation in marine populations (Manel and Holderegger, 2013; Riginos et al., 2016; Xuereb et al., 2020). Currently, these putative divergent populations are being managed as combined stocks, according to the management stocks of their prey(e.g. AFMA, 2019b), with no specific consideration of genetic or genomic differentiation. Results of this study disclosed up to five putatively adapted common dolphin populations in southern Australia that need to be considered as priority areas for conservation and management, taking into account the potential cumulative impacts of fisheries and other stressors in each local population, as well as across the metapopulation. This needs to be prioritised in common dolphin local populations such as the one from Gulf of St Vincent, which has been and continuous to be impacted by human activities, exhibits the least amount of migration compared to locally adjacent sites based on neutral markers (Barceló et al. 2021, Chapter 2), and is a site where common dolphins present putative adaptation to their semi-enclosed embayment. Thus, results from neutral markers showed that these putatively adapted populations are likely to be demographically dependent, given the amount of gene flow between them (Barceló et al., 2021, Chapter 2). In contrast, candidate adaptive loci disclosed by the GEA analysis suggested that some of the dolphins' genomic differentiation is associated with environmental gradients that perhaps lead to a local adaptation. Thus, it is recommended that neutral and adaptive variation should be incorporated into policy for the management of common dolphin populations. Inter-state jurisdictional collaboration should aim to maintain connectivity across the locally adapted populations of the species, to ensure the persistence of high standing genetic variation across the region, which could act as an insurance for ongoing and future anthropogenic impacts and climatic changes.

Conclusion

This research used genome-wide SNPs to disclose fine-scale adaptive genomic differentiation for common dolphins inhabiting different regions of southern Australia. The adaptive dataset obtained from multivariate GEA and Bayesian analyses suggested the presence of up to five locally adapted populations. The GEA analysis indicated that the common dolphins genomic variation of these putatively local adapted populations are impacted by four key environmental variables related to three oceanographic phenomena characteristic of the region. Genomic variation in dolphins off the southern coast of western Australia was associated with current velocity, while genomic differentiation of common dolphins from sites along the continental shelf break were associated with primary productivity and sea surface temperature. The latter may relate to major upwelling centres, which could be promoting areas of seasonal aggregation. By contrast, genomic differentiation of common dolphins from protected coastal habitats and embayments were associated mainly with fluctuations in salinity. These environmental variables may present gradients and discontinuities, that in turn may create soft barriers among putatively adapted local populations. This study represents the first fine-scale seascape genomics assessment of common dolphins in a dynamic heterogeneous environment, in which the candidate genes described could be used for future comparative studies of common dolphins in the region and perhaps other delphinid species that share the area. Results highlight that conservation and policy efforts towards common dolphins should aim to preserve both neutral and adaptive genomic variation of populations, aiming to preserve diversity as well as connectivity, and taking into account cumulative impacts on the putatively five adaptive populations. Maintaining connectivity can lead to high standing genomic variation, which in turn will enhance their chances of survival into unfavourable anthropogenic impacts, including climatic events.

CHAPTER 4. ADAPTIVE DIVERGENCE IN THE AUSTRALIAN METAPOPULATION OF COMMON DOLPHINS (*DELPHINUS DELPHIS*)

Author contributions

Andrea Barceló Celis - Conceptualization and design of the study, DNA extractions, ddRAD library preparation, bioinformatics, data analyses, writing of the chapter and corresponding author.

Luciana Möller - primary supervisor - Conceptualization and design of the study, guidance on data analyses and interpretation, collection of samples and drafting manuscripts.

Luciano Beheregaray - associate supervisor- Guidance on data analyses and interpretation, and drafting manuscripts.

Kerstin Bilgmann - adjunct supervisor - Collection of samples and drafting manuscript.

Jonathan Sandoval-Castillo - Guidance on laboratory methods, bioinformatics and data analyses.

Chris Brauer – Guidance with data analyses.

Abstract

Assessing the environmental influences on adaptive diversity of marine metapopulations is fundamental to predict their resilience to environmental changes and to inform conservation management. Metapopulations of wide-ranging species are often connected across ocean basins, but may also exhibit localised adaptive divergence across heterogeneous regions due to the influence of local- and meso-scale oceanographic features. In this study, we used seascape genomic approaches to characterise and analyse putatively adaptive genomic variation across multiple segments of the Australian metapopulation of common dolphins (*Delphinus delphis*). Analyses were implemented for the entire metapopulation level using 17,539 filtered SNPs (i.e. the broad-scale dataset) and for the eastern coast metapopulation segment using 16,326 SNPs (i.e. the fine-scale dataset). At the metapopulation level, two regional and potential adaptively divergent populations were identified after accounting for the effects of spatial distance. Genomic variation in these putatively populations appeared strongly associated with variation in sea surface temperature, current velocity, salinity, bathymetry and primary productivity. Much lower adaptive divergence was detected along the eastern coast segment, which appeared associated mainly to variation in primary productivity. We proposed that both broad- and fine-scale adaptive divergence in Australian common dolphins is influenced by three main oceanographic and coastal features: (i) ocean circulation patterns at range edges, (ii) areas of eddies and upwellings, and (iii) semi-enclosed coastal habitats. Preliminary evidence found for repetitive selection in some regions of the genome is speculated here in the context of parallel evolution of dolphins on separate coasts. Our results provide novel information for the conservation and management of multiple segments of the Australian metapopulations of common dolphins, within the context of a highly dynamic and heterogeneous marine environment.

Introduction

Complex interactions of ecological processes can shape the spatial structure of populations, and information about these interactions are essential for the conservation and management of biodiversity (Levins, 1969; Hanski, 1998; Saccheri and Hanski, 2006). Molecular ecology involves the understanding of ecological and evolutionary processes that generate and maintain neutral and adaptive genetic variation (Funk et al., 2012; Grummer et al., 2019; Rajora, 2019). In metapopulations, which comprises species distributed over large spatial scales, these processes can occur along highly heterogeneous and dynamic environments (Gagnaire et al., 2015; Riginos et al., 2016). In these types of populations, the heterogeneity of habitats and selective pressures impacting local populations and the dispersal of individuals can lead to differences in life history traits (e.g. feeding, reproduction), which in turn affect their contribution to ecosystem functioning (Hanski, 1998; Bonte and Bafort, 2019). If selection occurs in traits that favour the survival and reproduction of individuals that disperse, the metapopulation or population fitness can be impacted (Wright, 1968; Crow and Kimura, 1970; Hanski, 1998). However, if natural selection or selective pressures occur at a specific habitat, it may only impact the local population (Wright, 1968; Crow and Kimura, 1970; Hanski and Saccheri, 2006). The maintenance of connectivity within a species allows the persistence of standing genetic variation and evolutionary potential that may enable populations to adapt to pressures such as climatic changes (Wright, 1968; Crow and Kimura, 1970; Hanski, 1998).

Marine ecosystems are dynamic heterogeneous environments, where the majority of species exhibit high dispersal potential at some stage of their life (Palumbi, 2003; Shafer et al., 2015; Kelley et al., 2016). This dispersal is, in most cases, modulated by oceanic circulation and food availability, in which marine species seek the optimal foraging for achieving their energy requirements (Emlen, 1966; MacArthur and Pianka, 1966; Spitz et al., 2012). Thus, marine species are influenced by abiotic (i.e. oceanographic and environmental features) and biotic (i.e. predator-prey interactions) factors, which impact the movement of individuals between environments and can lead to genetic differentiation among their populations (Manel and Holderegger, 2013; Rajora, 2019; Oleksiak and Rajora, 2020). Genetic variation can be different between individuals inhabiting contrasting environments, which impacting on their individual fitness (Riginos and Liggins, 2013; Hanson et al., 2017; Waters et al., 2020).

The use of methodologies that combine spatial and environmental data with genomic variation in marine systems (i.e. seascape genomics), enable the assessment of how environmental heterogeneity leads to adaptive divergence of marine populations (Manel and Holderegger, 2013; Selkoe et al., 2016; Oleksiak and Rajora, 2020). In metapopulation systems, understanding how genomic variation is associated with environmental and geomorphological gradients and discontinuities can provide vital information for the conservation and management of a species (Benestan et al., 2015; Oleksiak and Rajora, 2020; Xuereb et al., 2020). Despite many marine taxa exhibiting a metapopulation structure (Kritzer and Sale, 2004; Riginos et al., 2016), studies assessing these systems using a seascape genomics framework are still scarce (e.g. Bradbury et al., 2010; Sandoval-Castillo et al., 2018; D'Aloia et al., 2020). The few seascape genomic studies of cetaceans have shown that population structure in species with high connectivity can be impacted by ecological gradients or discontinuities (e.g. Pratt, 2020; Andrews et al., 2021; Morin et al., 2021). The potential effects of environmental heterogeneity on the divergence of marine predators within metapopulations remains poorly understood.

Large marine predators, such as the common dolphin (*Delphinus delphis*), are essential for the equilibrium and maintenance of food webs and ecosystem functioning (Goldsworthy et al., 2013; Castro-Tavares et al., 2019; Bestley et al., 2020). The movements of common dolphins are mainly driven by the distribution and density of their prey (e.g. Natoli et al., 2006; Möller et al., 2011; Bilgmann et al., 2018). Some populations of common dolphins exhibit differences in feeding specializations and strategies depending on the environment they inhabit and their target prey (e.g. Neumann and Orams, 2003; Meynier et al., 2008). In Australia, common dolphins feed mainly upon abundant small pelagic fish species such as jack mackerel (*Trachurus declivis, T.s. murphyi*), sardines (*Sardinops sagax*) and anchovies (*Engraulis australis*), and some cephalopods, such as arrow squid (*Nototodarus gouldi)* (Banks et al., 2019; Goldsworthy et al., 2019b). However, they can also target different prey species depending on the seasonal food availability and area they inhabit (e.g. Filby et al., 2010; Mason et al., 2016).

Common dolphins are widely distributed around the world (Perrin, 2021). In Australia, their group sizes range from about 2-20 individuals in shallow waters (e.g. Filby et al., 2010; Mason et al., 2016) to over 500 individuals in oceanic waters (Bilgmann et al., 2018). The species live in fission-fusion societies (Möller, 2011; Mason et al., 2016), with some group sizes related to their abundance and foraging strategies in an area (Filby et al., 2010; Mason et al., 2016). Their movement patterns also differ, with groups or individuals presenting high site fidelity to relatively small areas (<200 km) (e.g. Filby et al., 2013; Mason et al., 2016; Hupman et al., 2018), while others perform long-distances movements (>1,000 km) (e.g. Genov et al., 2012). Common dolphins in Australasia inhabit a variety of habitats along southern and eastern Australia, Tasmania and New Zealand, with contemporary gene flow within and among regional populations (>1,000 km) exhibiting a hierarchical metapopulation (Barceló et al., 2021, Chapter 2).

The formation of Australian coasts in modern ocean basins occurred during the Pleistocene-Holocene (~2.8 Ma), with distinctive topographic, oceanographic and climatic ranges (Brooke et al., 2012; Brooke et al., 2017) leading to several distinct marine habitats (Bird, 2005; Steeman et al., 2009; Kämpf and Bell, 2014). These events also led to the submergence of the Tasmanian land bridge (i.e. Bassian Isthmus), which separates three biogeographical provinces, the Flinders on the south-west, the Peronia in the east, and the Maugea in the south-east (York et al., 2008; Waters et al., 2010; Teske et al., 2017). These bioregions align closely with the neutral hierarchical metapopulation structure of Australasian common dolphins (south-west, east and south-east) previously disclosed (Barceló et al., 2021, Chapter 2).

The genetic differentiation among populations of Australian common dolphin could also be influenced by oceanographic conditions (Möller et al., 2011; Bilgmann et al., 2014), which are driven by two main currents. The first one follows the eastern Australian coast, and forms the south flowing East Australian current. The second surrounds Indonesia and creates a poleward current along the western Australian coast; the warm Leeuwin current that flows into the southern Australian coast from west to east (Bird, 2005; Brooke et al., 2012). Both of these branches have counter currents of cold water that promote seasonal upwellings in southern Australia, as well as cyclonic and anticyclonic eddies along eastern Australia, leading to differences in water masses across the two coasts (Condie et al., 2011; Suthers et al., 2011; Kämpf and Chapman, 2016). These currents in turn are known to impact on the distribution of marine taxa with passive dispersal and the genetic differentiation of their populations (e.g. Waters et al., 2005; Costello et al., 2017), possibly including common dolphins and their prey (e.g. Möller et al., 2011; Bilgmann et al., 2014). All these different geomorphological, oceanographic and biological characteristics across Australian temperate marine bioregions provide a system for natural selection to act upon populations of common dolphins. In this study, we use two filtered SNP datasets to characterise and analyse putatively adaptive genomic variation across multiple segments of the Australian metapopulation of common dolphins (*D.*

delphis). The analyses were carried out at the level of the entire metapopulation (i.e. the broad-scale dataset, details below) and at the level of the eastern coast segment (i.e. the fine-scale dataset). This arbitrary division builds on the main results of the two previous chapters, one that characterised neutral metapopulation structure across Australasia and the other which characterised adaptive divergence across the better sampled and highly heterogeneous marine environment of southern Australia. The two-scale strategy used in this chapter allowed us to test the relative influence of environmental heterogeneity and oceanographic features across multiple, hierarchically structured population segments. The inferences made allowed us to assess the roles of connectivity and adaptation over a range of spatial scales and selective environments, providing new perspectives towards a better understanding of adaptive resilience in a near-top marine predator.

Methods

Sample collection and study area

Common dolphins were biopsy sampled along eastern and southern Australia between 2000 and 2017 (same individuals utilised in Chapters 2 and 3) across a total of 13 sites. At-sea GPS locations were obtained for each biopsy sampled individual, providing a total of 302 biopsies for genomic analyses (Figure 4.1). Note that given the proximity of <50 km, eight individuals from Forster were considered as Broughton Island (BI). These sites were chosen for a comparative broad and fine spatial scale analysis encompassing the distribution of the species along the two main Australian temperate marine bioregions (i.e. southern and eastern Australia). Each sample was collected from a free-ranging individual using a hand held biopsy pole (Bilgmann et al., 2007a) or a remote biopsy gun (PAXARMS) (Krutzen et al., 2002). In an attempt to avoid the inclusion of closely related individuals, dependent calves were not sampled. Biopsies were preserved in 90% ethanol or in a 20% salt-saturated solution of dimethyl sulphoxide (DMSO), and kept in a -80^{0}C freezer until laboratory analyses took place, as suggested in Smith and Morin (2005).

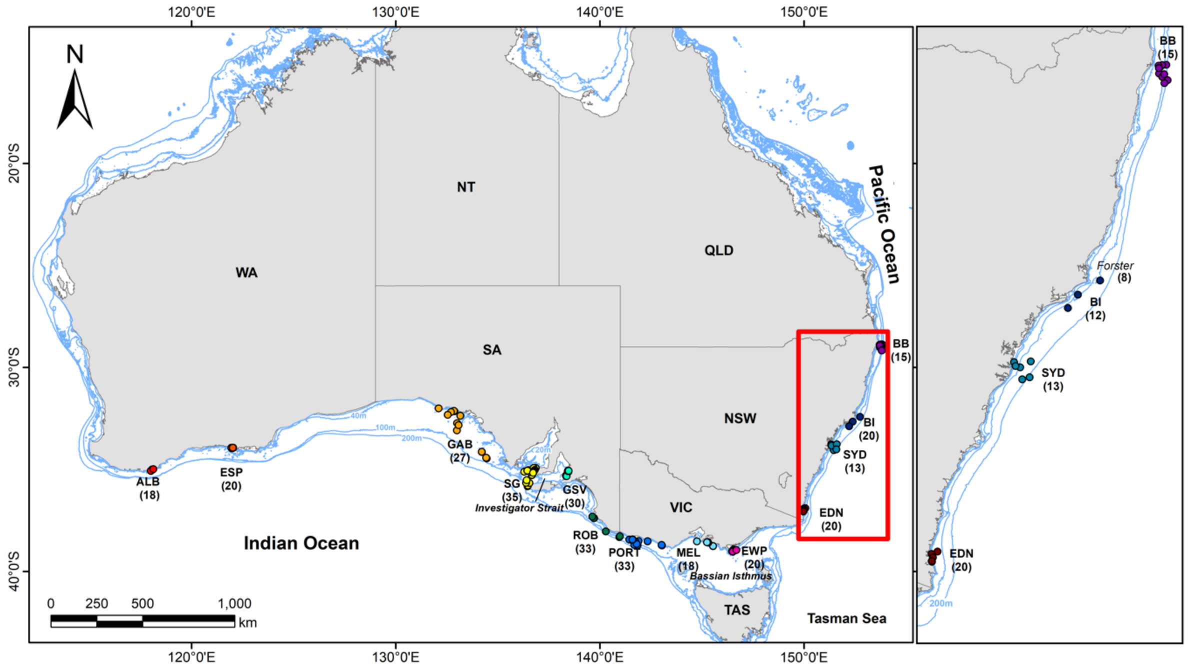


Figure 4.1 Study area in southern and eastern Australia showing the geolocations for common dolphin (*Delphinus delphis*). A total of 302 individuals were used at broad-scale (southern and eastern Australia) and 65 at fine-scale (eastern Australia). Acronyms: *Albany (ALB); Esperance (ESP); Great Australian Bight (GAB); shelf waters, Spencer Gulf (SG); Gulf St Vincent (GSV); Robe (ROB); Portland (PORT); Melbourne (MEL); East, Wilson Promontory (EWP); Ballina (BB); Broughton Island (BI); Sydney (SYD) and Eden (EDN).

Laboratory analyses and bioinformatics

DNA extraction from skin samples were performed using a salting-out protocol (Sunnucks and Hales, 1996). Quantity and quality controls, a total of 300ng and >5,000 bp per sample, were determined using a Qubit 2.0 fluorometer (Life 178 Technologies), and a Nanodrop spectrophotometer (Thermo Scientific).

Library preparation for the double digest restriction-site associated (ddRDA) was performed following a modified protocol from Peterson et al. (2012). We used 96 individual barcodes per lane in a total of four lanes with known replicate samples. These were single-ended sequenced in an Illumina HiSeq 2500 platform at the South Australian Health & Medical Research Institute (SAHMRI).

The raw data quality was assessed and demultiplexed using process_radtags, with STACKS v1.48 (Catchen et al., 2011; Catchen et al., 2013) and the dDocent2.2.19 pipeline 219 (Puritz et al., 2014). The resulting sequences were filtered using a modified protocol of VCFtools. The quality-filtered reads were then mapped against the genome of a closely related dolphin species from southern Australia (Indo-Pacific bottlenose dolphin, *Tursiops aduncus*; Batley et al., 2021), due to the absence of a high-quality genome for *D. delphis.* Detailed information of laboratory and bioinformatics analyses are provided elsewhere (Barceló et al., 2021, Chapter 2).

For this study, two datasets were selected based on the Australian metapopulation neutral structure, and availability of samples from free-ranging individuals. The first one included samples of common dolphins from the eastern Australia segment, corresponding to 68 individuals. The second dataset was selected based on the Australian common dolphin metapopulation, which included 302 biopsy samples from both segments: eastern, 68 biopsies; and southern, 234 biopsies (Chapters 2 and 3). Each dataset was analysed separately according to their sampled sites (i.e. four and 13 sites, respectively). The arrangement of sites at the two spatial scales provided similar number of samples per site for a comparison between and among them. For each dataset, non-polymorphic loci were excluded using a Minor Allele Count (MAC) of 1, as suggested in Tabangin et al. (2009) and Linck and Battey (2018).

Genotype-Environment Association (GEA)

A seascape genomics framework with a multivariate Redundancy Canonical Analysis (RDA) was implemented to detect loci putatively under selection (as detailed in Brauer et al., 2016). Based on the distribution of common dolphins and environmental heterogeneity along southern and eastern Australia, this study utilised six available and relevant environmental variables to test for associations to the dolphins' genomic variation.

Selection of environmental variables

Environmental variables were selected following the same framework previously detailed (Chapter 3), where six variables were used to tested for associations to the genomic variation of common dolphins in Australia. These variables were bathymetry, sea surface temperature, chlorophyll *a*, current velocity, primary productivity, and salinity. For each environmental variable, annual maximum, mean, minimum, and range values between 2000 to 2014 were downloaded from the database BioOracle at a resolution of ~9.2 km using the R package ‘sdmpredictors’ (Tyberghein et al., 2012; Assis et al., 2018) (see Appendix E, Table E.1). The range of bathymetry was not available from BioOracle database, and therefore it was calculated based on the range of the minimum and the maximum values of the bathymetry. These resulted in a total of 24 variables to be tested for each spatial scale.

Due to the complexity and heterogeneity of the Australian coasts, pairwise geographic distances were calculated on an individual level for each dataset using GPS coordinates of each individual and the R function *viamaris* from the ‘MELFU’ package (MELFU/pigmyperch Github). This was done at a resolution of 5000 pixels accounting for complex coastlines and avoiding land crossing. Pairwise geographic distances were then transformed to a Moran’s eigenvector map (MEM) using the package ‘memgene’ (Galpern et al., 2014). The explanatory MEM axes were then used as spatial variables.

Environmental variables were selected by first implementing a standardisation of the 24 variables with the package ‘pysch’ (Blanchet et al., 2008). After that two tests for multicollinearity were implemented to avoid overfitting the model: excluding highly correlated variables ($|r| > 0.7$) (Dormann et al., 2013; Prunier et al., 2015; 2017), and using a conservative variance inflation factor (VIF) maximum of 3 (O’brien, 2007). All the selected variables were identified using the forward selection method, and those included in the models had to explain a significant portion ($p < 0.05$) of the genomic variation of common dolphins to be included in the final model (Blanchet et al., 2008; Legendre et al., 2011).

Redundancy Canonical Analysis (RDA)

A multivariate RDA was chosen due to its robust performance in detecting loci associated with multiple environmental variables (e.g. Capblancq et al., 2018; Forester et al., 2018; Grummer et al., 2019). The RDA analyses were implemented for both datasets using the R package ‘vegan’ (Oksanen et al., 2019). Additionally, for the metapopulation level analysis, regional neutral population structure was taken into account to avoid confounding patterns of gene flow and demographic history (e.g. Forester et al., 2018). This was done by incorporating the Q values from the Admixture analysis as an additional condition in the RDA analyses.

The RDA was performed separately for each spatial scale, with selected environmental variables and axes calculated through 1,000 permutations in an analysis of variance. Only RDA axes that explained a significant portion ($p < 0.05$) of the genomic variation were considered for the locus selection, and only loci that scored greater than three standard deviations (± 3SD) from the mean locus scores were considered as under selection (Legendre et al., 2011; Capblancq et al., 2018; Forester et al., 2018). For the final step, Spearman's correlation was calculated between each candidate locus and selected environmental variable to establish which variable had a greater association to a particular locus.

Test for outlier selection (F_{ST} outlier)

Bayescan v2.1 analyses were implemented (Foll and Gaggiotti, 2008) for each dataset independently, to compare with results from the RDA multivariate analyses with a GEA approach . This method does not test for associations with environmental variables, however, it is robust and conservative to identify loci putatively under selection. This method identifies outlier loci through a logistic regression model; it considers the demographic population component, and decomposes F_{ST} values into locus-specific components (Foll and Gaggiotti, 2008), reducing the number of false positives (e.g. Narum and Hess, 2011; Rellstab et al., 2015). The outlier test was once again performed for each spatial scale separately, with the same previously used parameters (Chapter 3), and a multinomial Dirichlet model. Loci were considered candidates if their q-value was <0.1 (false discovery rate (FDR) <10%). This allowed the identification of additional loci putatively under divergent selection, as this software has a good performance in complex demographic scenarios (Foll and Gaggiotti, 2008).

Adaptive population structure

Based on the full dataset, loci that were identified as potentially under selection for each scale independently, by both methodologies (RDA and Bayescan), were extracted to obtain two unique putatively adaptive SNP datasets. The first dataset includes individuals only from the eastern Australia segment, whereas the second dataset includes individuals from the Australian-wide metapopulation, with the exception of Tasmania, as no samples from free-ranging animals were available from this area. Adaptive genomic diversity and population structure were assessed for each dataset. Measures of genomic diversity per site were calculated, including expected heterozygosity (H_E) and observed heterozygosity (H_O), using the software Genodive 2.0b27 (Meirmans and Van Tienderen, 2004).

Principal Component Analysis (PCA) was implemented to investigate adaptive population genomic structure using the R package ‘Adegenet’ (Jombart, 2008; Jombart and Ahmed, 2011). The Bayesian Information Criterion (BIC) and Akaike Information Criterion (AIC) provided the best-supported number of clusters for each spatial scale using the snapclust.chooseK function (Beugin et al., 2018). Population stratification based on a Bayesian clustering approach that estimates individual ancestries was also investigated using Admixture v1.3.0 (Alexander et al., 2009). This analysis was used only to compare the results to those based on the putatively neutral dataset (Barceló et al., 2021, Chapter 2), given that Hardy-Weinberg assumptions of equilibrium are likely violated by adaptive datasets (Funk et al., 2012). Maximum likelihood estimates were calculated using the ancestry proportions and population allele frequencies to identify the most likely number of K (i.e. populations) in the dataset, and to model the probability of observed genotypes (Alexander and Lange, 2011). The broad-scale dataset was tested for K 1-13, while the fine-scale dataset was tested for K 1-4, which related to the number of sampling sites. Subsequently, cross validation with ten replicates for each of the K values was performed to confirm and provide an accurate estimation on the number of populations at each spatial scale.

Putatively adaptive genomic differentiation among sites was estimated as pairwise F_{ST} (Weir and Cockerham, 1984) using Genodive 2.0b27, for each spatial scale separately. Significance levels were assessed using 10,000 permutations (FDR = 10%), and corrected by the B-Y method (Benjamini and Yekutieli, 2001). Heatmap plots of F_{ST} were constructed with the R package ‘ggplot2’ (Wickham, 2016).

Functional enrichment analysis and annotation

A functional enrichment analysis was performed using the candidate loci detected with the RDA for each dataset separately. For these analyses, the same analytical framework previously detailed in Chapter 3 was used. First, the full dataset was compared to all available cetacean nucleotides and non-redundant proteins available within the NCBI database at time of analysis (Appendix E, Table E.2) (NCBI, 2020) for 601-bp length flanked sequences, with an e-value threshold of $1X10^{-3}$, which was based on the linkage disequilibrium filter. The 601-bp sequences represent 300-bp either side of every candidate SNP, and obtained from the full dataset of 17,875 SNPs. Subsequently, an enrichment GO term analysis was performed for the candidate loci (601-bp) at each scale. This was done using a Fisher’s exact test and a FDR of

<5% (Gene Ontology, 2015). Specific candidate genes were obtained from the resulting GO terms, in which each SNP with a variant in a candidate gene was further examined for its position in an intronic or exonic region using snpEFF (Cingolani et al., 2012). Finally, using the Reactome and UnitProtKB databases (UnitPro Consortium 2018), each SNP found in coding and non-coding regions were further related to a gene pathway and function.

Results

Population genomic dataset

A total of 700 million filtered sequence reads were generated for the 302 common dolphin samples. After filtering using stringent criteria, a high-resolution dataset of 17,875 filtered SNPs was obtained, with 1% average missing data per locus (Appendix D, Table D.1) (detailed in Barceló et al. 2021, Chapter 2). Exclusion of low quality, replicate samples, and closely related individuals (i.e. three samples from eastern Australia and 20 from southern Australia), resulted in two datasets: a broad-scale SNP dataset based on 279 common dolphins across southern and eastern Australia; and a fine-scale dataset encompassing 65 individuals from eastern Australia (Figure 4.1). After further filtering for non-polymorphic loci, the two final, high quality datasets comprised of 17,539 SNPs at broad-scale and 16,326 SNPs at fine-scale (Appendix D, Table D.1).

Genotype-Environment Association

After testing for multicollinearity ($|r| > 0.7$ and VIF ≤ 3) and significance of the RDA analyses ($p < 0.05$), six environmental variables were retained out of the 24 initially tested (Appendix D, Figure D.1). At broad-scale (Australian-wide), the retained, significant variables were surface temperature range, sea surface temperature mean, current velocity maximum, salinity range, bathymetry and primary productivity minimum (Table 4.1 and Figure 4.2). At fine-scale (eastern Australia), the only environmental variable retained was primary productivity minimum (Table 4.1 and Figure 4.3). At broad and fine scales, the selected environmental variables exhibited a contrasting visual gradient across the Australian temperate coasts (Figure 4.4).

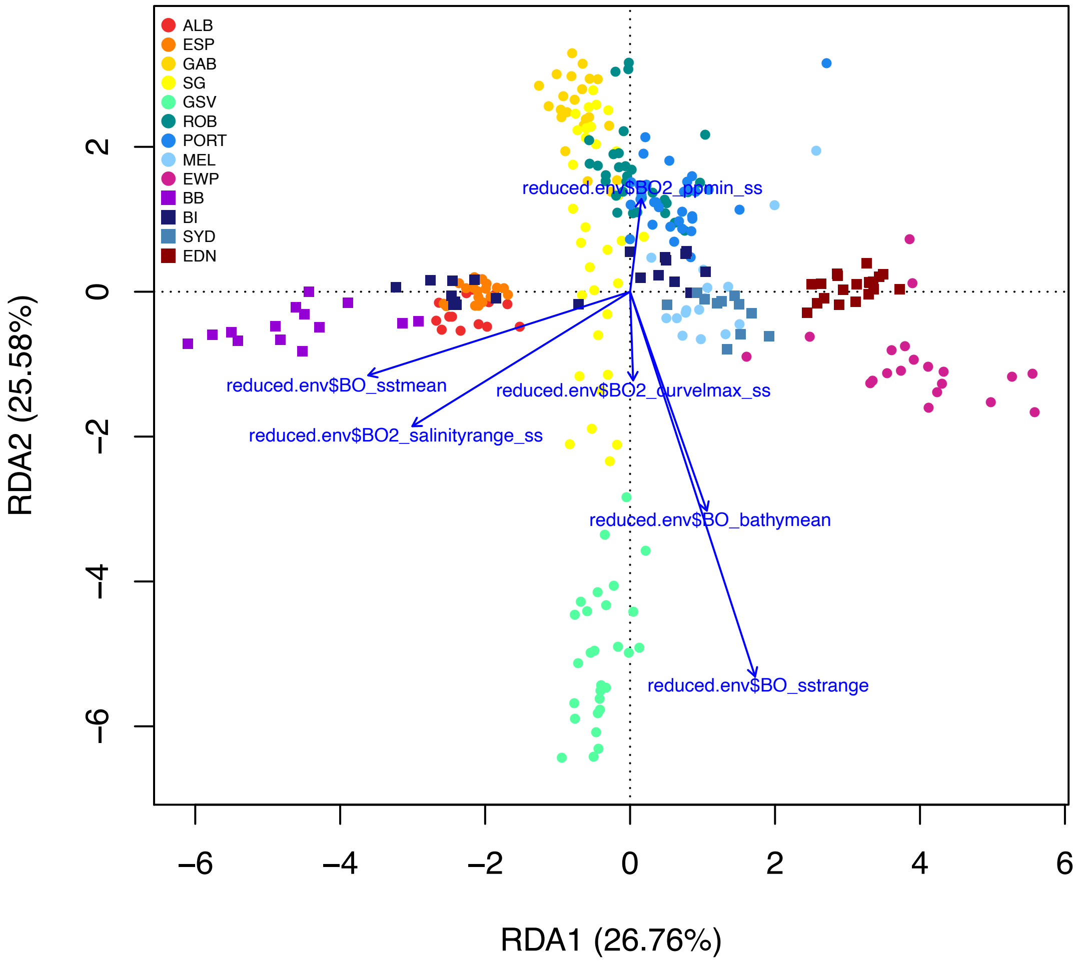


Figure 4.2 Redundancy Canonical Analyses (RDA) displaying the influence of the six significant environmental variables on individual genomic variances of Australian common dolphins (*Delphinus delphis*). Analysis based on 279 samples and 13 sites from southern and eastern Australia. The overall variance of the model explained was 3954 (p = 0.001) (see Appendix D and Table 2 for more details). Legend displays sites from west to east, and north to south, respectively in each coast, and colours correspond to the site membership where common dolphins were sampled (as in Figure 4.1).

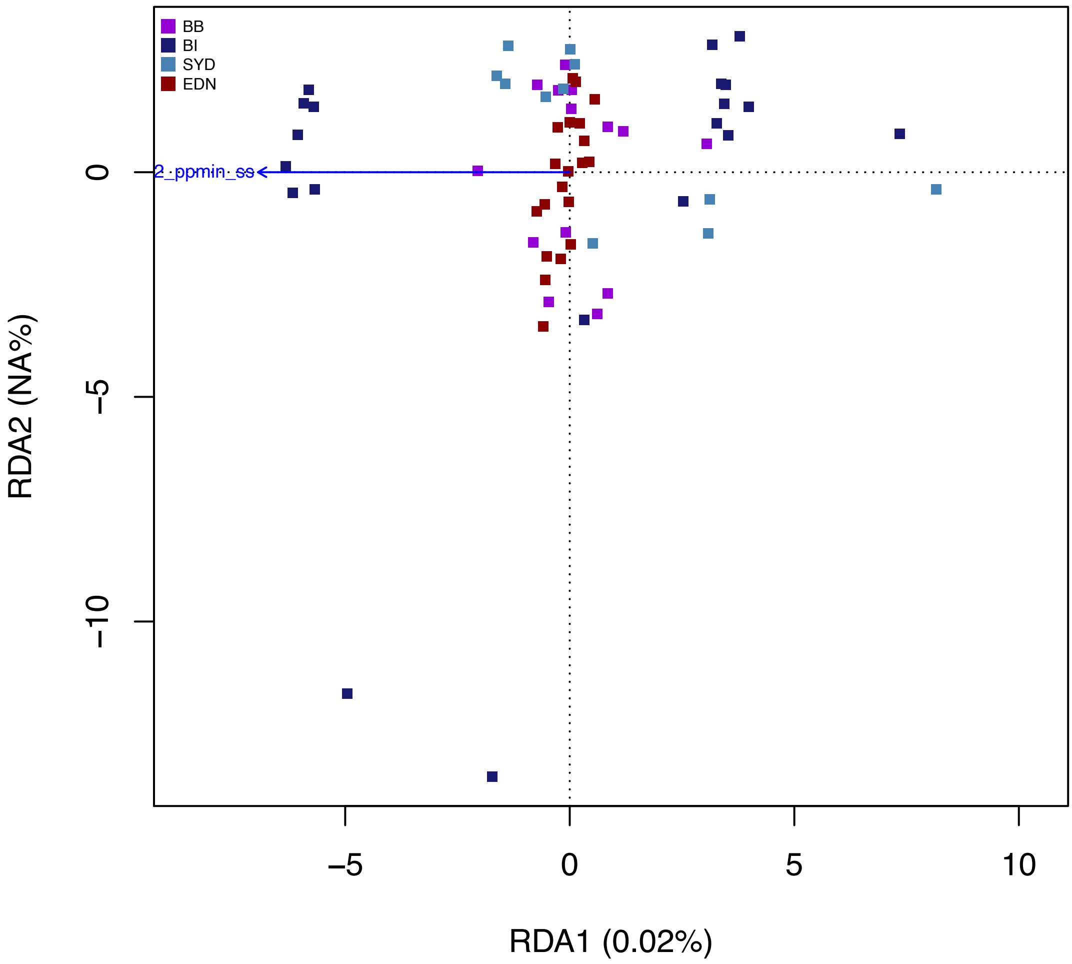
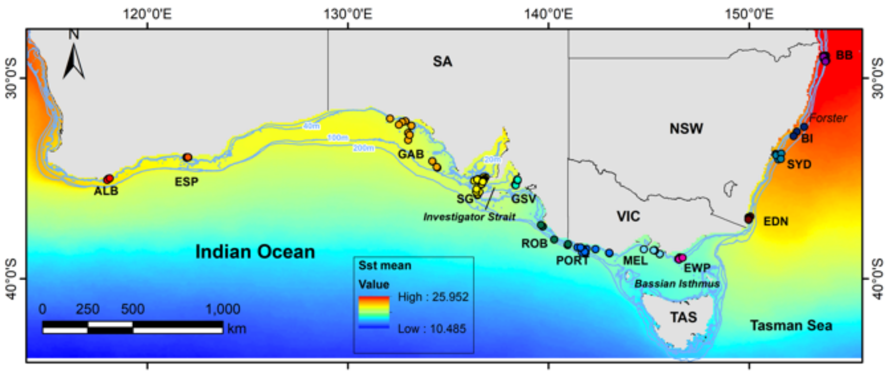


Figure 4.3 RDA displaying the influence of the significant ecological variable of primary productivity on genomic variances of eastern Australian common dolphins (*Delphinus delphis*). Analysis based on 65 samples and 4 sites from eastern Australia. The overall variance of the model explained was 3948 ($p = 0.001$) (see Appendix D and Table 2 for more details). The second component was not significant and was only used for visualisation. Legend displayed from north to south, and colours correspond to the site membership where common dolphins were sampled (as in Figure 4.1).

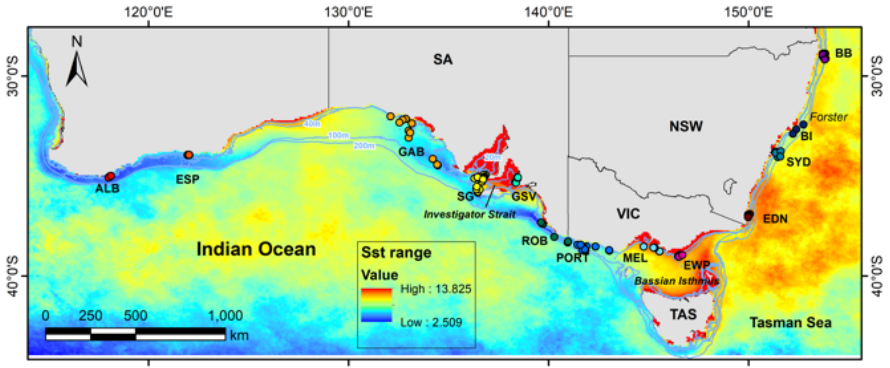
The overall models of the RDA were significant ($p < 0.001$) at both broad and fine spatial scales (Table 4. 1). At the broad-scale, genotype and spatial variables explained 1.3% of the variation in the full model, while the environmental variables explained 3.3% of the variation. At the fine-scale, genotype and spatial variables explained 8.9% of the variation in the full model, while the primary productivity explained 1.9% of the variation. The number of loci retained as adaptive candidates was 646 SNPs at broad-scale, and 172 at fine-scale.

Table 4.1 Significance of the environmental variables selected in the MEM axis and in the Redundancy Canonical Analysis model for southern and eastern Australian common dolphins (*Delphinus delphis*) based on the full dataset of 17,539 SNPs at broad-scale, and on 16,236 SNPs at fine-scale. Portion of the constrained variance explained by each environmental variable and the number of putative candidate loci is also presented.

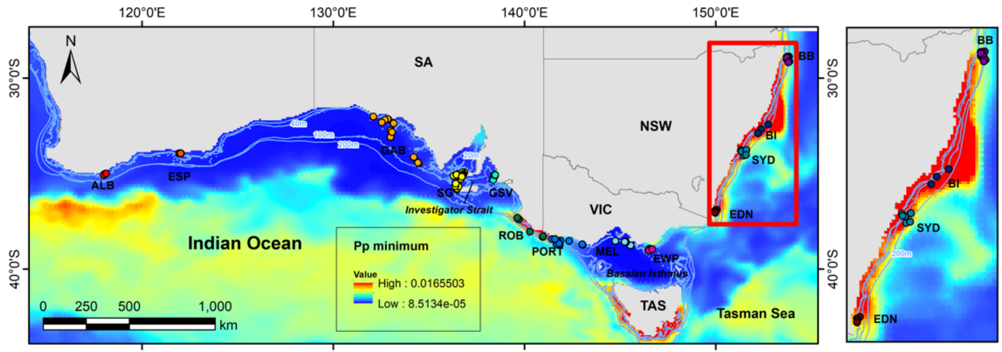
	Environmental variable	**p- value**	**Percentage explained by the model**	**No. of candidate loci**
Eastern and Southern Australia, broad-scale	Sea surface temperature range	0.001 ***	0.6196257	103
	Sea surface temperature mean	0.001 ***	0.5867476	225
	Current velocity maximum	0.001 ***	0.46788063	76
	Primary productivity minimum	0.001 ***	0.44511887	110
	Salinity range	0.001 ***	0.37936267	122
	Bathymetry mean	0.001 ***	0.35154274	11
Eastern Australia, fine-scale	Primary productivity minimum	0.001 ***	1.84903749	172


120°0'E
130°0'E
140°0'E
150°0'E
30°0'S
40°0'S
N
SA
NSW
VIC
TAS
BB
Forster
BI
SYD
EDN
GAB
ALB
ESP
SG
GSV
Investigator Strait
ROB
PORT
MEL
EWP
Bassian Isthmus
Indian Ocean
Tasman Sea
40m
100m
200m
Sst mean
Value
High : 25.952
Low : 10.485
0 250 500 1,000
km

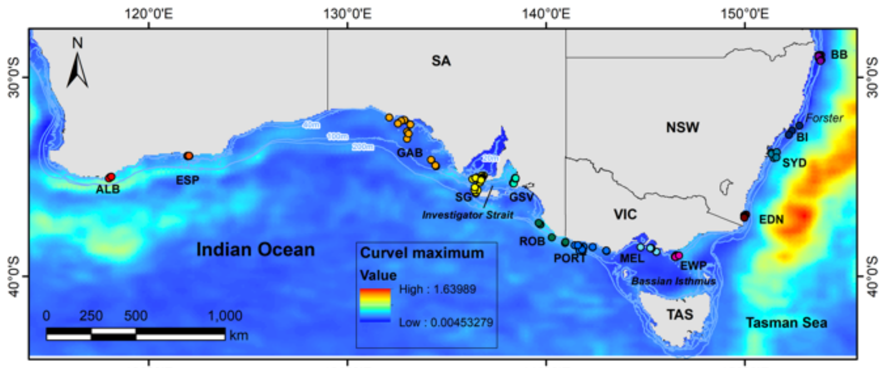
(A)


120°0'E
130°0'E
140°0'E
150°0'E
30°0'S
40°0'S
N
SA
NSW
VIC
TAS
BB
Forster
BI
SYD
EDN
GAB
ALB
ESP
SG
GSV
Investigator Strait
ROB
PORT
MEL
EWP
Bassian Isthmus
Indian Ocean
Tasman Sea
40m
100m
200m
Sst range
Value
High : 13.825
Low : 2.509
0 250 500 1,000
km

(B)


120°0'E
130°0'E
140°0'E
150°0'E
30°0'S
40°0'S
N
SA
NSW
VIC
TAS
BB
BI
SYD
EDN
GAB
ALB
ESP
SG
GSV
Investigator Strait
ROB
PORT
MEL
EWP
Bassian Isthmus
Indian Ocean
Tasman Sea
40m
100m
200m
Pp minimum
Value
High : 0.0165503
Low : 8.5134e-05
0 250 500 1,000
km

(C)


120°0'E
130°0'E
140°0'E
150°0'E
30°0'S
40°0'S
N
SA
NSW
VIC
TAS
BB
Forster
BI
SYD
EDN
GAB
ALB
ESP
SG
GSV
Investigator Strait
ROB
PORT
MEL
EWP
Bassian Isthmus
Indian Ocean
Tasman Sea
40m
100m
200m
Curvel maximum
Value
High : 1.63989
Low : 0.00453279
0 250 500 1,000
km

(D)

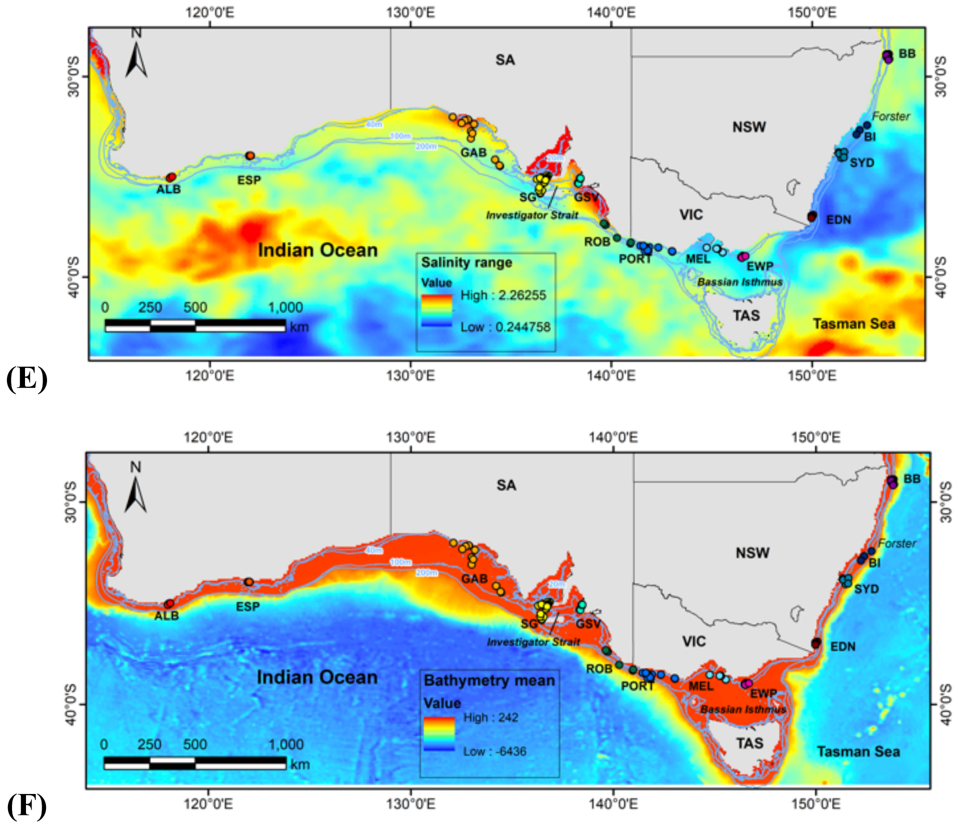


Figure 4.4 Environmental variables retained for the Genotype-Environment Association analyses in southern and eastern Australian common dolphins (*Delphinus delphis*). (A) Sea surface temperature mean (B) Sea surface temperature range, (C) Primary productivity minimum, (D) Current velocity maximum (E) Salinity range, and (F) Bathymetry mean. *Acronyms used as in Figure 4.1.

At the broad-scale, the first component explained 0.1% of the full model and 26.8% of the constrained variance, while the second component explained 0.1% of the full model and 25.6% of the constrained variance (Appendix D, Table D.2). In contrast, the only significant component at the fine-scale explained 0.02% of the full model and 100% of the constrained variance. The visualisation of each component of the RDA demonstrated how genomic variation (i.e. individuals per site) covary in response to the retained environmental variable at each spatial scale (Figure 4.2 and 4.3). Changes in sea surface temperature and salinity seem to affect genomic differentiation of common dolphins mainly at the edge of their distribution. These are represented by both the northern sites in eastern Australia, and the western sites in southern Australia. At the contact zone of the two oceans, Pacific and Indian, represented by the Bass Strait, RDA analysis clustered adjacent sites (i.e. Wilsons Promontory, Victoria; and Eden, New South Wales) together. These were correlated to sea surface temperature and salinity. By contrast, sea surface temperature range, bathymetry mean, and current velocity maximum appear to be separating common dolphins from Gulf St Vincent and some individuals from Investigator Strait from all other sites in Australia. Finally, genomic variation of common dolphins at the remaining sites along southern and eastern Australia (i.e. Great Australian Bight, Spencer Gulf, Robe, Portland and Melbourne, and Broughton Island-Forster) appears to be mainly influenced by primary productivity minimum.

Test for outlier loci under selection

At broad-scale, a total of 1,016 loci were identified by the Bayescan outlier test as being putatively under selection (Figure 4.5), while at fine-scale, 33 loci were identified as such (Figure 4.6). Subsequent analyses of adaptive population structure at each spatial scale were implemented using a combined SNP dataset based on those identified as candidate loci by the RDA and outlier loci identified by the Bayescan tests, which resulted in a putatively adaptive dataset of 1,586 loci at broad-scale, and 205 at fine-scale (Appendix D, Figure D.2).

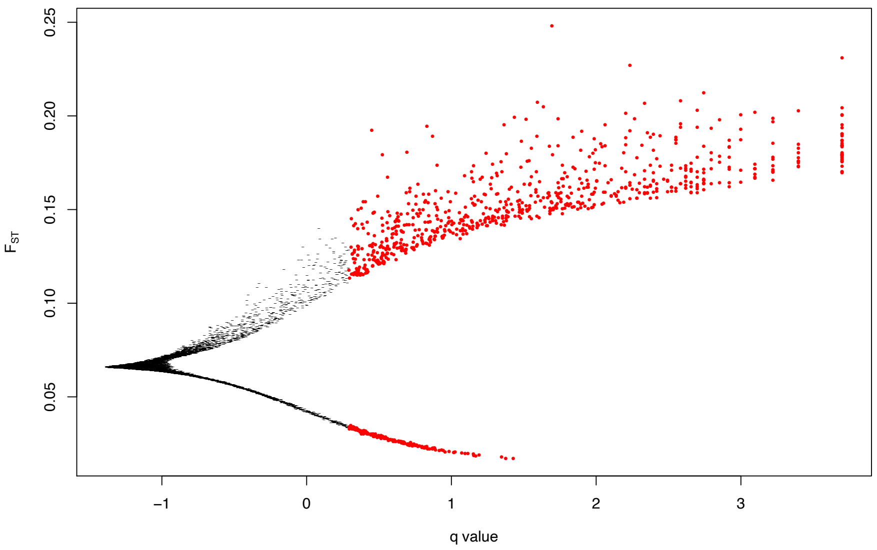


Figure 4.5 Result of the Bayescan analysis to detect outlier loci in common dolphins (*Delphinus delphis*) from southern and eastern Australia. Locus specific F_{ST} plotted against q values with a false discovery rate (FDR) of 10%. Outlier loci are represented by the red dots.

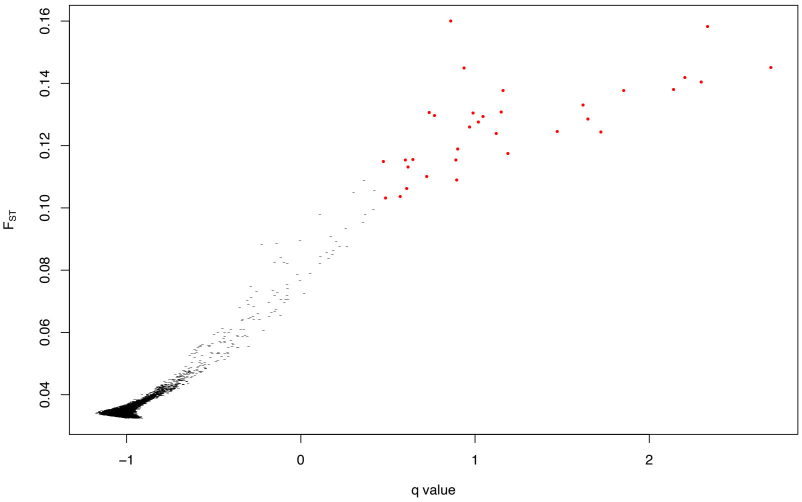


Figure 4.6 Result of the Bayescan analysis to detect outlier loci in common dolphins (*Delphinus delphis*) from eastern Australia, Locus specific F_{ST} plotted against q values with a false discovery rate (FDR) of 10%. Outlier loci are represented by the red dots.

Adaptive diversity and population genomic structure

The loci retained for the analyses at each spatial scale were independently extracted from the filtered dataset (Appendix D, Figure D.2). The inferred levels of genome-wide diversity for the putatively adaptive metapopulation loci were relatively high for all sites (H_E 0.265 to 0.345; H_O 0.266 to 0.367) compared to the putatively neutral metapopulation (H_E 0.160 to 0.212; H_O 0.154 to 0.225) (Table 4.2A; Appendix D, Figure D.13). For eastern Australia, adaptive diversity based on putative loci was also higher (H_E 0.359 to 0.424; H_O 0.407 to 0.424) compared to the putative neutral loci (H_E 0.189 to 0.209; H_O 0.189 to 0.225) (Table 4.2B). Across the Australian metapopulation, the adaptive loci presented the lowest diversity at the edge of the distribution of common dolphins in both northern New South Wales (i.e. Ballina and Forster) and southwestern Western Australia (i.e. Albany, Esperance), with the exception of the semi-enclosed environment of Gulf St Vincent.

Admixture analyses of the putatively adaptive datasets indicated the presence of two highly distinct regional populations at broad-scale (Figure 4.7; Appendix D, Figure D.5 and D.6), represented by southern and eastern Australia; these are the same two regional populations disclosed by the neutral dataset (Barceló et al., 2021, Chapter 2). In comparison, analyses using the fine-scale dataset, indicated the presence of up to four putatively distinct adaptive populations of common dolphins in eastern Australia, supported by BIC analysis (Appendix D, Figure D.5). The fine-scale, Admixture analysist exhibited a clear separation between individuals from Eden (EDN) at New South Wales' south coast, individuals from Forster (FOR) and Byron Bay (BB) on New South Wales' north coast, with the more admixed individuals from Sydney (SYD) to Broughton Island (BI) (Figure 4.8; Appendix D, Figure D.5 and D.7). Results from the PCA also supported the broad-scale (Appendix D, Figure D.8) and fine-scale findings (Appendix D, Figure D.9).

Table 4.2 Measures of genomic diversity based on 14,799 putatively neutral SNPs for both spatial scales, and putatively adaptive SNPs for (A) broad-scale (1,586 SNPs), and (B) fine-scale (205 SNPs) in Australian common dolphins (*Delphinus delphis*). Observed heterozygosity (H_O), expected heterozygosity (H_E) and Number of samples (N). * Acronyms used as in Figure 1.

(A)

		neutral		**adaptive**	
Site	**N**	**H_o**	**H_E**	**H_o**	**H_E**
ALB	15	0.167	0.166	0.306	0.301
ESP	18	0.171	0.172	0.317	0.314
GAB	22	0.170	0.176	0.313	0.325
SG	32	0.172	0.172	0.326	0.321
GSV	28	0.154	0.160	0.292	0.297
PORT	31	0.172	0.175	0.323	0.326
ROB	32	0.169	0.175	0.317	0.329
MEL	16	0.169	0.177	0.321	0.338
EWP	20	0.175	0.181	0.332	0.345
EDN	20	0.202	0.209	0.339	0.345
SYD	11	0.225	0.212	0.367	0.337
BI	20	0.201	0.205	0.304	0.306
BB	14	0.189	0.189	0.266	0.265
Total average		*0.180*	*0.182*	*0.317*	*0.319*
Total SD		*0.019*	*0.017*	*0.024*	*0.023*

(B)

		neutral		adaptive	
Site	**N**	**H_o**	**H_E**	**H_o**	**H_E**
EDN	20	0.202	0.209	0.347	0.369
SYD	11	0.225	0.212	0.424	0.407
BI	20	0.201	0.205	0.355	0.424
BB	14	0.189	0.189	0.355	0.359
Total average		*0.204*	*0.204*	*0.370*	*0.390*
Total SD		*0.015*	*0.010*	*0.036*	*0.031*

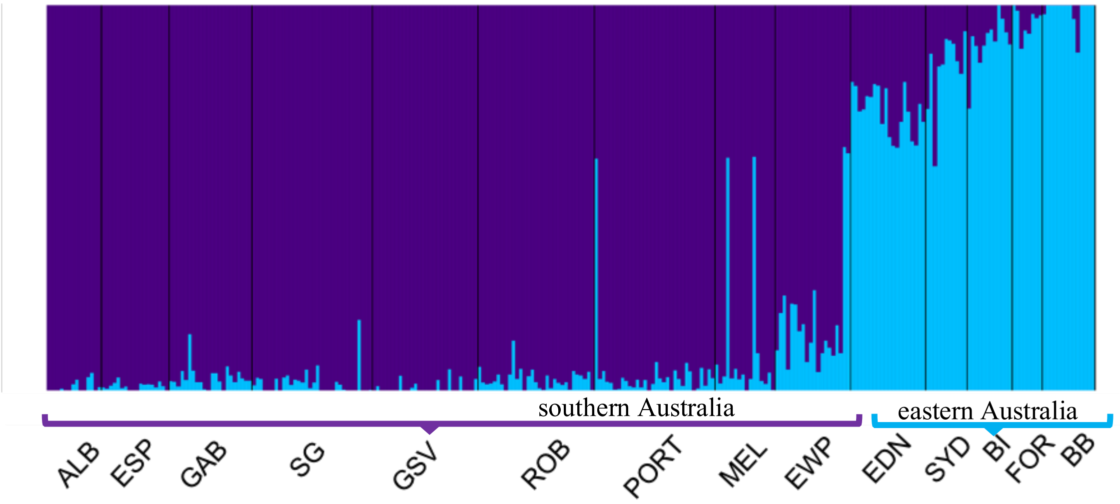


Figure 4.7 Analysis of population genomic structure using Admixture, based on 1,586 putative adaptive SNPs for southern and eastern Australian common dolphins (*Delphinus delphis*). The results depict levels of admixture for each individual sample grouped into two genomic clusters. Each sample is represented by one vertical line and is colour-coded by the membership probability to one of the locally adaptive populations. *Acronyms used as in Figure 4.1.

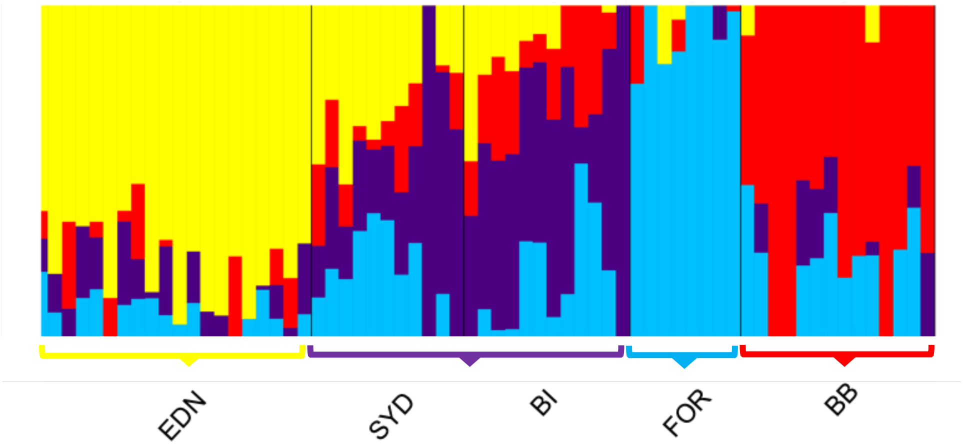


Figure 4.8 Analysis of population genomic structure analysis using Admixture, based on 205 putative adaptive SNPs for eastern Australian common dolphins (*Delphinus delphis*). The results depict levels of admixture for each individual sample grouped into four genomic clusters. Each sample is represented by one vertical line and is colour-coded by the membership probability to one of the locally adaptive populations. *Acronyms used as in Figure 4.1.

Fixation indices indicated low to relatively high putatively adaptive genomic differentiation between sites (broad-scale pairwise F_{ST} = 0.003 to 0.442; fine-scale pairwise F_{ST} = 0.025 to 0.153) (Appendix D, Figure D.3. and Table D.3). At broad-scale, the highest F_{ST} values were observed in comparisons between sites of the two main regional populations (southern vs eastern Australia = 0.140 to 0.442), while in eastern Australia the highest F_{ST} values were observed in comparisons between sites in northern and southern New South Wales (BB vs EDN = 0.153) (Appendix D, Figure D.4. and Table D.3).

Functional enrichment and annotation using cetacean nucleotides and proteins

A total of 1,871 SNPs (~10%) out of the full dataset of 17,875 SNPs (Appendix D, Table D.1) scored BLAST hits that annotated to the currently available cetacean nucleotides and non-redundant proteins NCBI databases. For the broad-scale dataset, 132 SNPs were annotated out of 646 SNPs identified as potentially under selection (~20%). At fine-scale, 25 SNPs were annotated out of 172 SNPs retained (~15%). Functional enrichment analyses identified several GO terms over-represented when comparing the SNPs from the full dataset to the SNPs identified as potentially under selection. At broad-scale, 11 over-represented GO terms corresponding to 23 SNPs in candidate genes were found (Appendix D, Table D.4). At the fine-scale, four over-represented GO terms corresponding to 13 SNPs in candidate genes were disclosed (Appendix D, Table D.5).

At broad-scale, three of these SNPs were in exonic regions and non-synonymous (NR2F6, RPS8, and Protrudin), whereas at fine-scale only one was in an exonic region and non-synonymous (PDCD2L) (Appendix D, Table D.5; D.6). NR2F6, which is related to white adipogenesis, was associated with salinity range. RPS8, which is related to structural constitution of the ribosome, was associated with sea surface temperature mean. Protrudin, related to metal-ion binding, and PDCD2L, related to programmed cell death, were both associated with primary productivity minimum. The correlations between the candidate genes and the environmental variables were low ($r^2 < 0.5$), but still significant (Fisher's p-value < 0.05). Noticeable changes in the allele frequencies of these candidate SNPs can be seen across gradients of the seascape (Appendix D, Figures D.10; D.11; D.12).

Discussion

Metapopulations of marine species can show genetic connectivity over large spatial scales (Watson et al., 2012; Gagnaire et al., 2015; Riginos et al., 2016). However, they can also exhibit local adaptation, when ecological gradients or discontinuities lead to selective pressures on their gene variants (Manel and Holderegger, 2013; Benestan et al., 2015; Xuereb et al., 2020). The potential for both large-scale connectivity and local adaptation in marine metapopulations makes them particularly sensitive to anthropogenic and climatic changes (Funk et al., 2019; Xuereb et al., 2020), and it is paramount that they are conserved and managed at appropriate scales (Oleksiak and Rajora, 2020). This study disclosed signals of adaptive divergence in Australian common dolphins that varied depending on the metapopulation hierarchy tested. Across the entire coastal range of the species in Australia, a combination of environmental variables (i.e. sea surface temperature, current velocity, salinity, bathymetry, and primary productivity) appeared to influence genomic divergence between Indian Ocean (southern Australia) and Pacific Ocean (eastern Australia) dolphins. In the Pacific segment of the metapopulation, only primary productivity was identified as a driver of population divergence along Australia's eastern coast. It appears that adaptive genomic variation between oceans (Australian metapopulation) and within coastal segments (eastern coast) is influenced by three main oceanographic phenomena. These include (i) ocean circulation patterns at the edge of the distribution of common dolphin in each coast; (ii) areas of eddies and upwellings promoted by seasonal wind patterns; and (iii) the presence of protected, semi-enclosed coastal habitats. The results suggest that broad scale environmental heterogeneity may impact upon genomic diversity and structure of Australian common dolphins, including after taking into account the effect of spatial distances.

Genomic diversity and population structure: adaptive *vs* neutral

Species with wide ranges, large population sizes, and capable of maintaining high levels of gene flow generally present high genetic diversity (Wright, 1968; Hanski, 1998). In metapopulations, the persistence of genetic connectivity over large spatial scales may promote evolutionary potential by the rapid spread of beneficial mutations through the interconnectedness of populations (Slatkin, 1987; Palumbi, 2003; Saccheri and Hanski, 2006). In this study, results based on putatively candidate adaptive loci suggested a hierarchical population structure for common dolphins in Australia. At a broader spatial scale, the most supported number of dolphin populations was two, which was the same number suggested using putatively neutral loci (Barceló et al., 2021, Chapter 2). These populations are located at the interface between the Indian and the Pacific Oceans. As expected, the dolphins' genomic diversity was higher for the putatively adaptive markers compared to the neutral markers (e.g. Frankham et al., 2017). However, one of the most distinct patterns at broad-scale was only disclosed by the putatively adaptive markers. This was that adaptive diversity is lower at the edge of the species' distribution in the Australian metapopulation, compared to the central sites where the two oceans meet. Lower adaptive genomic diversity at the edge of a species' distribution has been described for other taxa, both in terrestrial and marine systems, and it is attributed to lower levels of connectivity (e.g. Bradbury et al., 2010; Smith et al., 2020; Yiming et al., 2020). These populations, peripherals and central, are relevant for the conservation and management of the evolutionary diversity of this species in the region, for the persistence of the high standing genetic variation.

At fine-scale in eastern Australia, adaptive loci suggested a different number of common dolphin populations compared to neutral markers (Möller et al., 2011; Barceló et al., 2021, Chapter 2). The adaptive markers suggested the presence of a maximum of four local populations, while the neutral loci suggested a maximum of three populations (Möller et al., 2011; Barceló et al., 2021, Chapter 2). Similarly, a fine-scale study of southern Australian common dolphins using an adaptive SNP dataset suggested a larger number of populations (Chapter 3) compared to results of studies using neutral loci (Bilgmann et al., 2014; Barceló et al., 2021, Chapter 2). Neutral and adaptive markers can account for different evolutionary forces, and therefore cannot be a proxy for each other in population genomic assessments (Wright, 1968; Crow and Kimura, 1970). Similar results, disclosing a larger number of populations based on loci under putative selection compared to neutrality, have been shown in studies of other marine taxa (e.g. Gastropoda: *Haliotis laevigata*, Sandoval-Castillo et al., 2018; Stichopodidae: *Parastichopus californicus*, Xuereb et al., 2020), including for one small delphinid from Australian coastal waters (Indo-Pacific bottlenose dolphins, Delphinidae*: T. aduncus*; Pratt et al., 2018; Pratt, 2020). The results highlight the importance of considering both types of genomic markers, neutral and adaptive, for the assessment of metapopulations, in which high standing genetic variation may assist with evolutionary adaptations when faced with rapid climatic changes (Barrett and Schluter, 2008) and potential anthropogenic impacts (Reed et al., 2020).

Selective environmental pressures on dolphin populations

Different environmental processes (e.g. currents, nutrient cycling) can produce analogous genomic patterns of marine populations in different habitats (e.g. Bradbury et al., 2010; Benestan et al., 2016a). In marine systems, genomic studies of adaptation in organisms with passive and active dispersal have mostly demonstrated adaptive responses to thermal (e.g. Decapoda: *Homarus americanus,* Benestan et al., 2016a; Stichopodidae*: P. californicus*, Xuereb et al., 2018a; Phocoenidae: *Phocoena phocoena,* Morin et al., 2021) and salinity variation (e.g. Perciforme: *Mullus surmuletus*, Dalongeville et al., 2018; Cottidae: *Trachidermus fasciatus*, Li et al., 2019; Delphinidae: *T. aduncus*, Pratt, 2020). However, other environmental variables such as depth and dissolved oxygen can promote gradients in the water column that may exert selective pressures on marine populations (Oleksiak and Rajora, 2020). Although gradients in water characteristics may not be directly impacting on common dolphins, it could be affecting prey composition and abundance, and since common dolphins closely associate with their prey (e.g. Möller et al., 2011; Bilgmann et al., 2014), it may indirectly impact on dolphin movements and dispersal patterns.

Genomic variation in Australian common dolphins was associated with various environmental variables at the metapopulation level, and with one main variable (i.e. primary productivity) at Australia's east coast. The Australian metapopulation is impacted by two main currents (i.e. Leeuwin Current and East Australia Current), which could be creating somewhat analogous genomic patterns between these two heterogeneous environments. In contrast, specific environmental heterogeneity in the Pacific coast (i.e. upwelling centres, eddies formation, topographic discontinuities and embayments), could be shaping the adaptive divergence of common dolphins in this region. These could be explained by three major oceanographic phenomena occurring along the metapopulation in the Pacific and Indian Ocean coasts, discussed separately below.

Lower adaptive diversity at the distributional edge of the Australian metapopulation

At the edge of the distribution of common dolphins in Australia, represented by the sites of Albany and Esperance (southwestern Western Australia) and Ballina and Forster (northern New South Wales), common dolphins were differentiated by the GEA and samples from the localities were associated with two main variables, sea surface temperature and salinity (Figure 4.2). Common dolphins in these peripheral environments also exhibited lower levels of adaptive diversity compared to the other sites. In these areas, the warm water masses with seasonal fluctuations of salinity are represented by the Leeuwin Current in Western Australia in the region of the Albany Canyon (Condie et al., 2011; Kämpf and Chapman, 2016), and the northern part of the Eastern Australian current in New South Wales (Keane and Neira, 2008; Suthers et al., 2011). These similar environmental conditions could be driving parallel adaptive patterns for common dolphins at each coast, which was not previously disclosed when analysing separately each coast or using the neutral datasets (i.e. Barceló et al. 2021, Chapter 2; Chapter 3). A comparable scenario has been reported for Atlantic cod (Gadidae: *Gadus morhua*), where parallel temperature patterns between populations at two coasts also similarly impacted on their divergence (e.g. Bradbury et al., 2010).

The adaptive genomic variation observed in common dolphins from these two Australian biogeographical regions included differences in minor allele frequencies of candidate gene CFAP54 in sampling sites at the edge of the dolphins' distribution compared to the other sites. In mammals, CFAP54 is related to the functioning of the musculoskeletal system (Barrington et al., 2015; Sha et al., 2020). Although information about functional validation of this gene in dolphins is non-existent, it is possible that differences in this gene may be somehow related to fluctuations in temperature and salinity. Associations between temperature and salinity gradients with genes related to the musculoskeletal system have also been suggested for Indo-Pacific bottlenose dolphins across Australian waters (Pratt, 2020). By contrast, the highest levels of adaptive diversity were found in dolphins at the sites near the Bass Strait, at the interface between the Indian and Pacific Oceans. Here, variations in sea surface temperature and salinity were also associated with the genomic variation. To the east and south of this region, the more admixed Tasmania/New Zealand population of common dolphins is present (Barceló et al., 2021, Chapter 2). Thus, these contact areas likely promote gene flow across ocean boundaries leading to higher diversity in dolphins from the region and are highly important areas for conservation. On the other hand, the Bass Strait presents seasonal circulation patterns with differences in salinity and temperature on either side of the region (Colton and Swearer, 2012). This is thought to act as barrier between common dolphins across the two oceans and the three coastal biogeographical regions (i.e. Flinders, Peronia and Maugea), as observed for other marine taxa (e.g. Crustacea: *Catomerus polymerus* York et al., 2008; macroalgae Waters et al., 2010; Gastropoda: *Nerita* sp. and Gastropoda: *Siphonaria* sp. Teske et al., 2017). The findings of higher adaptive diversity and occasional connectivity in the Bass Strait emphasise the importance of conservation and management efforts in the region for maintaining metapopulation processes and genomic variation in Australian common dolphins.

The GEA analyses at a fine-scale in eastern Australia did not detect significant temperature or salinity fluctuations at the edge of the common dolphin distribution in northern New South Wales. However, the fine-scale GEA in southern Australia detected genomic differentiation associated with current velocity in range-edge, westernmost common dolphins (Chapter 3). Within eastern Australia, dolphins' genomic differentiation appears to be mainly driven by variation in primary productivity as suggested by the GEA analysis. The findings of different GEA patterns at each region reinforce the importance of analysing genomic data at multiple scales and several environments to unravel environmental gradients and discontinuities that may impact upon local adaptation.

Influences of upwellings and eddies on common dolphin adaptive divergence

Similar levels of adaptive diversity were observed for common dolphins along the continental shelf in both southern and eastern coasts. The GEA analyses disclosed that variation in dolphins at these sites was associated with minimum primary productivity. Seasonal currents and wind patterns in these areas are known to promote upwellings and eddies, which are normally associated with primary productivity fluctuations (Condie et al., 2011; Kämpf and Chapman, 2016; Short, 2020). In southern Australia, the combination of the geomorphology, as well as current and wind patterns, promote major seasonal upwellings such as the Bonney upwelling and the western Tasmanian upwelling, where the nutrient-rich waters drives high biological productivity (Condie et al., 2011; Ridgway and Godfrey, 2015; Kämpf and Chapman, 2016). In eastern Australia, geomorphological features and current patterns create periodic cyclonic (cold core) and anticyclonic (warm core) eddies, leading to areas of high phytoplankton activity and prey biomass (Condie et al., 2011; Suthers et al., 2011).

As near-top marine predators, common dolphins tend to depend on prey species with high energy density (Spitz et al., 2010; Spitz et al., 2012), which in turn feed upon higher phytoplankton biomasses present in areas of upwellings and eddies. At fine-scale in eastern Australia, common dolphin genomic variation was associated with primary productivity minimum. This ecological driver seems to be particularly impacting upon dolphins from Forster and Broughton Island, located on the central-northern part of New South Wales (NSW), which corresponds to a different water mass than other parts of the state, and with different fish assemblages (e.g Keane and Neira, 2008). Different water masses in NSW may be indirectly leading to differentiation between common dolphins from the northern, central, and southern regions, as previously suggested (Möller et al., 2011). This resembles results from southern Australian common dolphins, in which primary productivity seemed to be important in differentiating dolphins from several sites (i.e. Great Australian Bight, Spencer Gulf, Robe, Portland and Melbourne), which are known to be influenced by seasonal upwellings (Chapter 3). Seasonal upwellings and eddies present at each coast support high energy density species, such as sardines and anchovies, which common dolphins generally feed upon (Ward et al., 2006; Keane and Neira, 2008; Condie et al., 2011). These areas are also known to be seasonal feeding grounds for other marine mammals (e.g. Otariidae: *Arctocephalus forsteri*, Foo et al., 2020; Balanopteridae: *Balaenoptera musculus brevicauda*, Möller et al., 2020). Thus, for common dolphins that specialise in preying upon schooling fish, such as sardines and anchovies, seasonal oceanographic phenomena could be promoting adaptive genetic divergence between populations (e.g. Möller et al., 2011; Barceló et al., 2021, Chapter 2). On one hand, upwellings in Australia could be promoting gene flow between common dolphins from regions further afield when they travel to aggregation areas to feed upon these high productivity biomasses. On the other hand, the formation of different water masses in eastern and parts of southern Australia could be promoting adaptive genomic differentiation of common dolphins exerted by potential feeding specialisations on different fish assemblages.

Gradients in primary productivity and sea surface temperature created by eddies and upwelling formations along southern and eastern Australia could be promoting environmental discontinuities (Lourey et al., 2006; Kämpf, 2010; 2015; Kämpf and Chapman, 2016). Common dolphins from sites where seasonal upwellings and eddies occur exhibited differences in minor allele frequencies in the candidate gene ERC2, which was associated with sea surface temperature. ERC2 has been associated with heat stress metabolism in other taxa (e.g. Emami et al., 2020) and was also found to be positively selected when analysing data from only southern Australian common dolphins (Chapter 3). It is possible this gene could be regulating pathways of energy intake (e.g. Turcot et al., 2018; Boonanuntanasarn et al., 2019), particularly in common dolphins from sites influenced by high fluctuations in sea surface temperatures in areas of seasonal upwellings and eddies. These periodic, highly productive waters where common dolphins and other marine mammals feed (e.g. *A. forsteri*, Foo et al., 2020; *B. m. brevicauda*, Möller et al., 2020), could lead to parallel patterns of adaptive variation in common dolphins from southern and eastern Australia.

The impact of protected, semi-enclosed coastal habitats on common dolphins

Common dolphins inhabit a wide range of environments along southern and eastern Australia (e.g. Möller et al., 2011; Bilgmann et al., 2014; Bilgmann et al., 2018), but only two of them are characterised as protected or semi-enclosed areas and potential year-round habitats for the species (e.g. Filby et al., 2010; Mason et al., 2016). The first environment encompasses the inverse estuary of Gulf St Vincent and Investigator Strait in South Australia, an area protected by Kangaroo Island (Ward et al., 2006; Kämpf and Bell, 2014). The second, Port Phillip Bay, is a semi-enclosed embayment with a narrow entrance at the western side of Bass Strait, protected by Tasmania and characterised as a marine biogeographic boundary for many species (Colton and Swearer, 2012; Short, 2020). Both areas show seasonal fish assemblages due to periodic fluctuations in salinity and temperature (e.g. Ward et al., 2006; Colton and Swearer, 2012).

Previous GEA studies for the southern Australian segment grouped common dolphins from the two protected coastal habitats separately to other shelf water sites (Gulf St Vincent and Wilson Promontory) due to the dolphins' genomic variation association with salinity, primary productivity and sea surface temperature (Chapter 3). However, at the metapopulation level, GEA results showed that genomic variation of dolphins off Wilson Promontory appeared more similar to the adjacent site in eastern Australia (i.e. Eden) than to Gulf St Vincent, although there is a clear biogeographic separation between ocean basins. This emphasises the importance of analyses at multiple spatial scales to assess GEA in metapopulations.

At a metapopulation level, results differentiated common dolphins from the protected habitat of Gulf St Vincent and some individuals sampled around the mouth of Spencer Gulf and Investigator Strait. These differentiations were mainly driven by associations with sea surface temperature, bathymetry and salinity, with dolphins showing lower diversity compared to most other Australian sites. This lower diversity could be related to the semi-closeness of the environment, and lower levels of gene flow between embayment dolphins to individuals found elsewhere (see Barceló et al. 2021, Chapter 2, for details on migration rates). Moreover, minor allele frequency differences for common dolphins from Gulf St Vincent were found in the gene IGFBP7, which has been associated with osmoregulation (Yau et al., 2015; Breves et al., 2017; Strobel et al., 2020). IGFBP7 was also found to be positively selected at fine-scale in southern Australian common dolphins, with differences in minor allele frequencies in the protected coastal habitats (Chapter 3). In marine fishes (Salmonidae: *Salmo salar* and Cottidae: *Scorpaenichthys marmoratus*), other members of the IGFBP gene family have been associated with physiological adaptations between freshwater and marine environments (e.g Breves et al., 2017; Strobel et al., 2020). This is relevant for Australian common dolphins as genes such as IGFBP could be assisting with osmoregulation in individuals inhabiting hyper-saline environments, such as the waters of Gulf St Vincent.

Gene ontology

For non-model species, it is generally difficult to elucidate complex oceanographic and demographic scenarios, and associations between key available environmental variables and candidate loci or genes do not necessarily infer causality (Sandoval-Castillo et al., 2018; Smith et al., 2020). Nonetheless, provisional inferences about adaptive responses can be made based on genes studied in model species (e.g. Vincent et al., 2013; Dalongeville et al., 2018; Oleksiak and Rajora, 2020). At the fine-scale, the only candidate adaptive SNP within an exonic region were found in the gene PDCD2L, which was associated with primary productivity. The function of this gene has been associated with programmed cell death (i.e. apoptosis) and the stability of genome, and was also found to be positively selected in humpback whales (Balanopteridae: *Megaptera novaeangliae*) and elasmobranchs (e.g. Marra et al., 2019; Tollis et al., 2019).

At broad-scale, three candidate adaptive SNPs were found in exonic regions and were also non-synonymous. ZFYVE27 (also known as Protrudin and part of the Zinc Finger family) was associated with primary productivity, and is involved in the regulation of neurite traffic and formation (UnitProt Consortium, 2018). Genes of the Zinc Finger protein family can be involved in a variety of biological roles (Matthews and Sunde, 2002). Another member of this large family (ZFP57) has been shown to be positively selected in southern Australia common dolphins (Chapter 3), whereas others genes in the same family were selected in the Antarctic ecotype of killer whales (Delphinidae: *Orcinus orca*) (Foote et al., 2016). In our results, another SNP in an exonic region was found in gene RPS8 (also known as 40S ribosomal protein 58), which was associated with sea surface temperature, and is involved in KEGG pathways acting at the ribosome level (e.g. hypoxia stress) (Desert et al., 2018). Some RPS genes have been found to be positively selected in the transient ecotype of killer whales (*O. orca*) (Foote et al., 2016), whale sharks (Rhincodontidae: *Rhincodon typus*) (Marra et al., 2019), and in delphinids (*T. truncatus* and Monodontidae: *Delphinapterus leucas*) (Chen et al., 2015; Chen et al., 2016), playing a role in basic metabolism as well as stability and maintenance of the cell. The third candidate adaptive SNP in an exonic region was in gene NR2F6 (also known as CoupTFII). This gene was also found to be positively selected in the fine-scale dataset of southern Australian common dolphins (Chapter 3), and was correlated to salinity. NR2F6 has been associated with the regulation of adipogenesis, glucose, homeostasis and metabolism of energy (Li et al., 2009; Jeong et al., 2014; Baldwin et al., 2017).

All the four exonic SNPs disclosed here are associated within the stability of cell functions, involved in many pathways, and may be responding to environmental pressures such as salinity, temperature and primary productivity. However, there were also other positively selected SNPs identified in non-coding regions. For eastern Australian common dolphins, several SNPs were located in intronic regions (i.e. genes MYH14, PLEKHA8, INMT, HNRNPUL1, ZC4H2, ABCC2 and PHEX), as well as in intergenic regions (i.e. genes RPL13A, CCDC188, SOX, TEAD2 and ZNF516). For the Australian-wide dataset, SNPs were located in promoter regions (i.e. genes LMX1A, RPS8 and CNIH3), introns (i.e. genes DRC1, SYT6, ERC2, OSBPL7, HIRA, CADPS2, KIAA1549, TLN2, STX7, CFAP45 and CFAP54), as well as intergenic regions (i.e. genes LZTS1, PMSG4, LMX1A, IGFBP7, NKD2, TAS1R2, EYA, AP1AR and CNIH3).

There is limited information about the relevance of non-coding regions, especially in marine species, although some reports in other taxa show evidence that they could be impacting adaptation (e.g. Andolfatto, 2005; Jones et al., 2012; Charlesworth et al., 2017). Some of these non-coding regions have been associated with the regulation of hypoxia (e.g. RPL13) (Luo et al., 2011), skeletal muscle regulation (e.g. MYH14, INMT, TLN2, CFAP, DRC1) (Conti et al., 2009; Ikeda et al., 2013; Sha et al., 2020; Takeuchi et al., 2020; Wu et al., 2020), homeostasis (e.g. STX7, NKD2, PHEX) (Zhang et al., 2007; Rowe, 2012; Roca-Agujetas et al., 2019), osmoregulation (e.g. IGFBP7, KRBA1, KCTD16) (Breves et al., 2017), adipogenesis (e.g. LZTS1, NR2F6, PLEKHA8, RPS8) (Qiu et al., 2007; Li et al., 2009; Desert et al., 2018; Xing et al., 2020), and thermogenesis (e.g. ERC2, HNRNPUL1) (Li et al., 2017; Turcot et al., 2018). They are also involved in the regulatory pathways of the sensory system, such as photoreceptors (e.g. ABCC2, KIAA1549) (Allikmets et al., 1997; deBruijn et al., 2018), inhibitors of taste receptors (e.g. TAS1R2, PKDL1) (Horio et al., 2011; Pang et al., 2014), and inhibitor of hearing receptors (e.g. EYA) (Abe et al., 2018). This could imply that multiple, complex gene pathways and their regulatory processes are involved in the fitness of common dolphins at different traits. Future comparative research using whole genomes from multiple delphinid species could possibly elucidate other regions and pathways behind genomic divergences.

Implications for conservation and management

The management of Australian common dolphin populations could benefit from assessing appropriate spatial scales to ensure maintenance of the dolphins' neutral and adaptive genomic variation. It is thought that this type of management could enhance their long-term survival, particularly in the face of rapid environmental change. In this study, putatively adaptive genomic markers revealed, at the broad-scale, the same number of regional populations of common dolphins than did the neutral markers (Barceló et al., 2021, Chapter 2). However, at the fine-scale in eastern Australia, adaptive markers suggested the presence of putatively local adapted populations of common dolphins. This was comparable to the southern Australia GEA analysis that suggested fine-scale, putatively local adapted populations of common dolphins (Chapter 3). In both cases, fine-scale analyses suggested that the divergence of dolphin populations might be associated with a few but significant different environmental variables and potential oceanographic phenomena acting as barriers for dispersal at the region. Therefore, conservation and management policies for the species need to ensure two aspects: (i) maintenance of gene flow across the metapopulation of Australasian common dolphins, and (ii) protection of each putatively local adapted population. These two aspects are expected to promote the maintenance of standing genetic variation at both broad and fine spatial scales. This is particularly crucial in contact areas between the two regional populations (Bass Strait), and in sites where common dolphins are likely to aggregate seasonally (Bonney and Tasmania upwellings, and areas of eddy formations). Likewise, conservation and management should consider putatively local adapted populations as unique biological units. This is particularly important at range edges of the Australian common dolphin distribution, as well as in protected coastal environments. These sites, where lower adaptive diversity was exhibited, are likely the most vulnerable to potential anthropogenic impacts such as fisheries by-catch (e.g. Bilgmann et al., 2008; Bilgmann et al., 2018, Parra et al., in review), diseases outbreaks (e.g. Bossart, 2011; Kemper et al., 2016; Batley et al., 2021) and climate change.

Individuals from the putative divergent metapopulation of common dolphin in Australia are subject to interactions with several fisheries (e.g. Bilgmann et al., 2008; Goldsworthy et al., 2019b). Currently, several national (e.g. Australia, EPBC 1999, AFMA, 2020b; New Zealand, Pact 1978, MPI, 2020), and international (e.g. FAO, 1995; IUCN, Hammond et al., 2008; Bonn, CMS, 2020) agreements regulate the trade of these species and fisheries interactions with this specie. However, the species management zones do not correspond to their population genomic structure or stocks (e.g. AFMA, 2019b; Barceló et al., 2021, Chapter 2), making it difficult to assses interactions separately for each putative adaptive, local population, as well as across the metapopulation. Thus, future management plans of the species need to acknowledge the hierarchical metapopulation structure of common dolphins in the Australasia, especially in consideration of future climate change that could exacerbate the vulnerability of populations. This is particularly important for populations in semi-enclosed or sheltered waters, as reported for another small cetacean in the region (e.g. Bilgmann et al., 2019; Reed et al., 2020; Batley et al., 2021). Future research for the conservation and management of Australasian common dolphin populations should use boundaries of locally adapted populations to estimate local abundance and to simulate population-specific responses to anthropogenic disturbances such as bycatch, disease outbreaks, and climate change, among others (Reed et al., 2020). These results emphasise the importance of inter-state and trans-Tasman cooperation (Barceló et al., 2021, Chapter 2), in which efforts to preserve common dolphins' genomic variation should focus on the metapopulation level and at putative locally adapted populations, despite geopolitical boundaries and differences in current intra-jurisdictional policies.

Conclusion

Common dolphins are mostly considered as a highly migratory marine species. However, this study shows that they exhibit some neutral and adaptive hierarchical patterns of genomic differentiation and gene flow, depending on the spatial scale assessed. These results need to be considered during conservation and management of the species in the region. The GEA analyses disclosed links between genomic divergence of common dolphins and key environmental variables related to three oceanographic phenomena with somewhat analogous patterns along southern and eastern Australia. Adaptive genomic diversity in semi-enclosed habitat and at the edge of common dolphin distribution was lower compared to regions of interface where adjacent regional populations seem to maintain some level of gene flow. Moreover, signals of selection were found repetitively in some regions of the genome, a finding that could potentially indicate parallel adaptation of these dolphins at different regions. Our results provide novel baseline information for the conservation and management of common dolphins in the context of a highly dynamic and heterogeneous marine environment,and presents a first incursion towards our understanding about adaptive resilience of local and regional populations of small cetaceans to potential natural environmental changes and to anthropogenic selective pressures.

CHAPTER 5. GENERAL DISCUSSION

General overview

Anthropogenic impacts, including by-catch, diseases outbreaks and climatic changes, are affecting many marine metapopulations. It is therefore paramount to understand the genomic structure and connectivity of wide-ranging marine species to predict their evolutionary potential and identify populations for priority conservation management (Manel et al., 2019; Oleksiak and Rajora, 2020; Xuereb et al., 2020). For large marine predators, such as the common dolphin, seascape genomics provides a robust framework to identify environmental factors that are impacting the species' genomic variation. Several genetic studies around the world have previously hypothesised that the genetic differentiation of delphinid populations is associated with environmental variables, such as temperature (e.g. Mirimin et al., 2009), salinity (e.g. Natoli et al., 2005; Gaspari et al., 2015a), currents (e.g. Möller et al., 2011; Bilgmann et al., 2014; Gkafas et al., 2017), and bathymetry (e.g. Tezanos-Pinto et al., 2009; Stockin et al., 2014; Pratt et al., 2018), but few have explicitly tested for this (e.g. Mendez et al., 2010; Viricel and Rosel, 2014; Morin et al., 2021).

In delphinids, the first seascape genetics study used remote-sensing environmental data to test for associations with the mtDNA control region in isolated populations of the franciscana dolphins (*Pontoporia blainvillei*) (Mendez et al., 2010). Since then, some other cetacean studies have investigated associations between genetic variation and population structure with environmental variables, mainly based on few microsatellite markers and fragments of the mtDNA control region (e.g. *Sousa chinensis*, Mendez et al., 2011; *Delphinus delphis*, Amaral et al., 2012a; *Stenella frontalis*, Viricel and Rosel, 2014). More recently, cetacean studies have combined environmental data with genome-wide data (e.g. Indo-Pacific bottlenose dolphins, *Tursiops aduncus,* Pratt, 2020; spinner dolphins, *S. longirostris,* Andrews et al., 2021; harbor porpoises, *Phocoena phocoena*, Morin et al., 2021), offering new insights about population adaptations and their evolutionary potential.

The main objectives of this thesis were to integrate neutral and adaptive genomic variation of Australasian common dolphins to investigate population structure and connectivity, as well as to combine environmental data and genomics to assess adaptive divergence across the metapopulation. Over 18,000 SNPs were utilised to differentiate between neutral and adaptive genomic variation in these dolphins. For the first part of the thesis, the use of SNPs under putative neutrality allowed to compare and resolve neutral population structure and gene flow of common dolphins from Australia and New Zealand. Analyses suggested the presence of three regional populations, with connectivity and further substructure within them impacted mainly by signals of isolation by distance (Barceló et al., 2021, Chapter 2). For the second and third parts of this thesis, putative selection at several genetic variants associated with specific environmental variables suggested the presence of putatively adaptive, locally divergent populations in Australia (Chapters 3 and 4). These analyses also indicated a different number of common dolphin sub-populations in the southern and eastern Australian, providing further subdivisions at these fine-scales segments compared to that indicated based on the putatively neutral markers (Chapters 2, 3 and 4). This metapopulation assessment at different segments allowed the detection of environmental drivers likely affecting genomic variation of regional and local populations of common dolphins. Results also highlighted similarities and differences between southern and eastern Australian heterogeneous marine environments, particularly in regard to oceanographic and geomorphological features that may affect common dolphin dispersal and in turn shape their populations.

Signals of adaptation in common dolphins from Australia

Sampling over large spatial scales is required to assess eco-evolutionary processes impacting on the genomic variation of widely dispersed marine species. If we recognise that natural selection is the ultimate inventor of nature (Pianka, 2000), understanding adaptations between marine organisms and the environment could be key for well-informed conservation and management strategies. In large populations, such as those of the Australasian common dolphin hierarchical metapopulation (Chapter 2, 4), contemporary gene flow could act as a reservoir of high standing genetic variation for population persistence (Manel and Holderegger, 2013; Oleksiak and Rajora, 2020).

Microevolutionary studies of delphinids are still mainly limited to assessing selection on genes associated with ecological adaptations between ecotypes or subspecies (Moura et al., 2013b; Foote et al., 2016). To the best of my knowledge, only three microevolutionary studies using a reduced representation of the genome have been done between cetacean ecotypes and populations (Pratt, 2020; Andrews et al., 2021; Morin et al., 2021). This thesis used this type of genomic dataset for common dolphins to identify candidate loci under selection, disclosing over 1,500 loci across the southern and eastern Australia metapopulation, approximately 800 in the southern Australia segment, and about 200 in the eastern Australia segment (Chapters 3 and 4). A multivariate Genotype-Environment Association (GEA) analysis used to investigate the genomic basis of adaptation to different environmental variables disclosed selected variants in coding and non-coding regions of various genes across the common dolphin metapopulation. High standing genetic variation in large marine populations could act as a source for parallel adaptive evolution (Riginos et al., 2016). Several putatively selected loci were found repeatedly, supporting the idea of signals of parallel evolution in southern and eastern Australian common dolphins.

Oceanographic patterns occurring in areas of upwelling and eddies between southern and eastern Australia coast may explain variation at genes, such as ERC2, which is involved in thermogenesis. This gene was associated with temperature at fine-scale in southern Australia (Chapter 3) and at broad-scale across Australia (Chapter 4) in dolphins from areas of upwellings and eddies. The ERC family of genes has been identified as putatively selected in cetacean macroevolutionary studies (e.g. *T. truncatus,* McGowen et al., 2012; *Balanoptera acutorostrata*, Yim et al., 2014), suggesting selection and specialisation to different environments over time. For this gene, and other genes showing similar patterns (e.g. SYT6, TLN2), differences in allele frequencies at each coast could perhaps be related to gradients of temperature along eastern Australia (± 6º C) and southern Australia (± 3ºC). Australian common dolphins exhibited admixed populations (Chapter 2, 3, 4), with clear evidence of shared historical origin (e.g. Amaral et al., 2012b; Amaral et al., 2016). This shared historical origin and similar oceanographic circulation patterns of upwellings and eddies could in turn be creating similar adaptive responses in local populations of common dolphins.

The candidate NR2F6 (nuclear receptor), which is involved with the regulation of adipogenesis, glucose, homeostasis and metabolism of energy (Li et al., 2009; Jeong et al., 2014; Baldwin et al., 2017), was associated with differences in salinity and was putatively selected for common dolphins in southern Australia (Chapter 3), but also for dolphins at the Australian metapopulation level (Chapter 4). Nuclear receptor genes were suggested to be involved in the macroevolution of the common bottlenose dolphin (*T. truncatus*) when compared to other cetacean lineages (Nery et al., 2013). In the present study, common dolphin variation at the gene IGFBP7, which is involved in osmoregulation, was also associated with salinity gradients in southern Australia (Chapter 3) and across Australia (Chapter 4). Some IGF genes have been reported as important in the macroevolution of marine mammals (e.g. *Ursus maritimus*, Liu et al., 2014; *B. acutorostrata*, Yim et al., 2014; *Orcinus orca*, Foote et al., 2016). These candidate genes were correlated to salinity and could suggest adaptation of common dolphins to coastal, hyper-saline environments. This is similar to previous studies that found microevolutionary adaptation between ecotypes of toothed whales inhabiting freshwater and oceanic environments (finless porpoises, *Neophocaena phocaenoides*, Ruan et al., 2015; Zhou et al., 2018a) or hyper saline areas (Indo-Pacific bottlenose dolphins, *T. aduncus*, Pratt, 2020)

Candidate genes of the sensory system, which are involved as photoreceptors and receptors of taste (Allikmets et al., 1997; Pang et al., 2014), were also found to be putatively selected at fine and broad-scales (i.e. ABC and TAS1R; Chapters 3 and 4), and were associated with either primary productivity or sea surface temperature. These genes mainly showed differences in the allele frequencies of dolphins inhabiting coastal protected environments, and in eastern Australia. Sensory genes have been disclosed as under selection in cetacean macroevolutionary studies (e.g. Zhou et al., 2013; McGowen et al., 2014; Zhu et al., 2014), with ancestral cetacean lineages losing taste receptors genes (i.e. ABC, TAS1R and TAS2R) and not able to distinguish between many tastes (sweet, sour, umami and bitter), with the exception of salt (McGowen et al., 2014; Zhu et al., 2014). A sour taste receptor in potassium channels of the PKD gene (Zhou et al., 2018b) was also found putatively selected in common dolphins, and associated with the hyper-saline coastal environments of southern Australia (Chapter 3). It was previously suggested this is for cetaceans to further reduce their dependence in taste during optimal foraging in saline environments (e.g. McGowen et al., 2014; Zhu et al., 2014), which could also be occurring in common dolphins inhabiting hyper-saline environments.

Overall, the candidate genes identified suggest that selection in common dolphins has allowed them to colonise different environments and subsequently specialise in those habitats. Relatively fast adaptations are expected to have evolved from high standing genetic variation (Barrett and Schluter, 2008). In these cases, populations with high genetic diversity provide a reservoir to resilience upon ongoing and future climatic changes (Pespeni et al., 2013). Since this is the first investigation of microevolutionary adaptation in common dolphins, future research should verify the importance of these candidate genes in other populations and regions of the world.

Adaptive resilience of common dolphins to climate change

Changes in ocean circulation and temperature regimes, as well as various anthropogenic impacts, are threatening the connectivity of marine populations (Xuereb et al., 2018a; Manel et al., 2019). Due to the aquatic life cycle of cetaceans it is often difficult to monitor and describe patterns impacting their populations (Bestley et al., 2020). Thus, an understanding of the potential impacts of environmental factors on cetacean dispersal is essential for elucidating patterns and processes driving their population structure, and for designing well-informed and effective conservation management strategies (Baker et al., 2019; Stephenson et al., 2020).

The idea that breeding or feeding strategies of cetaceans and other marine mammal populations are influenced by ocean circulation patterns, such as upwelling centres, have been suggested by many non-genetic studies, including in Australia (e.g. *Arctocephalus forsteri*, Foo et al., 2020), New Zealand (e.g. *Cephalorhynchus hectori maui*, Derville et al., 2016; various cetaceans, Stephenson et al., 2020), and the Pacific Islands (e.g. *Megaptera novaengliae,* Derville et al., 2019; various cetaceans, Peters and Stockin, 2021). These findings are similar to genetic studies in Australia and New Zealand that suggest that ocean circulation and topography are delimiting factors for the dispersal of common and bottlenose dolphins (e.g. Möller et al., 2011; Stockin et al., 2014; Pratt et al., 2018). Indeed, the seascape genomics framework has confirmed theoretical predictions that the Australian common dolphin metapopulation has population segments that may be driven by putatively localised, adaptive divergence (Chapters 3 and 4). The putatively adaptive divergence suggested by the GEA analysis of common dolphins in southern Australia seems to be mainly associated with the tested variables, sea surface temperature, current velocity, salinity and primary productivity (Chapter 3). In eastern Australia, dolphin genomic variation in the GEA analysis was associated with one main ecological driver, primary productivity (Chapter 4). The same variables, in addition to bathymetry, were found to be associated with the dolphins' genomic variation at the Australian metapopulation level (Chapter 4). These findings are somewhat analogous to seascape genomic studies of cetaceans elsewhere that disclosed correlations between various environmental factors (e.g. gradients of temperature, salinity, current velocity) and genetic variation (*T. aduncus*, Pratt, 2020; *S. longirostris*, Andrews et al., 2021; *P. phocoena*, Morin et al., 2021). Cetacean species with locally adapted populations, particularly in regard to environmental factors known to be under considerable change, such as temperature and salinity, might be particularly vulnerable to future climatic scenarios.

Climatic changes may compromise cetacean populations and lead to declines or habitat displacements (e.g. Watson et al., 2013; Derville et al., 2019; Reed et al., 2020). Projections of increasing sea temperature and ocean acidification also suggest other catastrophic events, such as eutrophication of whole marine ecosystems (e.g. Hobday and Lough, 2011; Kämpf and Chapman, 2016). Such events may lead to changes in food-webs, displacement of migratory corridors, collapse of areas of high biological productivity, or fragmentation of marine ecosystems (e.g. Wernberg et al., 2011; Dunn et al., 2019; Bestley et al., 2020). For cetacean species, these changes may impact migratory timing, food availability, reproductive success, and overall health (e.g. Derville et al., 2019; Sousa et al., 2019; Bestley et al., 2020). In turn, these can influence the vulnerability of cetacean populations (e.g. Sousa et al., 2019) and potentially lead to extinctions. Given that lower genetic variation has been attributed to susceptibility of small cetacean populations to disease outbreaks (e.g. Cammen et al., 2015; Batley et al., 2021), persistence of genetic variation by gene flow is key for their resilience, as also suggested for other marine taxa (Xuereb et al., 2020). For some Indo-Pacific bottlenose dolphin populations, simulations of specific responses indicated their main vulnerability to disease outbreaks, anthropogenic impacts, and climate change (Reed et al., 2020). This thesis provides baseline information for future research that aims to investigate the long-term genomic vulnerability to climate change of common dolphins.

Delineating populations based on neutral and adaptive genomic variation

Studies assessing neutral and adaptive genomic variation bring a new perspective for delineating populations for conservation and management (Funk et al., 2012; Oleksiak and Rajora, 2020; Xuereb et al., 2020). Neutral and adaptive variation often respond to different evolutionary forces, with the former best suited for addressing questions about biogeography and gene flow, and the latter best suited for studying natural selection (Shafer et al., 2015; Benestan et al., 2016b; Cammen et al., 2016).

This thesis disclosed some similar patterns, while other where distinctive patterns of population differentiation and diversity between putatively neutral and adaptive datasets from common dolphins of Australasia. At the metapopulation level across Australia and New Zealand, putatively neutral markers indicated strong genetic differentiation mainly explained by geographical distance and biogeographic divergence between ocean basins (Barceló et al., 2021, Chapter 2). Using putatively adaptive markers for Australian common dolphins (except for Tasmania, as this part of the study was restricted to samples from free-ranging animals), two regional populations were identified, one in the Pacific and one in the Indian Ocean, and also lower diversity at semi-enclosed and peripheral environments (Chapter 4). These genomically differentiated populations are located at either side of an old biogeographical break, the Bass Isthmus, which currently exhibit different ocean circulation patterns, but limited migration between them still occur. These results are comparable to previous studies that disclosed significant genetic differences between common dolphins of these two oceans basins with share an ancestral origin (e.g. Amaral et al., 2012b; Bilgmann et al., 2014), a pattern also observed for various marine taxa (e.g. *Catomerus polymerus*, York et al., 2008; *Carcharodon carharias*, Blower et al., 2012; *Nerita atramentosa and Siphonaria diemenensis*, Teske et al., 2017).

In contrast, within the eastern and southern Australian segments, the analyses of the putatively adaptive datasets revealed further differentiation in the number of putatively, locally adapted populations compared to the neutral datasets. For southern Australia, results based on neutral markers suggested two sub-populations (Barceló et al., 2021, Chapter 2), whereas the adaptive markers suggested five sub-populations (Chapter 3). In the case of eastern Australia, two sub-populations were suggested based on the neutral markers (Barceló et al., 2021, Chapter 2), while the adaptive markers suggested up to four sub-populations (Chapter 4). For the Tasmanian/New Zealand regional population, results based on neutral markers suggested at least two sub-populations (Barceló et al., 2021, Chapter 2). However, for this last regional population, which also includes Tasmania, the adaptive genomic variation was not investigated using GEA methods since most samples originated from stranded individuals, and therefore at-sea geographic location of the animals was not known. It is important to note that the sub-populations identified with the putatively adaptive markers are not demographically independent from other adjacent sub-populations, as suggested by the moderate levels of gene flow disclosed based on the putatively neutral markers. Assessments of both neutral and adaptive genomic variation are useful for delineating marine populations and clarifying their evolutionary potential (Sandoval-Castillo et al., 2018; Xuereb et al., 2020). The results from this study indicates that both datasets should be incorporated in to the management and conservation strategies for the species in Australasia.

Wide-ranging marine species, such as cetaceans and other marine mammals, are currently safeguarded by several international (e.g. FAO, 1995; IUCN, Hammond et al., 2008; Bonn, CMS, 2020) and national agreements (e.g. Australia, EPBC 1999, AFMA, 2020b; New Zealand, Pact 1978, MPI, 2020). These regulations control the trade of these species and have greatly reduced their mortalities in fisheries (Tulloch et al., 2020; Fisheries New Zealand, 2020). However, to date, fishery interactions still occur (e.g. AFMA, 2020b; Tulloch et al., 2020; Fisheries New Zealand, 2020) despite agreements, implementations of codes of practice (e.g. SASIA, 2015) and/or even electronic monitoring of fisheries (e.g. AFMA, 2020a). Currently, one major problem is that fisheries manage interactions based on fishery defined stocks, which in many cases do not consider the population genetic structure of the target (e.g. Papa et al., 2020) or non-target species (e.g. Leslie and Morin, 2018; Barceló et al., 2021, Chapter 2). This lack of genetic information is also noticeable in international agreements that categorise species threats (e.g Gardner et al., 2020). Nowadays, conservation efforts mainly focus on small, isolated populations where high levels of genetic diversity may have been already lost (e.g. Tetushkin, 2013). In addition, these metrics of genetic diversity and differentiation tend to still focus on traditional, neutral genetic datasets and analytical frameworks, and do not include information about the potential capacity of populations to adapt to rapid environmental changes (e.g. Gagnaire et al., 2015; Funk et al., 2019; Xuereb et al., 2020).

This thesis provides evidence for a hierarchical metapopulation system from a context of both neutral and adaptive genomic variation of Australasian common dolphins. This needs to be considered for management of their populations and to reduce fisheries by-catch. It is therefore recommended that management plans should aim to maintain connectivity across all the metapopulation for the persistence of neutral and adaptive standing genetic variation (i.e. across the three regional populations). In addition, potentially adaptive divergent sub-populations (i.e. five sub-populations in southern Australia and four sub-populations in eastern Australia) should also be considered in common dolphins management plans, with a continuous assessment of anthropogenic impacts. This is particularly important for Gulf of St Vincent, which exhibits low genomic diversity, restricted gene flow to neighbouring populations, and a strong putative signal of local adaptation. However, other sub-populations could also benefit from long-term assessments given their unique local diversity and their role in contributing to genomic variation across the metapopulation.

Limitations and Future directions

This thesis elucidated patterns of neutral and adaptive genomic variation in Australasian common dolphins and eco-evolutionary processes shaping their populations at various spatial scales. However, limitations exist in relation to genomic coverage, availability of dispersal models, and environmental, ecological and biological information.

The use of a small representation of the genome (<2%) (Oleksiak and Rajora, 2020) can certainly answer questions about evolutionary history, population structure, and gene flow with more resolution than traditional genetic markers can. However, it exhibits limited resolution for comprehensively tackling questions about adaptation as many genomic variants under selection may go undetected (Rajora, 2019). These issues could be overcome by the use of Whole Genome Sequencing (WGS), which is becoming more accessible and affordable, except perhaps in the case of large sample sizes such as the one used in this study. WGS should be considered to elucidate both micro and macroevolutionary adaptations (Rajora, 2019), but cost-efficiency needs to be contemplated if the focus of the study is at multiscale and requires a large sample size (Manel et al., 2019). Thus, genome scans from a small fraction of the genome allows assessments with many more individuals, contributing to baseline knowledge of potential adaptive mechanisms, that can lead to future genome-wide association studies with fewer individuals (Rajora, 2019; Grummer et al., 2019). However, given the nature of marine species, inferring impacts fitness based on the understanding of gene functions is extremely difficult, especially in marine mammals with current limited genomic resources and deficiency of experimental validation.

Various studies have conducted simulations of passive dispersal for marine taxa based on both biological and physical models (e.g. Waters, 2008; Teske et al., 2016; Xuereb et al., 2018a). Marine organisms with active dispersal, such as large predators, are normally associated with their prey movements and there is limited data about their dispersal capability and migratory paths (but see fur seals, *A. forsteri*, Foo et al., 2020; pygmy blue whale, *B. musculus brevicauda*, Möller et al., 2020; various baleen whales, Stephenson et al., 2020). Terrestrial studies have addressed the active dispersal of large predators by analysing potential migratory paths, and integrating with data on genetic differentiation (e.g. Mateo-Sánchez et al., 2015; Draheim et al., 2020). Future studies of marine predators, such as common dolphins, should try to combine these types of data to predict migratory paths and dispersal potential.

Seascape genomics as a research field is still in its early stages. Analytical frameworks which demonstrate associations between environmental variables and candidate loci or genes do not imply causality (Sandoval-Castillo et al. 2018), and there are many limitations in regard to biologically relevant environmental data for marine species. For example, researchers working with terrestrial and freshwater systems can integrate environmental variables in their studies with WorldClim, which encompasses more than 19 broad predictors (Fick and Hijmans, 2017). In contrast, studies on marine systems are usually restricted to fewer environmental predictors (Tyberghein et al., 2012; Assis et al., 2018). Increased accessibility to remote-sensing oceanographic and topographic variables, as well as biological and ecological data can provide additional information on complex interactions at different life history traits (e.g. Castro-Tavares et al., 2019). Genotype-environment analyses can only identify loci that have allele frequencies associated with environmental variables included in the analyses. These environmental variables can be in some cases strongly correlated with each other and geographical distances (Hohenlohe et al., 2020), and if done without caution can lead to a high number of false positives, making associations difficult to detect (Forester et al., 2018; Rajora, 2019; Grummer et al., 2019). Thus, expanding accessibility of environmental data should f improve the ability to predict genomic divergences for marine species at various spatial scales in response to anthropogenic impacts and climatic changes.

Final Remarks

This thesis contributes towards elucidating population structure, connectivity and adaptive potential of an abundant marine predator in Australasian waters, the common dolphin *D. delphis*. The study represents one of the largest population genomic datasets for a cetacean species. The evidence presented here suggests that common dolphins in Australasia exhibit a hierarchical metapopulation system, with higher adaptive genomic diversity in areas where connectivity is maintained, and lower adaptive diversity at range edge populations in eastern and southern Australia, as well as in semi-enclosed coastal protected environments. The seascape genomics framework disclosed associations of genomic variation to primary productivity, sea surface temperature, salinity, current velocity and bathymetry. The novel information about metapopulation structure and adaptively divergent populations should be incorporated and prioritised in conservation and management plans, both at intra- and inter-jurisdiction levels. It is thought that promoting connectivity across the metapopulation system will ensure high standing genetic variation that acts as a reservoir for adaptive resilience. The work presented in this thesis represents an important step towards understanding the microevolutionary potential of wide-ranging marine species at the near-top of the trophic web. It is suggested that SNPs or/and candidate genes described here are used as a baseline for future comparative research, as these variants may be under selection in other closely related delphinid species. This catalogue could be used in combination with other genomic technologies, such as microarray chips, transcriptomics in a candidate gene approach or WGS, to compare signatures of selection. The integration of results across the main objectives of each chapter demonstrated that information about neutral and adaptive genomic variation needs to be considered into current conservation and management policies for marine populations.

This study reinforces the value of a seascape genomics framework at a metapopulation level for a wide-ranging species found over a dynamic and heterogeneous environment. This type of assessment enables to distinguish populations inhabiting interconnected habitats, as well as environmental variables influencing adaptive divergence. This framework could be quite relevant for managers and policy makers that aim to preserve genomic variation in wide-ranging, large marine predators.

APPENDIX A. ARTICLE

Full manuscript in journal format of Barceló et al., 2021

frontiers
in Marine Science

ORIGINAL RESEARCH
published: 16 February 2021
doi: 10.3389/fmars.2021.616673

A Matter of Scale: Population Genomic Structure and Connectivity of Fisheries At-Risk Common Dolphins (*Delphinus delphis)* From Australasia

Andrea Barceló[1,2*], *Jonathan Sandoval-Castillo*[1], *Karen A. Stockin*[3], *Kerstin Bilgmann*[1,2,4], *Catherine M. Attard*[1,2], *Nikki Zanardo*[1,2], *Guido J. Parra*[2], *Krista Hupman*[5], *Isabella M. Reeves*[1,2], *Emma L. Betty*[3], *Gabriela Tezanos-Pinto*[3,6], *Luciano B. Beheregaray*[1] *and Luciana M. Möller*[1,2]

[1] Molecular Ecology Laboratory, College of Science and Engineering, Flinders University, Bedford Park, SA, Australia, [2] Cetacean Ecology, Behaviour, and Evolution Laboratory, College of Science and Engineering, Flinders University, Bedford Park, SA, Australia, [3] Cetacean Ecology Research Group, School of Natural and Computational Sciences, College of Science, Massey University, Auckland, New Zealand, [4] Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia, [5] National Institute of Water & Atmospheric Research Ltd (NIWA), Wellington, New Zealand, [6] Laboratorio de Ecología Molecular de Vertebrados Acuáticos, Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá, Colombia

An understanding of population structure and connectivity at multiple spatial scales is required to assist wildlife conservation and management. This is particularly critical for widely distributed and highly mobile marine mammals subject to fisheries by-catch. Here, we present a population genomic assessment of a near-top predator, the common dolphin (*Delphinus delphis*), which is incidentally caught in multiple fisheries across the Australasian region. The study was carried out using 14,799 ddRAD sequenced genome-wide markers genotyped for 478 individuals sampled at multiple spatial scales across Australasia. A complex hierarchical metapopulation structure was identified, with three highly distinct and genetically diverse regional populations at large spatial scales (>1,500 km). The populations inhabit the southern coast of Australia, the eastern coast of Australia, New Zealand, and Tasmania, with the latter also showing a considerable level of admixture to Australia's east coast. Each of these regional populations contained two to four nested local populations (i.e., subpopulations) at finer spatial scales, with most of the gene flow occurring within distances of 50 to 400 km. Estimates of contemporary migration rates between adjacent subpopulations ranged from 6 to 25%. Overall, our findings identified complex common dolphin population structure and connectivity across state and international jurisdictions, including migration and gene flow across the Tasman Sea. The results indicate that inter-jurisdictional collaboration is required to implement conservation management strategies and mitigate fisheries interactions of common dolphins across multiple spatial scales in the Australasian region.

Keywords: delphinids, fisheries genomics, isolation-by-distance, migration, gene flow, metapopulation, conservation genomics

Edited by:
Michael Paul Jensen,
Southwest Fisheries Science Center
(NOAA), United States

Reviewed by:
Phillip A. Morin,
Southwest Fisheries Science Center
(NOAA), United States
Carlos Carreras,
University of Barcelona, Spain

***Correspondence:**
Andrea Barceló
andrea.barcelo@flinders.edu.au

Specialty section:
This article was submitted to
Marine Megafauna,
a section of the journal
Frontiers in Marine Science

Received: *12 October 2020*
Accepted: *14 January 2021*
Published: *16 February 2021*

Citation:
Barceló A, Sandoval-Castillo J, Stockin KA, Bilgmann K, Attard CM, Zanardo N, Parra GJ, Hupman K, Reeves IM, Betty EL, Tezanos-Pinto G, Beheregaray LB and Möller LM (2021) A Matter of Scale: Population Genomic Structure and Connectivity of Fisheries At-Risk Common Dolphins (Delphinus delphis) From Australasia. Front. Mar. Sci. 8:616673. doi: 10.3389/fmars.2021.616673

INTRODUCTION

Genetic connectivity and the delineation of populations, including their boundaries, are fundamental issues in conservation biology, because such information can advise on the scale of which to conserve and manage wildlife species (Leslie and Morin, 2016; Taylor et al., 2017; Dunn et al., 2019; Pierre, 2019; Sousa et al., 2019; Taft et al., 2020; Tulloch et al., 2020). Studies using molecular markers can inform on the number and distribution of populations, their genetic diversity, their resilience to environmental change, as well as their vulnerability to anthropogenic impacts and disease outbreaks (DiBattista et al., 2017; Holland et al., 2017; Bradburd et al., 2018; Batley et al., 2019; Breed et al., 2019; Grummer et al., 2019; Jasper et al., 2019; Perry and Lee, 2019; Leitwein et al., 2020). However, incorporating genetic data into conservation policy and management remains a challenge, and enhanced collaboration between conservation geneticists and wildlife managers is needed (Funk et al., 2012; Hendricks et al., 2018; Gardner et al., 2020; Holderegger et al., 2020; Taft et al., 2020).

Studies of population structure and dynamics emerged with the theories of island biogeography and metapopulation dynamics (MacArthur and Wilson, 1967; Levins, 1969; Hanski, 1998), and have evolved since then into characterizing connectivity of species among habitat patches in heterogeneous environments under different spatial and temporal scales (Waples and Gaggiotti, 2006; Compton et al., 2007; Manel et al., 2019). In marine environments, there is still limited information about how geographic barriers and spatial scales impact on population genetic structure (Riginos et al., 2016). Population structure and the dispersal of marine species may be associated with a range of factors such as spatial distance, oceanographic features (e.g., currents, upwellings, environmental gradients) and ecological traits (e.g., feeding ecology and life history), making it difficult to disentangle these factors (Selkoe et al., 2016; Bernatchez et al., 2018), and establishing policies for conservation and management.

The movement of marine species with active dispersal, such as delphinids, can occur at any life stage. Despite this, dolphins can exhibit population genetic structure at relatively small spatial scales (e.g., Hoelzel, 1998; Natoli et al., 2006; Möller et al., 2007; Quérouil et al., 2007) and are often subdivided into local populations (e.g., Natoli et al., 2005; Hoelzel et al., 2007; Mendez et al., 2008; Möller, 2011; Caballero et al., 2012; Nykanen et al., 2018; Parra et al., 2018; Pratt et al., 2018). When these populations are interconnected, but exhibit specific ecological and/or behavioral traits in a geographic area, a complex metapopulation system may arise (Riginos et al., 2016; Selkoe et al., 2016; Perry and Lee, 2019).

At large scales, the dispersal and population structure of dolphins is influenced by oceanographic or environmental variables such as depth, currents, upwellings, salinity gradients, sea surface temperatures, and primary productivity (Fullard et al., 2000; Natoli et al., 2005; Quérouil et al., 2007; Mirimin et al., 2009; Möller et al., 2011; Amaral et al., 2012a; Bilgmann et al., 2014; Fruet et al., 2014; Gaspari et al., 2015a; Pratt et al., 2018). At smaller scales, localized site fidelity, complex social behavior, and feeding specializations may result in adaptations to local environments, which leads to further population subdivision (Hoelzel et al., 2007; Möller et al., 2007; Ansmann et al., 2012; Fruet et al., 2014; Cammen et al., 2016; Foote et al., 2016; Zanardo et al., 2017; Pratt et al., 2018).

Common dolphins (*Delphinus delphis*) have a high dispersal potential and inhabit coastal and pelagic environments in temperate and subtropical waters of both southern and northern hemispheres (Natoli et al., 2008; Whitehead et al., 2008; Möller, 2011). In Australasia, common dolphin distribution ranges from embayment and gulf waters, to coastal and shelf waters of Australia and New Zealand (Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014; Mason et al., 2016; Zanardo et al., 2016; Dwyer et al., 2020; Peters and Stockin, 2021). At its most extreme, common dolphins in some semi-enclosed, relatively shallow embayments, show moderate to high site fidelity, such as in Port Phillip Bay (Victoria, Australia), Gulf St Vincent (South Australia) (Filby et al., 2010; Mason et al., 2016), and in the Hauraki Gulf (New Zealand) (Stockin et al., 2008; Hupman, 2016; Hupman et al., 2018; Pawley et al., 2018).

Differences in prey abundance, distribution and diversity can lead to feeding specializations in common dolphins (Neumann and Orams, 2003), which may shape their population structure at fine and medium spatial scales (Möller et al., 2007, 2011; Tezanos-Pinto et al., 2009). Movements of common dolphins are known to generally associated with the movement of their prey, which includes schooling fish such as jack mackerel (*Trachurus declivis, T. symmetricus. Murphyi,* and *T. novaezelandiae*), blue mackerel (*Scomber australasicus*), sardines (*Sardinops sagax*), southern calamari (*Sepioteuthis australis*), and anchovies (*Engraulis australis*) (e.g., Meynier et al., 2008; Goldsworthy et al., 2019a). In turn, most of these prey species are heavily targeted by fisheries, both for human consumption and to feed fish held in aquaculture farms, making common dolphins particularly susceptible to interactions with fisheries and to incidental mortalities (Kemper et al., 2003; Bilgmann et al., 2008; Stockin et al., 2009b).

Indeed, common dolphins in Australasia suffer mortalities as by-catch in multiple fisheries (Hamer et al., 2008; Thompson et al., 2013; Abraham et al., 2017; Tulloch et al., 2020). In Australia, common dolphins are incidentally by-caught in purse-seine, trawl, and gillnet fisheries (e.g., Hamer et al., 2008; AFMA, 2019b), with ∼380 mortalities recorded in purse-seine nets in 2004-2005 (Hamer et al., 2008), and more than 100 mortalities during 2011-2019 in gillnets (AFMA, 2019a, 2020). In New Zealand, common dolphins are mainly threatened by trawl and surface long-line fisheries (Abraham et al., 2017; Pierre, 2019), with at least 200 captures occurring from 2002 to 2017 in the trawl fishery (MPI, 2019). While mitigation of common dolphin by-catch in these countries has led to a general reduction in mortalities over time (Rowe, 2007; Ward and Grammer, 2018; Goldsworthy et al., 2019b), by-catch incidents have continued and occasionally spike in numbers (Abraham et al., 2017; Goldsworthy et al., 2019b). Notably, the cumulative impacts of dolphin-fishery interactions are currently unknown (Mackay et al., 2016), and by-catch is still managed separately by each fishery and based on fishing management zones, not based on dolphins' stock structure. These issues are exacerbated by limited information about dolphin abundance in Australasia, and how many dolphins can be caught without compromising the long-term viability of the populations. These estimates of potential biological removal (PBR), have been estimated based on aerial surveys and fisheries surveys. For South Australia, an aerial assessment done over 40,000 km2 led to an estimation of 21,733 common dolphins (CV = 0.25; 95% CI = 13,809–34,203) (Parra et al., in review), while in New Zealand an estimation for the Northern Island was of 18,145 common dolphins (CV = 0.33, 95% CI = 9,669–33,726) (Abraham et al., 2017).

In Australasia, common dolphins are known from previous studies to exhibit a degree of population genetic structure (Bilgmann et al., 2007b, 2014; Möller et al., 2011; Amaral et al., 2012a; Zanardo et al., 2016). These studies utilized traditional genetic markers such as mitochondrial DNA (mtDNA) and microsatellites and have identified population genetic differentiation at broad spatial scales (>1,500 km) between common dolphins of the Pacific and Indian Oceans (Amaral et al., 2012a; Bilgmann et al., 2014), as well as over finer spatial scales (<1,000 km; in southern (Bilgmann et al., 2014) and eastern Australia (Möller et al., 2011), and New Zealand (Stockin et al., 2014). However, studies based on a few molecular markers may not be accurate for determining spatial population structure (e.g., Teske et al., 2018; Rajora, 2019). The use of thousands of genome-wide markers circumvents this issue by providing powerful data to clarify spatially complex population structure (Frankham et al., 2010; Funk et al., 2012; Cammen et al., 2016; Teske et al., 2018; Manel et al., 2019).

Here, we assess the population genomic structure of common dolphins using a multi-scale approach across its distribution in Australasia. Our primary aims are to elucidate patterns of genomic diversity, population structure, and connectivity using a novel and powerful genome-wide dataset for common dolphins based on single nucleotide polymorphisms (SNPs). We complement this population genomic assessment with analyses of novel and previously published mtDNA sequences. Our study combines broad and fine-scale approaches to resolve structure and connectivity and provides detailed information to enhance the conservation management of common dolphins in Australasia.

METHODS

Study Area and Sampling

The study area encompasses two major oceanic regions, the southern Indian Ocean (Australia's southern coast) and the south-western Pacific Ocean (Australia's eastern coast, Tasmania and New Zealand). Skin samples were collected from live animals (i.e., biopsied) and carcasses (i.e., stranded and by-caught animals) over 17 years (2000-2017) at 16 localities across the species range in Australia and New Zealand (**Figure 1**). Samples from live individuals were obtained using a hand held biopsy pole (Bilgmann et al., 2007a) or a remote biopsy system (PAXARMS) (Krutzen et al., 2002). A total of 510 samples were analyzed for population genomics, including 310 biopsy samples and 200 stranding and by-catch samples, with the GPS location allocated to where an individual was found/caught (**Figure 1**).

DNA Extraction and Sex Determination

Genomic DNA was extracted from samples using a modified salting out protocol (Sunnucks and Hales, 1996). Extraction quality was then assessed using a NanoDrop-2000 (Thermo scientific) spectrophotometer, quantity estimated by a Qubit 2.0 fluorometer (Life Technologies), and integrity evaluated with agarose gels. If degradation was observed, DNA fragments >5 Kbp were selected using AMPure XP magnetic beads (Beckman Coulter Genomics), using a ratio of 0.8:1 (beads: DNA). The sex was genetically determined by the amplification of fragments of the *ZFX* and *ZFY* genes for all DNA samples, following Banks et al. (1995).

Mitochondrial DNA Control Region (mtDNA CR) Sequencing and Data Analysis

A fragment of the mtDNA CR of ~450 base pairs was amplified by the polymerase chain reaction (PCR) with primers DLP1.5 and DLP5, as modified by Möller and Beheregaray (2001), and sequenced in an Applied Biosystems 3730XL Sequencer. MtDNA CR sequences were then trimmed and aligned using Geneious v.6.0.4 (Kearse et al., 2012). ARLEQUIN v3.5.2.2 (Excoffier and Lischer, 2010) was used to estimate nucleotide and haplotype diversities overall and for each locality. To assess genetic differentiation between localities, pairwise Φ_{ST} (Weir and Cockerham, 1984) was estimated with significance assessed using 10,000 permutations False Discovery Rate (FDR = 10%) and corrected for multiple tests by the B-Y method (Benjamini and Yekutieli, 2001). Heatmap plots of pairwise Φ_{ST} values were then constructed in the language R (R Development Core Team, 2018), with the package ggplot2 (Wickham, 2016). A haplotype network was built in PopART 1.7, using the ancestral parsimony and 95% cut-off (Clement et al., 2002). The latter was carried out to assess evolutionary relationships of the inferred maternal lineages (i.e., mtDNA CR haplotypes). Together with estimates of nucleotide diversity, this provides an indication of long-term evolutionary divergence (or similarity) of common dolphin lineages. A total of 197 samples were sequenced and retained for analysis after filtering out poor quality peaks, and trimming to 440 base pairs to match the sequence fragments of Möller et al. (2011) ($N = 63$), Stockin et al. (2014) ($N = 24$), and Bilgmann et al. (2014) ($N = 110$). Altogether a total of 394 individual sequences were available for analyses based on mtDNA CR.

Genomic Library Preparation and ddRAD Sequencing

Double digest restriction-site associated DNA (ddRAD) libraries were prepared following Peterson et al. (2012), with modifications. Each sample was digested with two restriction enzymes *SbfI* and *MseI,* and then ligated with one of 96 individual barcodes designed in-house. Samples were then pooled into a multiplex of 12 individuals. Libraries were size selected for 250–800 bp fragments with a Pippin prep electrophoresis gel (Sage Science). The samples were amplified by PCR, and after this removal of PCR byproducts was done using AMPure XP

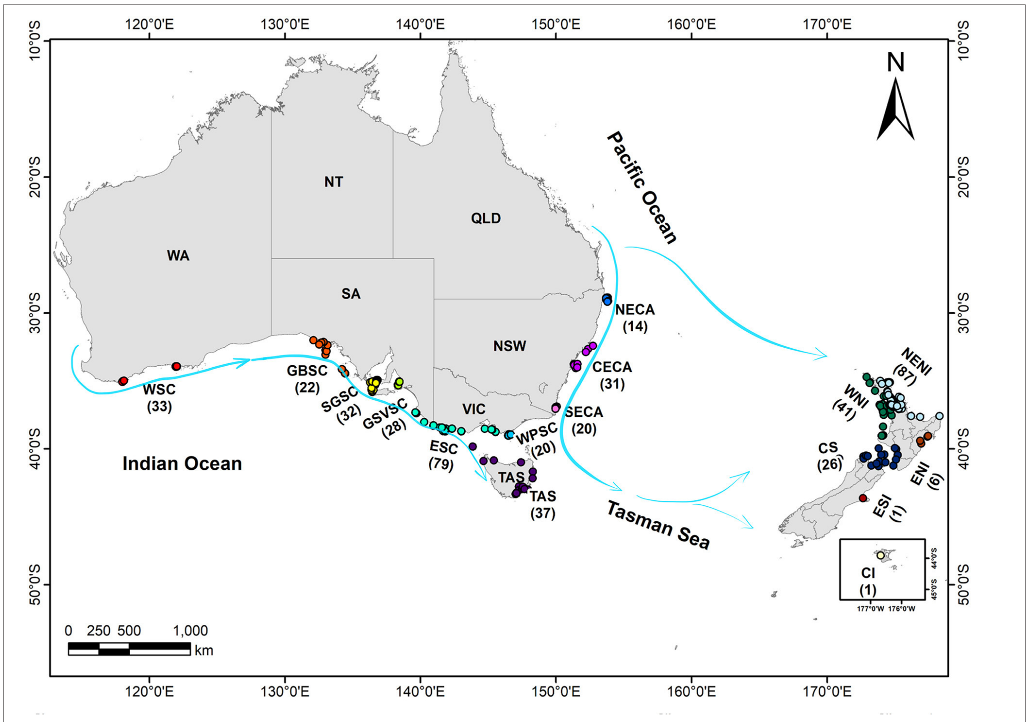


FIGURE 1 | Study area in the Australasian region showing the geolocations for 478 common dolphin (*Delphinus delphis*) samples used for the genome-wide analyses. Blue lines correspond to main current systems in Australasia. WSC, *West, Southern coast of Australia; GBSC, Great Australian Bight, Southern coast of Australia; SGSC, shelf waters in Spencer Gulf, Southern coast of Australia; GSVSC, Gulf St Vincent, Southern coast of Australia; ESC, East, Southern coast of Australia; WPSC, Wilson Promontory, Southern coast of Australia; NECA, North, Eastern coast of Australia; CECA, Central, Eastern coast of Australia; SECA, South, Eastern coast of Australia; CS, Cook Strait, New Zealand; WNI, West North Island, New Zealand; NENI, North East Island, New Zealand; ENI, East, North Island, New Zealand; CI, Chatman Island, New Zealand; ESI, East, South Island, New Zealand.

magnetic beads (ratio of 0.8:1). Real-time PCR was used to determine the DNA concentration to accurately pool eight libraries of 12 samples together in equal concentrations, creating one multiplex library of 96 uniquely barcoded samples sent for sequencing. The multiplex libraries were then single-end, 100 bp sequenced using multiple lanes in an Illumina HiSeq 2500 at the South Australian Health & Medical Research Institute (SAHMRI).

Sequences and SNP Filtering

Sequence quality checks were performed on the raw reads, followed by demultiplexing, trimming of barcodes and RAD tags (only one error allowed) and sorting into individual samples using process_radtags with STACKS v1.48 (Catchen et al., 2013). Next, filtered sequences were processed to generate a final SNP dataset using the dDocent2.2.19 pipeline (Puritz et al., 2014). The resulted variant calling file (VCF), with sequence variation across all samples (raw SNP catalog), was then filtered using VCFtools (Danecek et al., 2011) (for details see **Supplementary Material**). To further assess the quality of the SNP dataset and to exclude exogenous sequences, the quality-filtered reads were mapped against two genomes from closely related dolphin species: the *Tursiops truncatus* genome (Tur_tru_Illumina_phased_v1, GenBank Assembly ID: GCA_003435595.3) and the southern Australian bottlenose dolphin (SABD), *Tursiops aduncus* genome (Batley et al., unpublished). This was done using Bowtie2, following suggested standard procedures from Langmead and Salzberg (2012), allowing no mismatches in seed alignment and up to 20 consecutive seed fails. A linkage disequilibrium (LD) filter was implemented to obtain a dataset with the most likely number of independent markers (for details see **Supplementary Material**).

Detecting Neutral SNPs

SNPs putatively under selection were identified and removed from the dataset so that population structure analyses were based on markers conforming to neutral expectations (Luikart et al., 2003). This was done using an outlier test in BayeScan v2.1 (Foll and Gaggiotti, 2008) run with 100,000 iterations and prior odds of 10,000. Loci with a false discovery rate <10% were considered as not behaving as neutral and removed from the population analyses.

Relatedness Estimates for Excluding Potential Duplicate Samples

Relatedness between pairs of individuals was estimated using the triadic likelihood estimator (TrioML) in Coancestry v1.0.1.9 (Wang, 2011) to exclude potential re-sampled individuals (set at $r > 0.7$) from the population analyses. This method estimates pairwise relatedness (r) by using a third individual as a control, thus decreasing the chance of genes identical in state being mistakenly inferred as identical by descent (Wang, 2007).

Genomic Data Analyses

Genomic Diversity, Population Structure, and Genomic Differentiation

Genomic diversity was estimated for each locality sample as expected heterozygosity (H_E), observed heterozygosity (H_O), the inbreeding coefficient (F_{IS}), and percentage of polymorphic loci (P) using Genodive 2.0b27 (Meirmans and Van Tienderen, 2004). Population genetic structure was assessed using a Principal Component Analysis (PCA) and Discriminant Analysis of Principal Components (DAPC) with the R package Adegenet (Jombart and Ahmed, 2011) using an annealing simulation of 50,000 steps, and an optimal number of PCs to be retained, as suggested in Adegenet (Jombart and Collins, 2015). Both PCA and DAPC are model-free approaches for investigating population structure. The Bayesian information criterion (BIC) and Akaike information criterion (AIC) were then used to determine the best-supported number of clusters in the dataset, using the snapclust.chooseK function in the R package Adegenet (Beugin et al., 2018). Bayesian clustering was used to infer population stratification based on estimated individual ancestries using Admixture v1.3.0 (Alexander et al., 2009). This was done by performing a maximum likelihood estimates, using the ancestry portion and the population allele frequency to assign the most likely number of K (e.g., populations) in the dataset, testing for K1-16, and to model the probability of observed genotypes. The maximum likelihood of K and the fast-sequential quadratic algorithm were subsequently used as a cross validation with 10 replicates for each K value, using K1-8 (Alexander et al., 2009; Alexander and Lange, 2011). Genetic differentiation among localities was estimated as pairwise F_{ST} (Weir and Cockerham, 1984) using Genodive 2.0b27. Significance levels were assessed using 10,000 permutations (FDR = 10%), and then corrected by the B-Y method. Heatmap plots of F_{ST} were constructed with the R package ggplot2. A Mantel test (Mantel, 1967) was used to test for isolation by distance (IBD) using the shortest waterway distance matrix calculated in ArcMap v10.4 (Esri Inc., Redlands, CA) and a linearized pairwise F_{ST} matrix (F_{ST} /1- F_{ST}) as genetic distance. Scatterplots were then generated with the R package Adegenet.

Contemporary Migration Rates and First-Generation Migrants

Contemporary migration rates were estimated with BayesAss v3.0.4 (Wilson and Rannala, 2003) using the putatively neutral, unlinked SNPs. The method applies a Bayesian Markov chain Monte Carlo approach to estimate asymmetrical rates of recent migration (m), which represents the proportion of each population having migrant ancestry over the last generations. Common dolphins exhibit a long generation time ∼15 years, with interbirth intervals from 1 to 3 years (Taylor et al., 2007; Möller, 2011). The analysis was run with 10 million iterations and 1 million iterations as burn-in, and mixing parameters (allele frequencies, inbreeding coefficients, and migration rates) were adjusted to achieve recommended acceptance rates (Wilson and Rannala, 2003). Convergence was then inspected by plotting the cumulative log likelihoods of the iterations using TRACER 1.7 (Rambaut et al., 2018), with three runs used to verify consistency across runs.

First generation migrants were identified by performing a population assignment test in GeneClass2 (Piry et al., 2004), using the criteria of Rannala and Mountain (1997). This uses the multilocus genotypes and 1,000 simulations to provide a probability of an individual belonging to a population (Paetkau et al., 2004). An exclusion rate of 0.01 was applied. Only 800 SNPs were used due to the limitations of the software which only allowed successful runs to this maximum number of SNPs. The SNP subset was chosen using a random generator in R studio, and extracted from the full dataset of filtered putatively neutral SNPs.

RESULTS

Diversity and Differentiation Based on mtDNA CR

In the 440 bp of the mtDNA CR sequences of 394 Australasian common dolphins, three indels and 94 substitutions were observed. This resulted in 173 unique mtDNA haplotypes, 66 of which were not previously described for common dolphins in this region (Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014). Most haplotypes were represented by only one individual in the dataset. The overall haplotype diversity was high ($h = 0.860$), while the nucleotide diversity was low ($\pi = 0.0160$) (**Supplementary Table 4**). The haplotype diversity observed was similar to that previously reported for the eastern and southern Australia and for New Zealand (e.g., Möller et al., 2011; Bilgmann et al., 2014; Stockin et al., 2014). Fixation indices based on mtDNA CR indicated low to moderate differentiation between samples from the Pacific and the Indian Ocean (0.029–0.620) (**Supplementary Figure 2**, **Supplementary Table 7**). The haplotype network indicated very shallow phylogeographic structure (**Supplementary Figure 3**).

Genome-Wide SNP Data and Filtering for Putatively Neutral Loci

A total of 1,601,109,786 raw sequence reads were obtained, and a raw SNP catalog of 339,932 SNPs (**Supplementary Table 1**). The alignment rates with the *Tursiops* genomes were very high,

TABLE 1 | Measures of genomic diversity based on 14,799 SNPs for Australasian common dolphins (*Delphinus delphis*) by locality*.

Population	Locality	N	H_o	H_E	F_{IS}	P%
SC	WSC	33	0.169	0.172	0.015	73.295
	GBSC	22	0.170	0.176	0.032	74.816
	SGSC	32	0.172	0.172	0.000	81.053
	GSVSC	28	0.154	0.160	0.037	59.862
	ESC	79	0.170	0.176	0.033	91.155
	WPSC	20	0.175	0.181	0.033	71.005
EC	NECA	14	0.189	0.189	−0.001	58.862
	CECA	31	0.209	0.209	−0.003	80.587
	SECA	20	0.201	0.209	0.037	67.126
NZTAS	TAS	37	0.209	0.209	0.002	93.614
	CS	26	0.207	0.208	0.004	82.215
	WNI	41	0.204	0.206	0.013	87.209
	NENI	87	0.194	0.200	0.031	85.134
	ENI	6	0.179	0.190	0.061	52.760
	CI	1	NA	NA	NA	NA
	ESI	1	NA	NA	NA	NA
Total average	29.875	0.186	0.190	0.021	75.621	
Total SD			0.018	0.017	0.019	12.523

H_O, observed heterozygosity; H_E, expected heterozygosity; F_{IS}, inbreeding coefficient; P%, percentage of polymorphic loci; NA, not applicable (due to only one sample available). SC, *Southern coast of Australia; EC, Eastern coast of Australia; TAS, Tasmania; NZ, New Zealand. WSC, West, Southern coast of Australia; GBSC, Great Australian Bight, Southern coast of Australia; SGSC, shelf waters in Spencer Gulf, Southern coast of Australia; GSVSC, Gulf St Vincent, Southern coast of Australia; ESC, East, Southern coast of Australia; WPSC, Wilson Promontory, Southern coast of Australia; NECA, North, Eastern coast of Australia; CECA, Central, Eastern coast of Australia; SECA, South, Eastern coast of Australia; CS, Cook Strait, New Zealand; WNI, West North Island, New Zealand; NENI, North East Island, New Zealand; ENI, East, North Island, New Zealand; CI, Chatman Island, New Zealand; ESI, East, South Island, New Zealand.*

attesting to the high quality of the SNP dataset: 97% aligned with the *T. truncatus* genome and 99% with the SABD *T. aduncus* genome (retaining 26,199 SNPs, **Supplementary Table 1**). Filtering with stringent criteria resulted in a high-resolution dataset of 17,875 SNPs (**Supplementary Table 1**). The outlier test detected 3,076 SNPs likely not behaving as neutral, and these were excluded from the total dataset. This final dataset included 14,799 unlinked, putatively neutral SNPs (**Supplementary Table 1**, **Supplementary Figure 1**) that were used for the population structure analyses and to estimate migration rates.

Exclusion of Duplicate Samples

Thirty-two sample pairs were estimated as likely originating from duplicate individuals ($r \geq 0.7$), including 24 pairs of biopsies and eight pairs of stranding or by-caught individuals. One sample from each of the pairs was excluded, resulting in a final dataset of 478 individuals (**Figure 1**).

Genomic Diversity, Population Structure, and Genomic Differentiation

Genome-wide diversity was relatively high for all localities (**Table 1**) and there was no indication of population-level inbreeding (**Table 1**). When analyzing all samples combined, PCA and DAPC analyses suggested three distinct regional populations: (1) southern coast of Australia; (2) eastern coast of Australia; and (3) New Zealand and Tasmania, although the latter shows a degree of admixture to Australia's eastern coast (**Supplementary Figures 5, 6**). Admixture analysis suggested a hierarchical metapopulation structure in Australasia, with moderate levels of admixture within the regional populations (**Figure 2**, **Supplementary Figure 7**). At a metapopulation level, three clusters (K = 3), corresponding to geographical regional populations, were considered most likely (**Figure 2**). The membership probability of an individual belonging to a population varied according to the geographic position of the locality, with individuals from localities close to the interface between the Indian and Pacific Oceans (i.e., Wilsons Promontory in Victoria and southern localities in New South Wales, Australia), and between Tasmania and Australia's eastern coast being more admixed (**Supplementary Figure 7A**).

Further subdivision was disclosed within each regional population, when analyzing the three datasets separately, with two additional clusters (K = 2) within each region (**Figure 2**, **Supplementary Figures 7B–D**) best supported, but three and four clusters also highly supported for eastern and southern Australia (**Figure 2**, **Supplementary Figures 7B–D**), respectively. In the southern coast of Australia, the strongest separation was disclosed between individuals from Gulf St Vincent and the other localities, followed by Wilsons Promontory compare to the west coast individuals. In the case of Australia's eastern coast, the northern localities were most distinct from the central-south localities, with a greater proportion of admixed individuals in the central localities, possibly representing a further sub-population. For New Zealand and Tasmania, differentiation was disclosed mainly between localities in the east

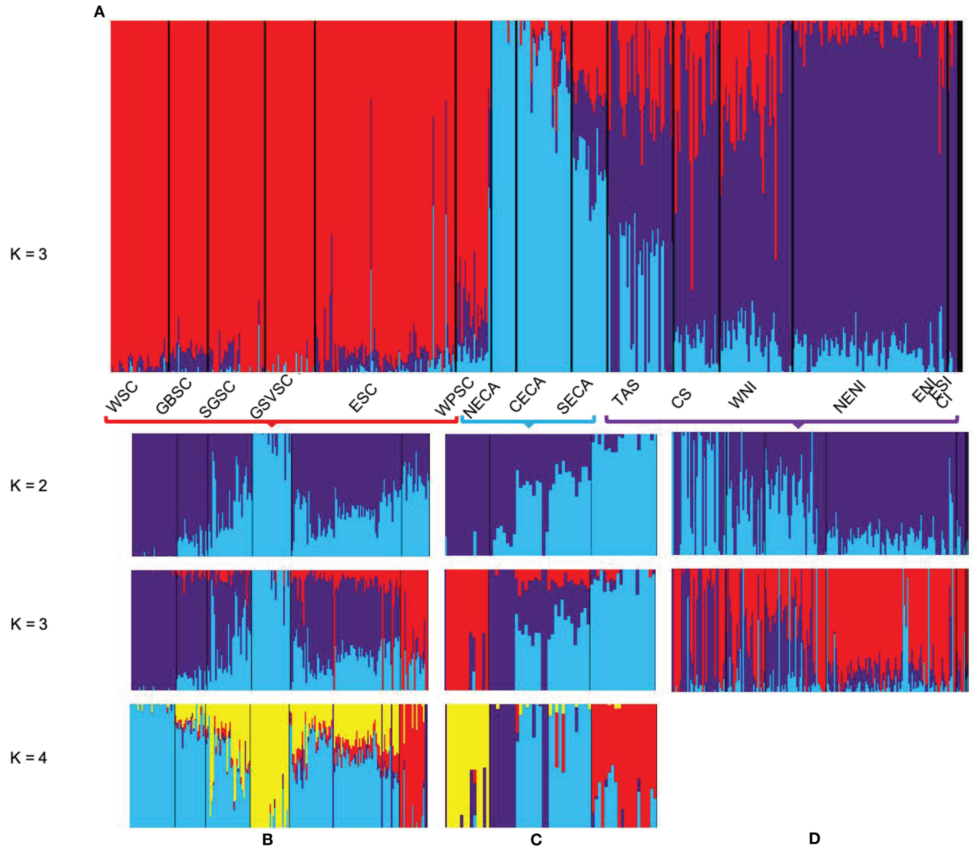


FIGURE 2 | Population genomic structure analysis using Admixture based on 14,799 SNPs for Australasian common dolphins (*Delphinus delphis*) (labeled by locality*). The results depict levels of admixture for each individual sample and grouping into two and/or three genomic clusters. Each sample (labeled by geographic sample groups in the x axis) is represented by one vertical line and is color-coded by the membership probability to **(A)** one of the three regional populations in Australia and New Zealand or **(B–D)** one of the potential local populations of the: **(B)** Southern coast of Australia; **(C)** Eastern coast of Australia; or **(D)** New Zealand and Tasmania. *Acronyms used as in **Figure 1**.

coast and west coast of New Zealand, with Tasmanian individuals considerable admixed. However, most of the Tasmanian common dolphins showed higher probability of assignment to the New Zealand population (~57%) based on Admixture's Q-values (>0.8), and DAPC results (**Supplementary Figures 6**, **7**), and were therefore considered primarily part of the New Zealand regional population.

Fixation indices indicated moderate genetic differentiation between the southern coast of Australia (SCA), eastern coast of Australia (ECA), and the New Zealand/Tasmania (NZT) regional populations (SCA vs. ECA = 0.060–0.213; SCA vs. NZT = 0.045–0.142; ECA vs. NZT = 0.018–0.142) (**Figure 3A**, **Supplementary Table 6**). In contrast, low genetic differentiation was observed between common dolphin subpopulations (**Figures 3B–D**). In the southern coast of Australia, the highest differences of F_{ST} were between Gulf St Vincent, Wilsons Promontory, and west southern coast vs. the other localities; whereas for the eastern coast of Australia, the northern localities showed the highest differentiation compared to the southern localities, followed by the central localities vs. the northern and southern localities. For New Zealand/Tasmania, the differentiation occurred between West coast of New

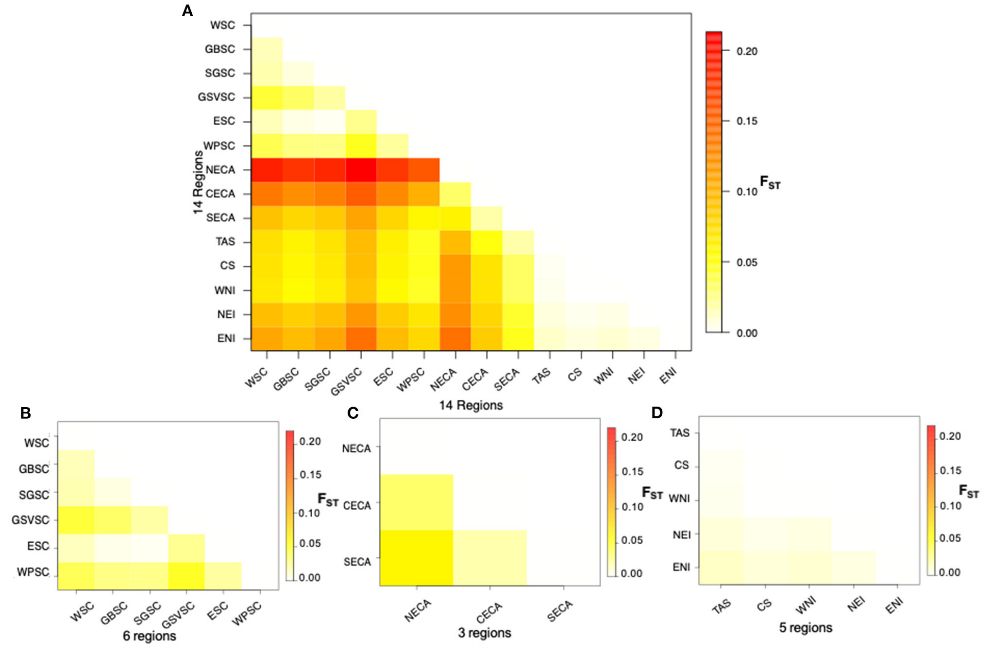


FIGURE 3 | Heatmap of pairwise F_{ST} values between localities* based on 14,799 SNPs for Australasian common dolphins (*Delphinus delphis*); **(A)** Australia and New Zealand; **(B)** Southern coast of Australia; **(C)** Eastern coast of Australia; and **(D)** New Zealand and Tasmania. *Acronyms used as in **Figure 1**.

Zealand/Tasmania vs. the localities from the east coast of New Zealand (**Figure 3**, **Supplementary Figure 8**).

A significant signal of IBD was observed at the metapopulation level ($r^2 = 0.084$, $p = 0.003$) (**Figure 4A**), and for the populations from the southern and eastern Australia ($r^2 = 0.346$, $p = 0.001$; $r^2 = 0.742$, $p = 0.03$, respectively). In contrast, there was no evidence of IBD in the New Zealand and Tasmania regional population ($r^2 = 0.005$, $p = 0.615$) (**Figures 4B–D**).

Contemporary Migration Rates and First-Generation Migrants

Estimates of contemporary migration rates based on BayesAss, that provide inferred rates of the portion of recent immigration over the last generations, indicated asymmetric migration between population pairs (**Supplementary Table 2**, **Figure 5**). There was relatively low estimates of migration (2–9%) between pairs of the three main regional populations, and moderate estimates of migration (6–25%) between pairs of the two subpopulations (**Figure 5**). First-generation migrants were detected in GeneClass between the three main regional populations, with 14 individuals rejected ($p < 0.01$) from the population they were sampled in **Supplementary Table 3**. These individuals were retained in all the population analyses to provide a representative picture of the metapopulation dynamics (**Supplementary Table 3**).

DISCUSSION

The delineation of populations and their respective geographic boundaries, as well as estimation of the degree of connectivity between populations are crucial for the conservation management of small cetaceans (Rosel et al., 2017; Taylor et al., 2017; Dunn et al., 2019; Pierre, 2019; Sousa et al., 2019; Taft et al., 2020). Integrating genomic technology for answering these questions can inform about the dolphin populations and scale at which anthropogenic activities may impact upon them (e.g., Leslie and Morin, 2016). Genomic analyses also provide baseline information for design of further studies and the monitoring of populations; for example, the area at which to estimate population abundance and trends, data on parameters for modeling population persistence, and for estimating sustainable by-catch rates (Waples and Gaggiotti, 2006; Allendorf et al., 2010; Frankham et al., 2010; Grummer et al., 2019; Manel et al., 2019).

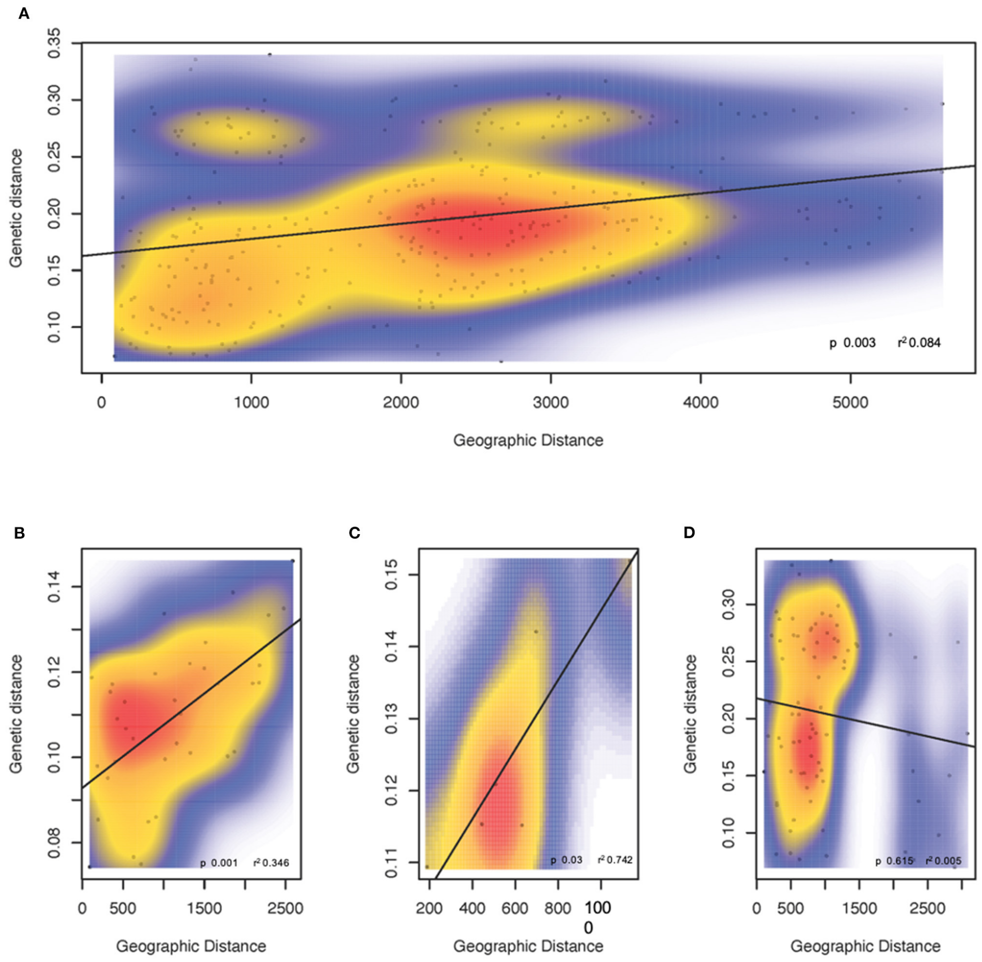


FIGURE 4 | Isolation by distance between F_{ST} values and the shortest waterway distance based on 14,799 SNPs for Australasian common dolphins (*Delphinus delphis*). **(A)** Australia and New Zealand metapopulation; and regional populations, **(B)** Southern coast of Australia, **(C)** Eastern coast of Australia, and **(D)** New Zealand and Tasmania.

This study revealed a hierarchical metapopulation structure for Australasian common dolphins, with high levels of genome-wide diversity and negligible inbreeding among them. At a broad scale, the southern Indian Ocean was represented by a single regional population inhabiting the southern coast of Australia. The south-west Pacific Ocean was represented by two regional populations, one along the eastern coast of Australia and the other in New Zealand/Tasmania, which suggests substantial connectivity across the Tasman Sea. Further subdivision was disclosed at finer scales, with evidence for at least two subpopulations within each regional population, but perhaps more. The varying levels of population connectivity identified across inter-state and international jurisdictions, have substantial implications for the conservation and management of common dolphins, which are subject to interactions and mortalities in multiple fisheries in the region.

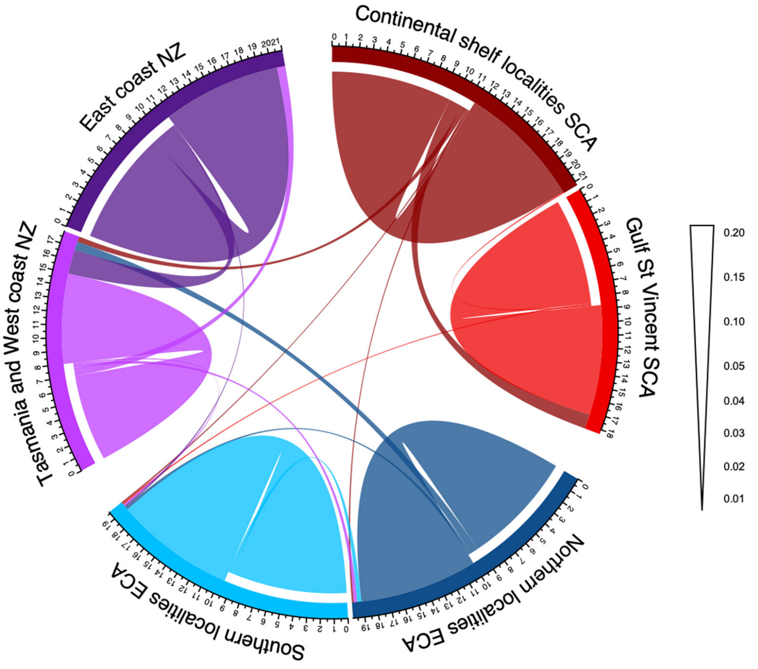


FIGURE 5 | Circos plot of inferred contemporary migration rates (per last generations) between local populations of Australasian common dolphins (*Delphinus delphis*) based on 14,799 SNPs. Plot corresponds to the migration directionally (full values from BayesAss are provided in **Supplementary Table 2**). Width of the curves indicates the amount of migration according to the scale going from one subpopulation into another one. Scale bar is in units of the proportion of migrations. Ticks represent the gross number of migrants per 100s. Migration rate < 0.01 is not shown. SCA, *****Southern coast of Australia; ECA, Eastern coast of Australia; NZ, New Zealand.

Population Structure of Australasian Common Dolphins

Studies investigating genetic partitioning at fine spatial scales in the sea usually provide evidence for distinct subpopulations, whereas metapopulations are generally disclosed when broader spatial scales are explored (Pitt and Kingsford, 2000; Dawson et al., 2014; Calò et al., 2016; Almany et al., 2017; Jasper et al., 2019). Nonetheless, sampling effort often makes it difficult to assess marine systems over broad scales, and as a consequence metapopulations may remain largely undisclosed (Manel et al., 2019). We assessed the population structure of common dolphins over a broad geographical area and revealed a hierarchical metapopulation structure across Australasia. Metapopulations have also been described for other dolphin species, such as spinner dolphins (*Stenella longirostris*) among Pacific Islands (Oremus et al., 2007), Hector's dolphins (*Cephalorhynchus hectori hectori*) between the west and east coasts of New Zealand (Heimeier et al., 2018), bottlenose dolphins (*Tursiops truncatus*) in the North Atlantic Ocean and Mediterranean Sea (Louis et al., 2014; Gaspari et al., 2015b), and Indo-Pacific bottlenose dolphins (*Tursiops cf. australis*) in southern Australia (Pratt et al., 2018). Although our sampling took place over 17 years, we believe there was little impact on the population genetic structure disclosed given than common dolphins exhibit a long generation time (∼15 years; Taylor et al., 2007). In addition, we found similar patterns of genomic diversity for sites sampled in multiple years, and similar levels of genomic differentiation between sites sampled in same and different years (data not shown).

At a broad scale, Australasian common dolphins showed moderate genomic differentiation at the level of the two ocean basins investigated, the Indian and Pacific Oceans. The mtDNA dataset provided enough resolution to distinguish historical population structure between the two oceans basins, as previously demonstrated in other genetic studies of common dolphins (e.g. Amaral et al., 2012a,b), bottlenose dolphins (*Tursiops* spp.) (e.g., Tezanos-Pinto et al., 2009; Charlton-Robb et al., 2011), and killer whales (*Orcinus orca*) (e.g., Reeves et al., in review). This regional distinction was also clear based on analyses of the SNP dataset. In Australia, we found pronounced genomic divergence between common dolphins of the southern coast, the eastern coast, and Tasmania. This split was evident along the Wilsons Promontory, which was once a land-bridge (the Bassian Isthmus, ∼14,000 ybp), which connected mainland Australia with Tasmania (Waters, 2008; Condie et al., 2011). The Wilsons Promontory region has been described as a prominent biogeographic boundary for many marine species (e.g., invertebrates, algae, small pelagic fish), accounting for many of the genetic discontinuities observed today along these coastlines (York et al., 2008; Teske et al., 2015, 2017; Costello et al., 2017).

An oceanographic perspective can also assist the interpretation of the pattern of regional genomic differentiation inferred in this study. The East Australian current (EAC) flows from the western boundary current into a southward direction, bringing warm and productive waters along the coast. The EAC is dominated by anticyclonic eddies, that creates three different water masses, and gradients of oceanographic variables along the coast, represented by northern, central and southern areas (Suthers et al., 2011). It then becomes weaker as it enters Tasmania and diverges eastward into New Zealand via the Tasman Front, where upwelling occurs mainly on the west coast (York et al., 2008; Flynn et al., 2018). These may impact on common dolphin movements along the eastern Australian region, leading to the pattern of local differentiation (Möller et al., 2011) and Tasman Sea regional separation.

The warm Leeuwin current runs south from western Australia into the southern coast of Australia. It then becomes the Great Australian Bight current, and later the Zeehan current, which extends from western Victoria into western Tasmanian waters, excluding the Bass Strait where currents in shallow waters tend to follow an eastward direction (York et al., 2008; Kämpf, 2015). Likewise, these currents may impact on common dolphin movements along the southern Australian region, leading to the proposed differentiation at finer-scales. The Zeehan current is weaker, and during the summer it is replaced by the cold Flinders current that enters from the west coast of Tasmania into the southern coast of Australia, bringing productive waters toward the continental shelf and leading to upwelling events (York et al., 2008; Lynch et al., 2014; Kämpf, 2015; Flynn et al., 2018). These complex oceanographic features cause variations in primary and secondary productivities along the two Australian coasts and in Tasmania, and may act as contemporary barriers that maintain historical divisions between marine organisms (Waters, 2008; Condie et al., 2011; Teske et al., 2017). While common dolphins have a high dispersal capability, their distributions are known to associate closely with that of their prey movements (e.g., Bilgmann et al., 2008; Meynier et al., 2008; Natoli et al., 2008; Zanardo et al., 2016; Peters et al., 2020), which may coincide with areas of high primary productivity along the two Australian coasts, as well as in New Zealand and Tasmania.

Previous population genetic studies of common dolphins based on microsatellite DNA markers suggested five subpopulations along the southern coast of Australia, including Tasmania (Bilgmann et al., 2014), three in the eastern coast of Australia (Möller et al., 2011), and three in New Zealand (Stockin et al., 2014), with the last two studies not including samples from Tasmania. At finer spatial scales, the genetic differences disclosed in our study suggested further subdivision within the identified Australasian regional populations. Two additional sub-populations were disclosed for New Zealand/Tasmania, two to four in southern Australia, and two to three in eastern Australia. These could potentially be explained by geological and oceanographic features (as mentioned above) reflecting on the contemporary population and feeding ecology of common dolphins. In the Australasian region, common dolphins are mainly found along continental shelf waters between the 20 and 200 m isobaths (Stockin et al., 2008, 2014; Möller et al., 2011; Meissner et al., 2015; Bilgmann et al., 2018; Peters and Stockin, 2021). By contrast, in the Gulf St Vincent, common dolphins are present in relatively shallow, protected waters (∼20 m) of the inner gulf (**Supplementary Figure 4**), with seasonal circulation year-round and may represent a resident population (Filby et al., 2010; Kämpf and Bell, 2014). The geological formation during the Cenozoic, established the Gulf St Vincent and Spencer Gulf as inverse estuaries (Bourman et al., 2016). These unique formations provide highly productive ecosystems, offering shelter for common dolphin prey species, such as sardines (*S. sagax*) and anchovies (*E. australis*) (Filby et al., 2010; Kämpf and Bell, 2014). These characteristics may have impacted on site fidelity of dolphins to this area and over time leading to genetic differentiation of Gulf St Vincent animals to those outside the gulf.

In the case of the eastern Australia, the northern localities are oceanographically and biologically differentiated due to the presence of a distinct water mass (Keane and Neira, 2008; Suthers et al., 2011). This could affect the distribution of common dolphins if they feed upon particular fish assemblages (Möller et al., 2011), and in turn lead to restricted movement and genetic differentiation between subpopulations. Common dolphins along the continental shelf of southern and eastern Australia presented a strong signal of IBD, a finding consistent with other common dolphin studies carried out across different ocean basins (Amaral et al., 2012a; Bilgmann et al., 2014). With the use of genomic markers, the pattern of IBD was also disclosed in this study at smaller spatial scales.

In the New Zealand and Tasmania regional population, genetic subdivision was found between the west and east coasts of New Zealand. This pattern between west and east coast subdivision has also been reported for Hector's dolphins that inhabit the southern island of New Zealand (Heimeier et al., 2018). Common dolphins from the west coast of New Zealand and Tasmania appear to comprise a subpopulation exhibiting moderate gene flow to dolphins on New Zealand's east coast and, to a lesser extent, with populations in Australia's eastern coast. The latter could also be due to historical factors. After the last glacial cycle (12,000–120,000 ybp) (Ashe and Wilson, 2019), subpopulation differentiation of dolphins across the Tasman Sea could have occurred due to habitat preferences and changes in prey availability. In New Zealand, differences in major currents, such as the east and the west Auckland current in the North Island, and the D'Urville current in the Cook Strait (Ayers and Waters, 2005; Ross et al., 2009; Chiswell et al., 2015), may influence fish distribution (Papa et al., 2020), and could have also led to restrictions on dolphin movement, and subsequent genetic differentiation.

Contemporary Migration Within and Between Ocean Basins

In an idealized population, individuals that are closer to each other, are genetically more similar than individuals that are further apart (Hanski, 1998). This may lead to a pattern of IBD, which was a common finding of the study across both broad and fine spatial scales. Migration of individuals between populations can also be shaped by intrinsic and extrinsic factors, promoting genetic discontinuities across heterogeneous environments (Armansin et al., 2019; Grummer et al., 2019; Rajora, 2019). For example, individuals may be unable or unlikely to disperse across physical or environmental barriers, and thus gene flow between populations may become compromised (Armansin et al., 2019). The estimated migration rates were relatively small between ocean basins (i.e., Pacific and Indian Oceans) and the regional populations (i.e., Southern Australia, Eastern Australia, and New Zealand/Tasmania, as described above) (<6%), separated by strong oceanographic discontinuities (i.e., unique biogeographic region in the Bassian Isthmus (Waters et al., 2010; Teske et al., 2017) (**Figure 5**). By contrast, estimated migration rates between subpopulations within ocean basins and between more homogeneous environments were higher (<18%). The migration rates and the number of first-generation migrants identified support the idea that genetic connectivity mainly occurs between subpopulations nested within regional populations. This suggests that if an extinction event was to occur, by either natural or anthropogenic causes, a subpopulation's home range will more likely be recolonized by individuals from within that region (e.g., Sandoval-Castillo et al., 2018; Riginos et al., 2019; Waters et al., 2020). However, if such events are strong enough to prevent gene flow and change the availability of prey resources, the subpopulation could decline without replacement. These types of events have been recorded for common dolphin populations from the Mediterranean Sea, which suffered dramatic declines due to combined impacts from by-catch mortalities, reduction of prey availability, and habitat degradation (Genov et al., 2020).

It appears that, in addition to spatial distance, heterogeneous marine environments found across the distribution of Australasian common dolphins have led to low and moderate connectivity between and within regional populations, respectively. In southern Australia, gene flow is restricted from continental shelf waters to Gulf St Vincent (∼5%). This protected environment allows common dolphin prey species to be locally available throughout the year (Filby et al., 2013; Ward et al., 2017; Goldsworthy et al., 2019a). The year-round availability of food resources could influence the feeding behavior of the common dolphins, maximizing their energy efficiency due to a lesser need for long-range movements, and perhaps increase reproductive success and lifetime fitness. All of these could lead to high site fidelity and residency by common dolphins to Gulf St Vincent, which while rare for the species, has been suggested for other semi-enclosed embayments in Australia, such as Port Philip Bay (Mason et al., 2016), and the Hauraki Gulf in New Zealand (Stockin et al., 2008, 2009a; Hupman, 2016; Peters et al., 2020). These characteristics, which may have led to genetic divergence of the Gulf St Vincent dolphins, also make them particularly at risk of decline due to interactions with fisheries in Gulf St Vincent and Investigator Strait (Hamer et al., 2008; Goldsworthy et al., 2019b).

In eastern Australia, stronger differentiation of common dolphins from the northern and southern localities translated in the lowest estimated migration rates (∼3%) between any two subpopulations in Australasia. In this area, the EAC creates eddies, which act as barriers for eggs and larval fish (Condie et al., 2011; Suthers et al., 2011). Thus, given the close association of common dolphins' distribution to that of their prey, these circulation patterns and differences in water masses could potentially act as oceanographic barriers for dolphin movements and gene flow (Möller et al., 2011).

Within the New Zealand and Tasmania population, moderate migration rates were estimated between the two subpopulations (∼18%). Migration here was strongly asymmetric, occurring mostly from the east into the west coast of New Zealand. Along the east coast of New Zealand there are several habitats (e.g., Hauraki Gulf), which have been proposed as breeding and calving areas for groups of common dolphins (Stockin et al., 2008; Dwyer et al., 2020). In this regional population, New Zealand's east coast appears to be acting as a genetic source, while the west coast, which presents higher rates of dolphin mortality due to fisheries (Thompson et al., 2013; Abraham et al., 2017), may be acting as a sink, similar to source-sink dynamics observed in other marine species (e.g., Benestan et al., 2016; DiBattista et al., 2017; Lal et al., 2017; Manel et al., 2019). Interestingly, Tasmania in Australia and the west coast of New Zealand displayed high connectivity over more than 1,000 km across the Tasman Sea, and genetic signatures show that individuals from western New Zealand are also found in Tasmanian waters. However, to the best of our knowledge, movements of common dolphins over long distances (∼1,000 km) have only been document across the Mediterranean Sea through photo-ID (Genov et al., 2012). Similar patterns of connectivity across the Tasman Sea have been disclosed for other marine species, such as teleosts and invertebrates (e.g., *Hippocampus abdominalis, Hoplosthethus atlanticus, Nerita melanogastrus*) (Cumming et al., 2016; Flynn et al., 2018; Ashe and Wilson, 2019; Gardner et.al. unpublished). Historically, dispersal of marine species across the Tasman Sea seems to have occurred during the last glacial cycle (12,000–120,00 ybp), leading to the colonization of multiple areas by marine species in both countries (Ashe and Wilson, 2019). However, contemporary genetic connectivity seems to have been retained by oceanographic currents (Flynn et al., 2018). Further sampling and assessment of common dolphins from Tasmania may clarify whether this represents a contact area, and if they should be considered as a separate or combined unit for management with New Zealand. The latter would involve cross jurisdictional cooperation between policy makers.

Implications for Conservation and Management of Australasian Common Dolphins

Common dolphins in Australasia are mainly threatened due to by-catch in commercial fisheries (Abraham et al., 2017; Tulloch et al., 2020), and potentially by anthropogenic-associated competition for food resources. In Australia, incidental by-catch has occurred mainly in trawl fisheries and purse-seine fisheries that catch mackerel (*T. declivis, T.s. murphyi, T. novaezelandiae,* and *S. australasicus*) and sardines (*S. sagax)*, as well as in gillnet fisheries targeting gummy sharks (*Mustelus* sp.) (Australian Goverment, 2019b). In New Zealand the observed incidental by-catch of common dolphins occurs mainly in mid-water trawl fisheries that catch the same mackerel species (Thompson et al., 2013; Abraham et al., 2017). However, by-catch within recreational set nets has also been documented as a threat to these dolphins (Stockin et al., 2009b). These incidental catches are known to have resulted in mortalities of hundreds of common dolphins in at least two of these fisheries (Abraham et al., 2017; Goldsworthy et al., 2019b). High mortalities were disclosed in 2004-2005 in the South Australian Sardine Fishery (SASF) (Hamer et al., 2008), likely exceeding the potential biological removal of individuals for one of the population's segment (Parra et al., in review). For New Zealand, an increase of common dolphin mortalities was reported between 2002 and 2003 in the trawl fishery (Thompson et al., 2013; MPI, 2019). After these periods, codes of practices were implemented in both fisheries, leading to a reduction in mortality rates (Hamer et al., 2008; Goldsworthy et al., 2019b; Pierre, 2019). More recently the Small Pelagic and Gillnet fisheries of Australia also implemented a by-catch trigger limit of six dolphins per operator, leading to a temporally exclusion of the vessel for 6 months from the fishing management zone if that occurs (Mackay et al., 2016; AFMA, 2019a,b). A recent study in New Zealand also reported that common dolphins are still one of the main marine mammal species accidentally caught by commercial fisheries (Abraham et al., 2017), although use of mitigation measures in the jack mackerel trawl fisheries has reduced mortalities to negligible levels in 2016-18 (Fisheries New Zealand, 2020). In Australia's SASF, an upsurge in mortalities has been recorded between 2018-19, with discrepancy in the data recorded by fishermen and independent observers (Goldsworthy et al., 2019b). These issues suggest that information about common dolphin population structure, connectivity and abundance are critical to evaluate the risk of by-catch to particular dolphin populations, and to establish strategies to mitigate the combined interactions and mortalities within the multiple fisheries.

In the Australasian region, fisheries that threaten common dolphins operate under different jurisdictions based on geographic delimitation and stock delineation for each prey targeted (Abraham and Thompson, 2015a,b,c; Patterson et al., 2019). The delineation of fish stocks represents different management zones (e.g., **Supplementary Table 5**) and often it does not consider the population structure of the targeted fish species (Papa et al., 2020). In addition, these management zones are not only used to manage the targeted species, but also to manage interactions and mortalities of by-caught species, such as common dolphins (Abraham and Thompson, 2015a,b,c; Mackay et al., 2016; AFMA, 2019a,b; Goldsworthy et al., 2019b; Patterson et al., 2019). Our findings suggest that regional populations and subpopulations of Australasian common dolphins are currently allocated across and within different fishing management zones. This suggests that the use of the management zones as presently implemented (e.g., **Supplementary Table 5**) could differentially impact populations of common dolphins.

Marine species that present connectivity over large spatial scales, such as common dolphins, need planning and implementation of conservation and management strategies over broad spatial scales that can guarantee the long-term persistence of populations (Rosel et al., 2017; Taylor et al., 2017; Dunn et al., 2019; Grummer et al., 2019; Manel et al., 2019; Sousa et al., 2019; Taft et al., 2020; Tulloch et al., 2020). Some of the dolphin subpopulations identified here are potentially at higher-risk of negative impacts from the fisheries. For example, the Gulf St Vincent subpopulation, which is possibly resident and relatively small (Filby et al., 2010), suffers by-catch induced mortalities by the SASF (Goldsworthy et al., 2019b), and these could potentially impact their long-term viability. In the West coast of New Zealand-Tasmania subpopulation, interactions with common dolphins and other top predators occur mainly with the mid-water trawl fisheries (Kemper et al., 2003; Thompson et al., 2013; Hamilton and Baker, 2019). Both of these fisheries have implemented codes of practice to reduce the number of entanglements and mortalities, including not setting nets when a cetacean sighting occurs, reporting cetacean interactions, modifying the fishery's gear (FAO, 1995; Rowe, 2007; Hamer et al., 2008; Goldsworthy et al., 2019b), and/or implementing an annual assessment with independent observers (Hamer et al., 2008; Goldsworthy et al., 2019b). Nevertheless, the management zones used to mitigate common dolphin interactions with these fisheries (**Supplementary Table 5**) are not in concordance with the population genomic structure of common dolphin disclosed here (**Figure 2**).

In Australasia, small cetacean populations have been generally managed in zones or units that do not reflect their genetic structure (e.g., Möller et al., 2001, 2011; Krutzen and Sherwin, 2004; Möller and Beheregaray, 2004; Bilgmann et al., 2007b, 2008, 2014, 2018; Wiszniewski et al., 2009; Amaral et al., 2012a; Stockin et al., 2014; Zanardo et al., 2016, 2017; Pratt et al., 2018). These could potentially make dolphin populations more vulnerable to decline due to anthropogenic impacts, as exemplified for common dolphins in the Mediterranean Sea (e.g., Natoli et al., 2008; Moura et al., 2013; Genov et al., 2020). These challenges highlight the need of using genetics and genomics markers as a tool for delineating population and estimating connectivity for biological meaningful management zones to be implemented (Funk et al., 2012; Leslie and Morin, 2016; Rosel et al., 2017; Taylor et al., 2017; Dunn et al., 2019). In particular, genetic and genomic analyses provide an opportunity to identify populations or subpopulations that require prioritization or additional conservation policies.

In this study, we found that Australasian common dolphins present a complex hierarchical metapopulation, with nested subpopulations within regional populations. The estimated contemporary migration rates between most of these subpopulations suggest that they are not entirely genetically or demographically independent, and therefore common dolphins in the Australasian region should be managed on both meso-scale (regional population level) and fine-scale (subpopulation level). Each population and subpopulation are relevant to conserve for the maintenance of the complex metapopulation system. Subpopulations with potentially high-risk of anthropogenic impacts due to fisheries may act as sink population as previously reported for other marine species with sink-source dynamics (e.g., Benestan et al., 2016; Lal et al., 2017; Manel et al., 2019; Rajora, 2019). However, the levels of contemporary migration suggest that the subpopulations identified cannot be managed entirely separately. Thus, we suggest that assessment and management of by-catch interactions and mortalities of common dolphins needs to be considered across multiple fisheries, management zones, and jurisdictions for adequate conservation management to occur. For example, interactions and mortalities in the West coast of New Zealand need to be perhaps considered in conjunction with impacts on common dolphins in Tasmania, as they (provisionally) appear to belong to the same subpopulation, albeit with moderate connectivity to other southeastern Australian localities. The equivalent level of management should be applied within southern Australian states (southern Western Australia, South Australia, Victoria) and within eastern Australia states (New South Wales and southern Queensland). Therefore, potential management zones for mitigation and assessments of common dolphin by-catch in Australasia need to be based on populations' boundaries and connectivity, and through collaboration between inter-state and international jurisdictions.

Our findings integrating genetics and genomics markers provide reliable estimates of population structure and connectivity at broad and fine spatial scales for common dolphins of Australasia. Future risk assessments of by-catch and potential biological removal will require an application of the population structure and connectivity information presented here. Genomic analyses are also essential in additional studies addressing adaptation in marine ecosystems, in which selection can potentially further clarify substructure within regional populations (e.g., Shafer et al., 2015; Bernatchez et al., 2018; Hendricks et al., 2018; Sandoval-Castillo et al., 2018; Xuereb et al., 2018; Rajora, 2019). This is a topical issue that needs to be considered in future conservation policies of marine ecosystems given the increase in anthropogenic impacts and ongoing changes of Earth's climate.

DATA AVAILABILITY STATEMENT

The datasets used for this study can be found in the online repository Figshare at: https://figshare.com/s/083be1832e010f249797, https://figshare.com/s/cff21a1394ad83c55f83, and https://figshare.com/s/683409860163e2d08e75

ETHICS STATEMENT

The animal study was reviewed and approved by under the ethics approval of the Flinders University Macquarie University, and Massey University animal ethics committees, and under research permits from Flinders University and South Australia Health Service Animal Welfare Committee (E326); DENR,SA (E25889); DEC,WA (SF008961); DSE,VIC (FF383247); DECCW, NSW (A2126); DEWHA (2008-001), SA State water a Ministerial Exemption PIRSA (9902404); KS and EB New Zealand Department of Conservation (RNW/HO/2008/03); GT-P New Zealand Department of Conservation (DOCDM-13171418); GT-P and KS New Zealand (AEC/17 14/25).

AUTHOR CONTRIBUTIONS

Conceptualization and first manuscript were developed by AB, LM, and LB. Samples were provided by KS, KB, LM, NZ, GT-P, EB, KH, and GP. Genetic data and analyses was performed by AB and JS-C. All authors have made contributions to the manuscript.

FUNDING

Ministry for Primary Industries of New Zealand (Project PRO201708A) and the National Institute of Water and Atmospheric Research (KH, KS, LM, and LB). The Australian Marine Mammal Centre (AMMC) Grants Program, Australian Antarctic Division (AAD) (project number 2010/3, LM, GP, KB, and LB). Ph.D. scholarship from the Mexican National Council for Science and Technology to AB, and Flinders University.

ACKNOWLEDGMENTS

AB is grateful for the support from CONACYT (the Mexican National Council for Science and Technology) Scholarship (Grant No. 440689) and sponsorship from Flinders University, as well as proof reading of the manuscript by Orlando Lam-Gordillo. We are thankful for all the samples provided and the work of many volunteers in the field. Biopsy samples were available through CEBEL/MELFU at Flinders University and the CERG at Massey University. We are thankful to the Massey University, University of Auckland, the National Institute of Water and Atmospheric Research and the Ministry of Primary Industries of New Zealand, the Tasmanian Museum and Art Gallery, Rosemary Gales, and Kris Carlyon and members of the Department of Primary Industries, Parks, Water and Environment of Tasmania, for providing tissues samples of stranding and by-catch individuals of common dolphins. Also, we thank the Ministry for Primary Industries, New Zealand, the Australian Marine Mammal Centre (AMMC) Grants Program and the Australian Antarctic Division (AAD) for funding part of this work. We thank the editor and the reviewers whose comments improved this manuscript. Finally but not least we are really thankful for Iwi collaborative partnership that permitted the genetic analyses of NZ cetacean samples. We acknowledge the biological whakapapa this research represents to mana whenua.

REFERENCES

Abraham, E. R., Neubauer, P., Berkenbusch, K., and Richard, Y. (2017). *Assessment of the Risk to New Zealand Marine Mammals From Commercial Fisheries.* New Zealand Aquatic Environment and Biodiversity Report No. 189: Ministry of Primary Industries.

Abraham, E. R., and Thompson, F. N. (2015a). *Captures of Common Dolphin in Setnet Fisheries, in the New Zealand Exclusive Economic Zone, During the 2017–18 Fishing Year* [Online]. Available online at: psc.dragonfly.co.nz/2019v1/released/common/dolphin/setnet/all/vessels/eez/2017/18/ (accessed September 24, 2020).

Abraham, E. R., and Thompson, F. N. (2015b). *Captures of Common Dolphin in Surface Longline Fisheries, in the New Zealand Exclusive Economic Zone, During the 2017–18 Fishing Year* [Online]. Available online at: psc.dragonfly.co.nz/2019v1/released/common/dolphin/surface/longline/all/vessels/eez/2017/18/ (accessed September 24, 2020).

Abraham, E. R., and Thompson, F. N. (2015c). *Captures of Common Dolphin in Trawl Fisheries, in the New Zealand Exclusive Economic Zone, During the 2017–18 Fishing Year* [Online]. Available online at: psc.dragonfly.co.nz/2019v1/released/common/dolphin/trawl/all/vessels/eez/2017/18/ (accessed September 24, 2020).

AFMA (2019a). *Gillnet Dolphin Mitigation Strategy. Minimising Dolphin Interactions With Gillnets in the Southern and Eastern Scalefish and Shark Fishery.* Australian Fisheries Management Authority (AFMA). Available online at: afma.gov.au/sites/default/files/gillnet_dolphin_mitigation_strategy_updated_aug_2019_accessible.pdf

AFMA (2019b). *Small Pelagic Fishery Dolphin Strategy. Minimising Dolphin Interactions in the Small Pelagic Fishery.* Australian Fisheries Management Authority (AFMA). Available online at afma.gov.au/sites/default/files/spf_dolphin_strategy_2019_updated_accessible.pdf

AFMA (2020). *Protected Species Interactions Quarterly Reports: 2012-2019.* Australian Fisheries Management Authority (AFMA). Available online at: afma.gov.au/sustainability/environment/protected/species/management/protected/species/interaction/reports

Alexander, D. H., and Lange, K. (2011). Enhancements to the ADMIXTURE algorithm for individual ancestry estimation. *BMC Bioinformatics* 12:246. doi: 10.1186/1471-2105-12-246

Alexander, D. H., Novembre, J., and Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* 19, 1655–1664. doi: 10.1101/gr.094052.109

Allendorf, F. W., Hohenlohe, P. A., and Luikart, G. (2010). Genomics and the future of conservation genetics. *Nat. Rev. Genet.* 11, 697–709. doi: 10.1038/nrg2844

Almany, G. R., Planes, S., Thorrold, S. R., Berumen, M. L., Bode, M., Saenz-Agudelo, P., et al. (2017). Larval fish dispersal in a coral-reef seascape. *Nat. Ecol. Evol.* 1:148. doi: 10.1038/s41559-017-0148

Amaral, A. R., Beheregaray, L. B., Bilgmann, K., Boutov, D., Freitas, L., Robertson, K. M., et al. (2012a). Seascape genetics of a globally distributed, highly mobile marine mammal: the short-beaked common dolphin (Genus *Delphinus*). *PLoS ONE* 7:e31482. doi: 10.1371/journal.pone.0031482

Amaral, A. R., Beheregaray, L. B., Bilgmann, K., Freitas, L., Robertson, K. M., Sequeira, M., et al. (2012b). Influences of past climatic changes on historical population structure and demography of a cosmopolitan marine predator, the common dolphin (genus *Delphinus*). *Mol. Ecol.* 21, 4854–4871. doi: 10.1111/j.1365-294X.2012.05728.x

Ansmann, I. C., Parra, G. J., Lanyon, J. M., and Seddon, J. M. (2012). Fine-scale genetic population structure in a mobile marine mammal: inshore bottlenose dolphins in Moreton Bay, Australia. *Mol. Ecol.* 21, 4472–4485. doi: 10.1111/j.1365-294X.2012.05722.x

Armansin, N. C., Stow, A. J., Cantor, M., Leu, S. T., Klarevas-Irby, J. A., Chariton, A. A., et al. (2019). Social barriers in ecological landscapes: the social resistance hypothesis. *Trends Ecol. Evol.* 35, 137–148. doi: 10.1016/j.tree.2019.10.001

Ashe, J. L., and Wilson, A. B. (2019). Navigating the southern seas with small fins: genetic connectivity of seahorses (*Hippocampus abdominalis*) across the Tasman Sea. *J. Biogeogr.* 47, 207–219. doi: 10.1111/jbi.13733

Ayers, K. L., and Waters, J. M. (2005). Marine biogeographic disjunction in central New Zealand. *Mar. Biol.* 147, 1045–1052. doi: 10.1007/s00227-005-1632-7

Banks, J., Levine, K., Syvanen, M., Theis, J., and Gilson, A. (1995). *DNA Tissue Gender Typing. Standard Operating Procedure of the Wildlife Forensic Laboratory of the California Department of Fish and Game.* Sacramento, CA: California Department of Fish and Game.

Batley, K. C., Sandoval-Castillo, J., Kemper, C. M., Attard, C. R. M., Zanardo, N., Tomo, I., et al. (2019). Genome-wide association study of an unusual dolphin mortality event reveals candidate genes for susceptibility and resistance to cetacean morbillivirus. *Evol. Appl.* 12, 718–732. doi: 10.1111/eva.12747

Benestan, L., Quinn, B. K., Maaroufi, H., Laporte, M., Clark, F. K., Greenwood, S. J., et al. (2016). Seascape genomics provides evidence for thermal adaptation and current-mediated population structure in American lobster (*Homarus americanus*). *Mol. Ecol.* 25, 5073–5092. doi: 10.1111/mec.13811

Benjamini, Y., and Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *Ann. Statist.* 29, 1165–1188. doi: 10.1214/aos/1013699998

Bernatchez, S., Xuereb, A., Laporte, M., Benestan, L., Steeves, R., Laflamme, M., et al. (2018). Seascape genomics of eastern oyster (*Crassostrea virginica*) along the Atlantic coast of Canada. *Evol. Appl.* 12, 587–609. doi: 10.1111/eva.12741

Beugin, M. P., Gayet, T., Pontier, D., Devillard, S., and Jombart, T. (2018). A fast likelihood solution to the genetic clustering problem. *Methods Ecol. Evol.* 9, 1006–1016. doi: 10.1111/2041-210X.12968

Bilgmann, K., Griffiths, O. J., Allen, S. J., and Möller, L. M. (2007a). A biopsy pole system for bow-riding dolphins: sampling success, behavioral responses, and test for sampling bias. *Mar. Mamm. Sci.* 23, 218–225. doi: 10.1111/j.1748-7692.2006.00099.x

Bilgmann, K., Möller, L. M., Harcourt, R. G., Gales, R., and Beheregaray, L. B. (2008). Common dolphins subject to fisheries impacts in Southern Australia are genetically differentiated: implications for conservation. *Anim. Conserv.* 11, 518–528. doi: 10.1111/j.1469-1795.2008.00213.x

Bilgmann, K., Möller, L. M., Harcourt, R. G., Gibbs, S. E., and Beheregaray, L. (2007b). Genetic differentiation in bottlenose dolphins from South Australia: association with local oceanography and coastal geography. *Mar. Ecol. Prog. Ser.* 341, 265–276. doi: 10.3354/meps341265

Bilgmann, K., Parra, G. J., and Möller, L. M. (2018). Occurrence, distribution and abundance of cetaceans off the western Eyre Peninsula in the Great Australian Bight. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 157–158, 134–145. doi: 10.1016/j.dsr2.2017.11.006

Bilgmann, K., Parra, G. J., Zanardo, N., Beheregaray, L. B., and Möller, L. M. (2014). Multiple management units of short-beaked common dolphins subject to fisheries bycatch off southern and southeastern Australia. *Mar. Ecol. Prog. Ser.* 500, 265–279. doi: 10.3354/meps10649

Bourman, R. P., Murray-Wallace, C. V., and Harvey, N. (2016). *Coastal Landscapes of South Australia.* Adelaide, SA: University of Adelaide Press.

Bradburd, G. S., Coop, G. M., and Ralph, P. L. (2018). Inferring continuous and discrete population genetic structure across space. *Genetics* 210, 33–52. doi: 10.1534/genetics.118.301333

Breed, M. F., Harrison, P. A., Blyth, C., Byrne, M., Gaget, V., Gellie, N. J. C., et al. (2019). The potential of genomics for restoring ecosystems and biodiversity. *Nat. Rev. Genet.* 20, 615–628. doi: 10.1038/s41576-019-0152-0

Caballero, S., Islas-Villanueva, V., Tezanos-Pinto, G., Duchene, S., Delgado-Estrella, A., Sanchez-Okrucky, R., et al. (2012). Phylogeography, genetic

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.616673/full#supplementary-material

diversity and population structure of common bottlenose dolphins in the Wider Caribbean inferred from analyses of mitochondrial DNA control region sequences and microsatellite loci: conservation and management implications. *Anim. Conserv.* 15, 95–112. doi: 10.1111/j.1469-1795.2011.00493.x

Calò, A., Muñoz, I., Pérez-Ruzafa, Á., Vergara-Chen, C., and García-Charton, J. A. (2016). Spatial genetic structure in the saddled sea bream (*Oblada melanura* [Linnaeus, 1758]) suggests multi-scaled patterns of connectivity between protected and unprotected areas in the Western Mediterranean Sea. *Fish. Res.* 176, 30–38. doi: 10.1016/j.fishres.2015.12.001

Cammen, K. M., Andrews, K. R., Carroll, E. L., Foote, A. D., Humble, E., Khudyakov, J. I., et al. (2016). Genomic methods take the plunge: recent advances in high-throughput sequencing of marine mammals. *J. Hered.* 107, 481–495. doi: 10.1093/jhered/esw044

Catchen, J., Hohenlohe, P. A., Bassham, S., Amores, A., and Cresko, W. A. (2013). Stacks: an analysis tool set for population genomics. *Mol. Ecol.* 22, 3124–3140. doi: 10.1111/mec.12354

Charlton-Robb, K., Gershwin, L. A., Thompson, R., Austin, J., Owen, K., and McKechnie, S. (2011). A new dolphin species, the Burrunan Dolphin *Tursiops australis* sp. nov., endemic to southern Australian coastal waters. *PLoS ONE* 6:e24047. doi: 10.1371/journal.pone.0024047

Chiswell, S. M., Bostock, H. C., Sutton, P. J. H., and Williams, M. J. M. (2015). Physical oceanography of the deep seas around New Zealand: a review. *N. Z. J. Mar. Freswater Res.* 49, 286–317. doi: 10.1080/00288330.2014.992918

Clement, M., Snell, Q., Walke, P., Posada, D., and Crandall, K. (2002). "TCS: estimating gene genealogies," in *Proceedings 16th International Parallel and Distributed Processing Symposium* (Ft. Lauderdale, FL), 7. doi: 10.1109/IPDPS.2002.1016585

Compton, B. W., McGarigal, K., Cushman, S. A., and Gamble, L. R. (2007). A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conserv. Biol.* 21, 788–799. doi: 10.1111/j.1523-1739.2007.00674.x

Condie, S. A., Mansbridge, J. V., and Cahill, M. L. (2011). Contrasting local retention and cross-shore transports of the East Australian Current and the Leeuwin Current and their relative influences on the life histories of small pelagic fishes. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 58, 606–615. doi: 10.1016/j.dsr2.2010.06.003

Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z., and Chaudhary, C. (2017). Marine biogeographic realms and species endemicity. *Nat. Commun.* 8:1057. doi: 10.1038/s41467-017-01121-2

Cumming, R. A., Nikula, R., Spencer, H. G., and Waters, J. M. (2016). Trans-Tasman genetic connectivity in the intertidal air-breathing slug *Onchidella nigricans*. *Mar. Ecol. Prog. Ser.* 562, 93–100. doi: 10.3354/meps11926

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., et al. (2011). The variant call format and VCFtools. *Bioinformatics* 27, 2156–2158. doi: 10.1093/bioinformatics/btr330

Dawson, M. N., Cieciel, K., Decker, M. B., Hays, G. C., Lucas, C. H., and Pitt, K. A. (2014). Population-level perspectives on global change: genetic and demographic analyses indicate various scales, timing, and causes of *scyphozoan* jellyfish blooms. *Biol. Invas.* 17, 851–867. doi: 10.1007/s10530-014-0732-z

DiBattista, J. D., Travers, M. J., Moore, G. I., Evans, R. D., Newman, S. J., Feng, M., et al. (2017). Seascape genomics reveals fine-scale patterns of dispersal for a reef fish along the ecologically divergent coast of Northwestern Australia. *Mol. Ecol.* 26, 6206–6223. doi: 10.1111/mec.14352

Dunn, D. C., Harrison, A. L., Curtice, C., DeLand, S., Donnelly, B., Fujioka, E., et al. (2019). The importance of migratory connectivity for global ocean policy. *Proc. Biol. Sci.* 286:20191472. doi: 10.1098/rspb.2019.1472

Dwyer, S. L., Pawley, M. D. M., Clement, D. M., and Stockin, K. A. (2020). Modelling habitat use suggests static spatial exclusion zones are a non-optimal management tool for a highly mobile marine mammal. *Mar. Biol.* 167:62. doi: 10.1007/s00227-020-3664-4

Excoffier, L., and Lischer, H. E. (2010). Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* 10, 564–567. doi: 10.1111/j.1755-0998.2010.02847.x

FAO (1995). *Code of Conduct for Responsible Fisheries.* Rome: Food and Agriculture Organization of the United Nations (FAO).

Filby, N. E., Bossley, M., Sanderson, K. J., Martinez, E., and Stockin, K. A. (2010). Distribution and population demographics of common dolphins (*Delphinus delphis*) in the Gulf St. Vincent, South Australia. *Aquat. Mamm.* 36, 33–45. doi: 10.1578/am.36.1.2010.33

Filby, N. E., Bossley, M., and Stockin, K. A. (2013). Behaviour of free-ranging short-beaked common dolphins (*Delphinus delphis*) in Gulf St Vincent, South Australia. *Aust. J. Zool.* 61, 291–300. doi: 10.1071/zo12033

Fisheries New Zealand (2020). *Aquatic Environment and Biodiversity Annual Review 2019–20.* Compiled by the Aquatic Environment Team, Fisheries Science and Information, Fisheries New Zealand, Wellington New Zealand, 765. Available online at: www.mpi.govt.nz/dmsdocument/40980-aquatic-environment-and-biodiversity-annual-review-201920

Flynn, A. J., Kloser, R. J., and Sutton, C. (2018). Micronekton assemblages and bioregional setting of the Great Australian Bight: a temperate northern boundary current system. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 157–158, 58–77. doi: 10.1016/j.dsr2.2018.08.006

Foll, M., and Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics* 180, 977–993. doi: 10.1534/genetics.108.092221

Foote, A. D., Vijay, N., Avila-Arcos, M. C., Baird, R. W., Durban, J. W., Fumagalli, M., et al. (2016). Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nat. Commun.* 7:11693. doi: 10.1038/ncomms11693

Frankham, R., Ballou, J. D., and Briscoe, D. A. (2010). *Introduction to Conservation Genetics*, 2nd ed. (Cambridge, UK; New York, NY: Cambridge University Press).

Fruet, P., Secchi, E. R., Daura-Jorge, F., Vermeulen, E., Flores, P. A. C., Simões-Lopes, P. C., et al. (2014). Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. *Conserv. Genet.* 15, 879–895. doi: 10.1007/s10592-014-0586-z)

Fullard, K. J., Early, G., Heide-Jorgensen, M. P., Bloch, D., Rosing-Asvid, S. A., and Amos, W. (2000). Population structure of long-finned pilot whales in the North Atlantic: a correlation with sea surface temperature? *Mol. Ecol.* 9, 949–958. doi: 10.1046/j.1365-294x.2000.00957.x

Funk, W. C., McKay, J. K., Hohenlohe, P. A., and Allendorf, F. W. (2012). Harnessing genomics for delineating conservation units. *Trends Ecol. Evol.* 27, 489–496. doi: 10.1016/j.tree.2012.05.012

Gardner, B., Hoban, S., and Luikart, G. (2020). IUCN Red List and the value of integrating genetics. *Conserv. Genet.* 21, 795–801. doi: 10.1007/s10592-020-01301-6

Gaspari, S., Holcer, D., Mackelworth, P., Fortuna, C., Frantzis, A., Genov, T., et al. (2015a). Population genetic structure of common bottlenose dolphins (*Tursiops truncatus*) in the Adriatic Sea and contiguous regions: implications for international conservation. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 25, 212–222. doi: 10.1002/aqc.2415

Gaspari, S., Scheinin, A., Holcer, D., Fortuna, C., Natali, C., Genov, T., et al. (2015b). Drivers of Population Structure of the Bottlenose Dolphin (*Tursiops truncatus*) in the Eastern Mediterranean Sea. *Evol. Biol.* 42, 177–190. doi: 10.1007/s11692-015-9309-8

Genov, T., Bearzi, G., Bonizzoni, S., and Tempesta, M. (2012). Long-distance movement of a lone short-beaked common dolphin *Delphinus delphis* in the central Mediterranean Sea. *Mar. Biodivers. Rec.* 5:E9. doi: 10.1017/S1755267211001163

Genov, T., Kotnjek, P., and Centrih, T. (2020). Occurrence of common dolphins (*Delphinus delphis*) in the Gulf of Trieste and the northern Adriatic Sea. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 1–7. doi: 10.1002/aqc.3407

Goldsworthy, S. D., Bailleul, F., NurseyBray, M., Mackay, A., Oxley, A., Reinhold, S.-L., et al. (2019a). *Assessment of the Impacts of Seal Populations on the Seafood Industry in South Australia.* Adelaide, SA: South Australian Research and Development Institute (Aquatic Sciences).

Goldsworthy, S. D., Ferguson, G. J., and Ward, T. M. (2019b). *Assessment of Dolphin Interactions, Effectiveness of Code of Practice and Fishing Behaviour in the South Australian Sardine Fishery: 2018-19.* Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences). F2010/000726-10. SARDI Research Report Series No. 1041, 36.

Grummer, J. A., Beheregaray, L. B., Bernatchez, L., Hand, B. K., Luikart, G., Narum, S. R., et al. (2019). Aquatic landscape genomics and environmental effects on genetic variation. *Trends Ecol. Evol.* 34, 641–654. doi: 10.1016/j.tree.2019.02.013

Hamer, D. J., Ward, T. M., and McGarvey, R. (2008). Measurement, management and mitigation of operational interactions between the South Australian Sardine Fishery and short-beaked common dolphins (*Delphinus delphis*). *Biol. Conserv.* 141, 2865–2878. doi: 10.1016/j.biocon.2008.08.024

Hamilton, S., and Baker, G. B. (2019). Technical mitigation to reduce marine mammal bycatch and entanglement in commercial fishing gear: lessons learnt and future directions. *Rev. Fish Biol.* 29, 223–247. doi: 10.1007/s11160-019-09550-6

Hanski, I. (1998). Metapopulation dynamics. *Nature* 396, 41–49. doi: 10.1038/23876

Heimeier, D., Alexander, A., Hamner, R. M., Pichler, F., and Baker, C. S. (2018). The influence of selection on MHC DQA and DQB haplotypes in the endemic New Zealand hector's and maui dolphins. *J. Hered.* 109, 744–756. doi: 10.1093/jhered/esy050

Hendricks, S., Anderson, E. C., Antao, T., Bernatchez, L., Forester, B. R., Garner, B., et al. (2018). Recent advances in conservation and population genomics data analysis. *Evol. Appl.* 11, 1197–1211. doi: 10.1111/eva.12659

Hoelzel, A. R. (1998). Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. *J. Hered.* 89, 451–458. doi: 10.1093/jhered/89.5.451

Hoelzel, A. R., Hey, J., Dahlheim, M. E., Nicholson, C., Burkanov, V., and Black, N. (2007). Evolution of population structure in a highly social top predator, the killer whale. *Mol. Biol. Evol.* 24, 1407–1415. doi: 10.1093/molbev/msm063

Holderegger, R., Schmidt, B. R., Grünig, C., Meier, R., Csencsics, D., Gassner, M., et al. (2020). Ready-to-use workflows for the implementation of genetic tools in conservation management. *Conserv. Genet. Resour.* 12, 691–700. doi: 10.1007/s12686-020-01165-5

Holland, L. P., Jenkins, T. L., and Stevens, J. R. (2017). Contrasting patterns of population structure and gene flow facilitate exploration of connectivity in two widely distributed temperate octocorals. *J. Hered.* 119, 35–48. doi: 10.1038/hdy.2017.14

Hupman, K. (2016). *Photo-identification and its application to gregarious delphinids: Common dolphins (Delphinus sp.) in the Hauraki Gulf, New Zealand* (Doctor of Philosophy). Massey University, Albany, New Zeland.

Hupman, K., Stockin, K. A., Pollock, K., Pawley, M. D. M., Dwyer, S. L., Lea, C., et al. (2018). Challenges of implementing Mark-recapture studies on poorly marked gregarious delphinids. *PLoS ONE* 13:e0198167. doi: 10.1371/journal.pone.0198167

Jasper, M., Schmidt, T. L., Ahmad, N. W., Sinkins, S. P., and Hoffmann, A. A. (2019). A genomic approach to inferring kinship reveals limited intergenerational dispersal in the yellow fever mosquito. *Mol. Ecol. Resour.* 19, 1254–1264. doi: 10.1111/1755-0998.13043

Jombart, T., and Ahmed, I. (2011). adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics* 27, 3070–3071. doi: 10.1093/bioinformatics/btr521

Jombart, T., and Collins, C. (2015). *A Tutorial for Discriminant Analysis of Principal Components (DAPC) Using Adegenet 2.0.0*. Available online at: adegenet.r-forge.r-project.org/files/tutorial-dapc.pdf

Kämpf, J. (2015). Phytoplankton blooms on the western shelf of Tasmania: evidence of a highly productive ecosystem. *Ocean Sci.* 11, 1–11. doi: 10.5194/os-11-1-2015

Kämpf, J., and Bell, D. (2014). "The murray/coorong estuary: meeting of the waters?," in *Estuaries of Australia in 2050 and Beyond,* ed E. Wolanski (Dordrecht; Heidelberg; New York, NY; London: Springer), 31–47.

Keane, J. P., and Neira, F. J. (2008). Larval fish assemblages along the south-eastern Australian shelf: linking mesoscale non-depth-discriminate structure and water masses. *Fish. Oceanogr.* 17, 263–280. doi: 10.1111/j.1365-2419.2008.00478.x

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., et al. (2012). Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28, 1647–1649. doi: 10.1093/bioinformatics/bts199

Kemper, C., Pemberton, D., Cawthorn, M., Heinrich, S., Mann, J., Würsig, B., et al. (2003). "Aquaculture and marine mammals: co-existence or conflict?," in *Marine Mammals: Fisheries, Tourism and Management Issues*, eds N. Gales, M. Hindell and R. Kirkwood (Melbourne, VIC: CSIRO Publishing),208–225.

Krutzen, M., Barre, L., Möller, L. M., Heithaus, M. R., Simms, C., and Sherwin, W. B. (2002). A Biopsy System for small ceteceans: darting success and wound healing in *Tursiops* spp. *Mar. Mamm. Sci.* 18, 863–878. doi: 10.1111/j.1748-7692.2002.tb01078.x

Krutzen, M., and Sherwin, W. B. (2004). Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: Bottlenose dolphins (Tursiops Sp.) in Shark Bay Western Australia. *Mar. Mamm. Sci.* 20, 28–47. doi: 10.1111/j.1748-7692.2004.tb01139.x

Lal, M. M., Southgate, P. C., Jerry, D. R., Bosserelle, C., and Zenger, K. R. (2017). Swept away: ocean currents and seascape features influence genetic structure across the 18,000 Km Indo-Pacific distribution of a marine invertebrate, the black-lip pearl oyster *Pinctada margaritifera*. *BMC Genomics* 18:66. doi: 10.1186/s12864-016-3410-y

Langmead, B., and Salzberg, S. L. (2012). Fast gapped-read alignment with Bowtie 2. *Nat. Methods* 9:357. doi: 10.1038/nmeth.1923

Leitwein, M., Duranton, M., Rougemont, Q., Gagnaire, P. A., and Bernatchez, L. (2020). Using haplotype information for conservation genomics. *Trends Ecol. Evol.* 35, 245–258. doi: 10.1016/j.tree.2019.10.012

Leslie, M. S., and Morin, P. A. (2016). Using genome-wide SNPs to detect structure in high-diversity and low-divergence populations of severely impacted Eastern Tropical Pacific Spinner (*Stenella longirostris*) and Pantropical Spotted Dolphins (*S. attenuata*). *Front. Mar. Sci.* 3:253. doi: 10.3389/fmars.2016.00253

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15, 237–240. doi: 10.1093/besa/15.3.237

Louis, M., Viricel, A., Lucas, T., Peltier, H., Alfonsi, E., Berrow, S., et al. (2014). Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. *Mol. Ecol.* 23, 857–874. doi: 10.1111/mec.12653

Luikart, G., England, P. R., Tallmon, D., Jordan, S., and Taberlet, P. (2003). The power and promise of population genomics: from genotyping to genome typing. *Nat. Rev. Genet.* 4, 981–994. doi: 10.1038/nrg1226

Lynch, T. P., Morello, E. B., Evans, K., Richardson, A. J., Rochester, W., Steinberg, C. R., et al. (2014). IMOS National Reference Stations: a continental-wide physical, chemical and biological coastal observing system. *PLoS ONE* 9:e113652. doi: 10.1371/journal.pone.0113652

MacArthur, R. H., and Wilson, E. O. (1967). *The Theory of Island Biogeography.* Princeton, NJ: Princeton University Press

Mackay, A. I., Goldsworthy, S. D., and Harrison, P. (2016). *Critical Knowledge Gaps: Estimating Potential Maximum Cumulative Anthropogenic Mortality Limits of Key Marine Mammal Species to Inform Management in the Small Pelagic Fishery Area*. Adelaide, SA: S.A.R.a.D.I.A. Sciences.

Manel, S., Loiseau, N., Andrello, M., Fietz, K., Goni, R., Forcada, A., et al. (2019). Long-distance benefits of marine reserves: myth or reality? *Trends. Ecol. Evol.* 34, 342–354. doi: 10.1016/j.tree.2019.01.002

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Res.* 27, 209–220.

Mason, S., Salgado Kent, C., Donnelly, D., Weir, J., and Bilgmann, K. (2016). Atypical residency of short-beaked common dolphins (*Delphinus delphis*) to a shallow, urbanized embayment in south-eastern Australia. *R. Soc. Open Sci.* 3:160478. doi: 10.1098/rsos.160478

Meirmans, P. G., and Van Tienderen, P. H. (2004). GENOTYPE and GENODIVE: two programs for the analysis of genetic diversity of asexual organisms. *Mol. Ecol. Not.* 4, 792–794. doi: 10.1111/j.1471-8286.2004.00770.x

Meissner, A. M., Christiansen, F., Martinez, E., Pawley, M. D., Orams, M. B., and Stockin, K. A. (2015). Behavioural effects of tourism on oceanic common dolphins, *Delphinus* sp., in New Zealand: the effects of Markov analysis variations and current tour operator compliance with regulations. *PLoS ONE* 10:e0116962. doi: 10.1371/journal.pone.0116962

Mendez, M., Rosenbaum, H. C., and Bordino, P. (2008). Conservation genetics of the franciscana dolphin in Northern Argentina: population structure, by-catch impacts, and management implications. *Conserv. Genet.* 9, 419–435. doi: 10.1007/s10592-007-9354-7

Meynier, L., Stockin, K. A., Bando, M. K. H., and Duignan, P. J. (2008). Stomach contents of common dolphin (*Delphinus* sp.) from New Zealand waters. *N. Z. J. Mar. Freshw. Res.* 42, 257–268. doi: 10.1080/00288330809509952

Mirimin, L., Westgate, A., Rogan, E., Rosel, P. E., Read, A., Coughlan, J., et al. (2009). Population structure of short-beaked common dolphins (*Delphinus delphis*) in the North Atlantic Ocean as revealed by mitochondrial and nuclear genetic markers. *Mar. Biol.* 156, 821–834. doi: 10.1007/s00227-008-1120-y

Möller, L., and Beheregaray, L. (2001). Coastal Bottlenose dolphins from Southeastern Australia are *Tursiops Aduncus* according to sequences of the mitochondrial DNA control region. *Mar. Mamm. Sci.* 17, 249–263. doi: 10.1111/j.1748-7692.2001.tb01269.x

Möller, L. M. (2011). Sociogenetic structure, kin associations and bonding in delphinids. *Mol. Ecol.* 21, 745–764. doi: 10.1111/j.1365-294X.2011.05405.x

Möller, L. M., and Beheregaray, L. B. (2004). Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Mol. Ecol.* 13, 1607–1612. doi: 10.1111/j.1365-294X.2004.02137.x

Möller, L. M., Beheregaray, L. B., Harcourt, R. G., and Krutzen, M. (2001). Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proc. Biol. Sci.* 268, 1941–1947. doi: 10.1098/rspb.2001.1756

Möller, L. M., Valdez, F. P., Allen, S., Bilgmann, K., Corrigan, S., and Beheregaray, L. B. (2011). Fine-scale genetic structure in short-beaked common dolphins (*Delphinus delphis*) along the East Australian Current. *Mar. Biol.* 158, 113–126. doi: 10.1007/s00227-010-1546-x

Möller, L. M., Wiszniewski, J., Allen, S., and Beheregaray, L. (2007). Habitat type promotes rapid and extremely localised genetic differentiation in dolphins. *Mar. Freshw. Res.* 58, 640–648. doi: 10.1071/MF06218

Moura, A. E., Natoli, A., Rogan, E., and Hoelzel, A. R. (2013). Atypical panmixia in a European dolphin species (*Delphinus delphis*): implications for the evolution of diversity across oceanic boundaries. *J. Evol. Biol.* 26, 63–75. doi: 10.1111/jeb.12032

MPI (2019). *Aquatic Environment and Biodiversity Annual Review 2018*. Wellington: Ministry for Primary Industries. Compiled by the Fisheries Science Team, Ministry for Primary Industries.

Natoli, A., Birkun, A., Aguilar, A., Lopez, A., and Hoelzel, A. R. (2005). Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proc. Biol. Sci.* 272, 1217–1226. doi: 10.1098/rspb.2005.3076

Natoli, A., Canadas, A., Peddemors, V. M., Aguilar, A., Vaquero, C., Fernandez-Piqueras, P., et al. (2006). Phylogeography and alpha taxonomy of the common dolphin (*Delphinus* sp.). *J. Evol. Biol.* 19, 943–954. doi: 10.1111/j.1420-9101.2005.01033.x

Natoli, A., Cañadas, A., Vaquero, C., Politi, E., Fernandez-Navarro, P., and Hoelzel, A. R. (2008). Conservation genetics of the short-beaked common dolphin (*Delphinus delphis*) in the Mediterranean Sea and in the eastern North Atlantic Ocean. *Conserv. Biol.* 9, 1479–1487. doi: 10.1007/s10592-007-9481-1

Neumann, D. R., and Orams, M. B. (2003). Feeding behaviours of short-beaked common dolphins, *Delphinus delphis*, in New Zealand. *Aquat. Mamm.* 29, 137–149. doi: 10.1578/016754203101023997

Nykanen, M., Dillane, E., Englund, A., Foote, A. D., Ingram, S. N., Louis, M., et al. (2018). Quantifying dispersal between marine protected areas by a highly mobile species, the bottlenose dolphin, *Tursiops truncatus*. *Ecol. Evol.* 8, 9241–9258. doi: 10.1002/ece3.4343

Oremus, M., Poole, M. D., and Baker, C. S. (2007). Isolation and interchange among insular spinner dolphin communities in the South Pacific revealed by individual identification and genetic diversity. *Mar. Ecol. Prog. Ser.* 336, 275–289. doi: 10.3354/meps336275

Paetkau, D., Slade, R., Burden, M., and Estoup, A. (2004). Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Mol. Ecol.* 13, 55–65. doi: 10.1046/j.1365-294X.2003.02008.x

Papa, Y., Oosting, T., Valenza-Troubat, N., Wellenreuther, M., and Ritchie, P. A. (2020). Genetic stock structure of New Zealand fish and the use of genomics in fisheries management: an overview and outlook. *N. Z. J. Zool.* 1–31. doi: 10.1080/03014223.2020.1788612

Parra, G. J., Bilgman, K., Peter, K. J., Möller, L. M. (in review). Abundance and potential biological removal of common dolphins subject to fishery-impacts in South Australian Waters. *Front. Mar. Sci.*

Parra, G. J., Cagnazzi, D., Jedensjö, M., Ackermann, C., Frere, C., Seddon, J., et al. (2018). Low genetic diversity, limited gene flow and widespread genetic bottleneck effects in a threatened dolphin species, the Australian humpback dolphin. *Biol. Conserv.* 220, 192–200. doi: 10.1016/j.biocon.2017.12.028

Patterson, H., Williams, A., Woodhams, J., and Curtotti, R. (2019). *Fishery Status Reports 2019*. Canberra, ACT: Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES).

Pawley, M. D. M., Hupman, K. E., Stockin, K. A., and Gilman, A. (2018). Examining the viability of dorsal fin pigmentation for individual identification of poorly-marked delphinids. *Sci. Rep.* 8:12593. doi: 10.1038/s41598-018-30842-7

Perry, G. L. W., and Lee, F. (2019). How does temporal variation in habitat connectivity influence metapopulation dynamics? *Oikos*. 128, 1277–1286. doi: 10.1111/oik.06052

Peters, K. J., Bury, S. J., Betty, E. L., Parra, G. J., Tezanos-Pinto, G., and Stockin, K. A. (2020). Foraging ecology of the common dolphin *Delphinus delphis* revealed by stable isotope analysis. *Mar Ecol Prog Ser* 652:173–86. doi: 10.3354/meps13482

Peters, K. J., and Stockin, K. A. (2021). Cetacean sighting records in the New Caledonia Basin, Tasman Sea, New Zealand. *N. Z. J. Mar. Freshw. Res.* 1–15. doi: 10.1080/00288330.2020.1867201

Peterson, B. K., Weber, J. N., Kay, E. H., Fisher, H. S., and Hoekstra, H. E. (2012). Double digest RADseq: an inexpensive method for *de novo* SNP discovery and genotyping in model and non-model species. *PLoS ONE* 7:e37135. doi: 10.1371/journal.pone.0037135

Pierre, J. (2019). *Associated Species Marine Mammals*. Ministry for Primary Industries and Department of Conservations. Available online at: openseas.org.nz/wp/content/uploads/2019/05/SDRMarineMammals2019.pdf

Piry, S., Alapetite, A., Cornuet, J. M., Paetkau, D., Baudouin, L., and Estoup, A. (2004). GENECLASS2: a software for genetic assignment and first-generation migrant detection. *J. Hered.* 95, 536–539. doi: 10.1093/jhered/esh074

Pitt, K. A., and Kingsford, M. J. (2000). Geographic separation of stocks of the edible jellyfish *Catostylus mosaicus* (Rhizostomeae) in New South Wales, Australia. *Mar. Ecol. Prog. Ser.* 196, 143–155. doi: 10.3354/meps196143

Pratt, E. A. L., Beheregaray, L. B., Bilgmann, K., Zanardo, N., Diaz-Aguirre, F., and Möller, L. M. (2018). Hierarchical metapopulation structure in a highly mobile marine predator: the southern Australian coastal bottlenose dolphin (*Tursiops* cf. *australis). Conserv. Genet.* 19, 637–654. doi: 10.1007/s10592-017-1043-6

Puritz, J. B., Hollenbeck, C. M., and Gold, J. R. (2014). dDocent: a RADseq, variant-calling pipeline designed for population genomics of non-model organisms. *PeerJ* 2:e431. doi: 10.7717/peerj.431

Quérouil, S., Silva, M. A., Freitas, L., Prieto, R., Magalhães, S., Dinis, A., et al. (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conserv. Genet.* 8, 1405–1419. doi: 10.1007/s10592-007-9291-5

R Development Core Team (2018). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Rajora, O. P. (2019). *Population Genomics. Concepts, Approaches and Applications*. Cham: Springer.

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., and Suchard, M. A. (2018). Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. *Syst. Biol.* 67, 901–904. doi: 10.1093/sysbio/syy032

Rannala, B., and Mountain, J. (1997). Detecting immigration by using multilocus genotypes. *Proc. Natl. Acad. Sci. U.S.A.* 94, 9197–9201.

Riginos, C., Crandall, E. D., Liggins, L., Bongaerts, P., and Treml, E. A. (2016). Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. *Curr. Zool.* 62, 581–601. doi: 10.1093/cz/zow067

Riginos, C., Hock, K., Matias, A. M., Mumby, P. J., Oppen, M. J. H., and Lukoschek, V. (2019). Asymmetric dispersal is a critical element of concordance between biophysical dispersal models and spatial genetic structure in Great Barrier Reef corals. *Divers. Distrib.* 25, 1684–1696. doi: 10.1111/ddi.12969

Rosel, P. E., Taylor, B. L., Hancock-Hanser, B. L., Morin, P. A., Archer, F. I., Lang, A. R., et al. (2017). A review of molecular genetic markers and analytical approaches that have been used for delimiting marine mammal subspecies and species. *Mar. Mamm. Sci.* 33, 56–75. doi: 10.1111/mms.12412

Ross, P. M., Hogg, I. D., Pilditch, C. A., and Lundquist, C. J. (2009). Phylogeography of New Zealand's coastal benthos. *N. Z. J. Mar. Freshw. Res.* 43, 1009–1027. doi: 10.1080/00288330.2009.9626525

Rowe, S. J. (2007). *A Review of Methodologies for Mitigating Incidental Catch of Protected Marine Mammals*. Wellington: Science and Technical Publishing Department of Conservation.

Sandoval-Castillo, J., Robinson, N. A., Hart, A. M., Strain, L. W. S., and Beheregaray, L. B. (2018). Seascape genomics reveals adaptive divergence in a connected and commercially important mollusc, the greenlip abalone (*Haliotis laevigata*), along a longitudinal environmental gradient. *Mol. Ecol.* 27, 1603–1620. doi: 10.1111/mec.14526

Selkoe, K. A., D'Aloia, C. C., Crandall, E. D., Iacchei, M., Liggins, L., Puritz, J. B., et al. (2016). A decade of seascape genetics: contributions to basic and applied marine connectivity. *Mar. Ecol. Prog. Ser.* 554, 1–19. doi: 10.3354/meps11792

Shafer, A. B., Wolf, J. B., Alves, P. C., Bergstrom, L., Bruford, M. W., Brannstrom, I., et al. (2015). Genomics and the challenging translation into conservation practice. *Trends Ecol. Evol.* 30, 78–87. doi: 10.1016/j.tree.2014.11.009

Sousa, A., Alves, F., Dinis, A., Bentz, J., Cruz, M. J., and Nunes, J. P. (2019). How vulnerable are cetaceans to climate change? Developing and testing a new index. *Ecol. Indic.* 98, 9–18. doi: 10.1016/j.ecolind.2018.10.046

Stockin, K. A., Amaral, A. R., Latimer, J., Lambert, D. M., and Natoli, A. (2014). Population genetic structure and taxonomy of the common dolphin (*Delphinus* sp.) at its southernmost range limit: New Zealand waters. *Mar. Mamm. Sci.* 30, 44–63. doi: 10.1111/mms.12027

Stockin, K. A., Binedell, V., Wiseman, N., Brunton, D. H., and Orams, M. B. (2009a). Behavior of free-ranging common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. *Mar. Mamm. Sci.* 25, 283–301. doi: 10.1111/j.1748-7692.2008.00262.x

Stockin, K. A., Duignan, P. J., Alley, M., Roe, W. D., Meynier, L., and Fettermann, T. (2009b). Causes of mortality in stranded Common Dolphin (*Delphinus* sp.) from New Zealand waters between 1998 and 2008. *Pac. Conserv. Biol.* 15, 217–227. doi: 10.1071/PC090217

Stockin, K. A., Pierce, G. J., Binedell, V., Wiseman, N., and Orams, M. B. (2008). Factors Affecting the Occurrence and Demographics of Common Dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. *Aquat. Mamm.* 34, 200–211. doi: 10.1578/am.34.2.2008.200

Sunnucks, P., and Hales, D. F. (1996). Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the Genus *Sitobion* (Hemiptera: Aphididae). *Mol. Biol. Evol.* 13, 510–524.

Suthers, I. M., Young, J. W., Baird, M. E., Roughan, M., Everett, J. D., Brassington, G. B., et al. (2011). The strengthening East Australian Current, its eddies and biological effects — an introduction and overview. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 58, 538–546. doi: 10.1016/j.dsr2.2010.09.029

Taft, H. R., McCoskey, D. N., Miller, J. M., Pearson, S. K., Coleman, M. A., Fletcher, N. K., et al. (2020). Research–management partnerships: an opportunity to integrate genetics in conservation actions. *Conserv. Sci. Pract.* 2:e218. doi: 10.1111/csp2.218

Taylor, B. L., Archer, F. I., Martien, K. K., Rosel, P. E., Hancock-Hanser, B. L., Lang, A. R., et al. (2017). Guidelines and quantitative standards to improve consistency in cetacean subspecies and species delimitation relying on molecular genetic data. *Mar. Mamm. Sci.* 33, 132–155. doi: 10.1111/mms.12411

Taylor, B. L., Chivers, S. J., Larese, J., and Perrin, W. F. (2007). *Generation Length and Percent Mature Estimates for IUCN Assessments of Cetaceans*. La Jolla, CA: Southwest Fisheries Science Center; Southwest Fisheries Science Center Administrative Report, 24.

Teske, P. R., Golla, T. R., Sandoval-Castillo, J., Emami-Khoyi, A., van der Lingen, C. D., von der Heyden, S., et al. (2018). Mitochondrial DNA is unsuitable to test for isolation by distance. *Sci. Rep.* 8:8448. doi: 10.1038/s41598-018-25138-9

Teske, P. R., Sandoval-Castillo, J., van Sebille, E., Waters, J., and Beheregaray, L. B. (2015). On-shelf larval retention limits population connectivity in a coastal broadcast spawner. *Mar. Ecol. Prog. Ser.* 532, 1–12. doi: 10.3354/meps11362

Teske, P. R., Sandoval-Castillo, J., Waters, J., and Beheregaray, L. B. (2017). An overview of Australia's temperate marine phylogeography, with new evidence from high-dispersal gastropods. *J. Biogeogr.* 44, 217–229. doi: 10.1111/jbi.12783

Tezanos-Pinto, G., Baker, C. S., Russell, K., Martien, K., Baird, R. W., Hutt, A., et al. (2009). A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. *J. Hered.* 100, 11–24. doi: 10.1093/jhered/esn039

Thompson, F. N., Abraham, E. R., and Berkenbusch, K. (2013). Common dolphin (*Delphinus delphis*) bycatch in New Zealand commercial trawl fisheries. *PLoS ONE* 8:e64438. doi: 10.1371/journal.pone.0064438

Tulloch, V., Pirotta, V., Grech, A., Crocetti, S., Double, M., How, J., et al. (2020). Long-term trends and a risk analysis of cetacean entanglements and bycatch in fisheries gear in Australian waters. *Biodivers. Conserv.* 29, 251–282. doi: 10.1007/s10531-019-01881-x

Wang, J. (2007). Triadic IBD coefficients and applications to estimating pairwise relatedness. *Genet. Res.* 89, 135–153. doi: 10.1017/S0016672307008798

Wang, J. (2011). COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Mol. Ecol. Resour.* 11, 141–145. doi: 10.1111/j.1755-0998.2010.02885.x

Waples, R. S., and Gaggiotti, O. (2006). What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Mol. Ecol.* 15, 1419–1439. doi: 10.1111/j.1365-294X.2006.02890.x

Ward, T. M., and Grammer, G. L. (2018). *Commonwealth Small Pelagic Fishery: Fishery Assessment Report 2017*. Report to the Australian Fisheries Management Authority. South Australian Research and Development Institute (Aquatic Sciences). SARDI Publication No. F2010/000270-9. SARDI Research Report Series No. 982, 114.

Ward, T. M., Smart, J., and Ivey, A. (2017). *Stock assessment of Australian Sardine (Sardinops sagax) Off South Australia 2017*. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences). SARDI Publication No. F2007/000765-6. SARDI Research Report Series No. 971, 107.

Waters, J. M. (2008). Marine biogeographical disjunction in temperate Australia: historical landbridge, contemporary currents, or both? *Divers. Distrib.* 14, 692–700. doi: 10.1111/j.1472-4642.2008.00481.x

Waters, J. M., Emerson, B. C., Arribas, P., and McCulloch, G. A. (2020). Dispersal reduction: causes, genomic mechanisms, and evolutionary consequences. *Trends Ecol. Evol.* 35, 512–522. doi: 10.1016/j.tree.2020.01.012

Waters, J. M., Wernberg, T., Connell, S. D., Thomsen, M. S., Zuccarello, G. C., Kraft, G. T., et al. (2010). Australia's marine biogeography revisited: back to the future? *Austral Ecol.* 35, 988–992. doi: 10.1111/j.1442-9993.2010.02114.x

Weir, B. S., and Cockerham, C. C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution* 38, 1358–1370

Whitehead, H., McGill, B., and Worm, B. (2008). Diversity of deep-water cetaceans in relation to temperature: implications for ocean warming. *Ecol. Lett.* 11, 1198–1207. doi: 10.1111/j.1461-0248.2008.01234.x

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. New York, NY: Springer-Verlag.

Wilson, G. A., and Rannala, B. (2003). Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* 163, 1177–1191.

Wiszniewski, J., Beheregaray, L. B., Allen, S. J., and Möller, L. M. (2009). Environmental and social influences on the genetic structure of bottlenose dolphins (*Tursiops aduncus*) in Southeastern Australia. *Conserv. Genet.* 11, 1405–1419. doi: 10.1007/s10592-009-9968-z

Xuereb, A., Benestan, L., Normandeau, E., Daigle, R. M., Curtis, J. M. R., Bernatchez, L., et al. (2018). Asymmetric oceanographic processes mediate connectivity and population genetic structure, as revealed by RADseq, in a highly dispersive marine invertebrate (*Parastichopus californicus*). *Mol. Ecol.* 27, 2347–2364. doi: 10.1111/mec.14589

York, K. L., Blacket, M. J., and Appleton, B. R. (2008). The Bassian Isthmus and the major ocean currents of southeast Australia influence the phylogeography and population structure of a southern Australian intertidal barnacle *Catomerus polymerus* (Darwin). *Mol. Ecol.* 17, 1948–1961. doi: 10.1111/j.1365-294X.2008.03735.x

Zanardo, N., Bilgmann, K., Parra, G. J., and Möller, L. M. (2016). Socio-genetic structure of short-beaked common dolphins in southern Australia. *J. Zool.* 299, 89–97. doi: 10.1111/jzo.12330

Zanardo, N., Parra, G. J., Passadore, C., and Möller, L. M. (2017). Ensemble modelling of southern Australian bottlenose dolphin *Tursiops* sp. distribution reveals important habitats and their potential ecological function. *Mar. Ecol. Prog. Ser.* 569, 253–266. doi: 10.3354/meps12091

Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

APPENDIX B. ADDITIONAL INFORMATION FOR CHAPTER 2

SNP filtering

The resulted variant calling file (VCF) with sequence variation across all samples (raw SNP catalogue) was then filtered using VCFtools (Danecek et al., 2011) to remove SNPs that are likely to be the result of sequencing errors, paralogs, multi-copy loci, and/or artefacts of library preparation (Table B.1).

First, SNPs that were bi-allelic, genotyped in 80% of the individuals, with base quality ≥30 and minor allele frequency >0.03 were retained. In addition, individuals with more than 20% missing data were removed. Next, the allelic balance filter removed SNPs that deviated largely from the expected equal number of reads in each allele. Subsequently, loci with genotypic frequencies not consistent with Hardy-Weinberg equilibrium expectations ($p < 0.05$) were also removed. A linkage disequilibrium (LD) filter was implemented to improve the likelihood that the remaining SNPs in the dataset represented independent markers. This was done by using VCFtools (Danecek et al., 2011) to calculate the LD (r^2) for each pair of SNPs. After this, LD exponential decay was estimated using a spline that fitted the data. Using Tukey's criteria for anomalies (the 95% probability distribution; Tukey, 1949), we determined the genetic distance at which LD decay was no longer significant. Finally, we selected only one SNP within that distance (i.e. 330 base pairs, Figure B.1). Obtaining a final average missing data per sample and per locus of 1.3% and 1.2% respectively. These allowed us to generate a joint, unbiased, high-resolution SNP dataset for all Australian and New Zealand common dolphins.

Table B.1. Filtering steps and number of SNPs retained after each step in the double digest restriction-site associated DNA study of common dolphins (*Delphinus delphis*) in the Australasian region. AUS: Australia; NZ: New Zealand; SABD: southern Australian bottlenose dolphin; FDR: false discovery rate.

Filtering Step	**SNP count AUS/NZ**
Raw SNP catalogue	339,932
Genotyped in 80% of individuals, base quality ≥ 30, minor allele frequency >0.03 and bi-allelic.	33,467
Split multiple nucleotide polymorphisms into SNPs	33,010
Read depth ≤ mean depth + (2 x standard deviation)	32,031
Read quality (ratio quality/coverage depth > 0.2)	31,160
Allele balance > 20% and < 80%	31,020
Hardy–Weinberg equilibrium in > 80% localities	29,224
Present in 75% of individuals and in each putative populations	26,431
Alignment against SABD, *Tursiops aduncus* genome (Batley et al. unpublished)	26,199 (99% alignment)
Exclude all SNPs but one within 330bp	17,875
Exclude outliers (FDR = 10%) to retain only putatively neutral loci	14,799
Average depth coverage per locus and per individual	21.446

Table B.2. Estimates of contemporary migration rates (m) between and within identified regional populations and subpopulations of common dolphins (*Delphinus delphis*) in the Australasian region. Within-population rates are showed in italic. Migration rates between populations and sub-populations greater than 0.05 are in bold. 95% confidence intervals are showed in brackets. **Direction of migration is from columns to rows. (A)** Migration rates between regional populations: Southern coast of Australia, Eastern coast of Australia and New Zealand/Tasmania. **(B)** Migration rates between local populations: Southern coast of Australia (SC), Eastern coast of Australia (EC), Tasmania (TAS) and New Zealand (NZ). Gulf St Vincent, Southern coast of Australia (GSVSCA); Continental shelf localities, Southern coast of Australia (CSlSCA); Northern localities, East coast of Australia (NlECA); Southern localities, East coast of Australia (SlECA); West coast, New Zealand and Tasmania (WCNZ/TAS); East coast, New Zealand (ECNZ).

(A)

Population	**Southern coast of Australia**	**Eastern coast of Australia**	**New Zealand and Tasmania**
Southern coast of Australia	*0.9862* *(0.977-0.995)*	0.007 (0-0.014)	0.0061 (0-0.012)
Eastern coast of Australia	0.0098 (0-0.023)	*0.9314* *(0.900-0.963)*	**0.0588** (0.029-0.089)
New Zealand and Tasmania	0.0396 (0.025-0.054)	0.0380 (0.023-0.053)	*0.9225* *(0.903-0.942)*

(B)

Subpopulations	**CSlSCA**	**GSVSCA**	**SlECA**	**NlECA**	**WCNZ/TAS**	**ECNZ**
CSlSCA	*0.9705 (0.957-0.984)*	0.0104 (0.002-0.019)	0.0017 (0-0.005)	0.0087 (0.001-0.016)	0.0067 (0-0.013)	0.0019 (0-0.006)
GSVSCA	**0.1109** (0.054-0.168)	*0.8498 (0.790-0.909)*	0.0099 (0-0.029)	0.0098 (0-0.028)	0.0098 (0-0.028)	0.0098 (0-0.028)
SlECA	0.0118 (0-0.034)	0.0118 (0-0.034)	*0.9289 (0.879-979)*	0.0235 (0-0.055)	0.0119 (0-0.034)	0.0120 (0-0.035)
NlECA	0.0136 (0-0.032)	0.0068 (0-0.020)	0.0329 (0.005-0.061)	*0.9126 (0.871-0.954)*	0.0272 (0.002-0.052)	0.0068 (0-0.020)
WCNZ/TAS	0.0422 (0.021-0.064)	0.0061 (0-0.014)	0.0030 (0-0.009)	**0.0638** (0.039-0.088)	*0.6961 (0.676-0.716)*	**0.1888** (0.155-0.222)
ECNZ	0.0067 (0-0.016)	0.0033 (0-0.010)	0.0033 (0-0.010)	0.0033 (0-0.010)	**0.0648** (0.038-0.091)	*0.9186 (0.890-0.947)*

Table B.3. Number and most likely origin of first-generation migrants identified at a metapopulation level from each regional population of common dolphins (*Delphinus delphis*) in the Australasian region.

Population	**Southern coast of Australia**	**Eastern coast of Australia**	**New Zealand and Tasmania**
Number of individuals assigned to another population	4 (Eastern coast of Australia) 1 (New Zealand and Tasmania)	2 (New Zealand and Tasmania)	3 (Southern coast of Australia) 4 (Eastern coast of Australia)

Table B.4. Measures of genetic diversity at the mitochondrial DNA control region for Australasian common dolphins (*Delphinus delphis*) by locality, including number of samples (N), haplotype diversity (*h*), nucleotide diversity (π), and number of haplotypes (NH) (some haplotypes are shared between localities). *Acronyms used as in Figure 2.1.

Population	**Locality**	**N**	**h**	**π**	**NH**
SC	WSC	34	0.809	0.015	22
	GBSC	13	0.910	0.017	3
	SGSC	32	0.925	0.018	17
	GSVSC	26	0.932	0.018	3
	ESC	31	0.907	0.024	14
	WPSC	18	0.667	0.008	15
EC	NECA	14	0.494	0.007	7
	CECA	29	0.5665	0.006	2
	SECA	20	0.963	0.017	11
TASNZ	TAS	37	0.989	0.017	20
	CS	20	1.000	0.020	5
	WNI	38	0.990	0.018	30
	NENI	75	0.991	0.019	30
	ENI	5	0.900	0.016	1
	CI	1	NA	NA	1
	ESI	1	NA	NA	1
Total average		**28.000**	**0.860**	**0.016**	**12.857**
Total S.D.		**16.719**	**0.166**	**0.005**	**9.991**

Table B.5. Management zones used by each fishery that have recorded mortalities of common dolphins (*Delphinus delphis*) in the Australasian region, compared to the population genomic structure disclosed in the study.

	Type of Fishery	**Source**	**No. of fisheries management zones in the common dolphins' habitat and region**	**Objective of the management zones**	**Fishery implementations for mitigation of common dolphins' interactions**	**Does the management zones correspond to the genomic population structure?**
Australia	Small Pelagic Fisheries (SPF)	AFMA (AFMA, 2019b)	2 - Australian waters.	Management zones used in the by-catch work plan 2016, and Small pelagic fishery strategy report 2019.	Risk assessments, code of practices, some modification of fishing gear, a minimum 10% of independent observed coverage, and a trigger limit to cease or exclude from the fisheries for 6 months if 6 or more dolphin interactions occur.	No -The two management zones do not correspond to the dolphin population structure disclosed in Figure 2.2.
	Eastern tuna and Billfish Fishery (ETBF)	AFMA (Patterson et al., 2019)	1 - Eastern Australian waters.	Management zone reported by ETBF based on their fish stocks.	Risk assessments, code of practices, some fishing gear modification, a minimum 10% of independent observed coverage.	No -The management zone do not correspond to the dolphin population structure disclosed in Figure 2.2.
	Southern and Eastern Scalefish and Shark Fishery (SESSF)	AFMA (Patterson et al., 2019)	4 - Australian waters.	Management zones reported by SSESF based on their fish stocks.	Risk assessments, code of practices, some fishing gear modification, and a minimum 10% of independent observed coverage and a trigger limit of cease or exclusion from the fisheries for 6 months, with 6 or	No -The four management zones, which are in accordance to the sectors that operate in the region (Commonwealth Trawl and Scalefish Hook Sector, East Coast Deepwater trawl Sector, Great Australian Bight trawl sector and Shark Gillnet and Shark Hook), do not correspond to the

					more dolphin interactions. Closure of some areas.	dolphin population structure disclosed in Figure 2.2.
	Gillnet Hook and Trap Fishery (GHAT), a sector of SESFF	AFMA (AFMA, 2019a)	2-South Australian waters.	Management zones used in the Gillnet dolphin mitigation strategy report 2019.	Risk assessments, code of practices, some fishing gear modification, a minimum 10% of independent observed coverage, and a trigger limit to cease or exclude from the fisheries for 6 months if 6 or more dolphin interactions occur.	No -The two management zones do not correspond to the dolphin population structure disclosed in Figure 2.2.
	Sardine Fisheries (SASF)	PIRSA, SARDI (Goldsworthy et al., 2019b)	2-South Australian waters.	Management zones reported by SASF based on their fish stocks.	Annual risk assessments, code of practices, some fishing gear modification, and a minimum 10% of independent observed coverage.	No - The two management zones do not correspond to the dolphin population structure disclosed in Figure 2.2.
New Zealand	Trawl Fisheries	MPI (Abraham and Thompson, 2015c)	9-New Zealand waters.	Management zones reported by MPI based on their fish stocks.	Risk assessments, code of practices, some fishing gear modification, and a variable observed coverage.	No - The nine management zones do not correspond to the dolphin population structure disclosed in Figure 2.2.
	Set net	MPI (Abraham and Thompson, 2015a)	9-New Zealand waters.	Management zones reported by MPI based on their fish stocks.	Risk assessments, code of practices, some fishing gear modification, and a variable observed coverage.	No - The nine management zones do not correspond to the dolphin population structure disclosed in Figure 2.2.
	Surface long-line	MPI (Abraham and Thompson, 2015b)	9-New Zealand waters.	Management zones reported by MPI based on their fish stocks.	Risk assessments, code of practices, some fishing gear modification, and a variable observed coverage.	No - The nine management zones do not correspond to the dolphin population structure disclosed in Figure 2.2.

Table B.6. Pairwise F_{ST} values based on 14,799 SNPs dataset between different sampling sites of Australasian common dolphins (*D. delphis*). Lower left p-values and upper right significance of the p-values, ***0.0001, **0.001, *0.05. Acronyms used as in Figure 2.1.

	WSC	**GBSC**	**SGSC**	**GSVSC**	**ESC**	**WPSC**	**NECA**	**CECA**	**SECA**	**TAS**	**CS**	**WNI**	**NEI**	**ENI**
WSC	0	***	***	***	***	***	***	***	***	***	***	***	***	***
GBSC	0.015	0	***	***	***	***	***	***	***	***	***	***	***	***
SGSC	0.017	0.007	0	***	***	***	***	***	***	***	***	***	***	***
GSVSC	0.042	0.033	0.019	0	***	***	***	***	***	***	***	***	***	***
ESC	0.014	0.005	0.003	0.024	0	***	***	***	***	***	***	***	***	***
WPSC	0.036	0.026	0.025	0.047	0.020	0	***	***	***	***	***	***	***	***
NECA	0.193	0.180	0.189	0.213	0.178	0.157	0	***	***	***	***	***	***	***
CECA	0.138	0.124	0.133	0.154	0.127	0.103	0.032	0	***	***	***	***	***	***
SECA	0.092	0.079	0.087	0.110	0.079	0.060	0.061	0.018	0	***	***	***	***	***
TAS	0.073	0.062	0.070	0.095	0.063	0.047	0.095	0.050	0.018	0	***	***	***	***
CS	0.070	0.058	0.068	0.095	0.060	0.048	0.116	0.070	0.033	0.003	0	-	***	**
WNI	0.067	0.056	0.064	0.090	0.057	0.045	0.116	0.070	0.033	0.004	0.000	0	***	***
NEI	0.094	0.083	0.093	0.118	0.085	0.069	0.124	0.079	0.044	0.007	0.004	0.006	0	**
ENI	0.109	0.095	0.108	0.142	0.095	0.078	0.142	0.086	0.048	0.011	0.007	0.009	0.006	0

Table B.7. Pairwise Φ_{ST} values based on mtDNA CR dataset between different sampling sites of Australasian common dolphins (*D. delphis*). Lower left p-values and upper right significance of the p-values, ***0.0001, **0.001, *0.05. Acronyms used as in Figure 2.1.

	WSC	**GBSC**	**SGSC**	**GSVSC**	**ESC**	**WPSC**	**NECA**	**CECA**	**SECA**	**TAS**	**CS**	**WNI**	**NENI**	**ENI**
WSC	0	*	***	*	***	***	***	***	*	***	***	***	***	*
GBSC	0.134	0	-	-	*	***	***	***	*	***	***	**	***	-
SGSC	0.128	0.057	0	*	-	***	***	***	-	*	*	***	***	-
GSVSC	0.069	0.045	0.063	0	*	***	***	***	*	***	*	***	***	-
ESC	0.138	0.112	0.045	0.079	0	***	***	***	*	*	-	**	***	-
WPSC	0.228	0.381	0.246	0.202	0.203	0	***	*	***	***	***	***	***	-
NECA	0.503	0.489	0.400	0.410	0.269	0.620	0	***	***	***	***	***	***	*
CECA	0.344	0.464	0.311	0.278	0.244	0.134	0.619	0	***	***	**	***	***	-
SECA	0.132	0.114	0.029	0.058	0.070	0.171	0.425	0.224	0	-	-	*	-	-
TAS	0.172	0.142	0.058	0.080	0.071	0.150	0.362	0.167	0.001	0	-	-	-	-

CS	0.152	0.130	0.050	0.069	0.036	0.151	0.309	0.186	0.011	0.003	0	-	-	-
WNI	0.187	0.132	0.065	0.084	0.074	0.178	0.312	0.202	0.037	0.012	0.001	0	-	-
NENI	0.152	0.129	0.059	0.064	0.064	0.138	0.316	0.152	0.015	0.000	0.004	0.010	0	-
ENI	0.230	0.164	0.107	0.070	0.088	0.230	0.558	0.292	0.018	0.003	0.000	0.038	0.013	0

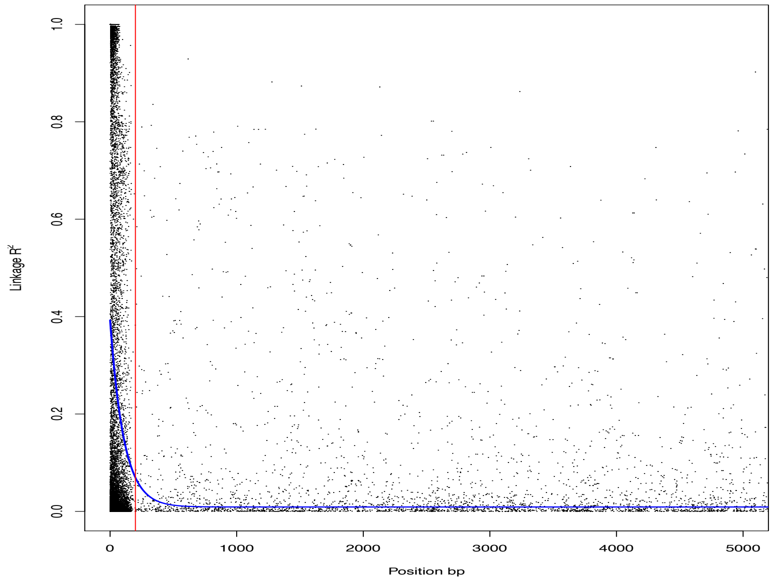


Figure B.1. Linkage disequilibrium (LD)-decay (R^2) for each pair of SNPs from Australasian common dolphins (*Delphinus delphis*), and their corresponding genetic distance.

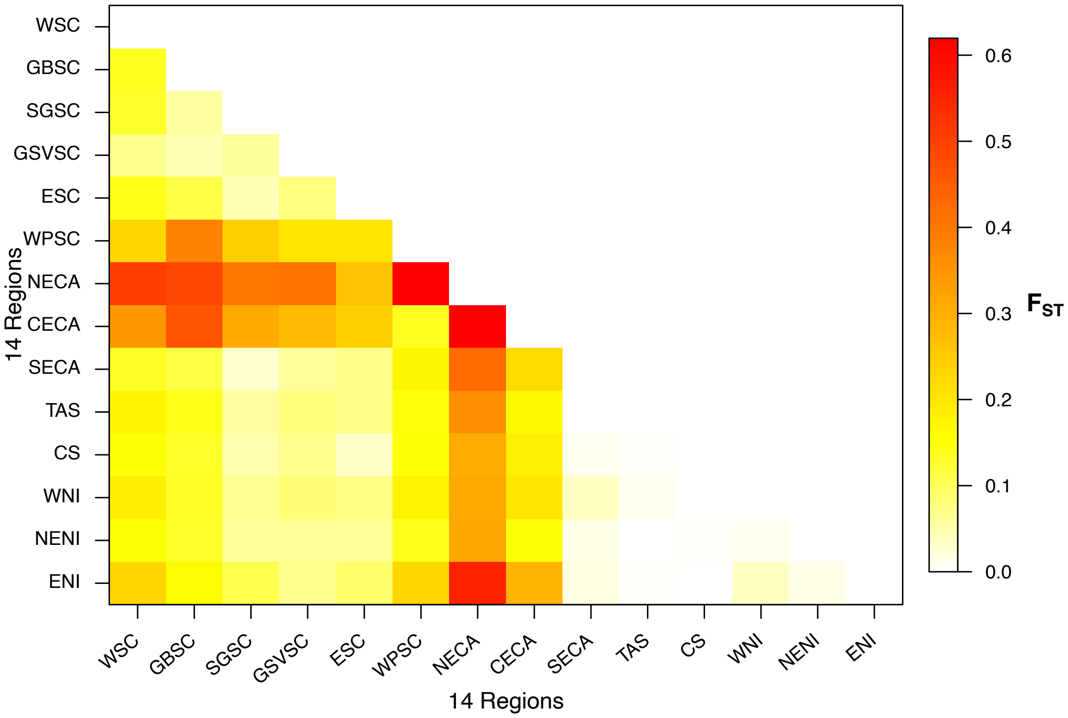


Figure B.2. Heatmap of pairwise F_{ST} values based on mtDNA CR dataset between different sampling sites of Australasian common dolphins (*Delphinus delphis*). *Acronyms used as in Figure 2.1.

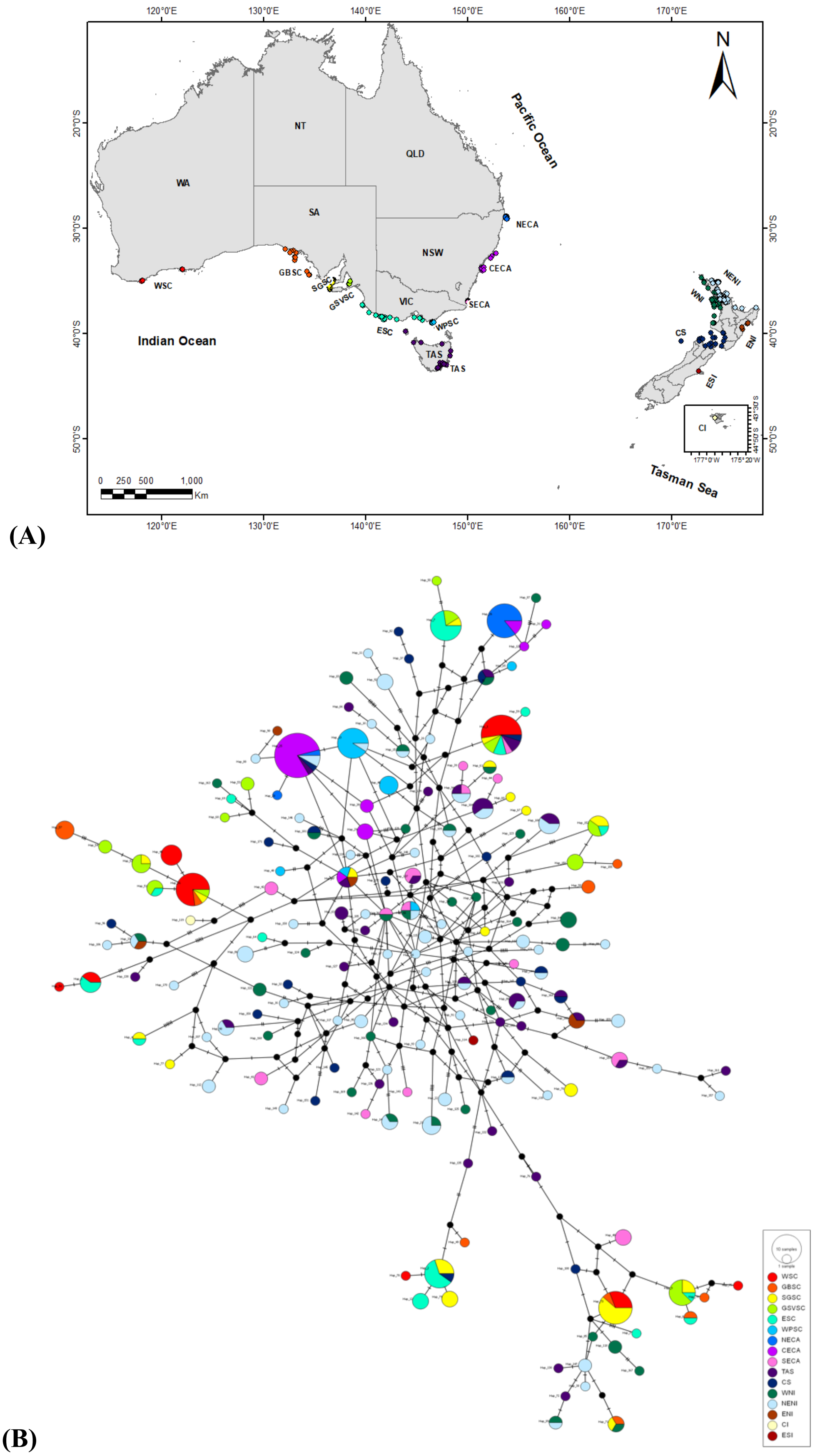
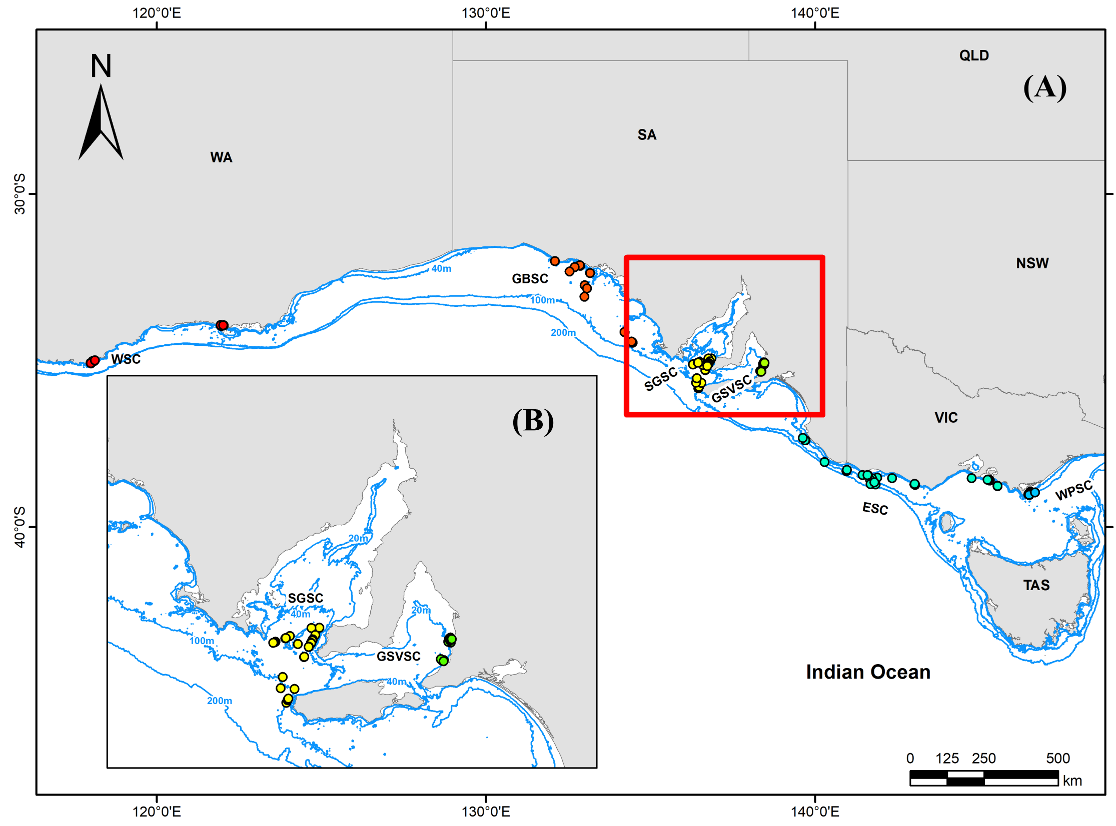


Figure B.3. Haplotype network of the mitochondrial DNA control region sequences of Australasian common dolphins (*Delphinus delphis*) showing (**A**) location of samples used in the map and (**B**) phylogenetic relationships among haplotypes across the 16 regions. Circles represent the observed haplotypes, with the size of the circle proportional to the number of individuals bearing a haplotype. Small circles in black represent haplotypes that were not observed (i.e. either not sampled or extinct). Each line between haplotypes indicates one mutational change. *Acronyms used as in Figure 2.1.



* West, Southern coast of Australia (WSC); Great Australian Bight, Southern coast of Australia (GBSC); Spencer Gulf, Southern coast of Australia (SGSC); Gulf St Vincent, Southern coast of Australia (GSVSC); East, Southern coast of Australia (ESC); Wilson Promontory, Southern coast of Australia (WPSC).

Figure B.4. Geolocations of the regional population of the southern coast of Australia used for the genomic analyses, compared to 20m, 50m, 100m and 200m isobaths. (**A**) Five localities* in the southern coast of Australia regional population. (**B**) Localities of Spencer Gulf (SGSCA) and the Gulf St Vincent (GSVSCA).

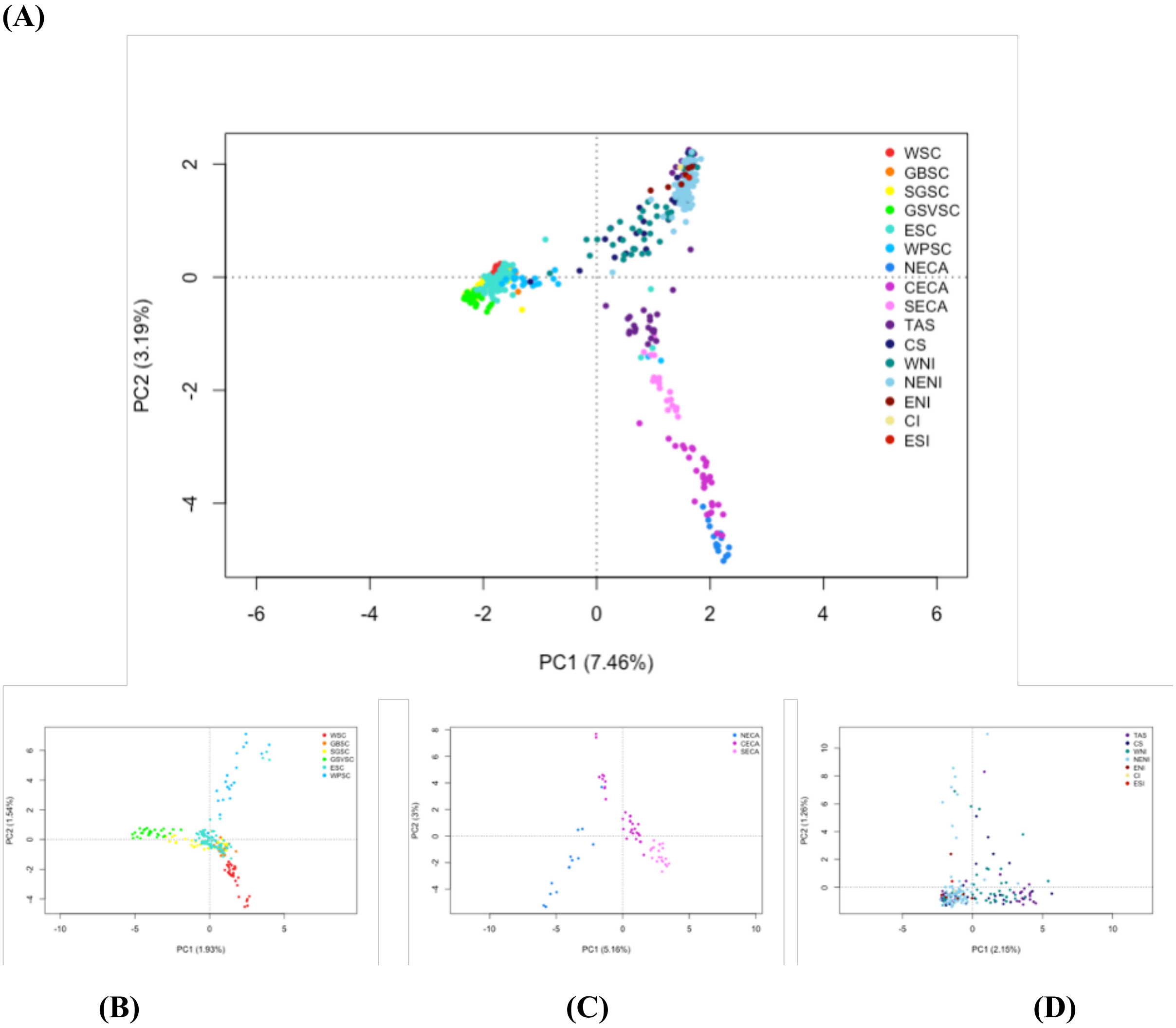


Figure B.5. Population genomic structure analysis using Principal Component Analysis (PCA), based on 14,799 SNPs for Australasian common dolphins (*Delphinus delphis*) (labelled by locality *) at metapopulation level and regional populations: **(A)** Australia and New Zealand; **(B)** Southern coast of Australia; **(C)** Eastern coast of Australia; and **(D)** New Zealand and Tasmania. *Acronyms used as in Figure 2.1.

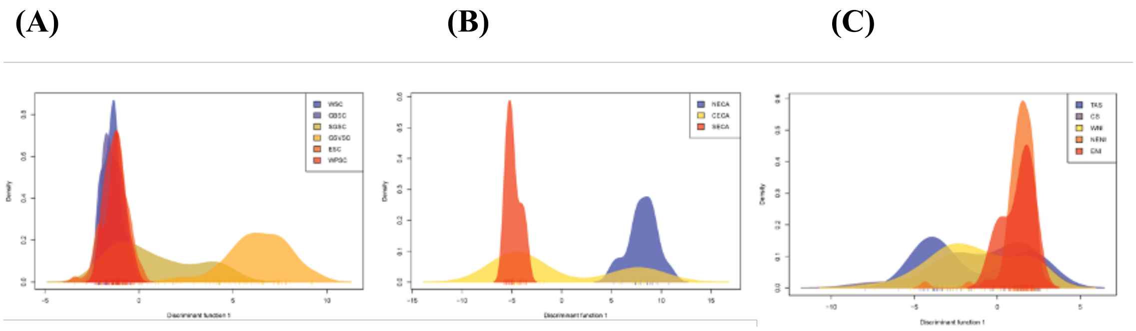
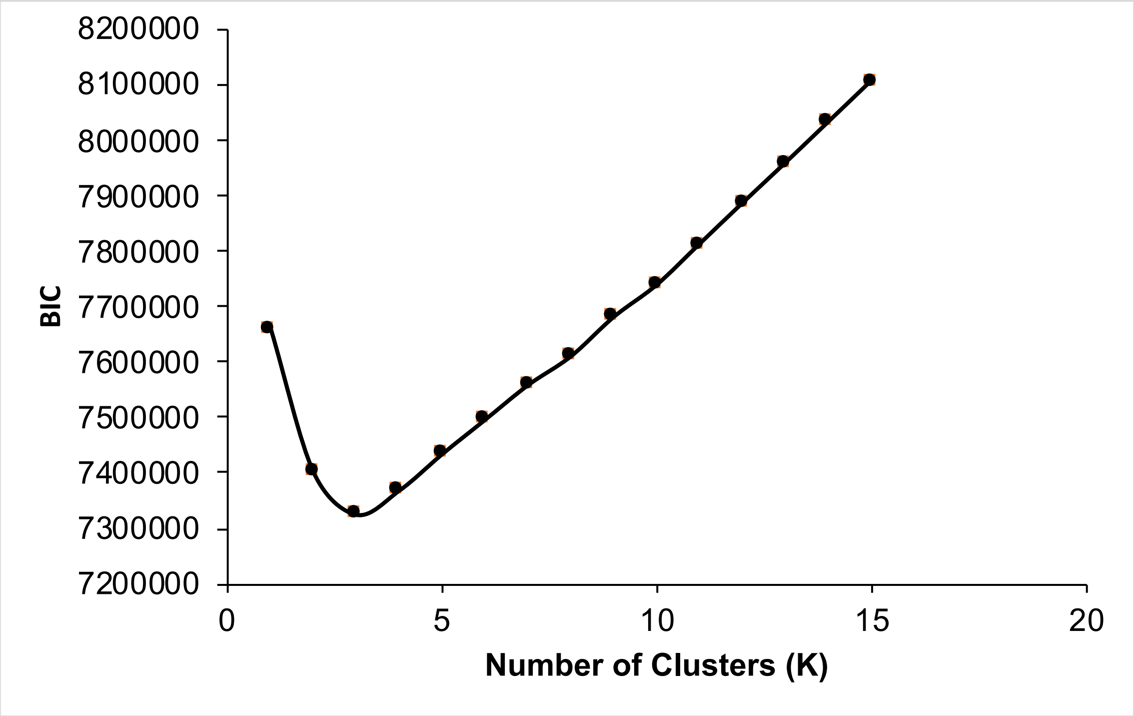
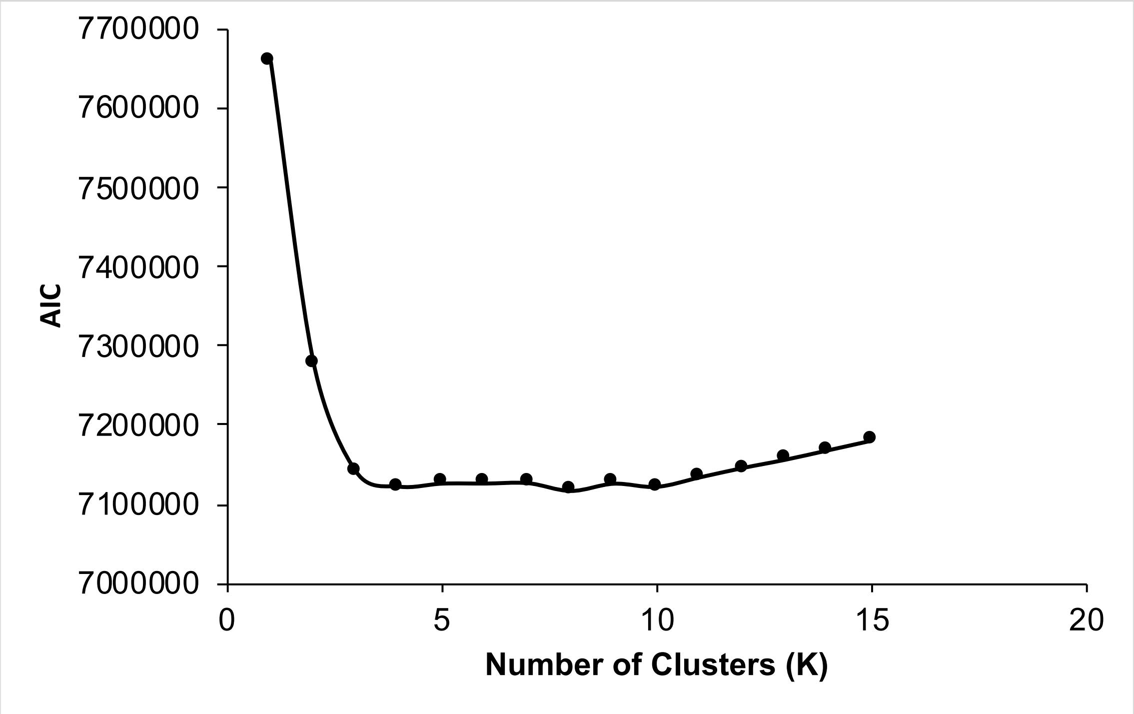


Figure B.6. Population structure analysis using Discriminant analysis of Principal Components (DAPC), based on genome-wide neutral SNPs for Australasian common dolphins (*Delphinus delphis*) per population and locality*: **(A)** Southern coast of Australia; **(B)** Eastern coast of Australia; and **(C)** New Zealand and Tasmania. *Acronyms used as in Figure 2.1.

(A)

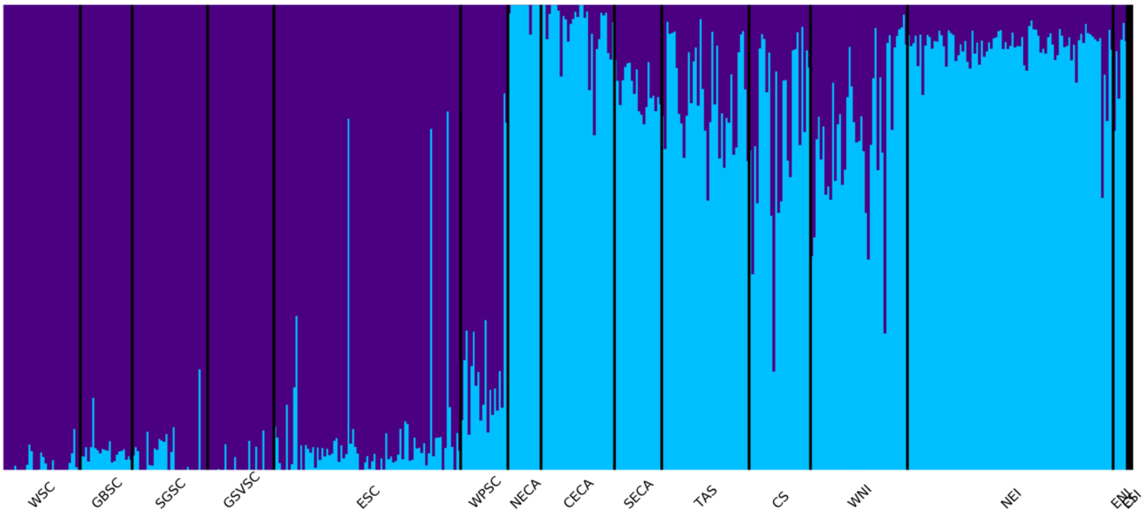


8200000
8100000
8000000
7900000
7800000
7700000
7600000
7500000
7400000
7300000
7200000
BIC
0
5
10
15
20
Number of Clusters (K)

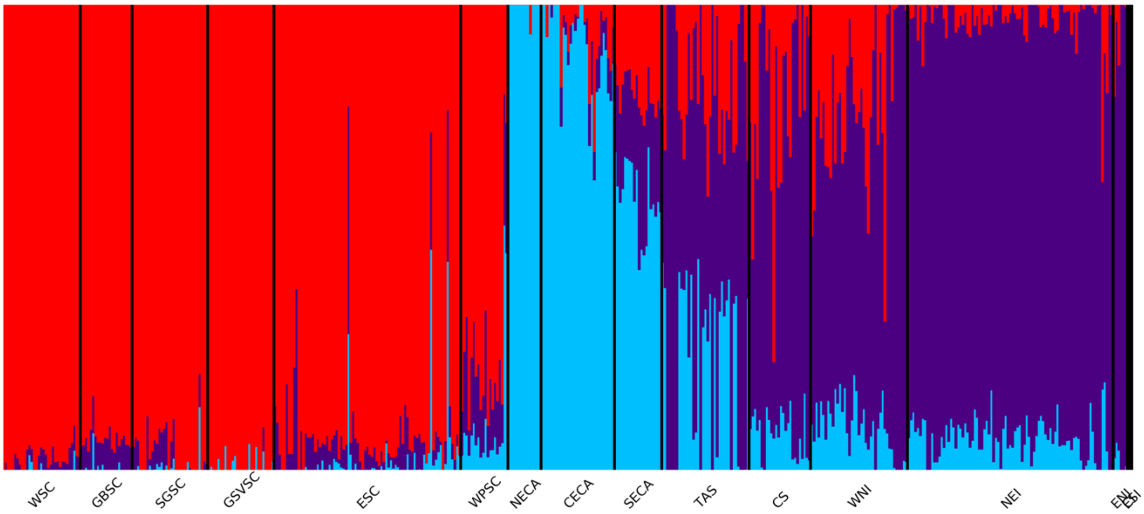


7700000
7600000
7500000
7400000
7300000
7200000
7100000
7000000
AIC
0
5
10
15
20
Number of Clusters (K)

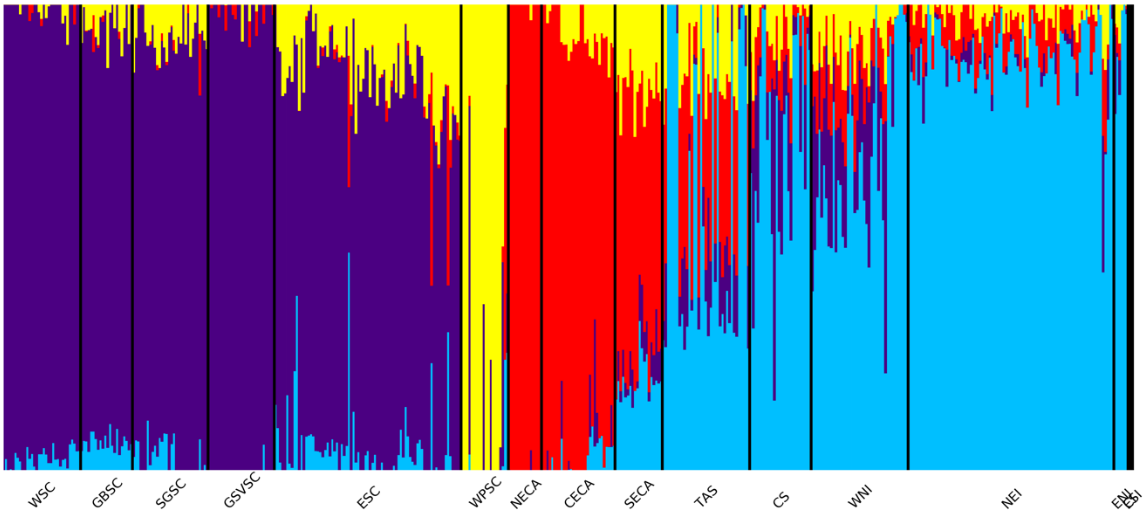
K2


WSC
GBSC
SGSC
GSVSC
ESC
WPSC
NECA
CECA
SECA
TAS
CS
WNI
NEI
ENI
ESI

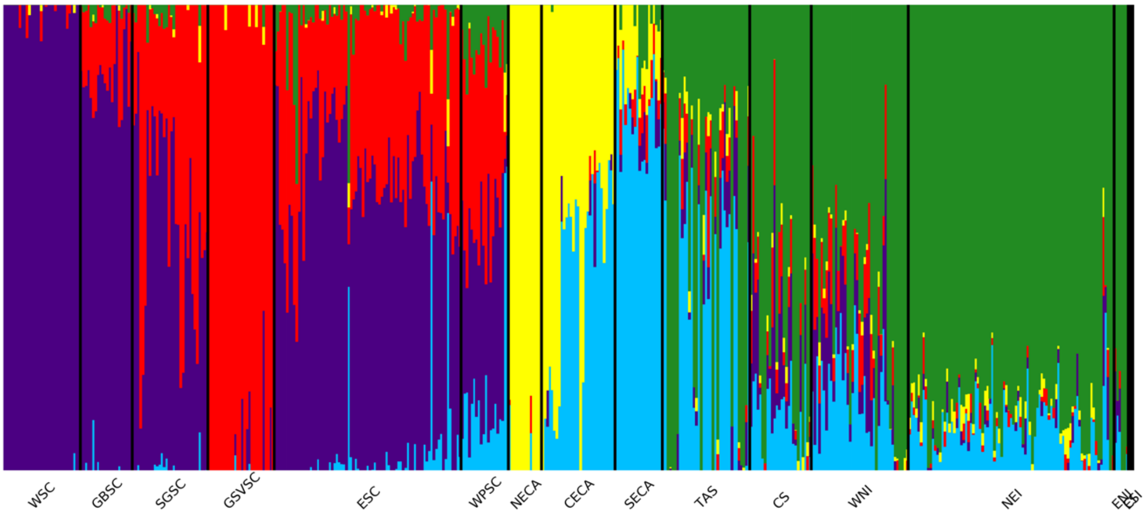
K3


WSC
GBSC
SGSC
GSVSC
ESC
WPSC
NECA
CECA
SECA
TAS
CS
WNI
NEI
ENI
ESI

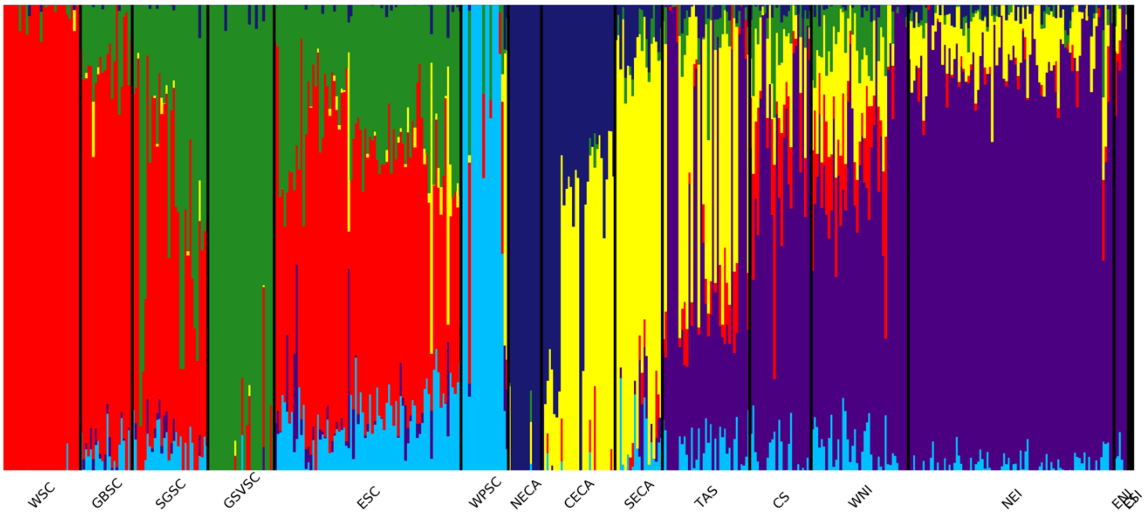
K4


WSC
GBSC
SGSC
GSVSC
ESC
WPSC
NECA
CECA
SECA
TAS
CS
WNI
NEI
ENI
ESI

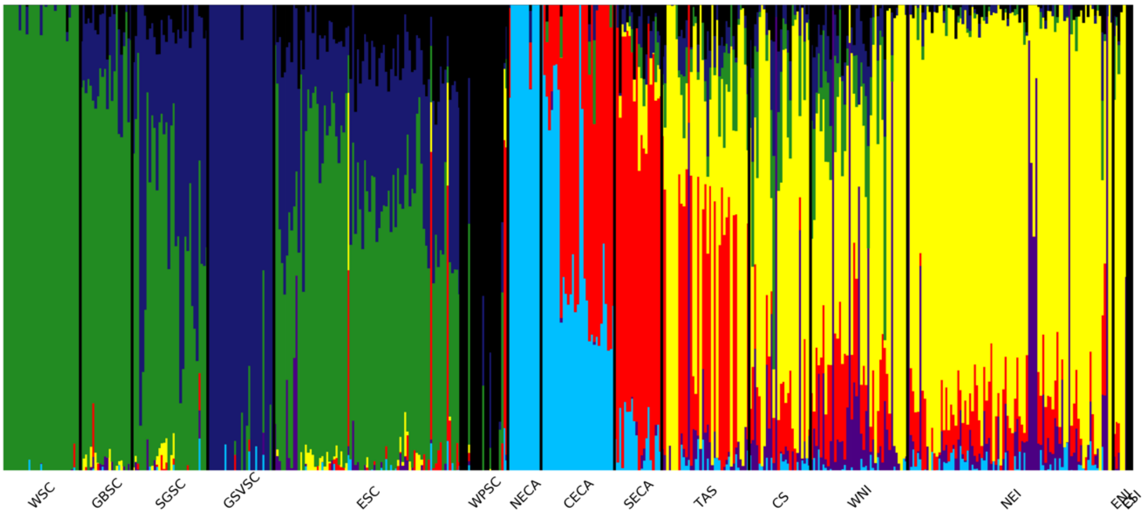
K5


WSC
GBSC
SGSC
GSVSC
ESC
WPSC
NECA
CECA
SECA
TAS
CS
WNI
NEI
ENI
ESI

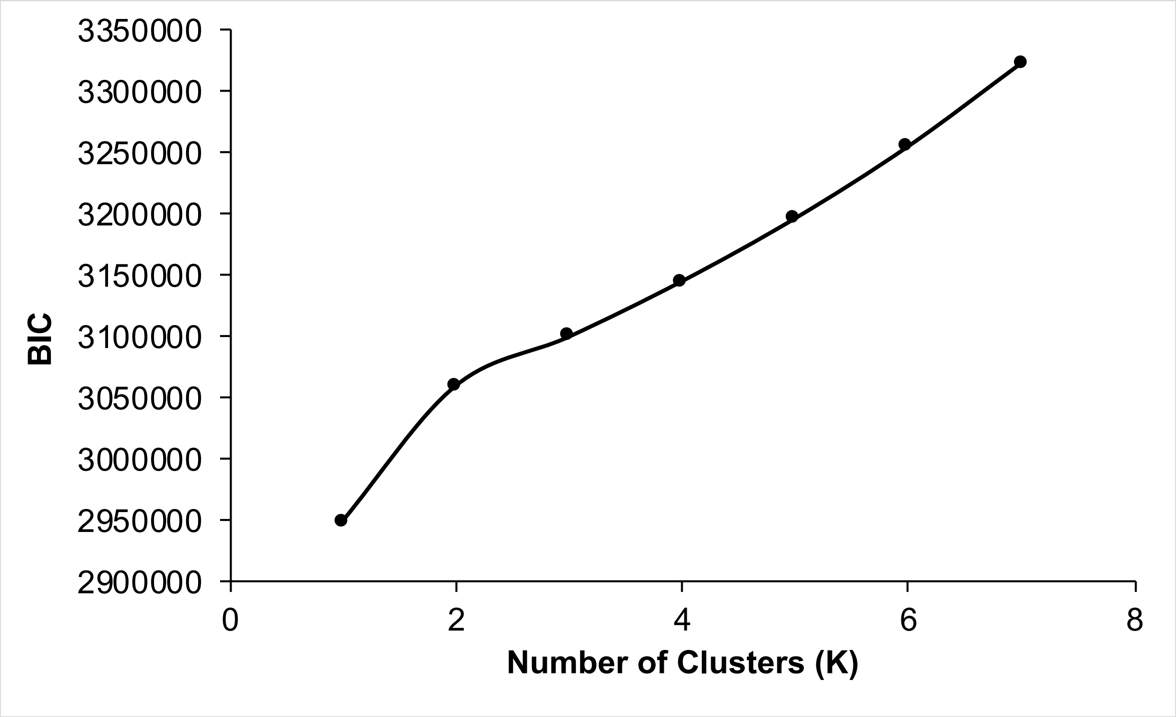
K6

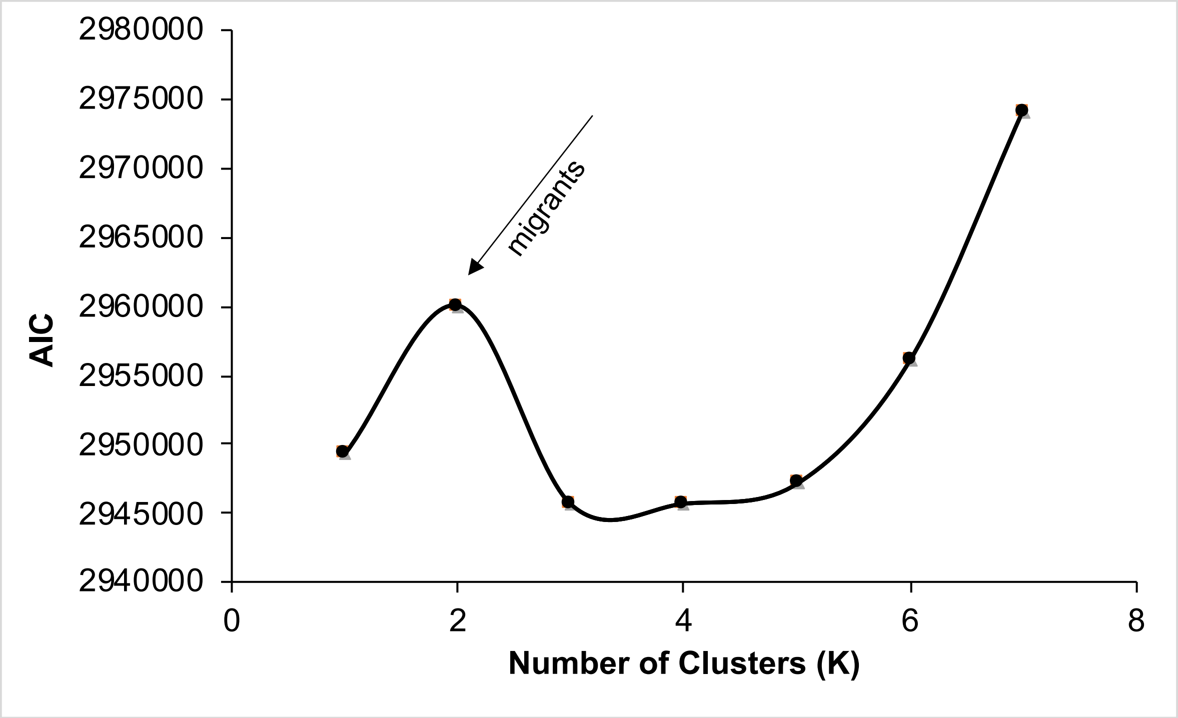

WSC
GBSC
SGSC
GSVSC
ESC
WPSC
NECA
CECA
SECA
TAS
CS
WNI
NEI
ENI
ESI

K7

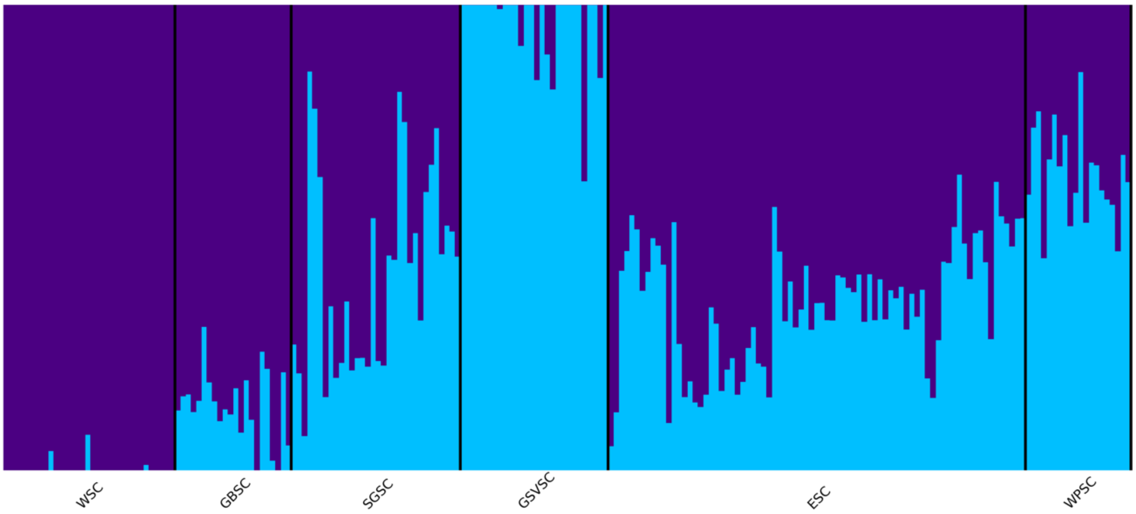

WSC
GBSC
SGSC
GSVSC
ESC
WPSC
NECA
CECA
SECA
TAS
CS
WNI
NEI
ENI
ESI

(B)

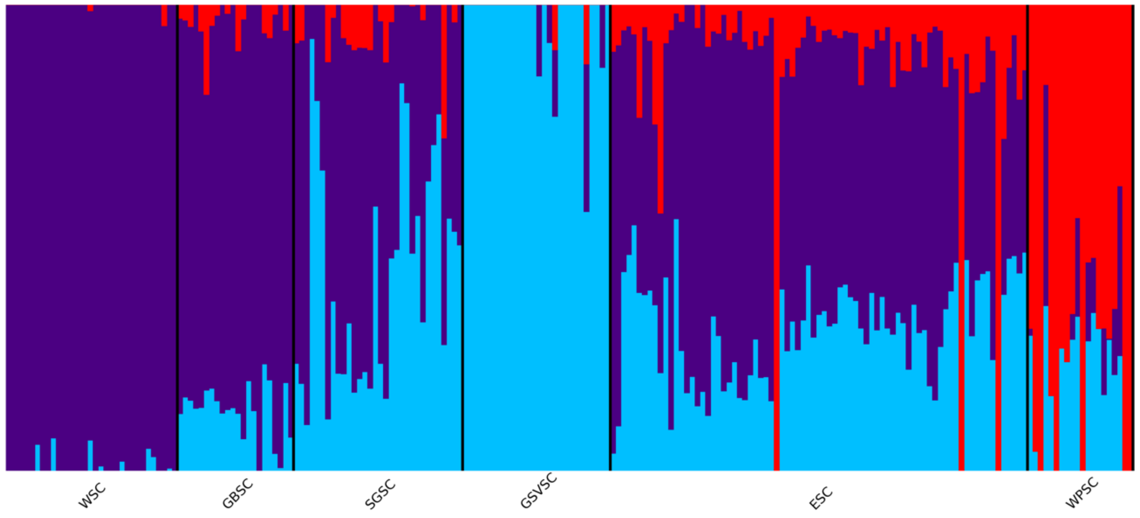

BIC
3350000
3300000
3250000
3200000
3150000
3100000
3050000
3000000
2950000
2900000
0
2
4
6
8
Number of Clusters (K)


2980000
2975000
2970000
2965000
2960000
2955000
2950000
2945000
2940000
AIC
migrants
0
2
4
6
8
Number of Clusters (K)

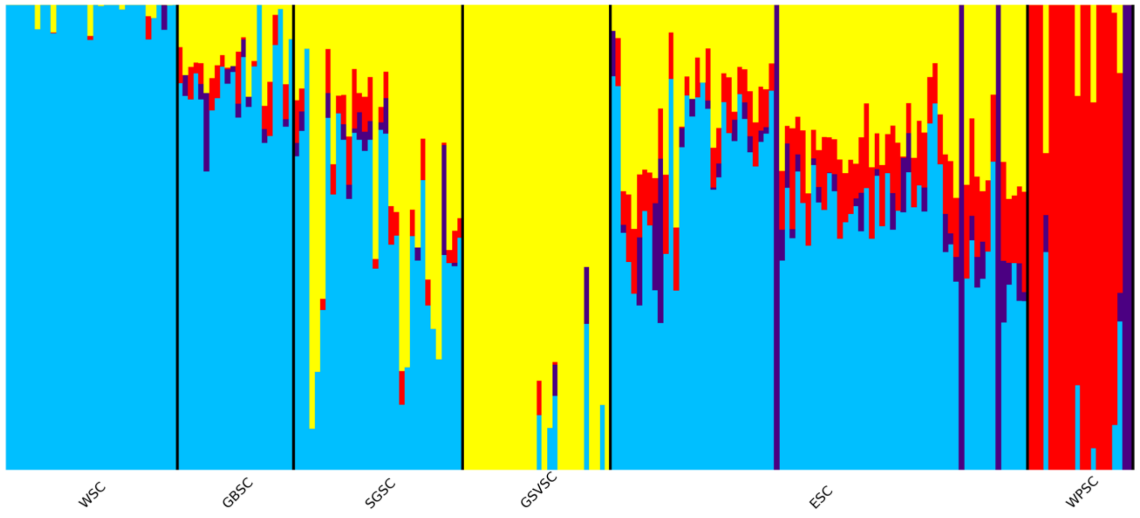
K2


WSC
GBSC
SGSC
GSVSC
ESC
WPSC

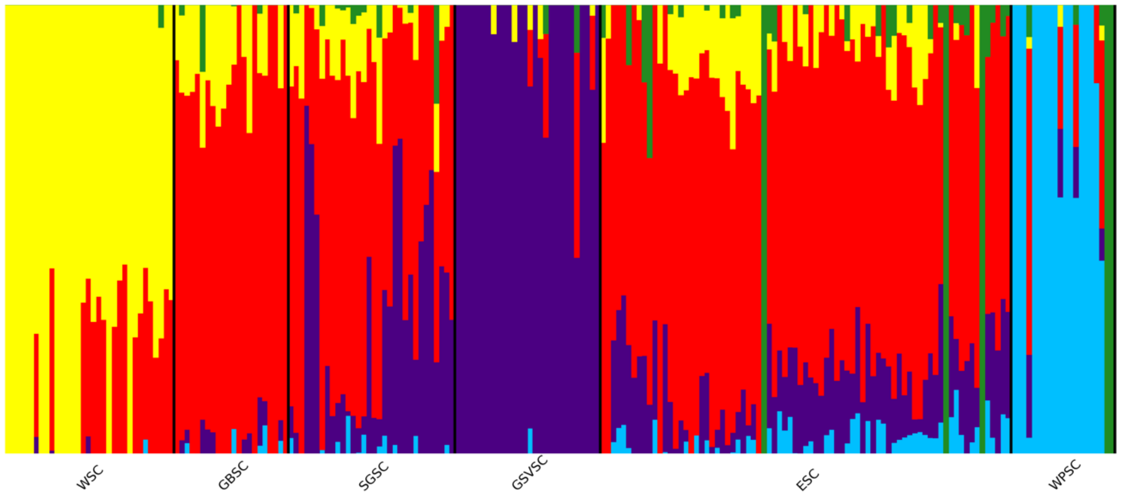
K3


WSC
GBSC
SGSC
GSVSC
ESC
WPSC

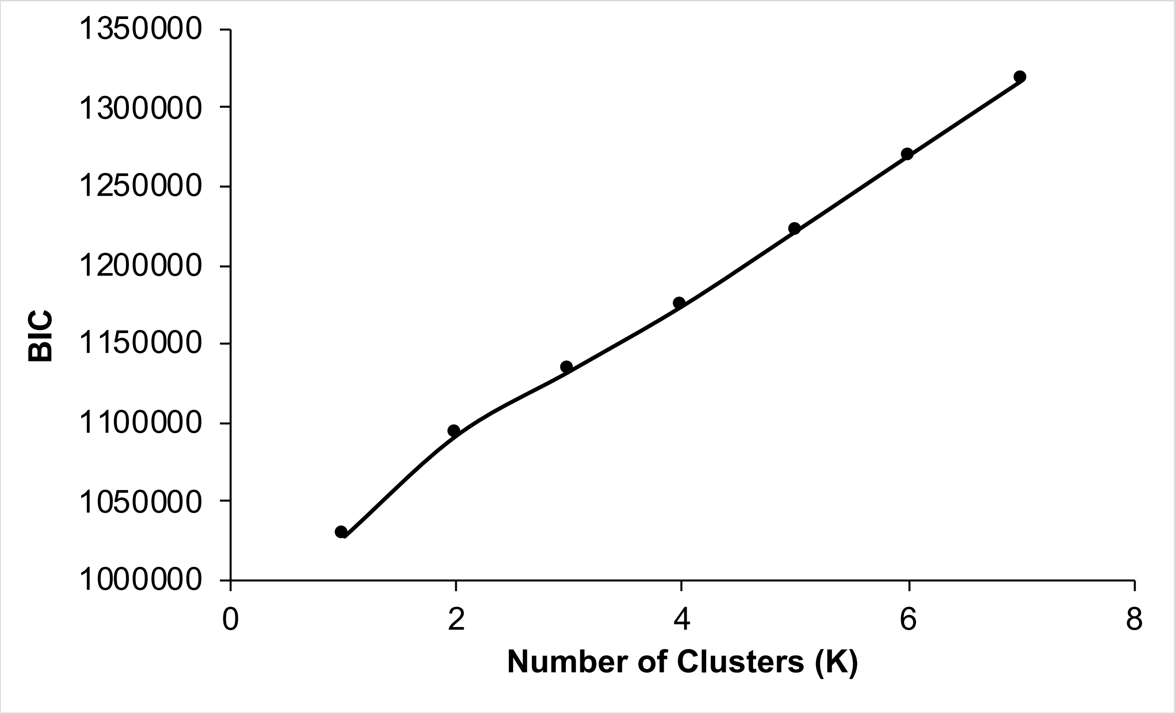
K4

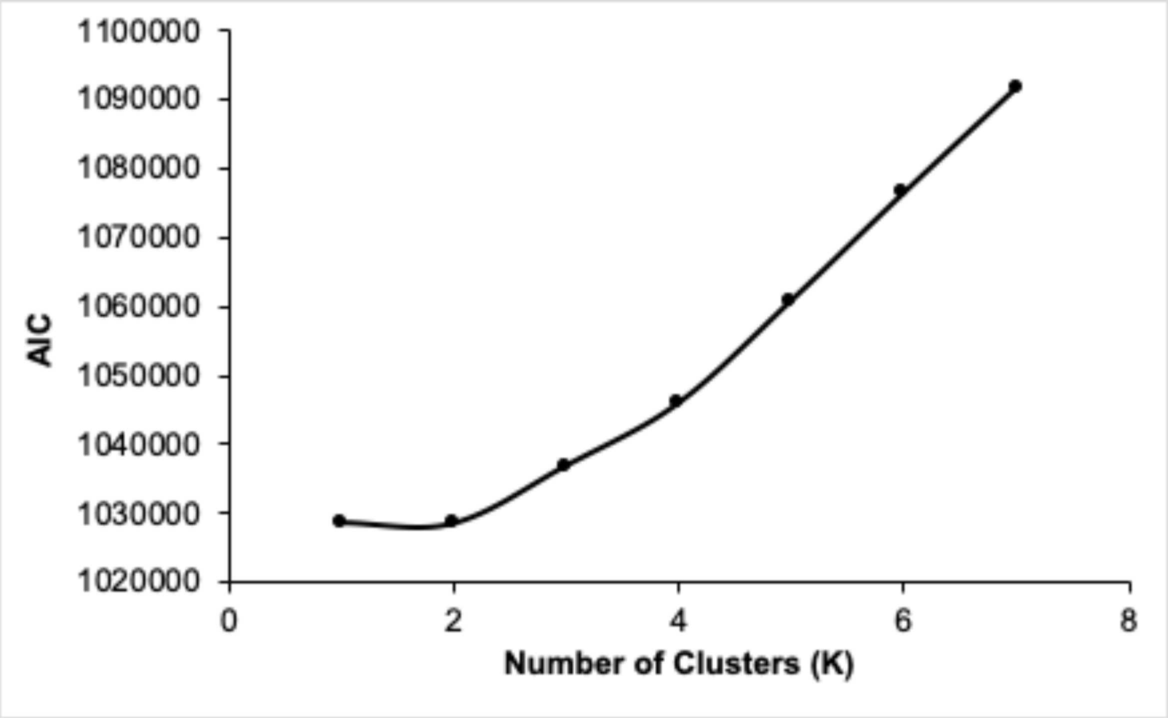

WSC
GBSC
SGSC
GSVSC
ESC
WPSC

K5

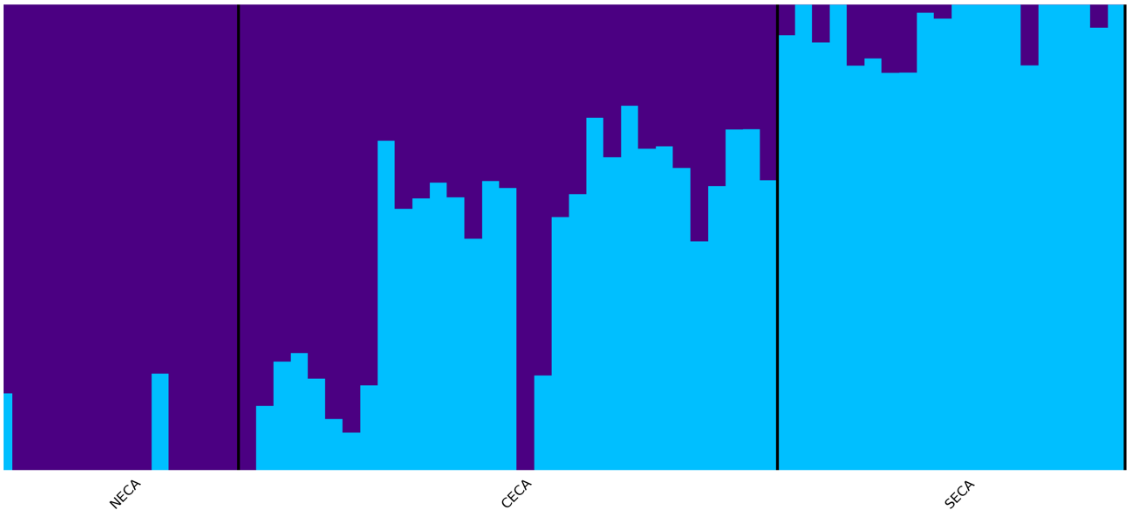

WSC
GBSC
SGSC
GSVSC
ESC
WPSC

(C)

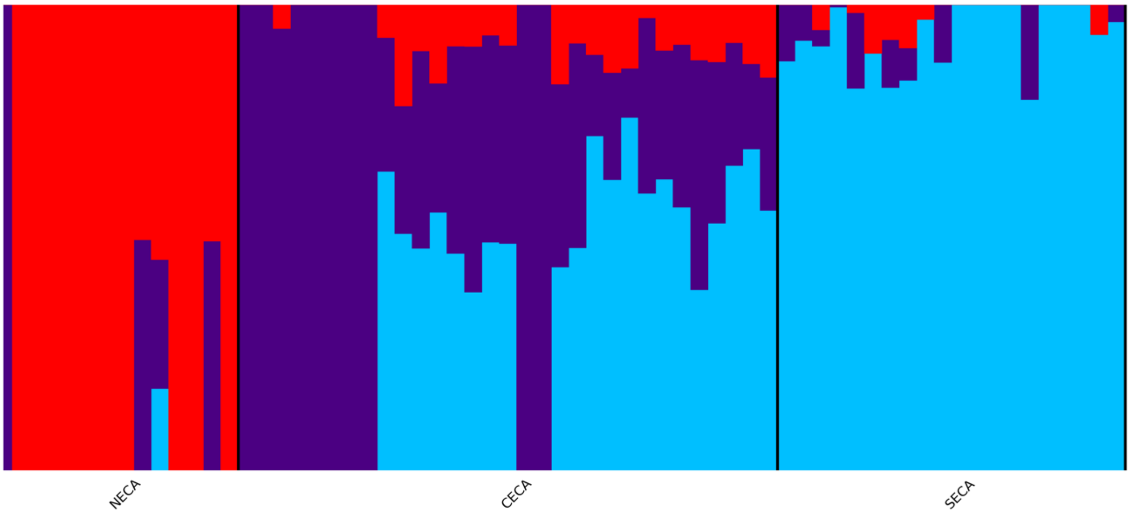

1350000
1300000
1250000
1200000
1150000
1100000
1050000
1000000
BIC
0
2
4
6
8
Number of Clusters (K)


1100000
1090000
1080000
1070000
1060000
1050000
1040000
1030000
1020000
AIC
0
2
4
6
8
Number of Clusters (K)

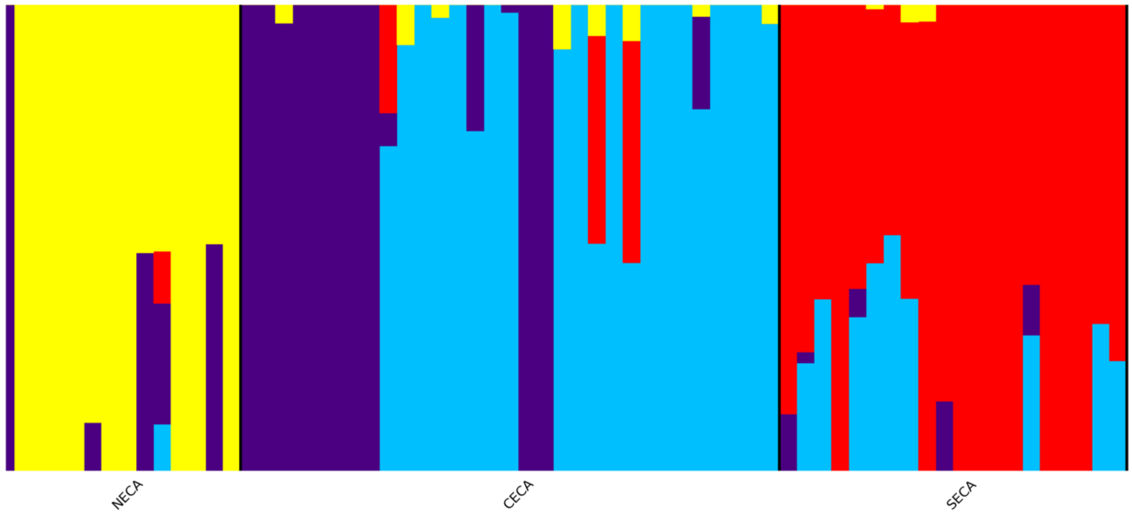
K2



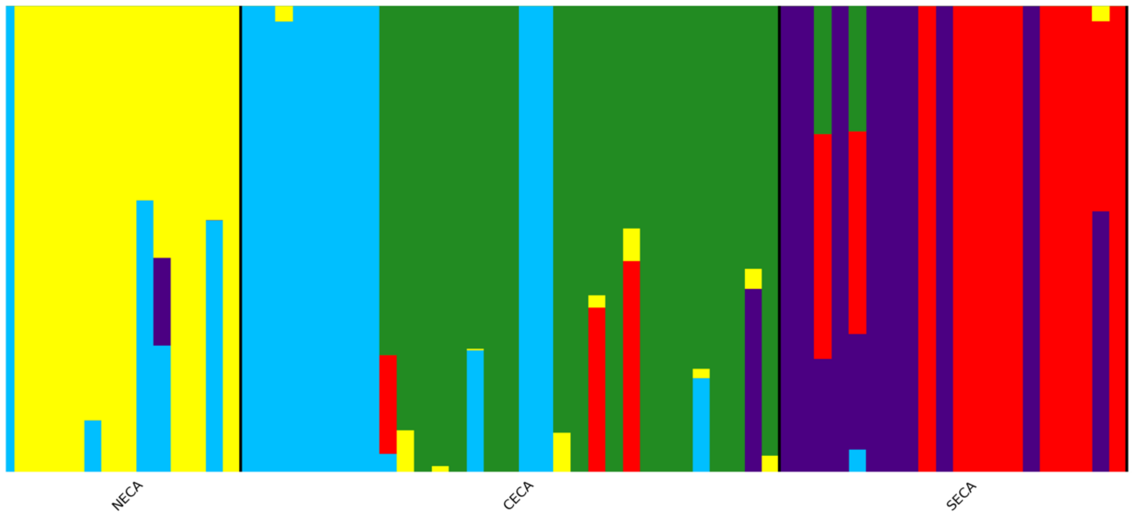
K3



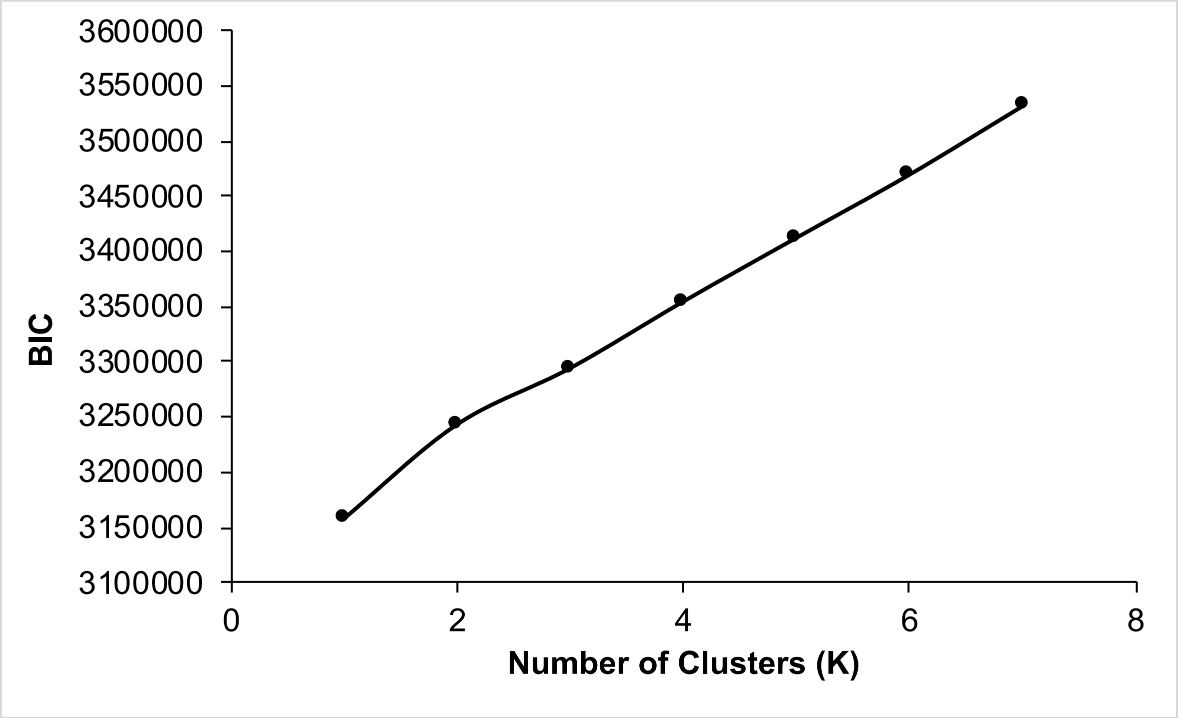
K4

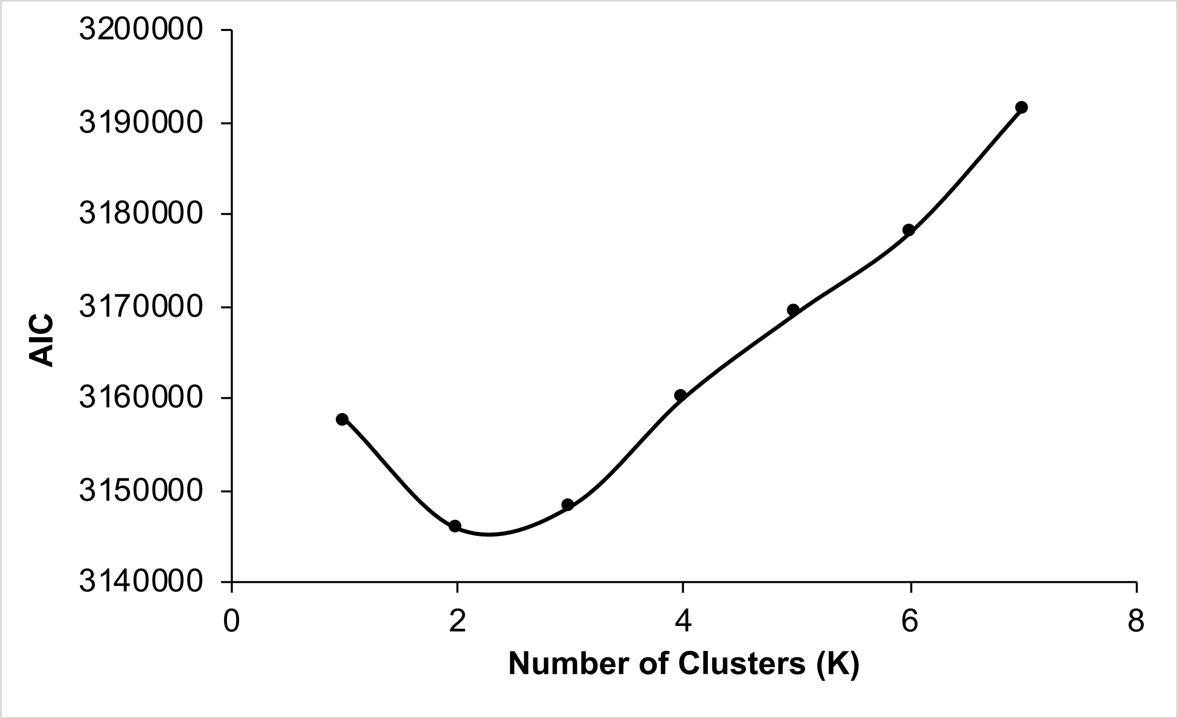


K5

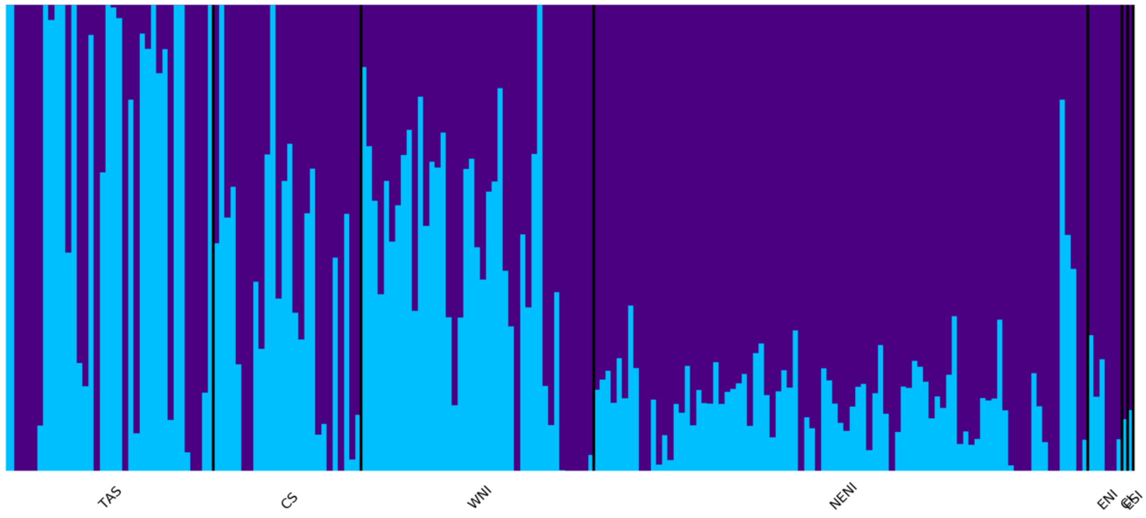


(D)

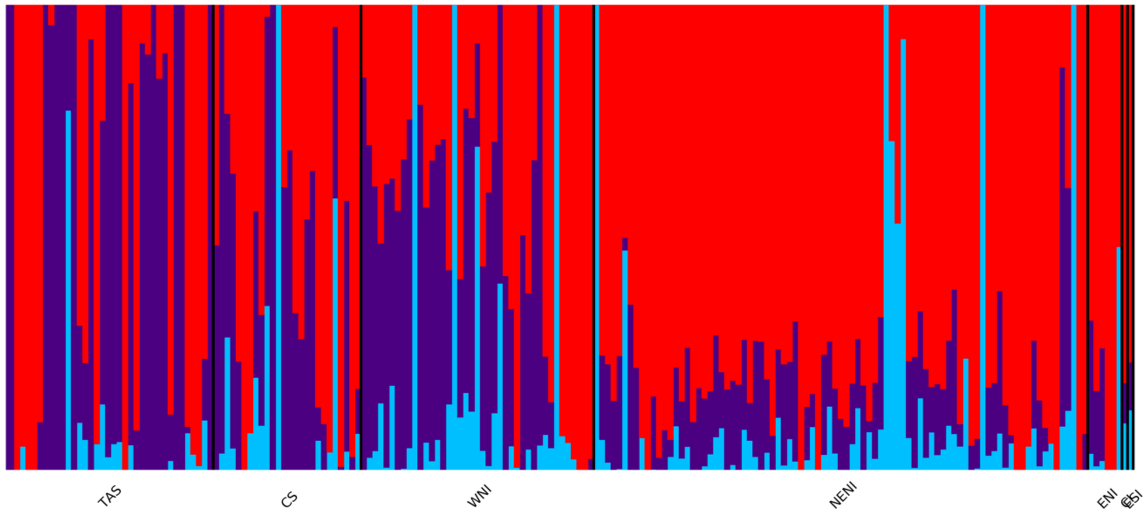

3600000
3550000
3500000
3450000
3400000
3350000
3300000
3250000
3200000
3150000
3100000
BIC
0
2
4
6
8
Number of Clusters (K)


3200000
3190000
3180000
3170000
3160000
3150000
3140000
AIC
0
2
4
6
8
Number of Clusters (K)

K2


TAS
CS
WNI
NENI
ENI
CI
ESI

K3


TAS
CS
WNI
NENI
ENI
CI
ESI

K4

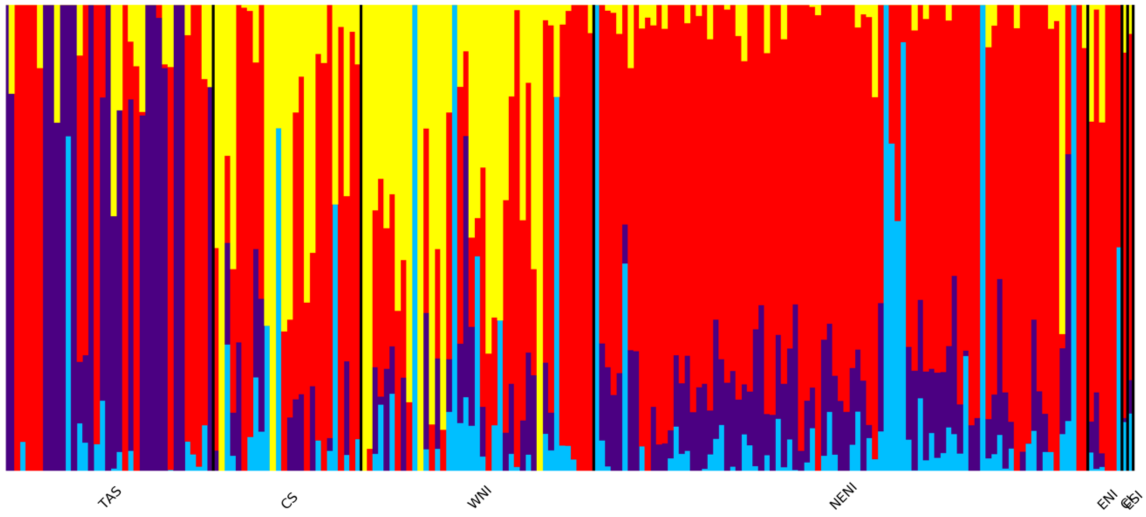

TAS
CS
WNI
NENI
ENI
CI
ESI

Figure B.7. Population genomic structure analysis using Admixture, based on genome-wide neutral SNPs of Australasian common dolphins (*Delphinus delphis*) (labelled by region). Showing Bayesian information criteria (BIC) and Akaike information criteria (AIC) for each scale **(A)** Australia and New Zealand hierarchical metapopulation. Subpopulations within each regional population: **(B)** Southern coast of Australia; **(C)** Eastern coast of Australia; or **(D)** Tasmania and New Zealand. *Acronyms used as in Figure 2.1.

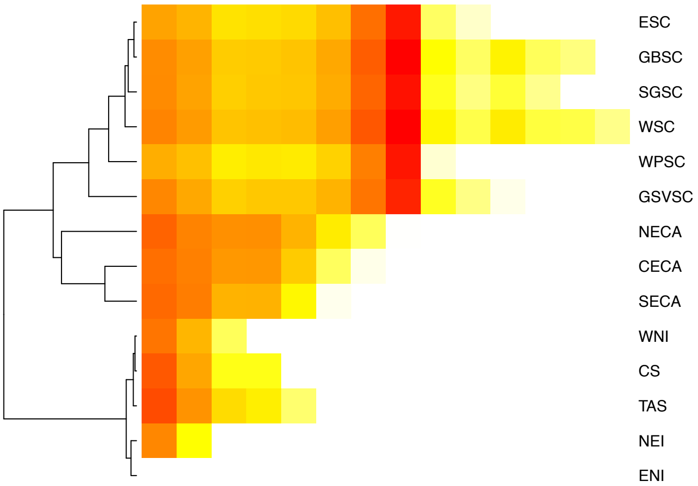


Figure B.8. Heatmap of pairwise F_{ST} values based on 14,799 putatively neutral SNPs between different sampling sites for Australasian common dolphins (*Delphinus delphis*), with the dendrogram clustering sites with the lowest F_{ST} values between them. *Acronyms used as in Figure 2.1.

APPENDIX C. ADDITIONAL INFORMATION FOR CHAPTER 3

Table C.1. Filtering steps and number of SNPs retained after each step for common dolphins (*Delphinus delphis*) in southern Australia. SABD: southern Australian bottlenose dolphin; FDR: false discovery rate.

Filtering Step	SNP count
Raw SNP catalogue	339,932
Genotyped in 80% of individuals, base quality ≥ 30, minor allele frequency >0.03 and bi-allelic.	33,467
Split multiple nucleotide polymorphisms into SNPs	33,010
Read depth ≤ mean depth + (2 x standard deviation)	32,031
Read quality (ratio quality/coverage depth > 0.2)	31,160
Allele balance > 20% and < 80%	31,020
Hardy–Weinberg equilibrium in > 80% localities	29,224
Present in at least 75% of individuals and in each putative population	26,431
Alignment against SABD, *Tursiops aduncus* genome (Batley et al. unpublished)	26,199 (99% alignment)
Best quality SNP (higher average Q) within 330bp	17,875
Minor allele count <0.01 based on the unrelated (R <0.7) 214 samples for southern Australian common dolphins	17,327
Average missing data per locus	1%

Table C.2. Significance of the RDA and the proportion explained by each component of the full model selection, with an overall significance of the model at p = 0.0001.

	Inertia	Proportion	Rank
Total	3.41E+03	1.00E+00	
Conditional	1.68E+02	4.92E-02	6
Constrained	1.20E+02	3.53E-02	5
Unconstrained	3.12E+03	9.16E-01	202

Table C.3. Pairwise F_{ST} values between sites based on putatively adaptive and neutral datasets for southern Australian common dolphins (*Delphinus delphis*). Upper right, neutral F_{ST} values, and lower left adaptive F_{ST} values, with their significance of the p-values by the B-Y method corrected represented by ***0.0001, **0.001, *0.05. Acronyms for sites as in Figure 3.1.

	ALB	**ESP**	**GAB**	**SG**	**GSV**	**ROB**	**PORT**	**MEL**	**EWP**
ALB	0	0.022***	0.026***	0.029***	0.056***	0.025***	0.026***	0.033***	0.047***
ESP	0.083***	0	0.015***	0.017***	0.044***	0.014***	0.015***	0.022***	0.036***
GAB	0.056***	0.025***	0	0.007***	0.034***	0.005***	0.006***	0.012***	0.026***
SG	0.059***	0.027***	0.014***	0	0.02***	0.004***	0.003***	0.010***	0.026***
GSV	0.120***	0.087***	0.081***	0.047***	0	0.027***	0.025***	0.029***	0.048***
ROB	0.055***	0.024***	0.007***	0.009***	0.060***	0	0.002***	0.007***	0.023***
PORT	0.056***	0.029***	0.009***	0.009***	0.058***	0.001	0	0.005***	0.021***
MEL	0.070***	0.030***	0.016***	0.011**	0.066***	0.010***	0.009***	0	0.02***
EWP	0.089***	0.066***	0.049***	0.038***	0.088***	0.048***	0.047***	0.033***	0

Table C.4. Significance of Gene Ontology (GO) Terms for southern Australian common dolphins (*Delphinus delphis*), comparing the full dataset with the putative candidate loci by Fisher's exact test. Biological Process (BP), Molecular Function (MF), Cellular Component (CC).

	GO.ID	**Term**	**Annotated**	**Significant**	**Expected**	**Fisher's p-value**
BP	GO:0019219	Regulation of nucleobase-containing compound metabolic process	86	9	20.67	0.0021
	GO:0019438	Aromatic compound biosynthetic process	111	9	26.68	0.005
	GO:1901362	Organic cyclic compound biosynthetic process	115	9	27.64	0.0052
	GO:0018130	Heterocycle biosynthetic process	111	9	26.68	0.0056
	GO:0032774	RNA biosynthetic process	88	9	21.15	0.0068
	GO:0009889	Regulation of biosynthetic process	84	8	20.19	0.009
	GO:0071705	Nitrogen compound transport	48	5	11.54	0.009
	GO:0034654	Nucleobase-containing compound biosynthetic process	105	9	25.24	0.0105
	GO:0008284	Positive regulation of cell proliferation	5	2	1.2	0.0111
	GO:0051171	Regulation of nitrogen compound metabolic process	100	9	24.03	0.0118
	GO:0006351	Transcription, DNA-templated	88	9	21.15	0.0127
	GO:0031326	Regulation of cellular biosynthetic process	83	8	19.95	0.0142
	GO:0009059	Macromolecule biosynthetic process	138	10	33.17	0.0207

	GO:0034645	Cellular macromolecule biosynthetic process	136	10	32.69	0.0215
	GO:0044271	Cellular nitrogen compound biosynthetic process	133	9	31.97	0.0241
	GO:0060255	Regulation of macromolecule metabolic process	105	9	25.24	0.0255
	GO:1905114	Cell surface receptor signaling pathway involved in cell-cell signaling	6	2	1.44	0.0326
	GO:0080135	Regulation of cellular response to stress	6	2	1.44	0.0406
	GO:0033036	Macromolecule localization	60	5	14.42	0.0536
	GO:0070647	Protein modification by small protein co.	16	2	3.85	0.0543
MF	GO:0030246	Carbohydrate binding	25	5	5.23	0.02
	GO:0001067	Regulatory region nucleic acid binding	12	3	2.51	0.025
	GO:0008234	Cysteine-type peptidase activity	22	3	4.6	0.027
	GO:0044212	Transcription regulatory region DNA bind.	12	3	2.51	0.05
	GO:0005506	Iron ion binding	17	3	3.56	0.079
	GO:1990837	Sequence-specific double-stranded DNA bi.	9	2	1.88	0.083
	GO:0048037	Cofactor binding	47	6	9.84	0.083
	GO:0016491	Oxidoreductase activity	67	7	14.02	0.102
	GO:0043169	Cation binding	297	25	62.16	0.109
	GO:0008092	Cytoskeletal protein binding	72	6	15.07	0.112
	GO:0060089	Molecular transducer activity	68	7	14.23	0.115

	GO:0004497	Monooxygenase activity	6	2	1.26	0.115
	GO:0016705	Oxidoreductase activity, acting on paire.	13	3	2.72	0.127
	GO:0016758	Transferase activity, transferring hexos.	13	2	2.72	0.148
	GO:0031406	Carboxylic acid binding	10	2	2.09	0.153
	GO:0043177	Organic acid binding	10	2	2.09	0.157
	GO:0005319	Lipid transporter activity	5	1	1.05	0.171
	GO:0005488	Binding	845	56	176.85	0.171
	GO:0008135	Translation factor activity, RNA binding	12	1	2.51	0.176
	GO:0008081	Phosphoric diester hydrolase activity	15	2	3.14	0.176
CC	GO:0030054	Cell junction	14	3	3.37	0.045
	GO:0042995	Cell projection	17	3	4.09	0.057
	GO:0030117	Membrane coat	9	2	2.16	0.074
	GO:0031410	Cytoplasmic vesicle	13	2	3.12	0.1
	GO:0048475	Coated membrane	9	2	2.16	0.108
	GO:0031982	Vesicle	13	2	3.12	0.121
	GO:0097708	Intracellular vesicle	13	2	3.12	0.127
	GO:0005929	Cilium	12	2	2.88	0.131
	GO:0031514	Motile cilium	5	2	1.2	0.152
	GO:0044433	Cytoplasmic vesicle part	6	1	1.44	0.194
	GO:0098796	Membrane protein complex	57	5	13.7	0.216

GO:0044429	Mitochondrial part	7	1	1.68	0.223
GO:0044456	Synapse part	16	2	3.85	0.243
GO:0016020	Membrane	577	37	138.7	0.243
GO:0005730	Nucleolus	8	1	1.92	0.27
GO:1904949	ATPase complex	6	1	1.44	0.274
GO:0044425	Membrane part	535	34	128.6	0.296
GO:0044451	Nucleoplasm part	16	1	3.85	0.308
GO:0012505	Endomembrane system	56	4	13.46	0.357
GO:0097458	Neuron part	8	1	1.92	0.361

Table C.5. Function of the candidate genes found in exonic regions, which were over enriched by the Gene Ontology analyses, for the 747 putatively adaptive SNPs discovered by the RDA of southern Australian common dolphins (*Delphinus delphis*).

Genes in exons	**Environmental variable associated**	**Pathway (reactome)**	**Function (Uniprot)**	**Family**	**General function described**	**References**
MAN2B1 Missense exon	RDA primary productivity max	Lysosome lumen: Lysosomal oligosaccharide catabolism mainly.	*Lipotes vexillifer* (Yangtze river dolphin) Protein Alpha-mannosidae. Human: Necessary for the catabolism of N-linked carbohydrates released during glycoprotein turnover.	MAN	Breaks complex sugar molecules "more energy" in the carbohydrate metabolism	(Dineshram et al., 2015; Lazzarotto, 2016; Sproles et al., 2019; Tivey et al., 2020)
NR2F2 Missense exon	RDA salinity max	Nucleoplasm- NR2F6:Gene expression in transcription pathway. Adipogenesis is the process of cell differentiation by which preadipocytes become adipocytes.	*Lipotes vexillifer* (Yangtze river dolphin) NR2F2-gene and COUP transcription factor 2-like isoform X3. Human: NR2F2 Ligand-activated transcription factor.	NR2	Regulation of adipogenesis, glucose, homeostasis and metabolism energy	(Li et al., 2009; Jeong et al., 2014; Baldwin et al., 2017)
ZPF57 Synonymous exon	RDA primary productivity max	ZPF: Nucleoplasm- Gene expression in transcription: generic transcriptions pathway, genes and factors involve in megakaryocyte differentiation, metabolism mRNA stability by proteins.	*Physeter macrocephalus* (Sperm whale). ZPF57-gene, zinc finger protein 57 homolog. Molecular function: metal ion binding and nucleic acid binding. Biological process: regulation of transcription DNA-templated. Human: Transcription regulator required to maintain maternal and paternal gene imprinting.	Part of the large group of ZPF	Acts by controlling DNA methylation during earliest multicellular stages of development and may be altered by nutrients in the diet.	(Amarasekera et al., 2014; Yim et al., 2014; Foote et al., 2016; Zglejc and Franczak, 2017; Irwin et al., 2019)

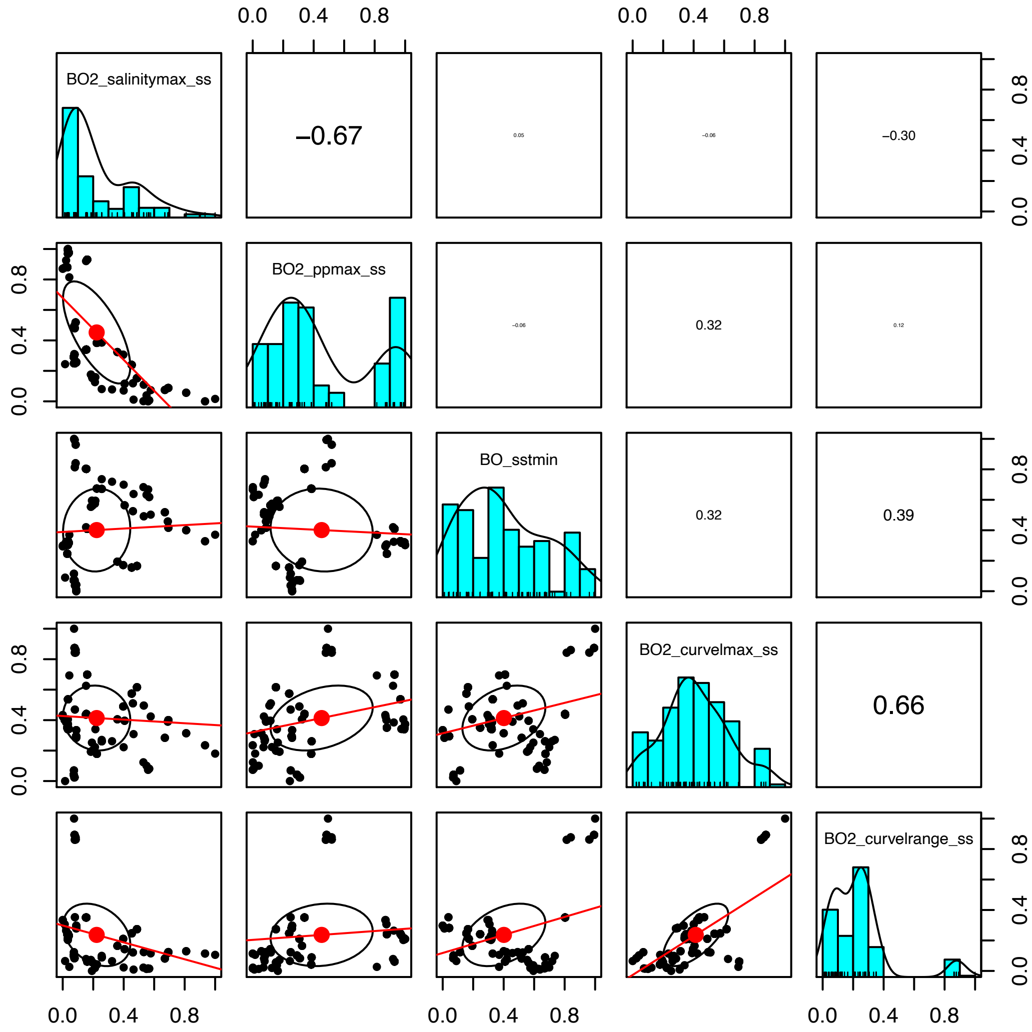


Figure C.1. Variance inflation factors (VIF) of the five environmental variables used for the RDA. Salinity maximum (BO2_salinitymax_ss), primary productivity maximum (BO2_ppmax_ss), sea surface temperature minimum (BO_sstmin), current velocity maximum (BO2_curvelmax_ss) and current velocity range (BO2_curvelrange_ss).

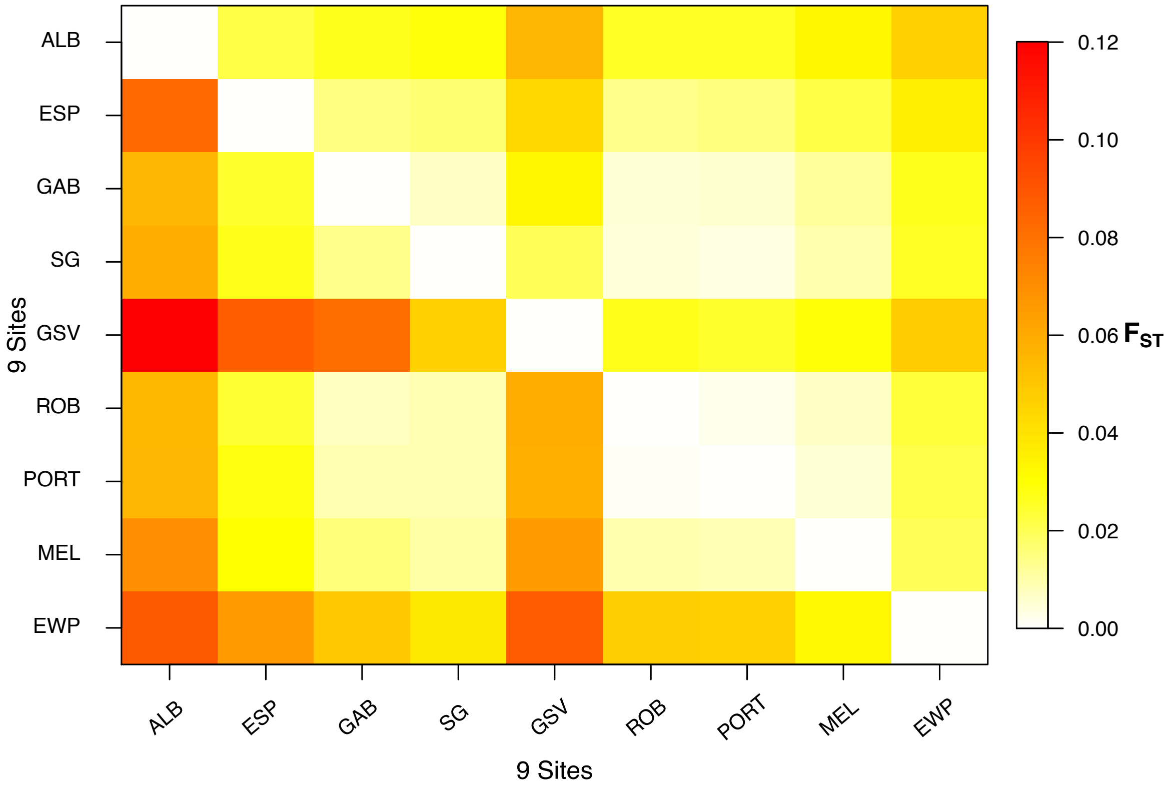


Figure C.2. Heatmap of pairwise F_{ST} values between sites * based on the adaptive and neutral SNP datasets for southern Australian common dolphins (*Delphinus delphis*). Upper right, neutral dataset, and lower left, adaptive dataset. Acronyms for sites as in Figure 3.1.

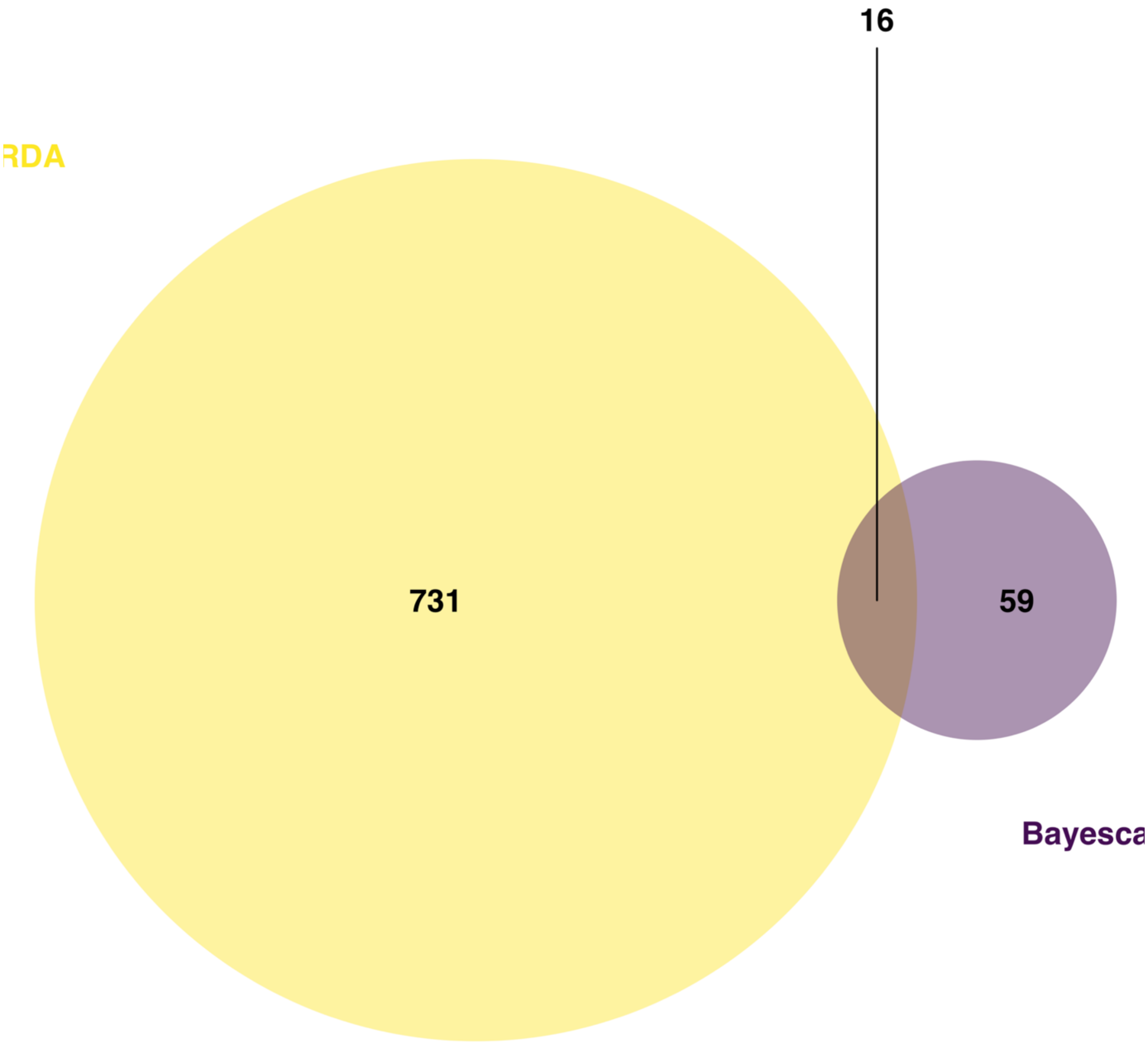


Figure C.3. Candidate loci putatively under selection for southern Australian common dolphins (*Delphinus delphis*) based on the candidate loci from RDA and the Bayesian outlier test.

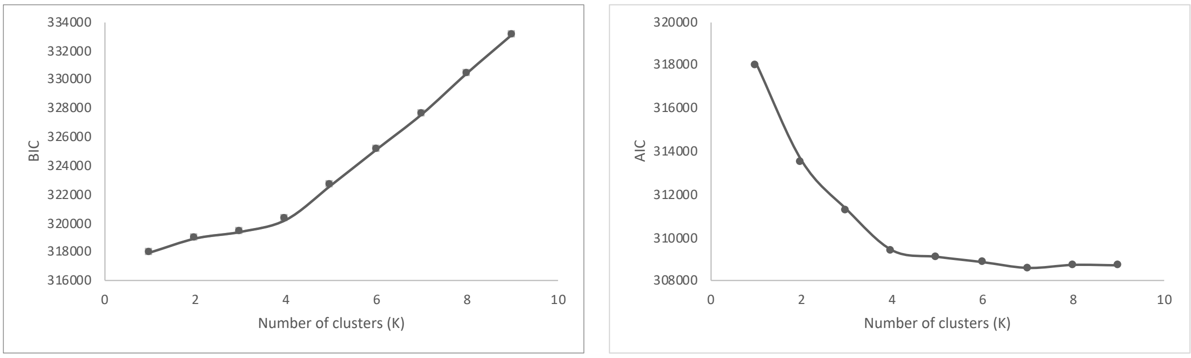
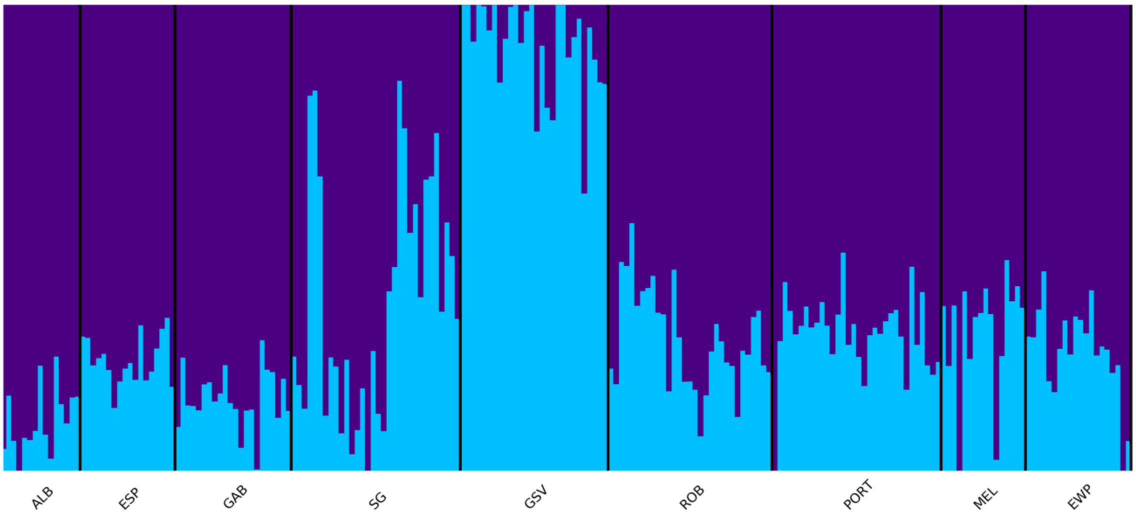
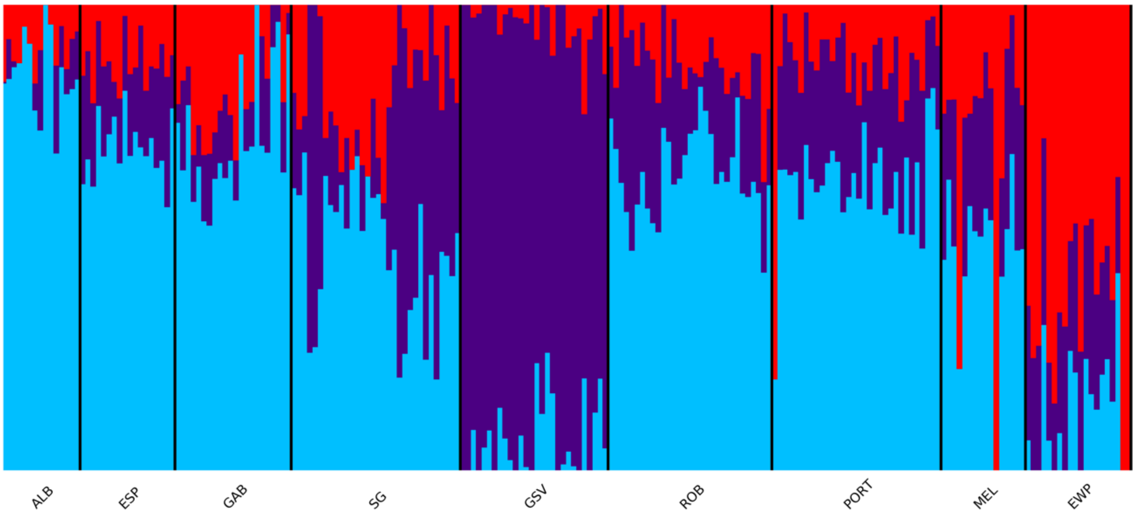


Figure C.4. Bayesian Information Criterion (BIC) and Akaike Information Criterion (AIC) used to determine the best-supported number of clusters in the putative adaptive datasets of southern Australia.

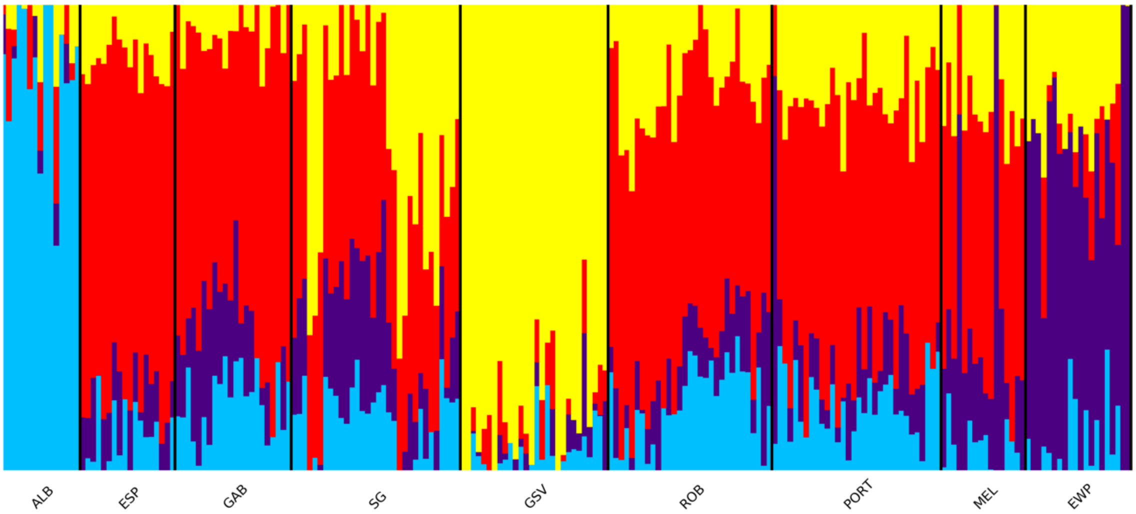
(A) K2



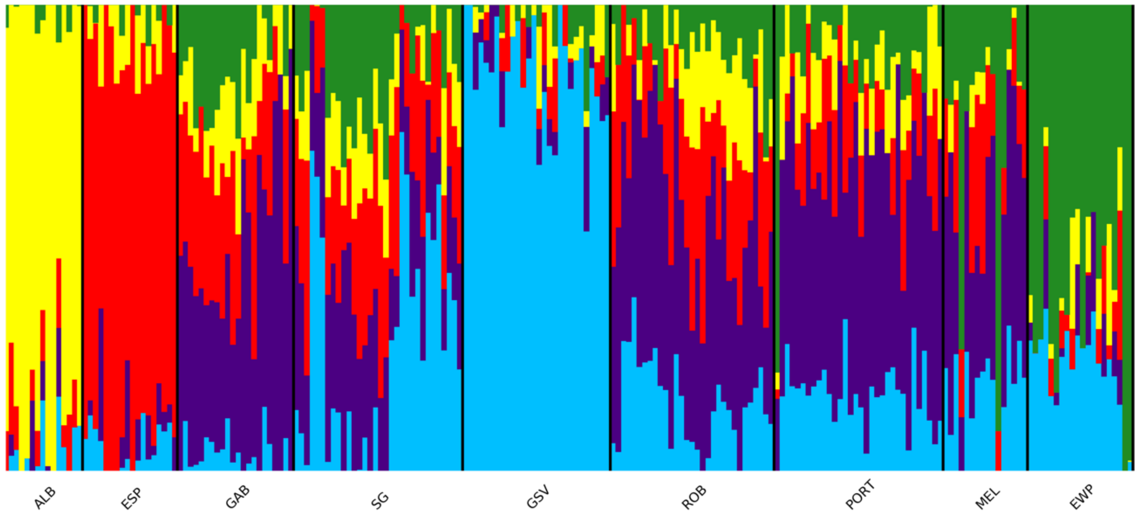
(B) K3


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP

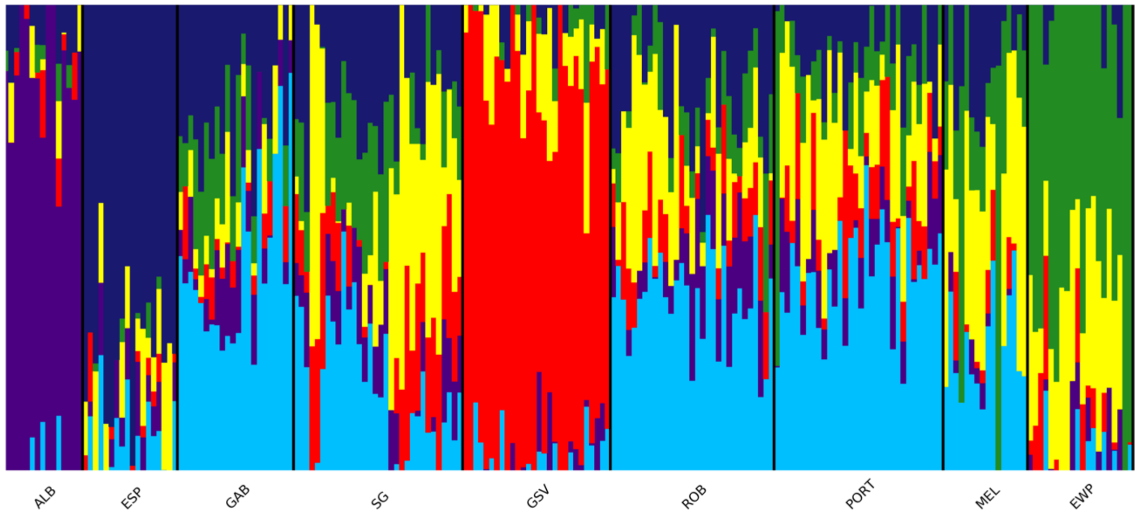
(C) K4*


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP

(D) K5*


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP

(E) K6


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP

(F) K7

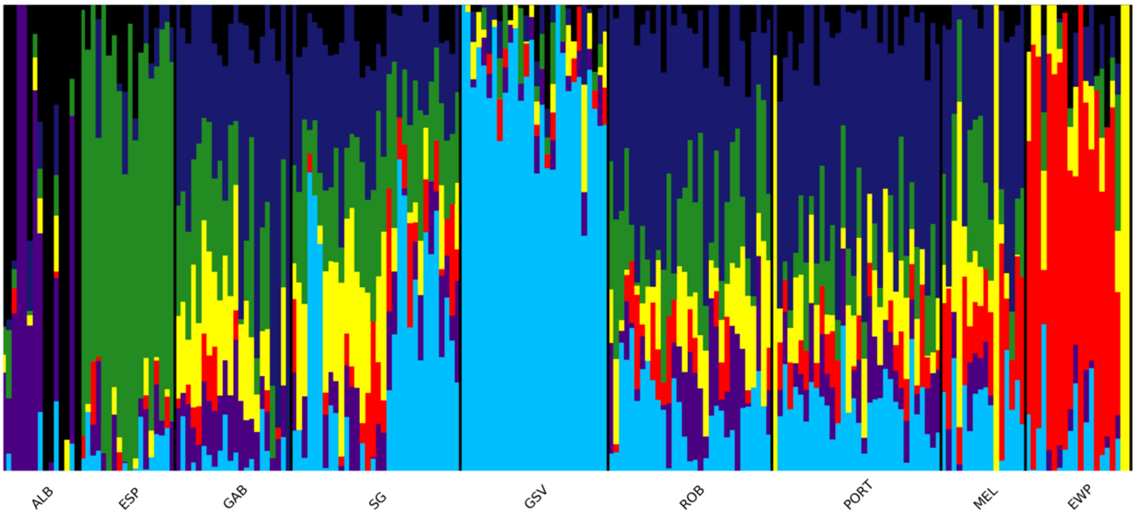


Figure C.5. Population genomic structure analysis using Admixture based on putatively adaptive SNPs for southern Australian common dolphins (*Delphinus delphis*) (labelled by sampling site and individual). K represents the number of populations tested (A to F), in which K4* and K5* are both correctly assigned as they are the most supported and highly likely number of local populations suggested by the analysis. Acronyms for sites as in Figure 3.1.

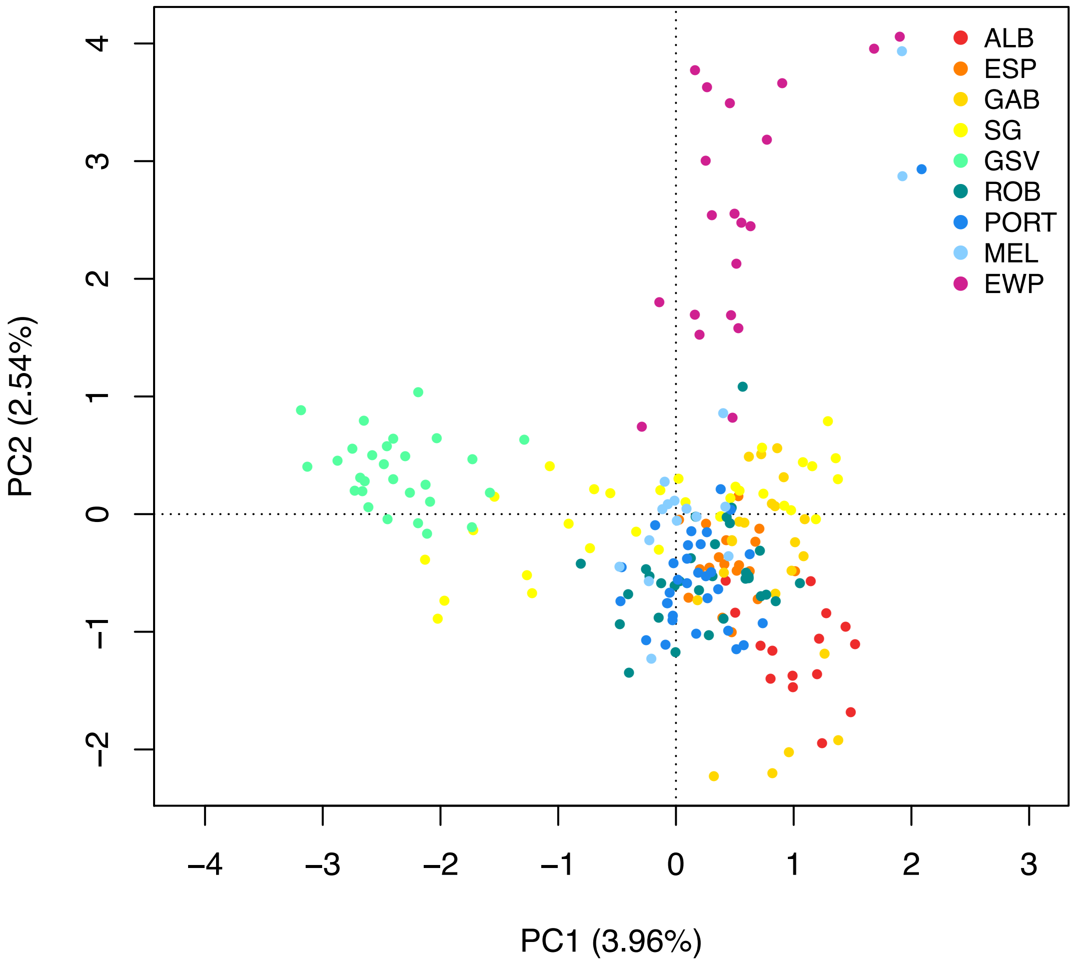


Figure C.6. Principal Component Analysis (PCA) based on 806 candidate adaptive loci for southern Australian common dolphins (*Delphinus delphis*). Acronyms for sites as in Figure 3.1.

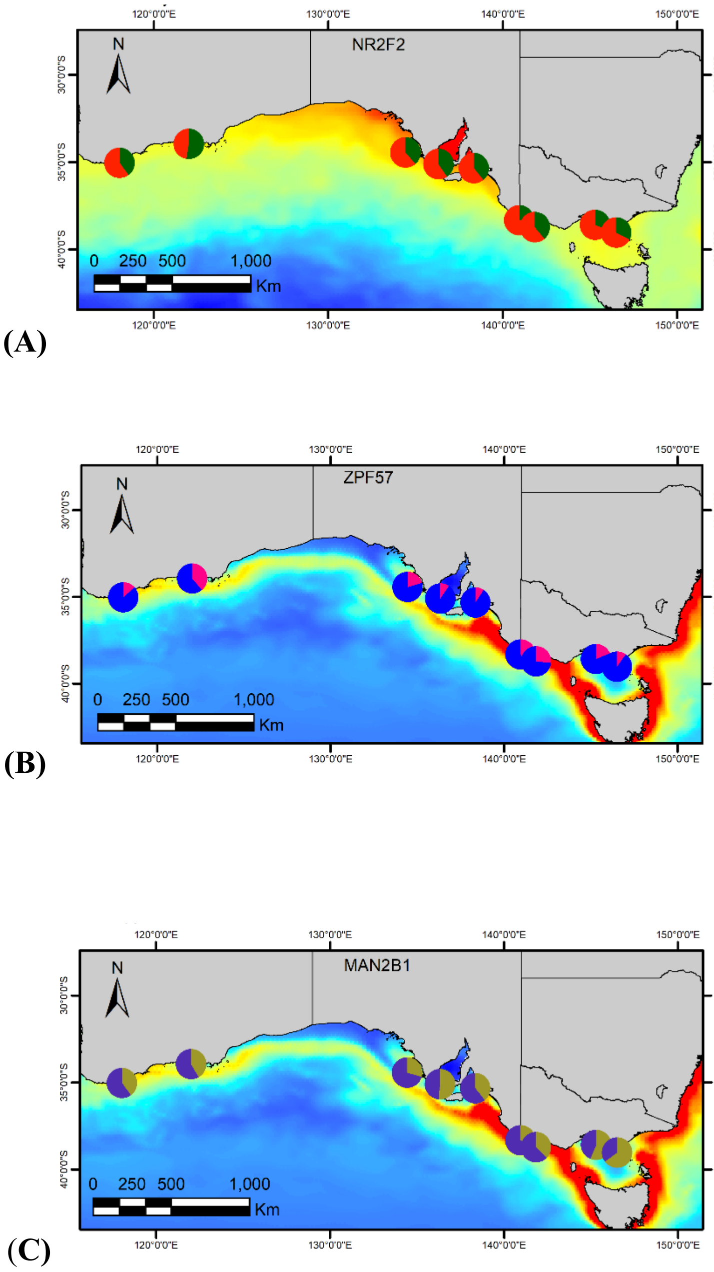


Figure C.7. Allele frequency changes for the candidate gene variants found in exonic regions across sampling sites of common dolphins (*Delphinus delphis*) in southern Australia. **(A)** NR2F6/NR2F2 was associated with maximum salinity, **(B)** ZFP57, with primary productivity maximum, and **(C)** MAN2B1, with primary productivity maximum.

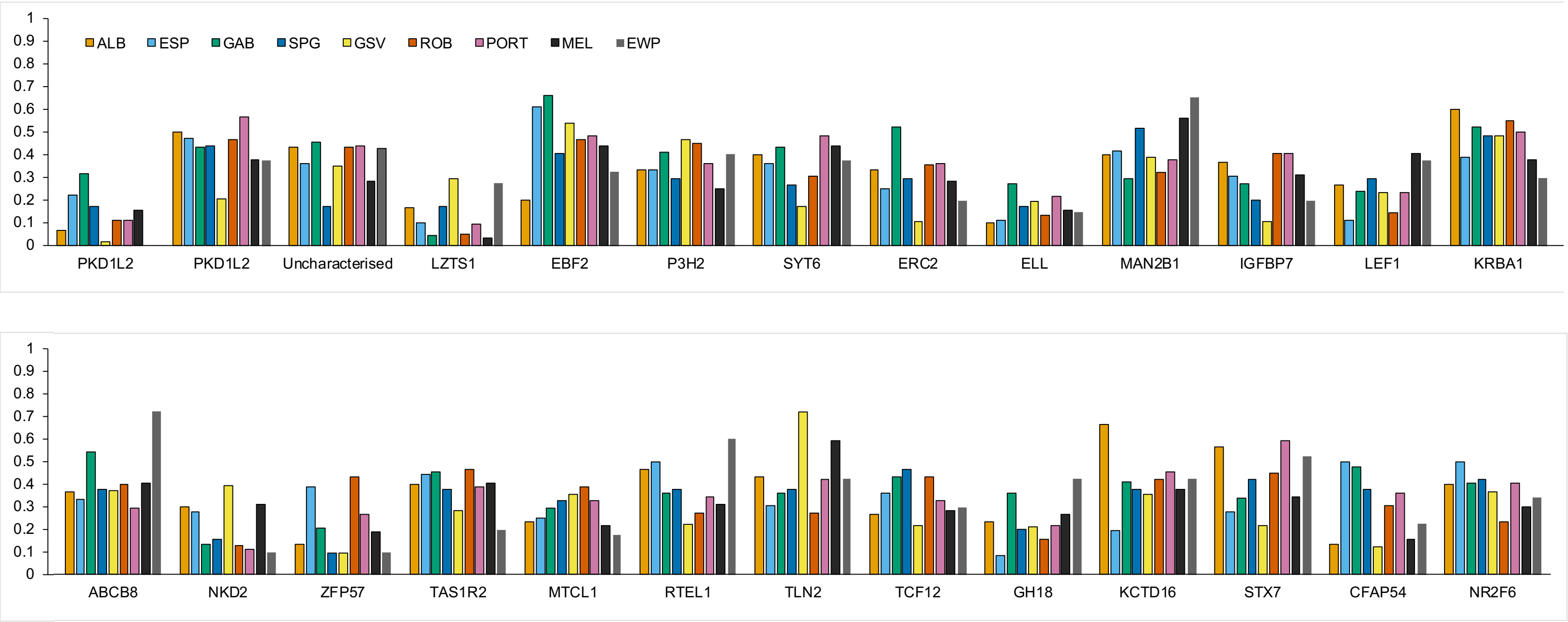


Figure C.8. Minor allele frequencies of 26 SNPs found to be positively selected by a gene enrichment test, with variants in coding or non-coding regions.

APPENDIX D. ADDITIONAL INFORMATION FOR CHAPTER 4

Table D.1. Filtering steps and number of SNPs retained after each step for common dolphins (*Delphinus delphis*) in southern and eastern Australia. AUS: Australia; SABD: southern Australian bottlenose dolphin; FDR: false discovery rate.

Filtering Step	SNP count
Raw SNP catalogue	339,932
Genotyped in 80% of individuals, base quality ≥ 30, minor allele frequency >0.03 and bi-allelic.	33,467
Split multiple nucleotide polymorphisms into SNPs	33,010
Read depth ≤ mean depth + (2 x standard deviation)	32,031
Read quality (ratio quality/coverage depth > 0.2)	31,160
Allele balance > 20% and < 80%	31,020
Hardy–Weinberg equilibrium in > 80% localities	29,224
Present in 75% of individuals and in each putative populations	26,431
Alignment against SABD, *Tursiops aduncus* genome (Batley et al., 2021)	26,199 (99% alignment)
Exclude all SNPs but one within 330bp	17,875
Minor allele count <0.01 based on the 279 samples for southern and eastern Australian common dolphins	17,539
Minor allele count <0.01 based on the 65 samples for eastern Australian common dolphins	16,236
Average missing per locus	1%

Table D.2. Significance of the RDA and the portion explained by each component of the full model selection, at each scale, with an overall significant model of p = 0.0001.

Scale	Component	Inertia	Proportion
Southern and Eastern Australia	Total	3.95E+03	1.00E+00
	Conditional	5.13E+02	1.30E-01
	Constrained	1.31E+02	3.32E-02
	Unconstrained	3.31E+03	8.37E-01
Eastern Australia	Total	3.95E+03	1.00E+00
	Conditional	3.52E+02	8.92E-02
	Constrained	7.30E+01	1.85E-02
	Unconstrained	3.52E+03	8.92E-01

Table D.3. Pairwise F_{ST} values between sites based on putatively adaptive and neutral datasets for common dolphins (*Delphinus delphis*) in (A) southern and eastern Australia (B) eastern Australia. Upper right, neutral values (as in chapter 2), and lower left, adaptive values with their significance of the p-values by the B-Y method corrected represented by ***0.0001, **0.001, *0.05. Acronyms used as in Figure 4.1.

(A)

	ALB	**ESP**	**GAB**	**SG**	**GSV**	**ROB**	**PORT**	**MEL**	**EWP**	**EDN**	**SYD**	**BI**	**BB**
ALB	0	0.022***	0.026***	0.029***	0.056***	0.025***	0.026***	0.033***	0.047***	0.096***	0.134***	0.157***	0.201***
ESP	0.027***	0	0.015***	0.017***	0.044***	0.014***	0.015***	0.022***	0.036***	0.088***	0.124***	0.148***	0.190***
GAB	0.036***	0.018***	0	0.007***	0.034***	0.005***	0.006***	0.012***	0.026***	0.079***	0.114***	0.139***	0.180***
SG	0.038***	0.018***	0.011***	0	0.020***	0.004***	0.003***	0.010***	0.026***	0.087***	0.124***	0.148***	0.189***
GSV	0.084***	0.067***	0.068***	0.038***	0	0.027***	0.025***	0.029***	0.048***	0.111***	0.150***	0.172***	0.214***
ROB	0.033***	0.015***	0.008***	0.007***	0.055***	0	0.002***	0.007***	0.023***	0.081***	0.117***	0.142***	0.182***
PORT	0.036***	0.018***	0.008***	0.007***	0.053***	0.003***	0	0.005***	0.021***	0.078***	0.115***	0.140***	0.180***
MEL	0.053***	0.031***	0.015***	0.016***	0.059***	0.012***	0.009*	0	0.020***	0.066***	0.099***	0.123***	0.165***
EWP	0.087***	0.069***	0.049***	0.051***	0.098***	0.047***	0.040***	0.031***	0	0.060***	0.092***	0.116***	0.158***
EDN	0.248***	0.235***	0.210***	0.229***	0.282***	0.212***	0.207***	0.182***	0.140***	0	0.010***	0.026***	0.062***
SYD	0.305***	0.290***	0.264***	0.286***	0.339***	0.267***	0.262***	0.237***	0.196***	0.017***	0	0.009***	0.043***
BI	0.353***	0.339***	0.314***	0.333***	0.383***	0.317***	0.312***	0.291***	0.251***	0.045***	0.011*	0	0.032***
BB	0.421***	0.401***	0.376***	0.392***	0.442***	0.379***	0.373***	0.355***	0.317***	0.113***	0.065***	0.044***	0

(B)

	BB	**BI**	**SYD**	**EDN**
BB	0	0.032***	0.043***	0.062***
BI	0.040*	0	0.009*	0.026***
SYD	0.070***	0.025	0	0.010***
EDN	0.153***	0.080***	0.026***	0

Table D.4. Gene Ontology (GO) Terms significance for southern and eastern Australian common dolphins (*Delphinus delphis*), comparing the full dataset with the putative candidate loci by Fisher's exact test. Biological Process (BP), Molecular Function (MF), Cellular Component (CC).

	GO.ID	**Term**	**Annotated**	**Significant**	**Expected**	**Fisher value**
BP	GO:0016192	vesicle-mediated transport	47	7	9.66	0.0058
	GO:0044271	cellular nitrogen compound biosynthetic process	133	7	27.34	0.0158
	GO:0007267	cell-cell signaling	26	4	5.34	0.0222
	GO:0019219	regulation of nucleobase-containing compound metabolic process	86	6	17.68	0.0231
	GO:0051252	regulation of RNA metabolic process	81	6	16.65	0.0304
	GO:0009889	regulation of biosynthetic process	84	6	17.27	0.0413
	GO:0018130	heterocycle biosynthetic process	111	6	22.82	0.0429

	GO:0032774	RNA biosynthetic process	88	6	18.09	0.0491
	GO:0070647	protein modification by small protein conjugation or removal	16	2	3.29	0.0543
	GO:0031326	regulation of cellular biosynthetic process	83	6	17.06	0.0574
	GO:0010256	endomembrane system organization	8	2	1.64	0.0581
	GO:1901615	organic hydroxy compound metabolic process	9	2	1.85	0.0589
	GO:0006508	proteolysis	27	3	5.55	0.0589
	GO:0034654	nucleobase-containing compound biosynthetic process	105	6	21.58	0.0641
	GO:0010556	regulation of macromolecule biosynthetic process	83	6	17.06	0.0712
	GO:0006351	transcription, DNA-templated	88	6	18.09	0.0729
	GO:0032940	secretion by cell	20	3	4.11	0.085
	GO:0010817	regulation of hormone levels	13	3	2.67	0.0888
	GO:0006979	response to oxidative stress	5	1	1.03	0.0893
	GO:0006887	exocytosis	10	3	2.06	0.0949
MF	GO:0008234	cysteine-type peptidase activity	22	3	3.63	0.027
	GO:0101005	ubiquitinyl hydrolase activity	13	2	2.14	0.059
	GO:0016614	oxidoreductase activity, acting on CH-OH group of donors	11	2	1.81	0.068
	GO:0030246	carbohydrate binding	25	3	4.12	0.086

	GO:0030594	neurotransmitter receptor activity	8	2	1.32	0.107
	GO:0004713	protein tyrosine kinase activity	7	1	1.15	0.119
	GO:0035639	purine ribonucleoside triphosphate binding	188	7	31	0.125
	GO:0044877	protein-containing complex binding	32	3	5.28	0.151
	GO:0060089	molecular transducer activity	68	5	11.21	0.155
	GO:0019199	transmembrane receptor protein kinase activity	5	1	0.82	0.175
	GO:0008081	phosphoric diester hydrolase activity	15	2	2.47	0.176
	GO:0019200	carbohydrate kinase activity	5	1	0.82	0.181
	GO:0043565	sequence-specific DNA binding	28	3	4.62	0.182
	GO:0004843	thiol-dependent ubiquitin-specific protease activity	6	2	0.99	0.192
	GO:0016209	antioxidant activity	5	1	0.82	0.195
	GO:0008092	cytoskeletal protein binding	72	5	11.87	0.202
	GO:0005088	Ras guanyl-nucleotide exchange factor activity	10	1	1.65	0.208
	GO:0005319	lipid transporter activity	5	1	0.82	0.209
	GO:0016684	oxidoreductase activity, acting on peroxide as acceptor	5	1	0.82	0.211
	GO:0008134	transcription factor binding	5	1	0.82	0.211
CC	GO:0099568	cytoplasmic region	5	2	0.95	0.015

GO:0042995	cell projection	17	3	3.23	0.035
GO:0005929	cilium	12	2	2.28	0.091
GO:0045202	synapse	23	3	4.36	0.095
GO:0005768	endosome	6	1	1.14	0.107
GO:0030054	cell junction	14	2	2.66	0.144
GO:0044441	ciliary part	6	1	1.14	0.153
GO:0099023	tethering complex	6	1	1.14	0.163
GO:0044456	synapse part	16	2	3.04	0.178
GO:0043233	organelle lumen	39	2	7.4	0.181
GO:0044429	mitochondrial part	7	1	1.33	0.223
GO:0044463	cell projection part	6	1	1.14	0.242
GO:0005815	microtubule organizing center	6	1	1.14	0.257
GO:0044421	extracellular region part	21	2	3.98	0.269
GO:0005875	microtubule associated complex	11	1	2.09	0.299
GO:0097458	neuron part	8	1	1.52	0.31
GO:0030117	membrane coat	9	1	1.71	0.315
GO:0098590	plasma membrane region	8	1	1.52	0.33
GO:1902494	catalytic complex	41	2	7.78	0.337
GO:0044444	cytoplasmic part	113	6	21.44	0.346

Table D.5. Gene Ontology (GO) Terms significance for eastern Australian common dolphins (*Delphinus delphis*), comparing the full dataset with the putative candidate loci by Fisher's exact test. Biological Process (BP), Molecular Function (MF), Cellular Component (CC).

	GO.ID	**Term**	**Annotated**	**Significant**	**Expected**	**Fisher value**
BP	GO:0032259	methylation	19	2	2.32	0.039
	GO:0006366	transcription by RNA polymerase II	20	2	2.44	0.05
	GO:0006357	regulation of transcription by RNA polymerase	19	2	2.32	0.054
	GO:0008152	metabolic process	399	7	48.72	0.057
	GO:0031328	positive regulation of cellular biosynthetic	8	1	0.98	0.085
	GO:0009891	positive regulation of biosynthetic proc.	9	1	1.1	0.09
	GO:0010557	positive regulation of macromolecule bio	8	1	0.98	0.107
	GO:0009890	negative regulation of biosynthetic proc	11	1	1.34	0.111
	GO:0031327	negative regulation of cellular biosynthetic	11	1	1.34	0.121
	GO:0051172	negative regulation of nitrogen compound	13	1	1.59	0.124
	GO:0010558	negative regulation of macromolecule bio	10	1	1.22	0.135
	GO:0010628	positive regulation of gene expression	7	1	0.85	0.137
	GO:0045934	negative regulation of nucleobase-contain	9	1	1.1	0.139
	GO:0051173	positive regulation of nitrogen compound	15	1	1.83	0.14

	GO:2000113	negative regulation of cellular macromolecule	10	1	1.22	0.141
	GO:0045935	positive regulation of nucleobase-contain	10	1	1.22	0.15
	GO:0009889	regulation of biosynthetic process	84	2	10.26	0.152
	GO:1902680	positive regulation of RNA biosynthetic	7	1	0.85	0.152
	GO:0051254	positive regulation of RNA metabolic pro.	7	1	0.85	0.153
	GO:0010467	gene expression	139	3	16.97	0.153
MF	GO:0140110	transcription regulator activity	42	3	4.72	0.014
	GO:0016741	transferase activity, transferring one-c.	29	2	3.26	0.079
	GO:0003712	transcription coregulator activity	8	2	0.9	0.088
	GO:0003676	nucleic acid binding	225	5	25.27	0.122
	GO:0016817	hydrolase activity, acting on acid anhyd.	92	2	10.33	0.125
	GO:0016740	transferase activity	230	4	25.83	0.166
	GO:0005515	protein binding	218	4	24.48	0.18
	GO:0005088	Ras guanyl-nucleotide exchange factor ac.	10	1	1.12	0.208
	GO:0022803	passive transmembrane transporter activi.	49	2	5.5	0.211
	GO:1901363	heterocyclic compound binding	435	6	48.85	0.283
	GO:0097159	organic cyclic compound binding	437	6	49.08	0.288
	GO:0044877	protein-containing complex binding	32	1	3.59	0.295
	GO:0046982	protein heterodimerization activity	7	1	0.79	0.304
	GO:0031267	small GTPase binding	15	1	1.68	0.306

	GO:0004386	helicase activity	17	1	1.91	0.34
	GO:0005267	potassium channel activity	14	1	1.57	0.341
	GO:0098772	molecular function regulator	98	2	11.01	0.351
	GO:0046983	protein dimerization activity	23	1	2.58	0.362
	GO:0015079	potassium ion transmembrane transporter	18	1	2.02	0.391
	GO:0016758	transferase activity, transferring hexos	13	1	1.46	0.394
CC	GO:0044464	cell part	445	10	56.19	0.013
	GO:0005623	cell	457	10	57.7	0.016
	GO:0043226	organelle	297	7	37.5	0.052
	GO:1902495	transmembrane transporter complex	23	1	2.9	0.163
	GO:0032991	protein-containing complex	174	4	21.97	0.17
	GO:0008076	voltage-gated potassium channel complex	8	1	1.01	0.17
	GO:0044427	chromosomal part	10	1	1.26	0.201
	GO:0016459	myosin complex	11	1	1.39	0.208
	GO:0005887	integral component of plasma membrane	30	1	3.79	0.214
	GO:0015629	actin cytoskeleton	14	1	1.77	0.215
	GO:0031226	intrinsic component of plasma membrane	31	1	3.91	0.219
	GO:0005694	chromosome	12	1	1.52	0.233
	GO:0044431	Golgi apparatus part	19	1	2.4	0.259
	GO:0044422	organelle part	143	3	18.06	0.275

GO:0043231	intracellular membrane-bounded organelle	199	6	25.13	0.318
GO:0031090	organelle membrane	30	1	3.79	0.33
GO:0005622	intracellular	350	9	44.19	0.334
GO:0044424	intracellular part	350	9	44.19	0.334
GO:0043227	membrane-bounded organelle	209	6	26.39	0.334
GO:0034705	potassium channel complex	8	1	1.01	0.4

Table D.6. Genes and function of the candidate genes found in exonic regions that were over enriched by the Gene Ontology analyses for the putatively adaptive SNPs discovered by the RDA of southern and eastern Australian common dolphins (*Delphinus delphis*). (A) 646 loci at broad-scale (southern and eastern Australian common dolphins), and (B) 172 at fine-scale (eastern Australian common dolphins).

(A)

Genes in exons	**Environmental variable associated**	**Pathway (reactome)**	**Function (Uniprot)**	**Family**	**General function described**	**References**
NR2F2/6 Missense exon	salinity range	Nucleoplasm-NR2F6:Gene expression in transcription pathway. Adipogenesis is the process of cell differentiation by which preadipocytes become adipocytes.	*Lipotes vexillifer* (Yangtze river dolphin) NR2F2-gene and COUP transcription factor 2-like isoform X3. Human: NR2F2 Ligand-activated transcription factor.	NR2	Regulation of adipogenesis, glucose, homeostasis and metabolism energy.	(Li et al., 2009; Jeong et al., 2014; Baldwin et al., 2017)
RPS8/40S ribosomal protein 58 Missense exon	sea surface temperature mean	RPS8 Humans Cytosol: Metabolism different routes	*Tursiops truncatus*: Molecular function structural constituent of ribosome and biological process-translation. Humans Bovine: RNA binding and structural constituent of ribosome and biological process-translation.	RPS	KEGG pathways acting at the ribosome level, that regulated lipogenesis when switching dietary source and ribosomal hypoxia stress	(Chen et al., 2015; Chen et al., 2016; Foote et al., 2016; Desert et al., 2018; Marra et al., 2019)
ZFYVE27/ Protrudin Missense exon	primary productivity minimum	ZFYVE: Early endosome membrane.	*Tursiops truncatus*: Metal ion binding. Humans: Key regulator of RAB-dependent vesicular trafficking during neurite	ZPF	Acts by controlling DNA methylation during earliest multicellular stages of development at multiple imprinting	(Matthews and Sunde, 2002;

			extension through polarized membrane transport.		control regions and may be altered by nutrients in the diet.	Foote et al., 2016; Lim et al., 2020)

(B)

Gene in exons	**Environmental variable associated**	**Pathway (reactome)**	**Function (Uniprot)**	**Family**	**General function described**	**References**
PDCD2L Missense exon	primary productivity	PDCD2: Interaction with Q16342 Metabolism of proteins PDCD1: Plasma membrane-immune system costimulation by the CD28 family (T cells).	*Physeter macrocephalus* (Sperm whale) PDCD2L-gene programmed cell death with no function provided Human: PDCD2L Over-expression suppresses AP1, CREB, NFAT, and NF-kB transcriptional activation, and delays cell cycle progression at S phase.	PDC	Program cell death (apoptosis), helps in the stability of the genome.	(Dineshram et al., 2015; Bidle, 2016; e.g. Marra et al., 2019; e.g. Tollis et al., 2019)

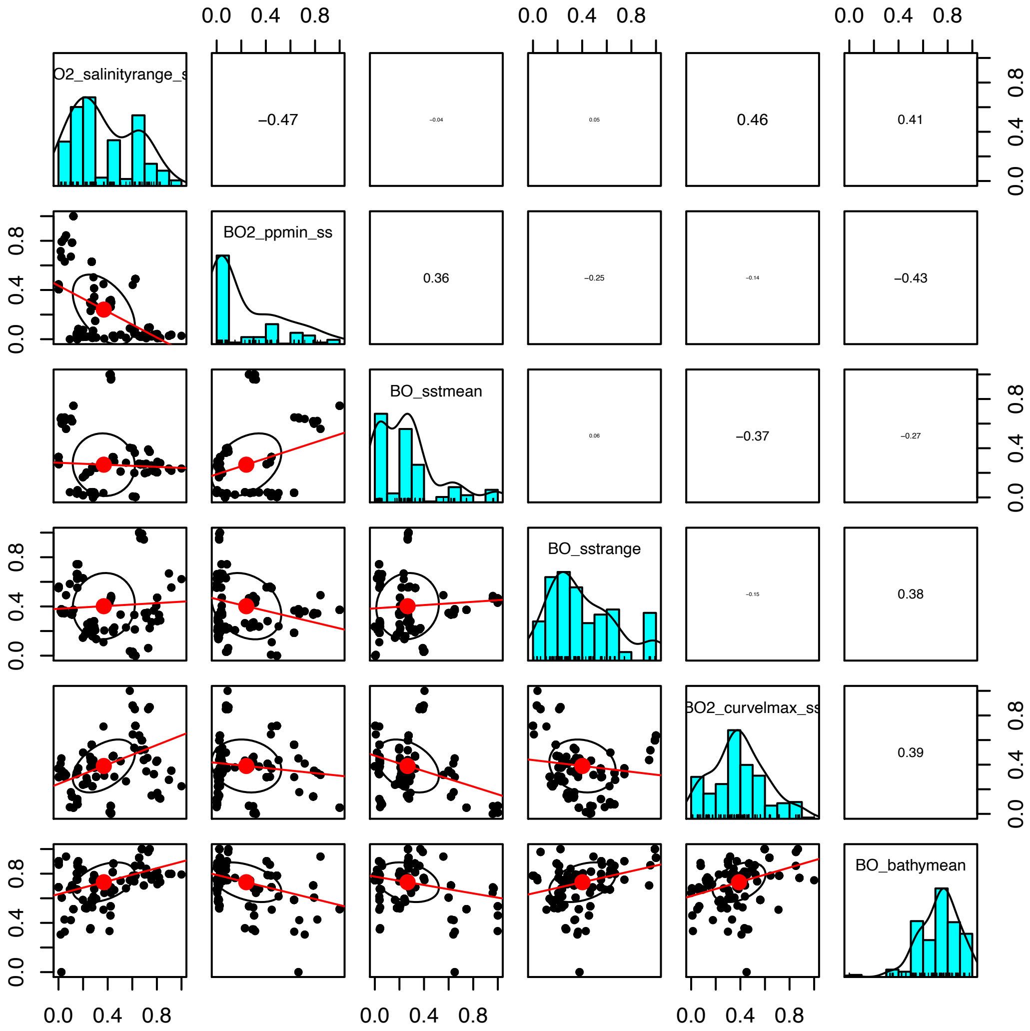
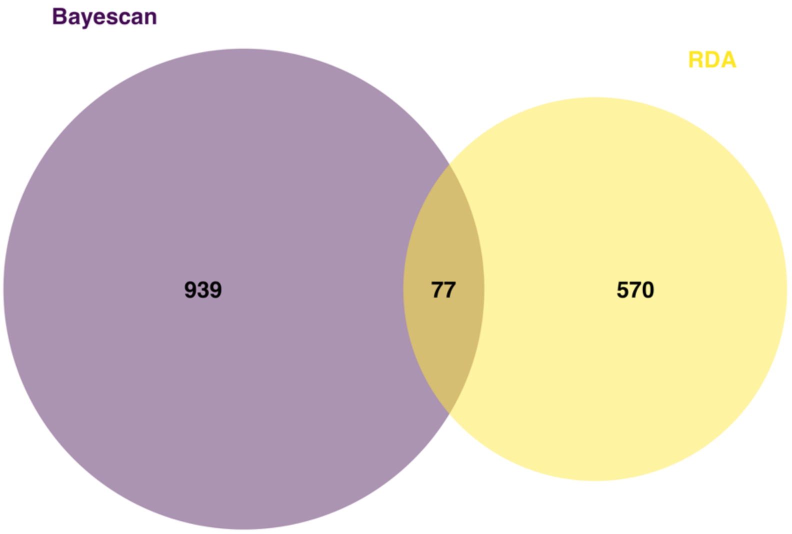
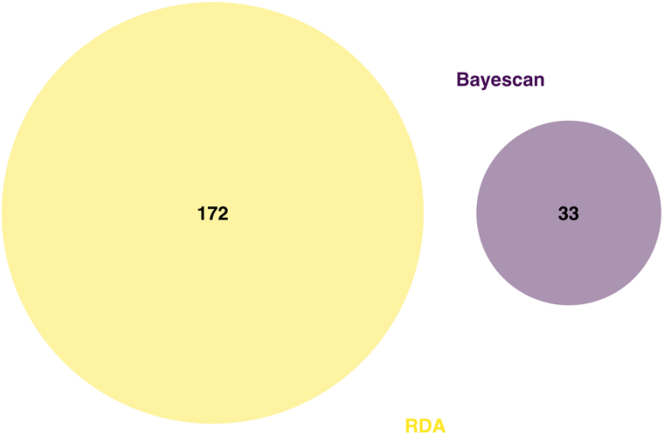


Figure D.1. Variance inflate factor (VIF) of the six environmental variables used for southern and eastern Australia analysis of RDA. Salinity range (BO2_salinityrange_ss), primary productivity minimum (BO2_ppmin_ss), sea surface temperature mean (BO_sstmean), sea surface temperature range (BO_sstrange), current velocity maximum (BO2_curvelmax_ss) and bathymetry mean (BO_bathymean).



(A)



(B)

Figure D.2. Candidate loci putatively under selection for southern and eastern Australian common dolphins (*Delphinus delphis*) based on the candidate loci RDA, and the Bayesian outlier test. (A) broad-scale, and (B) fine-scale.

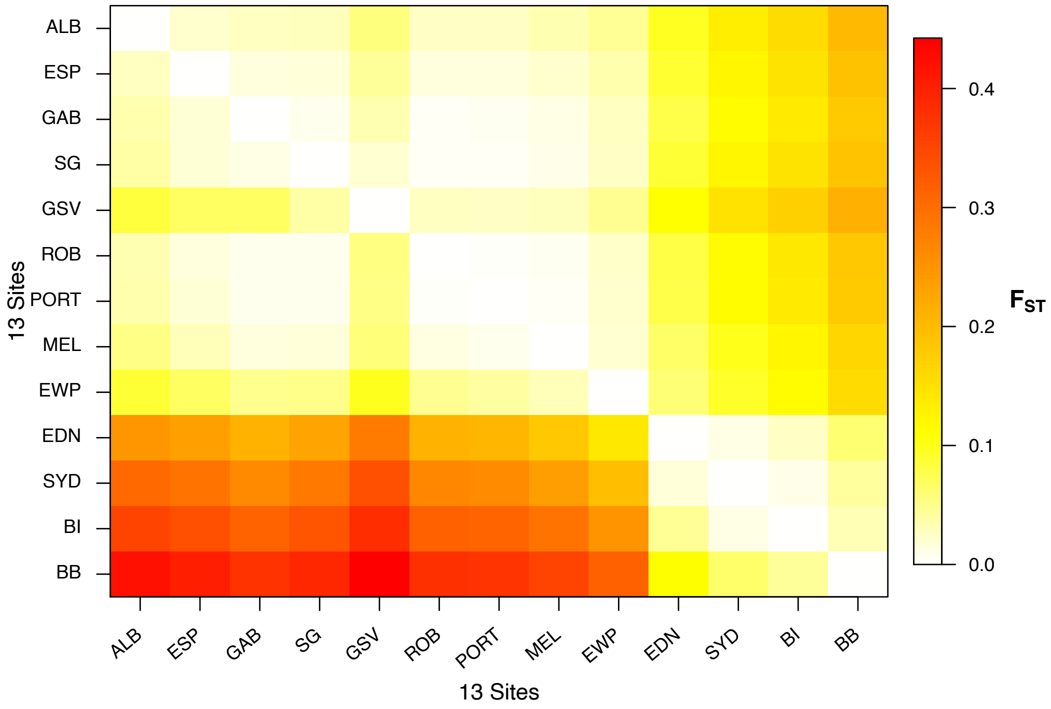


Figure D.3. Heatmap of pairwise F_{ST} values between sites* values based on the adaptive and neutral datasets for southern and eastern Australian common dolphins (*Delphinus delphis*). Upper right, neutral dataset (as in chapter 2), and lower left, adaptive dataset.

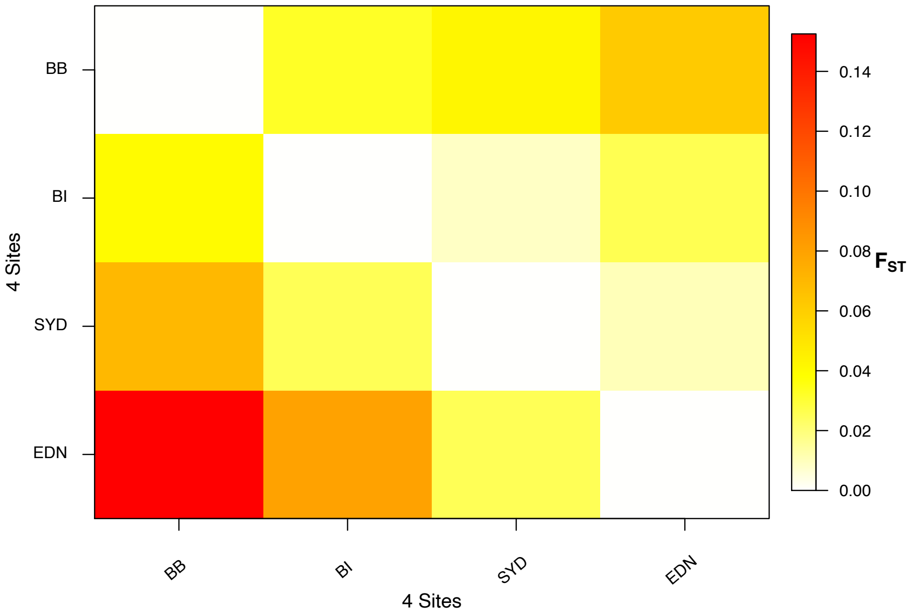


Figure D.4. Heatmap of pairwise F_{ST} values between sites* values based on the adaptive and neutral datasets for eastern Australian common dolphins (*Delphinus delphis*). Upper right, neutral dataset (as in chapter 2), and lower left, adaptive dataset.

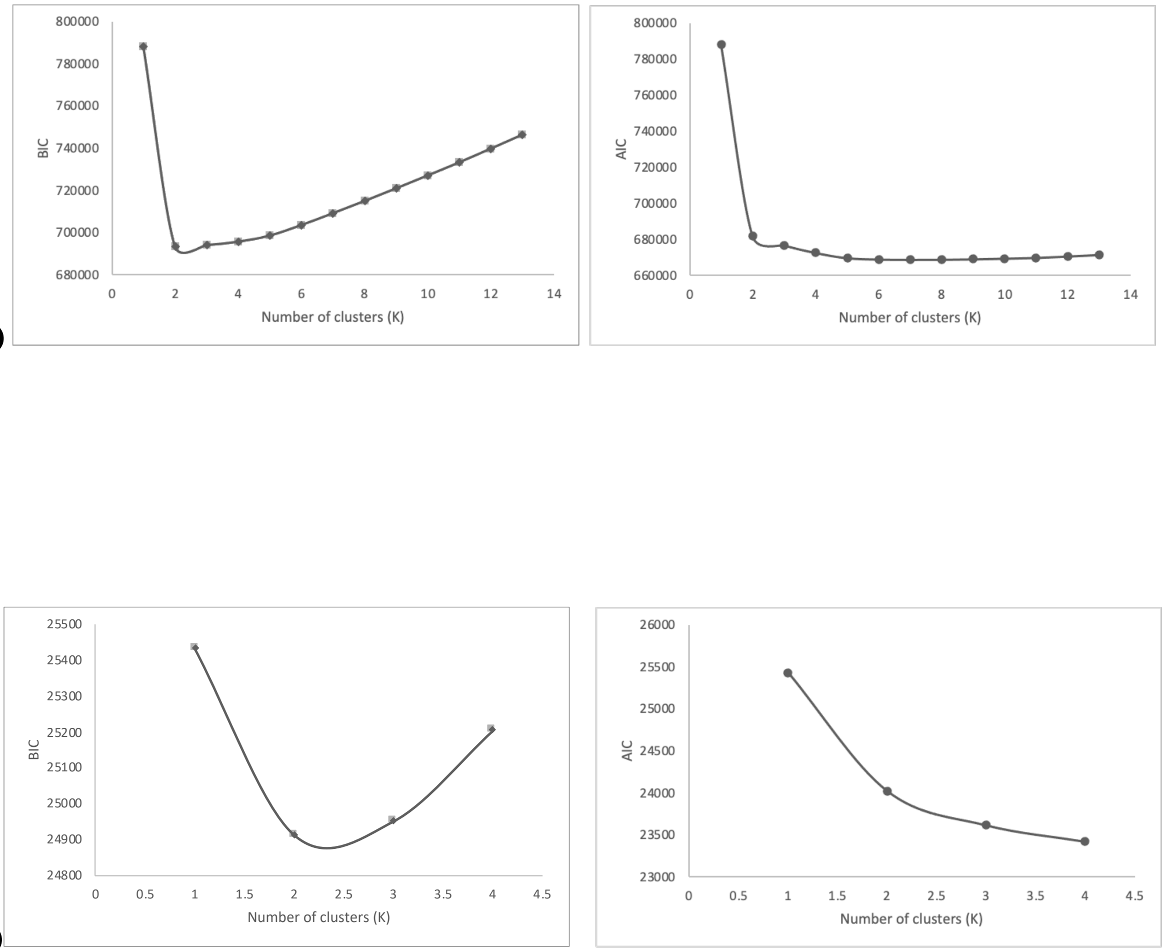
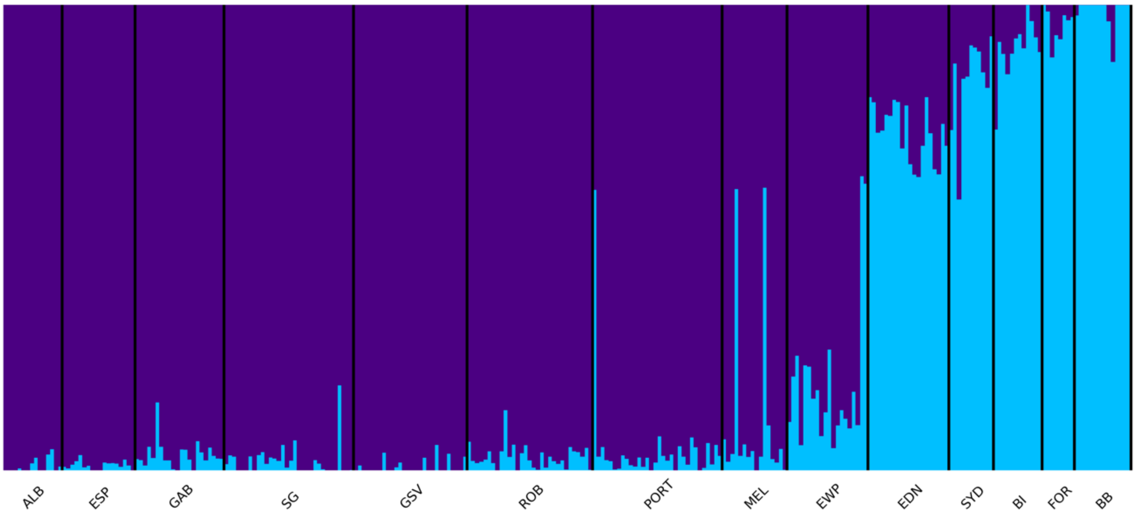
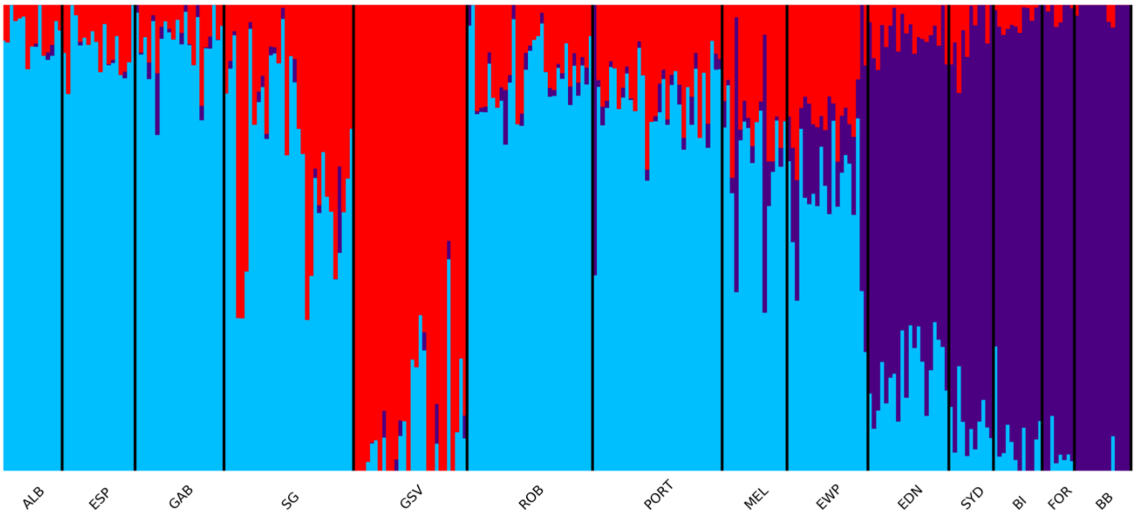


Figure D.5. Bayesian Information Criterion (BIC) and Akaike Information Criterion (AIC) used to determine the best-supported number of clusters in the putative adaptive datasets. (A) broad-scale, and (B) fine-scale.

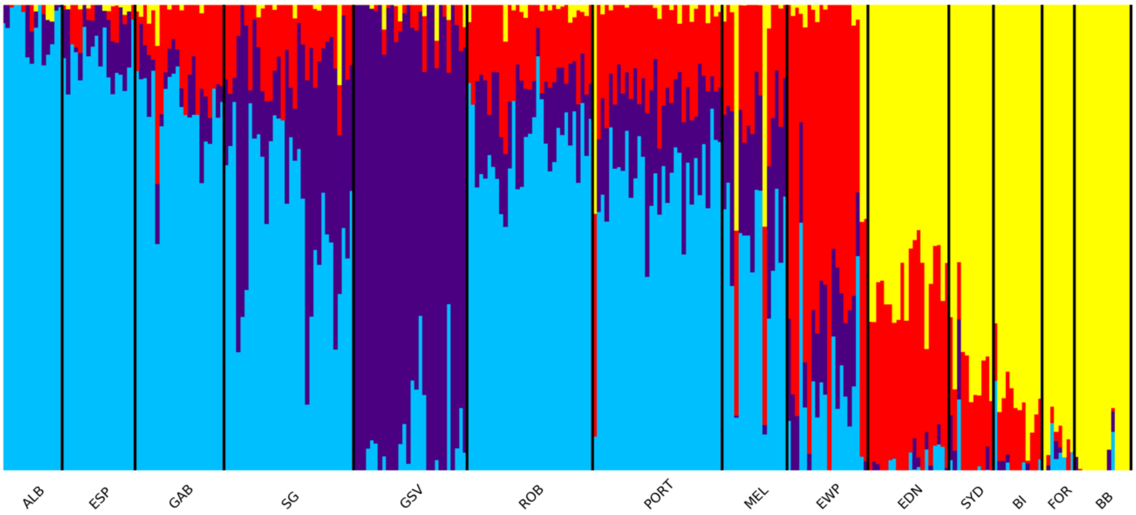
(A) K2*


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP
EDN
SYD
BI
FOR
BB

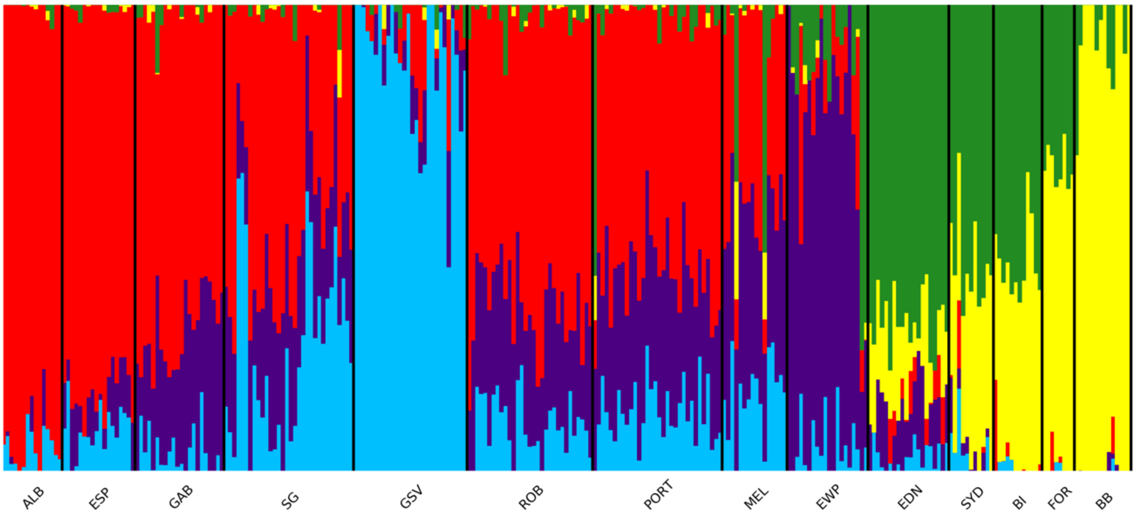
(B) K3


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP
EDN
SYD
BI
FOR
BB

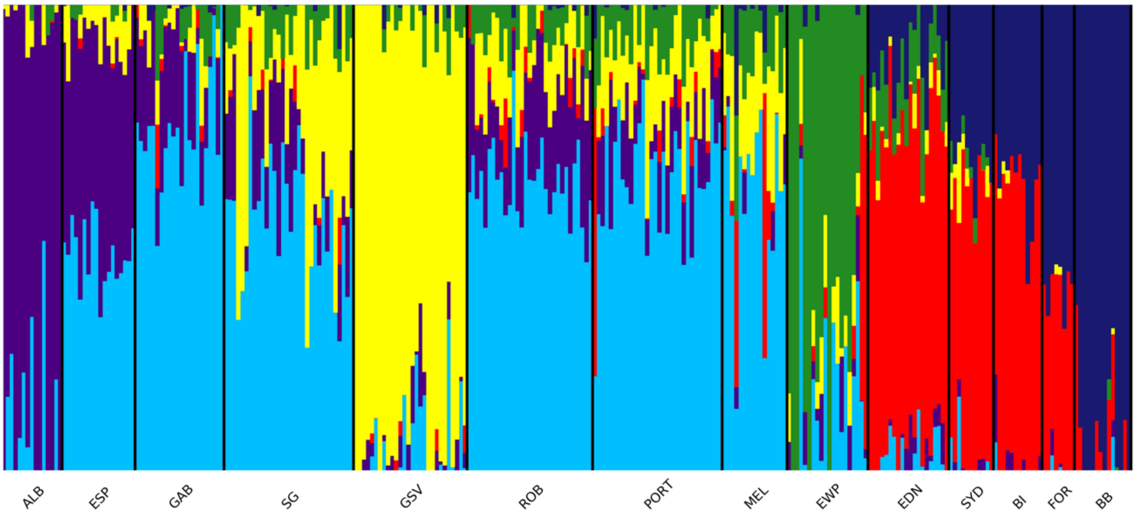
(C) K4


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP
EDN
SYD
BI
FOR
BB

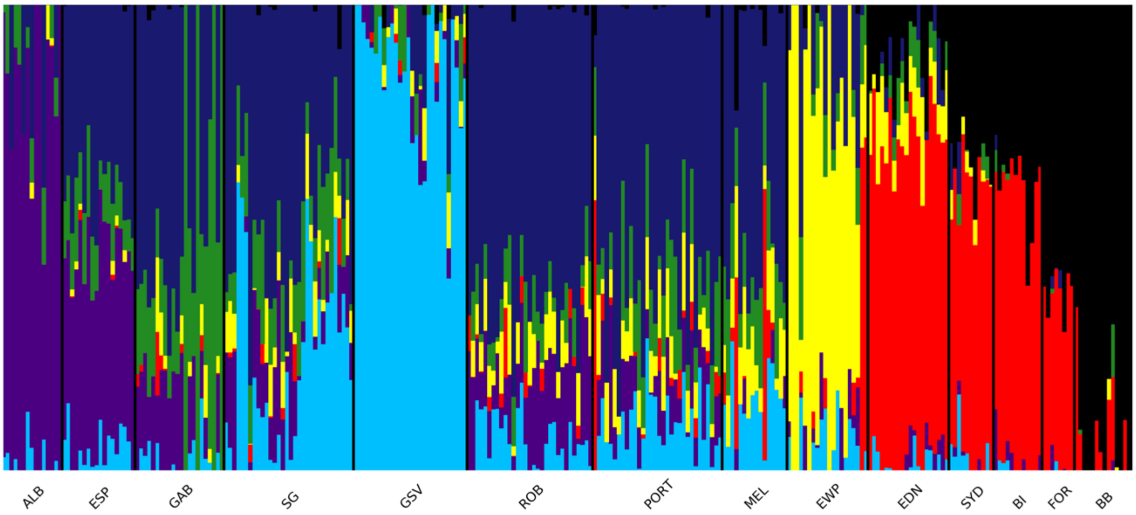
(D) K5


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP
EDN
SYD
BI
FOR
BB

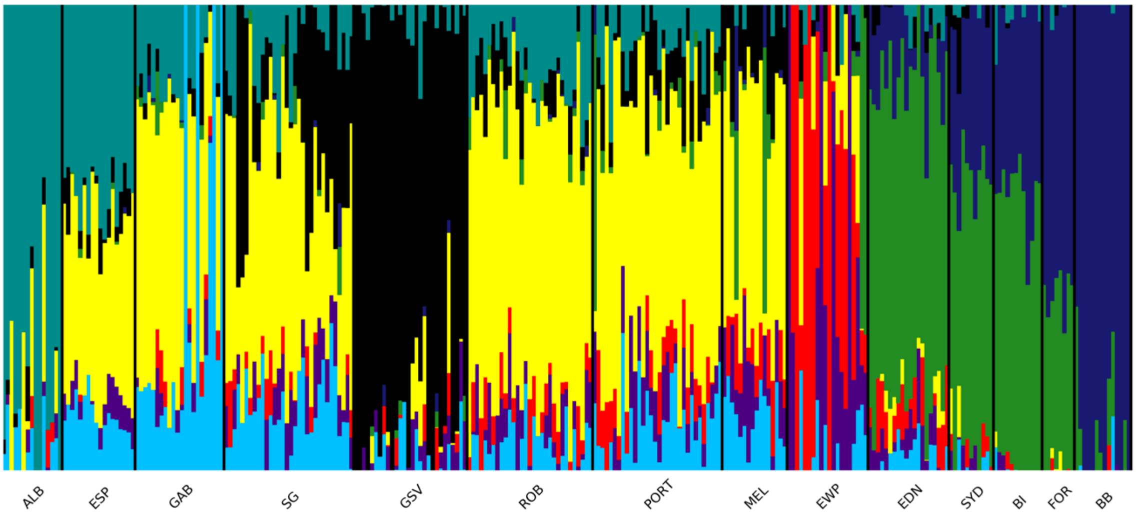
(E) K6


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP
EDN
SYD
BI
FOR
BB

(F) K7


ALB
ESP
GAB
SG
GSV
ROB
PORT
MEL
EWP
EDN
SYD
BI
FOR
BB

(G) K8



(H) K9

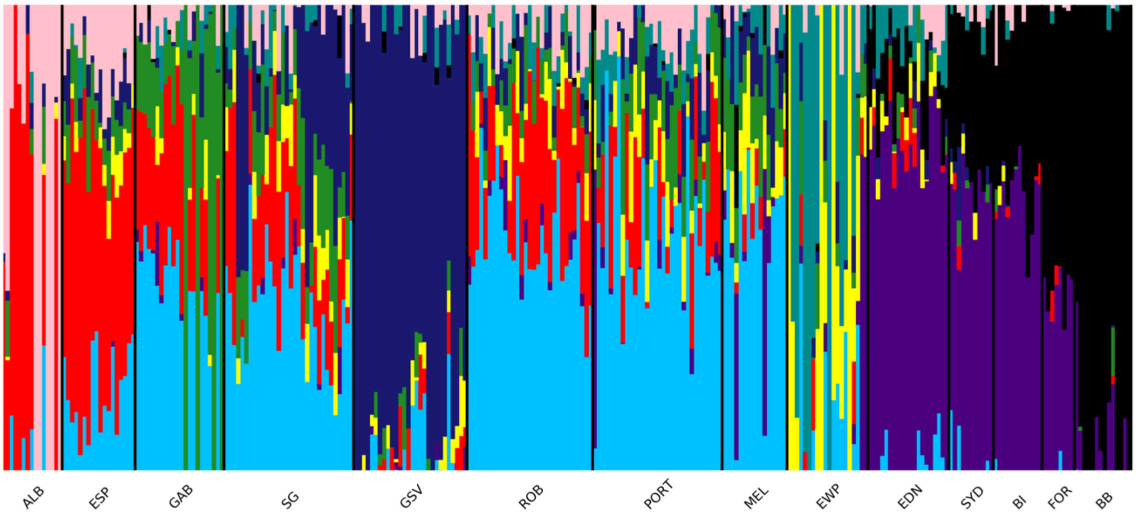
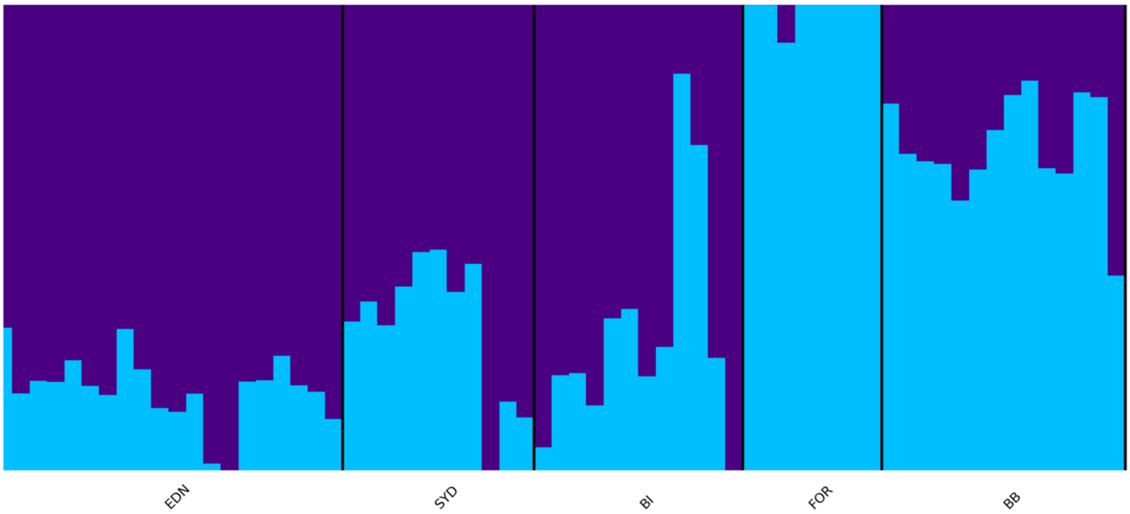
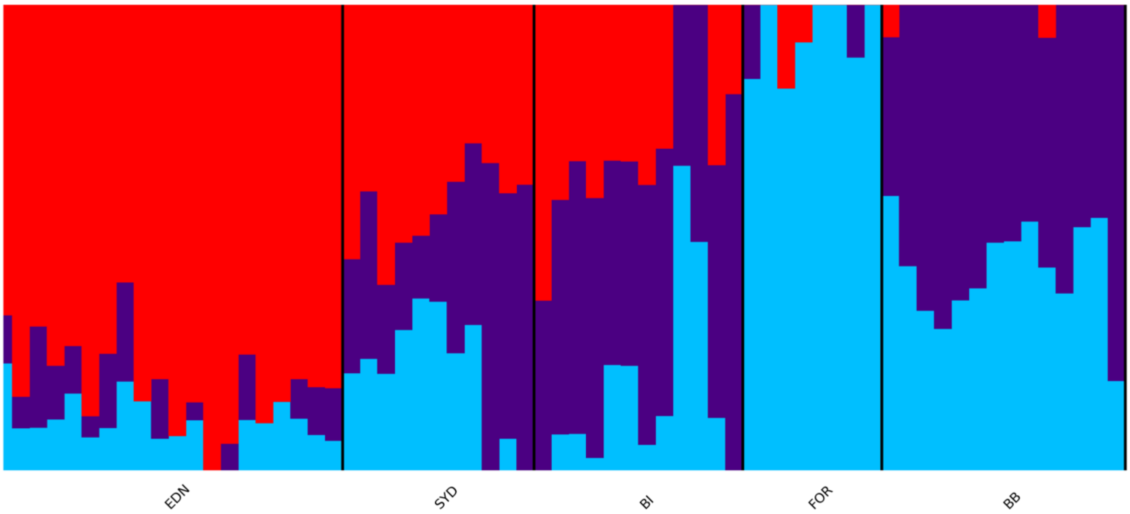


Figure D.6. Population genomic structure analysis using Admixture, based on putatively adaptive SNPs for southern and eastern Australian common dolphins (*Delphinus delphis*) (labelled by sampling site and individual). K represents the number of populations tested (A to H), in which K2* is the only most supported and highly likely number of populations suggested by the analysis. Acronyms used as in Figure 4.1.

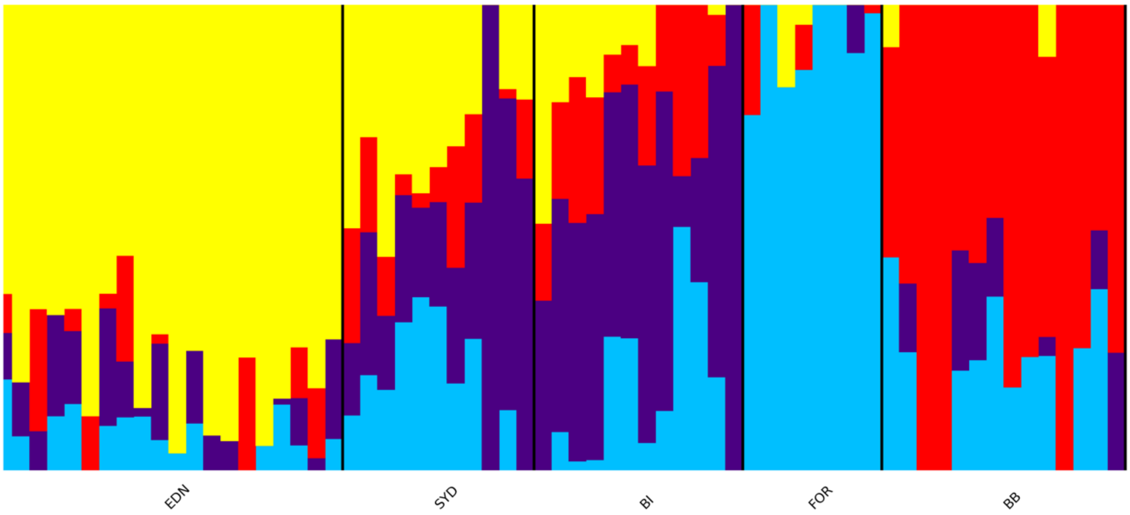
(A) K2



(B) K3*



(C) K4*



(D) K5

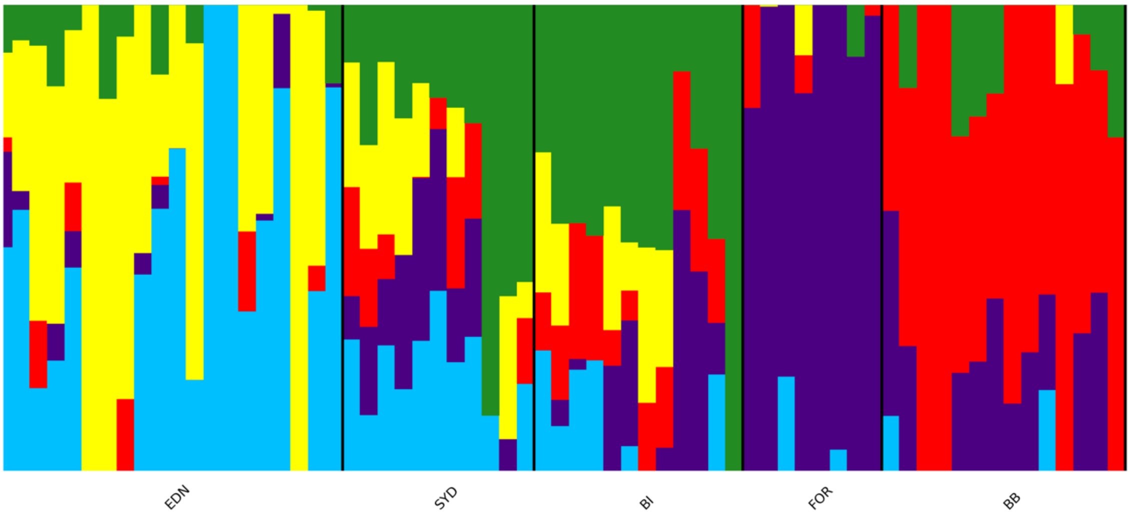


Figure D.7. Population genomic structure analysis using Admixture, based on putatively adaptive SNPs for eastern Australian common dolphins (*Delphinus delphis*) (labelled by sampling site and individual). K represents the number of populations tested (A to D), in which K3* and K4* are both correctly assigned as they are the most supported and highly likely number of local populations suggested by the analysis. Acronyms used as in Figure 4.1.

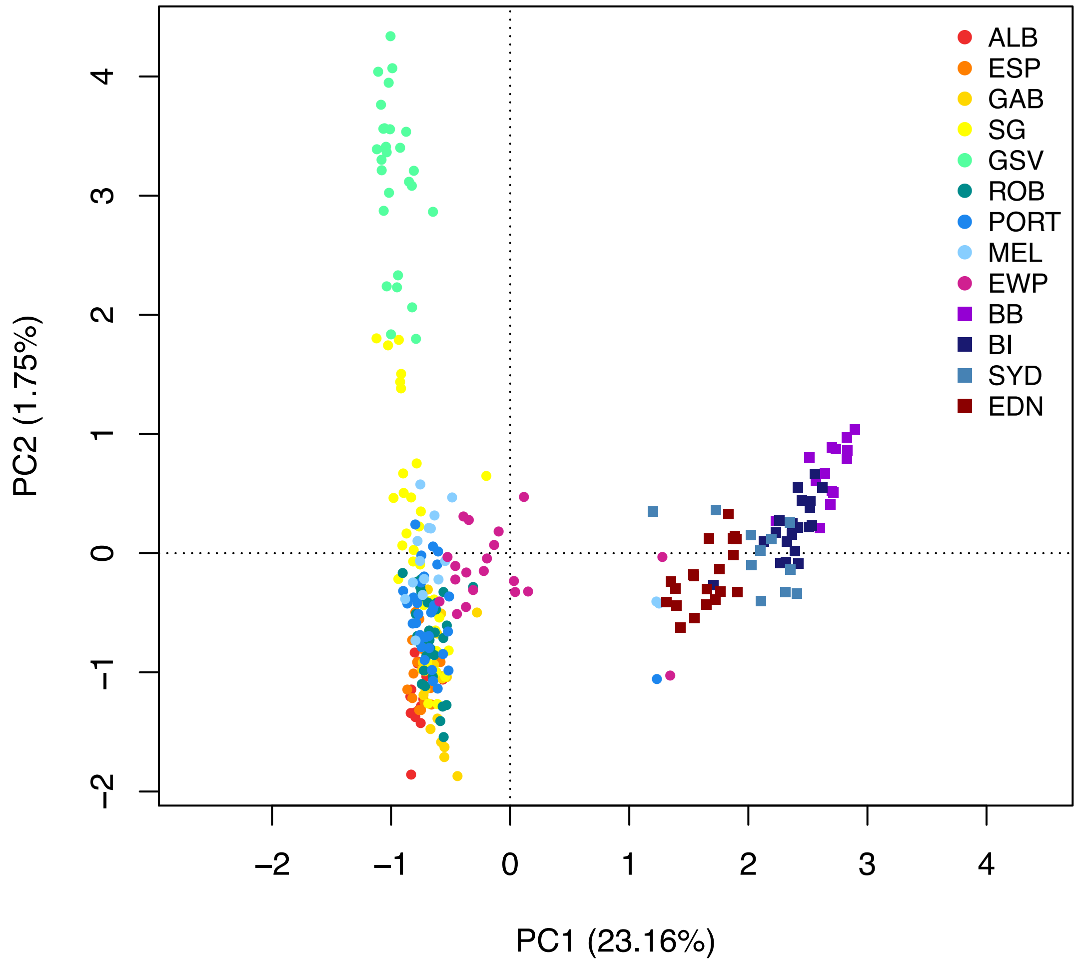


Figure D.8. Principal Component Analysis (PCA) based on 1586 candidate adaptive loci for southern and eastern Australasian common dolphins (*Delphinus delphis*). *Acronyms used as in Figure 4.1.

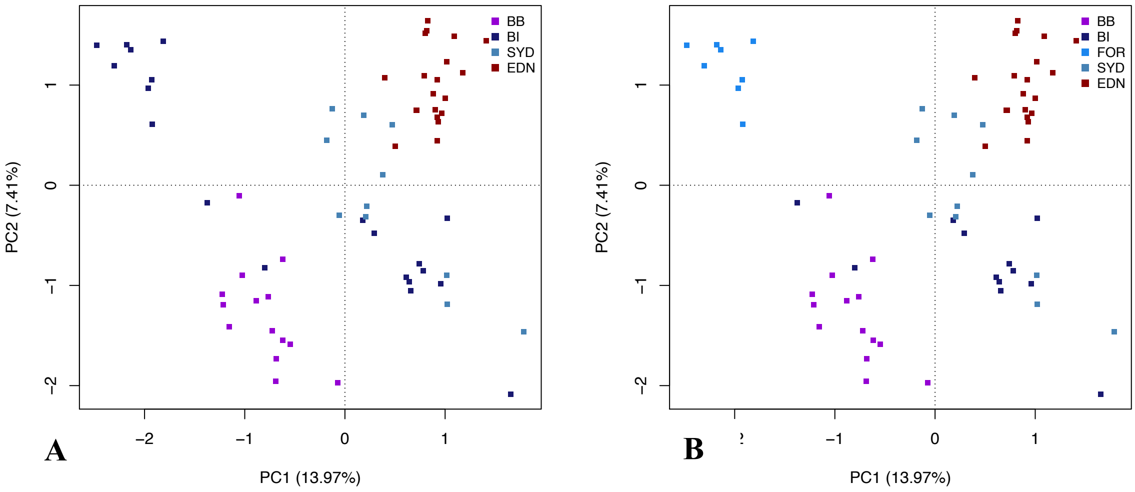


Figure D.9. PCA based on 205 candidate adaptive loci for eastern Australasian common dolphins (*Delphinus delphis*). **(A)** *Acronyms used as in Figure 4.1. **(B)** Alternative PCA separating individuals from Forster (FOR) and Broughton Island (BI).

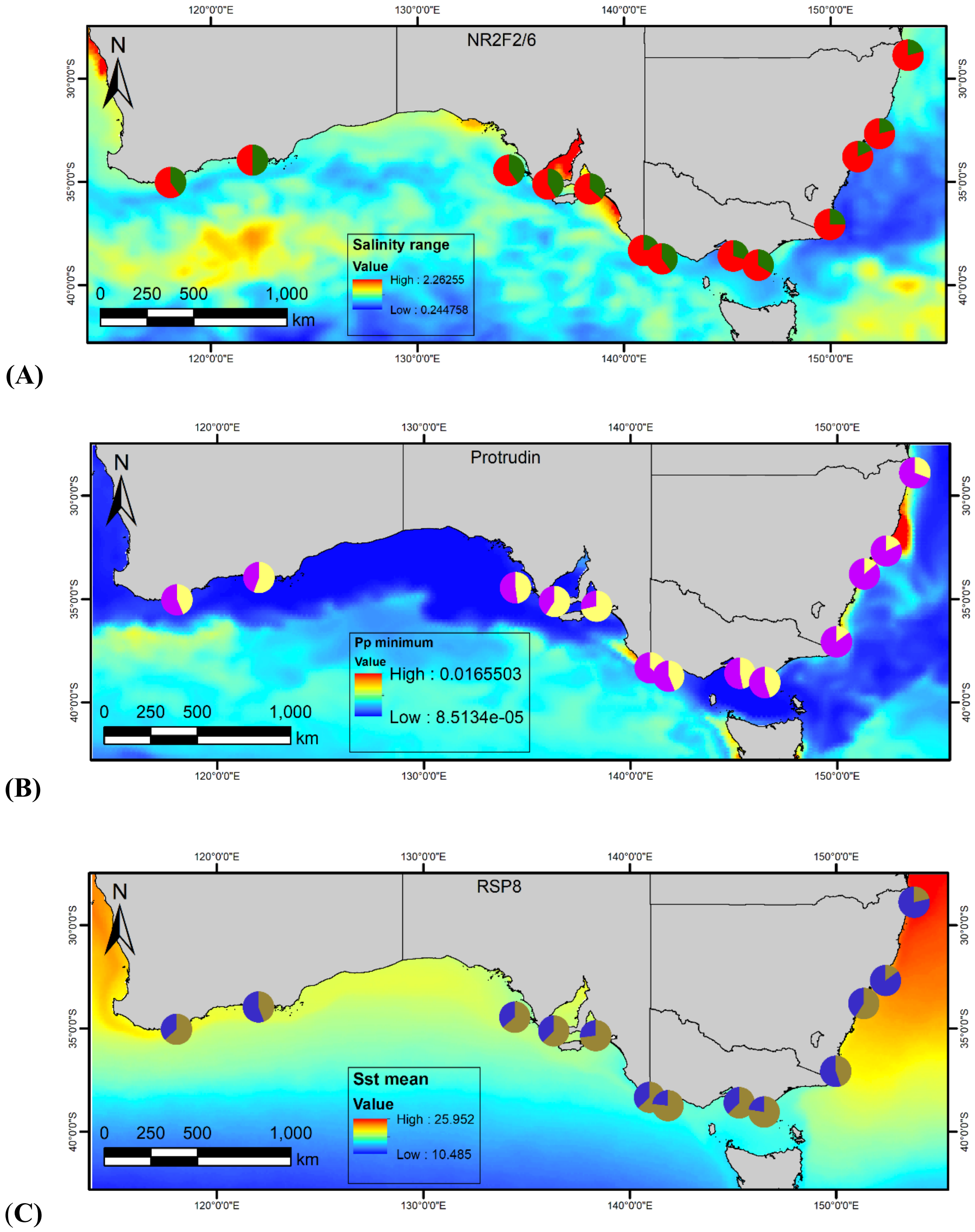


Figure D.10. Allele frequency changes for the candidate genes found in exonic regions across sampling sites of common dolphins (*Delphinus delphis*) in southern and eastern Australia. **(A)** NR2F6/NR2F2 associated with salinity. **(B)** Protrudin associated with primary productivity, and **(C)** RPS8 associated with temperature.

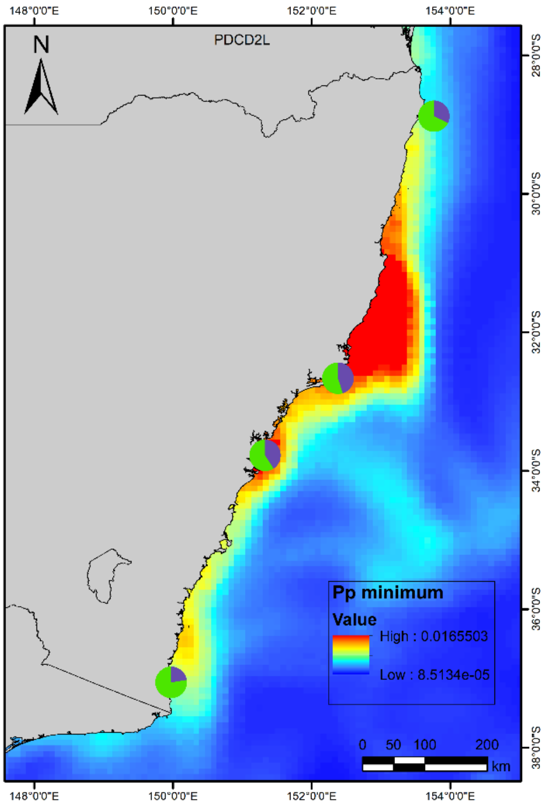
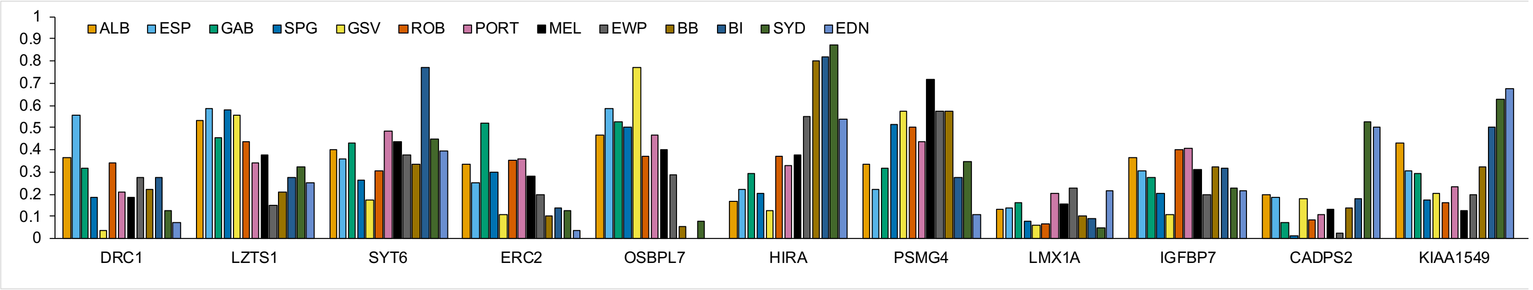
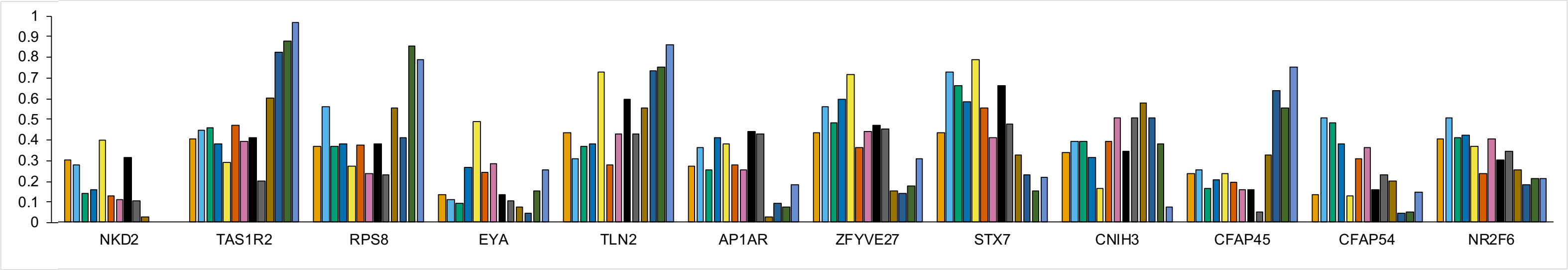


Figure D.11. Allele frequency changes for the candidate genes found in exonic regions across sampling sites of common dolphins (*Delphinus delphis*) in eastern Australia. PDCD2L associated with primary productivity.

(A)



1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
ALB
ESP
GAB
SPG
GSV
ROB
PORT
MEL
EWP
BB
BI
SYD
EDN
DRC1
LZTS1
SYT6
ERC2
OSBPL7
HIRA
PSMG4
LMX1A
IGFBP7
CADPS2
KIAA1549



1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
NKD2
TAS1R2
RPS8
EYA
TLN2
AP1AR
ZFYVE27
STX7
CNIH3
CFAP45
CFAP54
NR2F6

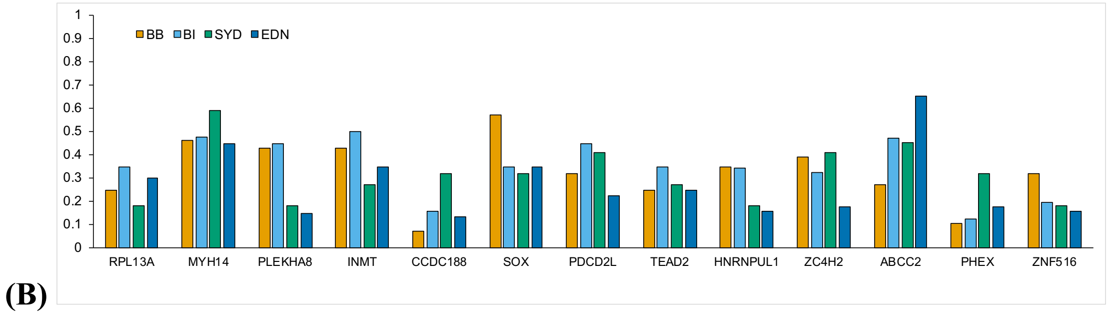


Figure D.12. Minor allele frequencies of positive selected SNPs by a gene enrichment test, with bearing variants in coding and non-coding regions. (**A**) 23 SNPs at broad-scale southern and eastern Australian common dolphins. (**B**) 13 SNPs at fine-scale eastern Australian common dolphins.

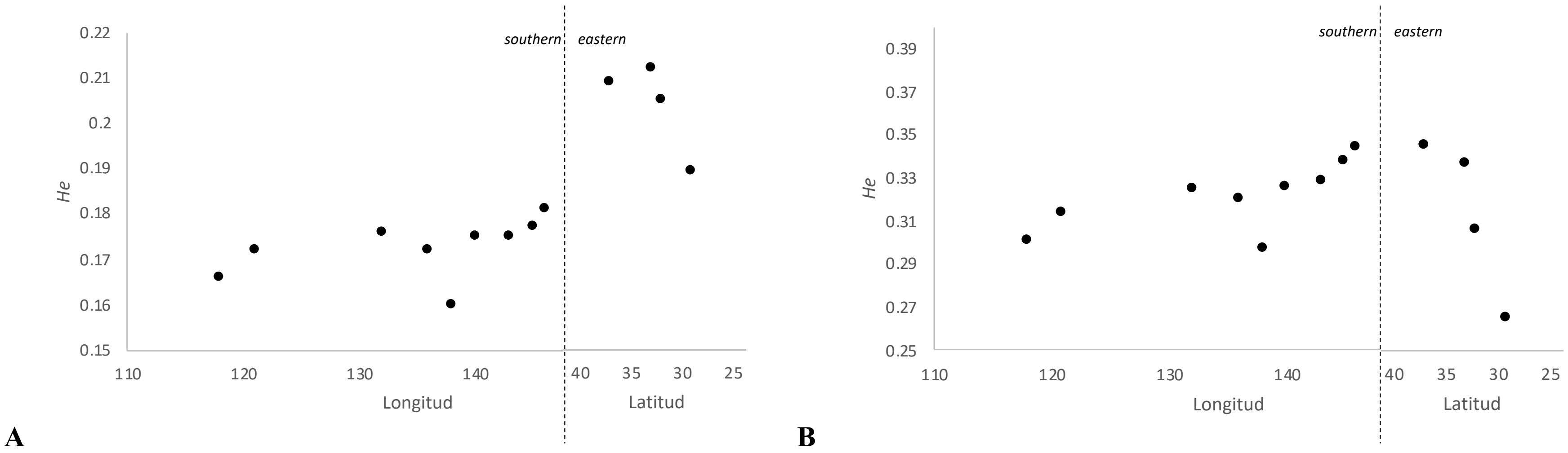


Figure D.13. Associations between heterozygosity and longitude/latitude location of sites at broad-scale in southern and eastern Australian common dolphins (*Delphinus delphis*). (**A**) Putative neutral dataset with 14,799 loci **(B)** Putative adaptive dataset with 1,586 loci.

APPENDIX E. ADDITIONAL INFORMATION USED FOR THE GEA AND BASH SCRIPTS

Environmental variables

Environmental variables used for the Genotype-Environment Association multivariable analyses were download from the updated datasets of BioOracle using the R package ‘sdmpredictors’ (Tyberghein et al., 2012; Assis et al., 2018).

Selected variables from BioOracle were originally measures of satellite Moderate Resolution Imaging Spectroradiometer (Aqua-MODIS) and in situ measurements, corresponding to sea surface temperature, salinity, primary productivity, current velocity and chlorophyll *a* (Tyberghein et al., 2012). These variables were then reanalysed by Global Ocean Physics Non-assimilative Hindcast (PISCES) and Global Observed Ocean Physics Reprocessing (ARMOR) for a monthly average measure from 2000-2014 and scale to resolution of ~9.2 km (Assis et al., 2018). Bathymetry is based on measures from the General Bathymetric Chart of the Oceans (GEBCO) (Tyberghein et al., 2012; Assis et al., 2018).

Table E.1. Environmental variables used for the Genotype-Environment Association multivariable analyses were download from the updated datasets of BioOracle using the R package ‘sdmpredictors’ (Tyberghein et al., 2012; Assis et al., 2018).

Name	Layer code	Units	Resolution	Date
Sea surface temperature (maximum)	BO_sstmax	Celsius	~9.2km	2000-2014
Sea surface temperature (mean)	BO_sstmean	Celsius	~9.2km	2000-2014
Sea surface temperature (minimum)	BO_sstmin	Celsius	~9.2km	2000-2014
Sea surface temperature (range)	BO_sstrange	Celsius	~9.2km	2000-2014
Chlorophyll concentration (maximum)	BO2_chlomax_ss	mg/mü	~9.2km	2000-2014
Chlorophyll concentration (mean)	BO2_chlomean_ss	mg/mü	~9.2km	2000-2014
Chlorophyll concentration (minimum)	BO2_chlomin_ss	mg/mü	~9.2km	2000-2014
Chlorophyll concentration (range)	BO2_chlorange_ss	mg/mü	~9.2km	2000-2014
Current velocity (maximum)	BO2_curvelmax_ss	m/s	~9.2km	2000-2014
Current velocity (mean)	BO2_curvelmean_ss	m/s	~9.2km	2000-2014
Current velocity (minimum)	BO2_curvelmin_ss	m/s	~9.2km	2000-2014
Current velocity (range)	BO2_curvelrange_ss	m/s	~9.2km	2000-2014
Primary production (maximum)	BO2_ppmax_ss	g/mü/day	~9.2km	2000-2014
Primary production (mean)	BO2_ppmean_ss	g/mü/day	~9.2km	2000-2014
Primary production (minimum)	BO2_ppmin_ss	g/mü/day	~9.2km	2000-2014
Primary production (range)	BO2_pprange_ss	g/mü/day	~9.2km	2000-2014

Sea surface salinity (maximum)	BO2_salinitymax_ss	PSS	~9.2km	2000-2014
Sea surface salinity (mean)	BO2_salinitymean_ss	PSS	~9.2km	2000-2014
Sea surface salinity (minimum)	BO2_salinitymin_ss	PSS	~9.2km	2000-2014
Sea surface salinity (range)	BO2_salinityrange_ss	PSS	~9.2km	2000-2014
Bathymetry (minimum)	BO_bathymin	meters	30 arcsec	2016
Bathymetry (maximum)	BO_bathymax	meters	30 arcsec	2016
Bathymetry (mean)	BO_bathymean	meters	30 arcsec	2016

Table E.2. NCBI database of cetaceans families of nucleotide and non-redundant proteins available at the time of analyses. Accessed August 2020

Mysticeti (baleen whales)	**Odontoceti (tooth whales)**
Balaenidae	*Delphinidae*
Balaenopteridae	*Iniidae*
Eschrichtiidae	*Lipotidae*
Neobalaenidae	*Monodontidae*
	Phocoenidae
	Physeteridae
	Platanistidae
	Pontoporiidae
	Ziphiidae

RDA bash script MEM selection and variance inflation factor (VIF) Southern Australia

```
> sel <- ordistep(rda(snps ~ 1, as.data.frame(MEM.sel)), scope = formula(mod0), scale= FALSE, direction="forward", pstep = 1000)

Start: snps ~ 1

      Df    AIC      F Pr(>F)
+ MEM1  1 1741.3 2.5604  0.005 **
+ MEM2  1 1741.6 2.2843  0.005 **
+ MEM3  1 1742.1 1.7362  0.005 **
+ MEM4  1 1742.5 1.4061  0.005 **
+ MEM5  1 1742.5 1.3882  0.005 **
+ MEM6  1 1742.7 1.1375  0.015 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1

      Df    AIC      F Pr(>F)
+ MEM2  1 1741.0 2.3013  0.005 **
+ MEM3  1 1741.5 1.7490  0.005 **
+ MEM4  1 1741.9 1.4164  0.005 **
+ MEM5  1 1741.9 1.3984  0.005 **
+ MEM6  1 1742.2 1.1459  0.010 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2
```

```
       Df    AIC      F Pr(>F)
+ MEM3  1 1741.2 1.7599  0.005 **
+ MEM4  1 1741.5 1.4252  0.005 **
+ MEM5  1 1741.6 1.4071  0.005 **
+ MEM6  1 1741.8 1.1530  0.010 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3

       Df    AIC      F Pr(>F)
+ MEM4  1 1741.8 1.4304  0.005 **
+ MEM5  1 1741.8 1.4122  0.005 **
+ MEM6  1 1742.0 1.1571  0.005 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4

       Df    AIC      F Pr(>F)
+ MEM5  1 1742.3 1.4151  0.005 **
+ MEM6  1 1742.6 1.1595  0.010 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4 + MEM5

       Df    AIC      F Pr(>F)
+ MEM6  1 1743.1 1.1619  0.005 **
---
```

```
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4 + MEM5 + MEM6



> R2.all.space
[1] 0.02158653



5env that are significant all        > w.lab   > w.lab
env_var <- as.matrix(ENV[,c(3,7,13,19,22)])       [1] "RDA1 (0.11%)"   [1] "RDA1 (32.3%)"
> R2.all.env        > x.lab   > x.lab
[1] 0.02228495       [1] "RDA2 (0.07%)"   [1] "RDA2 (20.29%)"
      > y.lab   > y.lab
      [1] "RDA3 (0.06%)"   [1] "RDA3 (17.99%)"
> keep.env <-vif_func(in_frame=env_var,thresh=3.1,trace=T)       > z.lab   > z.lab
 var               vif                  [1] "RDA4 (0.06%)"   [1] "RDA4 (16.01%)"
 BO2_salinitymax_ss 3.01623814015617       > zz.lab   > zz.lab
 BO2_ppmax_ss       2.99638081512828       [1] "RDA5 (0%)"   [1] "RDA5 (13.41%)"
 BO_sstmin          1.22882456945448
 BO2_curvelmax_ss   3.0221613403873
 BO2_curvelrange_ss 3.02339520128452       > length(cand1)
      [1] 244
All variables have VIF < 3.1, max VIF 3.02       > length(cand2)
      [1] 266
      > length(cand3)
> RDASCsites5env       [1] 227
Call: rda(formula = snps ~ reduced.env$BO2_salinitymax_ss +       > length(cand4)
reduced.env$BO2_ppmax_ss + reduced.env$BO_sstmin +       [1] 52
```

```
reduced.env$BO2_curvelmax_ss + reduced.env$BO2_curvelrange_ss +

Condition(MEM.sel), data = reduced.env)       > ncand

      [1] 789

 Inertia Proportion Rank

Total 3.41E+03 1.00E+00   3410

Conditional 1.68E+02 4.92E-02 6    > table(cand$predictor) duplicates

Constrained 1.20E+02 3.53E-02 5

Unconstrained  3.12E+03  9.16E-01  202                    BO_sstmin      BO2_curvelmax_ss
BO2_curvelrange_ss

Inertia is variance                  224             118              161

           BO2_ppmax_ss BO2_salinitymax_ss

Eigenvalues for constrained axes:                   95              191

 RDA1  RDA2  RDA3  RDA4  RDA5

38.85 24.41 21.63 19.26 16.12

      > length(cand$snp[duplicated(cand$snp)])

Eigenvalues for unconstrained axes:       [1] 42

  PC1    PC2    PC3    PC4    PC5    PC6    PC7    PC8          > env_mat <- cbind(cand$axis,
duplicated(cand$snp))

47.27 29.97 28.95 25.12 24.51 23.36 23.01 22.79         > table(env_mat[env_mat[,1]==1,2])#
none on axis 1

(Showing 8 of 202 unconstrained eigenvalues)

      0

      244

      > table(env_mat[env_mat[,1]==2,2])# 2 duplicates on axis 2

> mod_permRDASCsites5env

Permutation test for rda under reduced model        0   1

Permutation: free       258   8

Number of permutations: 999       > table(env_mat[env_mat[,1]==3,2])# n duplicates on axis 3


Model:      rda(formula      =      snps      ~      reduced.env$BO2_salinitymax_ss      +
reduced.env$BO2_ppmax_ss + reduced.env$BO_sstmin + reduced.env$BO2_curvelmax_ss +
reduced.env$BO2_curvelrange_ss + Condition(MEM.sel), data = reduced.env)        0   1

        Df Variance      F Pr(>F)          203  24
```

```
Model     5   120.26 1.5553  0.001 ***       > table(env_mat[env_mat[,1]==4,2])# n duplicates
on axis 4

Residual 202  3123.88

---       0  1

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1       42 10

> margin_permRDASCsites5env

Permutation test for rda under reduced model

Marginal effects of terms       747

Permutation: free

Number of permutations: 999

            BO_sstmin   BO2_curvelmax_ss BO2_curvelrange_ss

Model:     rda(formula     =     snps     ~     reduced.env$BO2_salinitymax_ss     +
reduced.env$BO2_ppmax_ss + reduced.env$BO_sstmin + reduced.env$BO2_curvelmax_ss +
reduced.env$BO2_curvelrange_ss + Condition(MEM.sel), data = reduced.env)             215
110              152

                         Df Variance     F Pr(>F)              BO2_ppmax_ss BO2_salinitymax_ss

reduced.env$BO2_salinitymax_ss  1  20.49  1.3247  0.001  ***  0.600879765                    88
182

reduced.env$BO2_ppmax_ss 1 21.03 1.3599 0.001 *** 0.616715543

reduced.env$BO_sstmin 1 24.25 1.568 0.001 *** 0.711143695

reduced.env$BO2_curvelmax_ss     1     17.64     1.1408     0.001     ***     0.517302053     >
envfit(RDASCsites5env,reduced.env)

reduced.env$BO2_curvelrange_ss 1 20.75 1.3415 0.001 *** 0.608504399

Residual                    202  3123.88                    ***VECTORS

---     3.054545455

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1                          RDA1     RDA2
r2 Pr(>r)

> axis_permRDASCsites5env      BO2_salinitymax_ss  0.97221  0.23412 0.1784  0.001 ***

Permutation test for rda under reduced model      BO2_ppmax_ss      -0.90346 -0.42866 0.1661
0.001 ***

Forward tests for axes      BO_sstmin          -0.96700 -0.25478 0.1470  0.001 ***

Permutation: free      BO2_curvelmax_ss    0.52393 -0.85176 0.2974  0.001 ***

Number of permutations: 999      BO2_curvelrange_ss  0.32560 -0.94551 0.3351  0.001 ***

    ---
```

```
Model: rda(formula = snps ~ reduced.env$BO2_salinitymax_ss + reduced.env$BO2_ppmax_ss + reduced.env$BO_sstmin + reduced.env$BO2_curvelmax_ss + reduced.env$BO2_curvelrange_ss + Condition(MEM.sel), data = reduced.env)   Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

         Df Variance      F Pr(>F)          Permutation: free

RDA1      1    38.85 2.5119  0.001 ***      Number of permutations: 999

RDA2      1    24.41 1.5782  0.001 ***

RDA3      1    21.63 1.3988  0.001 ***

RDA4      1    19.26 1.2453  0.001 ***

RDA5      1    16.12 1.0425  0.117

Residual 202  3123.88

---

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1



> RsquareAdj(RDASCsites5env)

$r.squared

[1] 0.03524924


$adj.r.squared

[1] 0.0129506


> RsquareAdj(RDASCsites5env)$r.squared #0.016  #0.0394

[1] 0.03524924

> # how much inertia is associated with each axis

> summary(eigenvals(RDASCsites5env,model = "constrained"))

Importance of components:

                      RDA1    RDA2    RDA3    RDA4    RDA5

Eigenvalue           38.845 24.4066 21.6319 19.2588 16.1216

Proportion Explained   0.323  0.2029  0.1799  0.1601  0.1341

Cumulative Proportion  0.323  0.5259  0.7058  0.8659  1.0000

> #visualize it
```

RDA bash script MEM selection and variance inflate factor (VIF) for broad and fine scale

```
// 279 individuals; 17,539 loci; 35,078 alleles; size: 46.6 Mb

 // Basic content
   @tab:  279 x 35078 matrix of allele counts
   @loc.n.all: number of alleles per locus (range: 2-2)
   @loc.fac: locus factor for the 35078 columns of @tab
   @all.names: list of allele names for each locus
   @ploidy: ploidy of each individual  (range: 2-2)
   @type:  codom
   @call: read.structure(file =
"../../Structurefiles/seascape279SCEC/StrMapLD_17539_279SCEC_ch_fmd.str",
    n.ind = 279, n.loc = 17539, onerowperind = FALSE, col.lab = 1,
    col.pop = 2, col.others = FALSE, row.marknames = 1, NA.char = "-9",
    pop = 13, ask = TRUE, quiet = FALSE)

 // Optional content
   @pop: population of each individual (group size range: 11-32)
   @other: a list containing: X
```

```
> indMEMPositive #8 eigenvectros 1  2  3  5  4  6 10 12       r2 0.1602329
$GlobalP
[1] 0.01

$selectedRsqAdj
[1] 0.192643
```

```
$selectedMEM
[1] 1 3 2 4 6 5 7 8 9

> ## Negative MEM eigenvectors (negative spatial autocorrelation) second
> indMEMNegative <- mgForward(psa,  indMEM$vectorsMEM[ , indMEM$valuesMEM <
0])
> indMEMNegative# 0    r2 0
$GlobalP
[1] 1

$selectedRsqAdj
[1] NA

$selectedMEM
[1] NA


> sel <- ordistep(rda(snps ~ 1, as.data.frame(MEM.sel)), scope = formula(mod0), scale=
FALSE, direction="forward", pstep = 1000)

Start: snps ~ 1

       Df    AIC       F Pr(>F)
+ MEM1  1 2291.5 23.0612  0.005 **
+ MEM2  1 2302.3 11.6865  0.005 **
+ MEM3  1 2311.8  1.9774  0.005 **
+ MEM5  1 2312.1  1.6921  0.010 **
+ MEM4  1 2312.1  1.6961  0.015 *
+ MEM6  1 2312.4  1.4424  0.040 *
+ MEM7  1 2312.7  1.1184  0.130
+ MEM8  1 2312.8  1.0501  0.180
```

```
+ MEM9  1 2312.8  1.0223  0.240
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1

       Df    AIC       F Pr(>F)
+ MEM2  1 2281.0 12.6582  0.005 **
+ MEM3  1 2291.3  2.1356  0.005 **
+ MEM4  1 2291.7  1.8316  0.005 **
+ MEM5  1 2291.7  1.8273  0.005 **
+ MEM6  1 2291.9  1.5575  0.005 **
+ MEM7  1 2292.3  1.2075  0.030 *
+ MEM8  1 2292.4  1.1337  0.040 *
+ MEM9  1 2292.4  1.1037  0.100 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2

       Df    AIC      F Pr(>F)
+ MEM3  1 2280.7 2.2262  0.005 **
+ MEM4  1 2281.1 1.9092  0.005 **
+ MEM5  1 2281.1 1.9047  0.005 **
+ MEM6  1 2281.3 1.6235  0.005 **
+ MEM7  1 2281.7 1.2586  0.005 **
+ MEM8  1 2281.8 1.1817  0.005 **
+ MEM9  1 2281.8 1.1504  0.005 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
Step: snps ~ MEM1 + MEM2 + MEM3

      Df    AIC      F Pr(>F)
+ MEM4  1 2280.8 1.9178  0.005 **
+ MEM5  1 2280.8 1.9133  0.005 **
+ MEM6  1 2281.1 1.6307  0.005 **
+ MEM7  1 2281.5 1.2642  0.005 **
+ MEM8  1 2281.5 1.1869  0.005 **
+ MEM9  1 2281.6 1.1555  0.005 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4

      Df    AIC      F Pr(>F)
+ MEM5  1 2280.8 1.9197  0.005 **
+ MEM6  1 2281.1 1.6362  0.005 **
+ MEM7  1 2281.5 1.2684  0.005 **
+ MEM8  1 2281.6 1.1909  0.005 **
+ MEM9  1 2281.6 1.1594  0.005 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4 + MEM5

      Df    AIC      F Pr(>F)
+ MEM6  1 2281.2 1.6417  0.005 **
+ MEM7  1 2281.5 1.2727  0.005 **
+ MEM8  1 2281.6 1.1949  0.005 **
+ MEM9  1 2281.7 1.1633  0.005 **
---
```

```
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4 + MEM5 + MEM6

       Df    AIC      F Pr(>F)
+ MEM7  1 2281.8 1.2757  0.005 **
+ MEM8  1 2281.9 1.1978  0.005 **
+ MEM9  1 2282.0 1.1660  0.005 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4 + MEM5 + MEM6 + MEM7

       Df    AIC      F Pr(>F)
+ MEM8  1 2282.6 1.1990  0.005 **
+ MEM9  1 2282.7 1.1672  0.005 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4 + MEM5 + MEM6 + MEM7 + MEM8

       Df    AIC      F Pr(>F)
+ MEM9  1 2283.4 1.1681  0.005 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3 + MEM4 + MEM5 + MEM6 + MEM7 + MEM8 +
MEM9



> keep.env <-vif_func(in_frame=env_var,thresh=3,trace=T)
```

```
 var                vif
 BO2_salinityrange_ss 1.93404090081921
 BO2_ppmin_ss        1.84803878817885
 BO_sstmean          1.57111646972974
 BO_sstrange         1.37294904016057
 BO2_curvelmax_ss    1.84505504860759
 BO_bathymean        1.76642071555321
```

All variables have VIF < 3, max VIF 1.93

```
> summary(eigenvals(RDASCECsites6envadmix,model = "constrained"))
Importance of components:
                     RDA1    RDA2    RDA3    RDA4    RDA5    RDA6
Eigenvalue           35.1050 33.5536 18.1479 17.0106 14.1419 13.2089
Proportion Explained   0.2676  0.2558  0.1384  0.1297  0.1078  0.1007
Cumulative Proportion  0.2676  0.5234  0.6618  0.7915  0.8993  1.0000

> RDASCECsites6envadmix
Call: rda(formula = snps ~ reduced.env$BO2_salinityrange_ss +
reduced.env$BO2_ppmin_ss + reduced.env$BO_sstmean +
reduced.env$BO_sstrange + reduced.env$BO2_curvelmax_ss +
reduced.env$BO_bathymean + Condition(MEMRDA2.sel), data = reduced.env)
```

```
// 65 individuals; 16,236 loci; 32,472 alleles; size: 16.6 Mb

 // Basic content
```

```
)

  @tab:  65 x 32472 matrix of allele counts
  @loc.n.all: number of alleles per locus (range: 2-2)
  @loc.fac: locus factor for the 32472 columns of @tab
  @all.names: list of allele names for each locus
  @ploidy: ploidy of each individual  (range: 2-2)
  @type:  codom
  @call:                                        read.structure(file                                        =
"../../Structurefiles/seascape279SCEC/StrMapLD_16236_65EC_ch_fmd.str",
   n.ind = 65, n.loc = 16236, onerowperind = FALSE, col.lab = 1,
   col.pop = 2, col.others = FALSE, row.marknames = 1, NA.char = "-9",
   pop = 4, ask = TRUE, quiet = FALSE)

 // Optional content
  @pop: population of each individual (group size range: 11-20)
  @other: a list containing: X



> indMEMPositive #8 eigenvectros 1  2  3  5  4  6 10 12       r2 0.1602329
$GlobalP
[1] 0.01

$selectedRsqAdj
[1] 0.05141609

$selectedMEM
[1] 2 1 3

> ## Negative MEM eigenvectors (negative spatial autocorrelation) second
> indMEMNegative <- mgForward(psa,  indMEM$vectorsMEM[ , indMEM$valuesMEM <
0])
> indMEMNegative# 0    r2 0
```

```
> sel <- ordistep(rda(snps ~ 1, as.data.frame(MEM.sel)), scope = formula(mod0), scale=
FALSE, direction="forward", pstep = 1000)

Start: snps ~ 1

      Df    AIC      F Pr(>F)
+ MEM1  1 538.16 3.0710  0.005 **
+ MEM2  1 539.56 1.6642  0.005 **
+ MEM3  1 540.14 1.0853  0.120
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1

      Df    AIC      F Pr(>F)
+ MEM2  1 538.38 1.7199  0.005 **
+ MEM3  1 538.99 1.1210  0.015 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2

      Df    AIC      F Pr(>F)
+ MEM3  1 539.18 1.1341   0.01 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: snps ~ MEM1 + MEM2 + MEM3

> sel <- attributes(sel$terms)$term.labels
```

```
> keep.env <-vif_func(in_frame=env_var,thresh=3,trace=T)
 var                vif
 BO2_salinitymin_ss 98.7219107200853
 BO2_ppmin_ss       8.56203436264875
 BO_sstmean        1314.34791143214
 BO_sstmin         807.323945580225
 BO_chlomax        4.52182995197209

removed:  BO_sstmean 1314.348

 var                vif
 BO2_salinitymin_ss 32.7316563751939
 BO2_ppmin_ss       7.44749901397238
 BO_sstmin         31.9599933981168
 BO_chlomax        2.22545370786853

removed:  BO2_salinitymin_ss 32.73166

> #env_var <- env_var[,c(1,2)]
> reduced.env <- subset(as.data.frame(env_var), select=c(keep.env))
> keep.env <-vif_func(in_frame=reduced.env,thresh=4,trace=T)
 var          vif
 BO2_ppmin_ss 1.02399581933712
 BO_sstmin    1.99550878228608
 BO_chlomax   2.00467525610965

All variables have VIF < 3, max VIF 2
```

```
Model: rda(formula = snps ~ reduced.env$BO2_ppmin_ss + reduced.env$BO_sstmin +
reduced.env$BO_chlomax + Condition(MEM.sel), data = reduced.env)

                          Df Variance      F Pr(>F)

reduced.env$BO2_ppmin_ss  1     71.2 1.2141  0.001 ***

reduced.env$BO_sstmin     1     61.2 1.0429  0.232

reduced.env$BO_chlomax    1     60.0 1.0228  0.317

Residual                 58   3402.2

---

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


> summary(eigenvals(RDAECsites1envppmin,model = "constrained"))

Importance of components:

                        RDA1

Eigenvalue             72.96

Proportion Explained   1.00

Cumulative Proportion  1.00




> RDAECsites1envppmin

Call: rda(formula = snps ~ reduced.env$BO2_ppmin_ss +

Condition(MEM.sel), data = reduced.env)


                Inertia Proportion Rank

Total    3.95E+03        1.00E+00

Conditional     3.52E+02        8.92E-02        3

Constrained     7.30E+01        1.85E-02        1

Unconstrained 3.52E+03        8.92E-01        60
```

REFERENCES

Abe, S., Takeda, H., Nishio, S.Y., and Usami, S.I. (2018). Sensorineural hearing loss and mild cardiac phenotype caused by an EYA4 mutation. *Hum Genome Var* 5, 23. doi: 10.1038/s41439-018-0023-9.

Abraham, E.R., Neubauer, P., Berkenbusch, K., and Richard, Y. (2017). "Assessment of the risk to New Zealand marine mammals from commercial fisheries". (New Zealand Aquatic Environment and Biodiversity Report No. 189: Ministry of Primary Industries).

Abraham, E.R., and Thompson, F.N. (2015a). *Captures of common dolphin in setnet fisheries, in the New Zealand Exclusive Economic Zone, during the 2017–18 fishing year* [Online]. psc.dragonfly.co.nz/2019v1/released/common-dolphin/setnet/all-vessels/eez/2017-18/. [Accessed September 24 2020].

Abraham, E.R., and Thompson, F.N. (2015b). *Captures of common dolphin in surface longline fisheries, in the New Zealand Exclusive Economic Zone, during the 2017–18 fishing year* [Online]. psc.dragonfly.co.nz/2019v1/released/common-dolphin/surface-longline/all-vessels/eez/2017-18/. [Accessed September 24 2020].

Abraham, E.R., and Thompson, F.N. (2015c). *Captures of common dolphin in trawl fisheries, in the New Zealand Exclusive Economic Zone, during the 2017–18 fishing year* [Online]. psc.dragonfly.co.nz/2019v1/released/common-dolphin/trawl/all-vessels/eez/2017-18/. [Accessed September 24 2020].

AFMA (2019a). "Gillnet Dolphin Mitigation Strategy. Minimising dolphin interactions with gillnets in the Southern and Eastern Scalefish and Shark Fishery", (ed.) C.A. Australian Fisheries Management Authority (AFMA). (Available at afma.gov.au/sites/default/files/gillnet_dolphin_mitigation_strategy_updated_aug_2019_accessible.pdf).

AFMA (2019b). "Small Pelagic Fishery Dolphin Strategy. Minimising dolphin interactions in the Small Pelagic Fishery", (ed.) C.A. Australian Fisheries Management Authority (AFMA). (Available at afma.gov.au/sites/default/files/spf_dolphin_strategy_2019_updated_accessible.pdf).

AFMA (2020a). "Australian Fisheries Management Authority Electronic Monitoring Program", (ed.) C.A. Australian Fisheries Management Authority (AFMA). (Available at: afma.gov.au/sites/default/files/australian_fisheries_management_authority_electronic_monitoring_program_june_2020.pdf).

AFMA (2020b). "Protected species interactions quarterly reports: 2012-2019", (ed.) C.A. Australian Fisheries Management Authority (AFMA). (Available at: afma.gov.au/sustainability-environment/protected-species-management/protected-species-interaction-reports).

Alexander, D.H., and Lange, K. (2011). Enhancements to the ADMIXTURE algorithm for individual ancestry estimation. *BMC Bioinformatics* 12. doi: 10.1186/1471-2105-12-246.

Alexander, D.H., Novembre, J., and Lange, K. (2009). Fast model-based estimation of ancestry in unrelated individuals. *Genome Res.* 19(9), 1655-1664. doi: 10.1101/gr.094052.109.

Allendorf, F.W. (2017). Genetics and the conservation of natural populations: allozymes to genomes. *Molecular Ecology* 26(2), 420-430. doi: 10.1111/mec.13948.

Allendorf, F.W., Hohenlohe, P.A., and Luikart, G. (2010). Genomics and the future of conservation genetics. *Nat. Rev. Genet.* 11(10), 697-709. doi: 10.1038/nrg2844.

Allikmets, R., Singh, N., Sun, H., Shroyer, N.F., Hutchinson, A., Chidambaram, A., et al. (1997). A photoreceptor cell-specific ATP-binding transporter gene (ABCR) is mutated in recessive Starqardt macular dystrophy. *Nat Genet* 15, 236–246. doi: 10.1038/ng0397-236.

Almany, G.R., Planes, S., Thorrold, S.R., Berumen, M.L., Bode, M., Saenz-Agudelo, P., et al. (2017). Larval fish dispersal in a coral-reef seascape. *Nat. Ecol. Evol.* 1(6), 148. doi: 10.1038/s41559-017-0148.

Amaral, A.R., Beheregaray, L.B., Bilgmann, K., Boutov, D., Freitas, L., Robertson, K.M., et al. (2012a). Seascape genetics of a globally distributed, highly mobile marine mammal: the short-beaked common dolphin (Genus *Delphinus*). *PLoS One* 7(2)**,** e31482. doi: 10.1371/journal.pone.0031482.

Amaral, A.R., Beheregaray, L.B., Bilgmann, K., Freitas, L., Robertson, K.M., Sequeira, M., et al. (2012b). Influences of past climatic changes on historical population structure and demography of a cosmopolitan marine predator, the common dolphin (genus *Delphinus*). *Mol. Ecol.* 21(19)**,** 4854-4871. doi: 10.1111/j.1365-294X.2012.05728.x.

Amaral, A.R., Jackson, J.A., Möller, L.M., Beheregaray, L.B., and Manuela Coelho, M. (2012c). Species tree of a recent radiation: the subfamily Delphininae (Cetacea, Mammalia). *Mol Phylogenet Evol* 64(1)**,** 243-253. doi: 10.1016/j.ympev.2012.04.004.

Amaral, K.B.d., Amaral, A.R., Ewan-Fordyce, R., and Moreno-Benites, I. (2016). Historical Biogeography of Delphininae Dolphins and Related Taxa (Artiodactyla: Delphinidae). *Journal of Mammalian Evolution*. doi: 10.1007/s10914-016-9376-3.

Amarasekera, M., Martino, D., Ashley, S., Harb, H., Kesper, D., Strickland, D., et al. (2014). Genome-wide DNA methylation profiling identifies a folate-sensitive region of differential methylation upstream of ZFP57-imprinting regulator in humans. *FASEB J* 28(9)**,** 4068-4076. doi: 10.1096/fj.13-249029.

Andolfatto, P. (2005). Adaptive evolution of non-coding DNA in *Drosophila*. *Nature* 437(7062)**,** 1149-1152. doi: 10.1038/nature04107.

Andrews, K.R., Epstein, B., Leslie, M.S., Fiedler, P., Morin, P.A., and Hoelzel, A.R. (2021). Genomic signatures of divergent selection are associated with social behavior for spinner dolphin ecotypes. *Mol Ecol*. doi: doi.org/10.1111/mec.15865.

Angueira, A.R., Shapira, S.N., Ishibashi, J., Sampat, S., Sostre-Colon, J., Emmett, M.J., et al. (2020). Early B Cell Factor Activity Controls Developmental and Adaptive Thermogenic Gene Programming in Adipocytes. *Cell Rep* 30(9)**,** 2869-2878 e2864. doi: 10.1016/j.celrep.2020.02.023.

Ansmann, I.C., Parra, G.J., Lanyon, J.M., and Seddon, J.M. (2012). Fine-scale genetic population structure in a mobile marine mammal: inshore bottlenose dolphins in Moreton Bay, Australia. *Mol. Ecol.* 21(18)**,** 4472-4485. doi: 10.1111/j.1365-294X.2012.05722.x.

Antao, L.H., Bates, A.E., Blowes, S.A., Waldock, C., Supp, S.R., Magurran, A.E., et al. (2020). Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nature Ecology and Evolution*. doi: 10.1038/s41559-020-1185-7.

Armansin, N.C., Stow, A.J., Cantor, M., Leu, S.T., Klarevas-Irby, J.A., Chariton, A.A., et al. (2019). Social Barriers in Ecological Landscapes: The Social Resistance Hypothesis. *Trends Ecol. Evol.* doi: 10.1016/j.tree.2019.10.001.

Arnason, U., Gullberg, A., and Janke, A. (2004). Mitogenomic analyses provide new insights into cetacean origin and evolution. *Gene* 333**,** 27-34. doi: 10.1016/j.gene.2004.02.010.

Ashe, J.L., and Wilson, A.B. (2019). Navigating the southern seas with small fins: Genetic connectivity of seahorses (*Hippocampus abdominalis*) across the Tasman Sea. *J. Biogeography* 47(1)**,** 207-219. doi: 10.1111/jbi.13733.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., and De Clerck, O. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography* 27(3)**,** 277-284. doi: 10.1111/geb.12693.

Ayers, K.L., and Waters, J.M. (2005). Marine biogeographic disjunction in central New Zealand. *Mar. Biol.* 147**,** 1045-1052. doi: 10.1007/s00227-005-1632-7.

Baker, C.S., Boren, L., Childerhouse, S., Constantine, R., van Helden, A., Lundquist, D., et al. (2019). "Conservation status of New Zealand marine mammals", in: *New Zealand Threat Classification Series.* (ed.) L. Clelland. (Department of Conservation,Wellington, New Zealand).

Baldwin, W.S., Boswell, W.T., Ginjupalli, G., and Litoff, E.J. (2017). Annotation of the Nuclear Receptors in an Estuarine Fish species, *Fundulus heteroclitus*. *Nucl Receptor Res* 4. doi: 10.11131/2017/101285.

Balkenhol, N., Cushman, S.A., Storfer, A., and Waits, L. (2016). *LANDSCAPE GENETICS concepts, methods and applications.*

Ball, L., Shreves, K., Pilot, M., and Moura, A.E. (2017). Temporal and geographic patterns of kinship structure in common dolphins (Delphinus delphis) suggest site fidelity and female-biased long-distance dispersal. *Behav Ecol Sociobiol* 71(8)**,** 123. doi: 10.1007/s00265-017-2351-z.

Banks, J., Levine, K., Syvanen, M., Theis, J., and Gilson, A. (1995). "DNA tissue gender typing. Standard operating procedure of the Wildlife Forensic Laboratory of the California Department of Fish and Game", (ed.) C. California Department of Fish and Game. Sacramento.).

Banks, R., Zaharia, M., Dixon, C., and Stern-Pirlot, A. (2019). "Australia Small Pelagic Fishery (Commonwealth) Final Report and Determination". (MRAG Americas: Ridley Agriproducts Pty Ltd.).

Banks, S.C., Ling, S.D., Johnson, C.R., Piggott, M.P., Williamson, J.E., and Beheregaray, L.B. (2010). Genetic structure of a recent climate change-driven range extension. *Mol Ecol* 19(10)**,** 2011-2024. doi: 10.1111/j.1365-294X.2010.04627.x.

Barceló, A., Sandoval-Castillo, J., Stockin, K.A., Bilgmann, K., Attard, C.R.M., Zanardo, N., et al. (2021). A Matter of Scale: Population Genomic Structure and Connectivity of Fisheries At-Risk Common Dolphins (*Delphinus delphis*) From Australasia. *Frontiers in Marine Science* 8. doi: 10.3389/fmars.2021.616673.

Barrett, R.D., and Hoekstra, H.E. (2011). Molecular spandrels: tests of adaptation at the genetic level. *Nat Rev Genet* 12(11)**,** 767-780. doi: 10.1038/nrg3015.

Barrett, R.D., and Schluter, D. (2008). Adaptation from standing genetic variation. *Trends Ecol Evol* 23(1)**,** 38-44. doi: 10.1016/j.tree.2007.09.008.

Barrington, W.T., Morgan, A.P., and Siracusa, L.D. (2015). The 28th International Mammalian Genome Conference--meeting report. *Mamm Genome* 26(5-6)**,** 201-209. doi: 10.1007/s00335-015-9561-3.

Basener, W.F., and Sanford, J.C. (2018). The fundamental theorem of natural selection with mutations. *J Math Biol* 76(7)**,** 1589-1622. doi: 10.1007/s00285-017-1190-x.

Batley, K.C., Sandoval-Castillo, J., Kemper, C.M., Attard, C.R.M., Zanardo, N., Tomo, I., et al. (2019). Genome-wide association study of an unusual dolphin mortality event reveals candidate genes for susceptibility and resistance to cetacean morbillivirus. *Evol. Appl.* 12(4)**,** 718-732. doi: 10.1111/eva.12747.

Batley, K.C., Sandoval-Castillo, J., Kemper, C.M., Zanardo, N., Tomo, I., Beheregaray, L.B., et al. (2021). Whole genome data reveals multiple candidate genes and pathways involved in the immune response of dolphins to a highly infectious virus. *Molecular Ecology*.

Becker, E.A., Carretta, J.V., Forney, K.A., Barlow, J., Brodie, S., Hoopes, R., et al. (2020). Performance evaluation of cetacean species distribution models developed using generalized additive models and boosted regression trees. *Ecology and Evolution*. doi: 10.1002/ece3.6316.

Benestan, L., Gosselin, T., Perrier, C., Sainte-Marie, B., Rochette, R., and Bernatchez, L. (2015). RAD genotyping reveals fine-scale genetic structuring and provides powerful population assignment in a widely distributed marine species, the American lobster (*Homarus americanus*). *Mol Ecol* 24(13)**,** 3299-3315. doi: 10.1111/mec.13245.

Benestan, L., Quinn, B.K., Maaroufi, H., Laporte, M., Clark, F.K., Greenwood, S.J., et al. (2016a). Seascape genomics provides evidence for thermal adaptation and current-mediated population structure in American lobster (*Homarus americanus*). *Mol. Ecol.* 25(20)**,** 5073-5092. doi: 10.1111/mec.13811.

Benestan, L.M., Ferchaud, A.-L., Hohenlohe, P.A., Garner, B.A., Naylor, G.J.P., Baums, I.B., et al. (2016b). Conservation genomics of natural and managed populations: building a conceptual and practical framework. *Mol Ecol* 25**,** 2967–2977. doi: 10.1111/mec.13647.

Benjamini, Y., and Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *Ann. Statist.* 29(4), 1165–1188. doi: 10.1214/aos/1013699998.

Bernatchez, S., Xuereb, A., Laporte, M., Benestan, L., Steeves, R., Laflamme, M., et al. (2018). Seascape genomics of eastern oyster (*Crassostrea virginica*) along the Atlantic coast of Canada. *Evol. Appl.* 12(3), 587-609. doi: 10.1111/eva.12741.

Bestley, S., Ropert-Coudert, Y., Bengtson Nash, S., Brooks, C.M., Cotté, C., Dewar, M., et al. (2020). Marine Ecosystem Assessment for the Southern Ocean: Birds and Marine Mammals in a Changing Climate. *Frontiers in Ecology and Evolution* 8. doi: 10.3389/fevo.2020.566936.

Beugin, M.P., Gayet, T., Pontier, D., Devillard, S., and Jombart, T. (2018). A fast likelihood solution to the genetic clustering problem. *Methods Ecol. Evol.* 9(4), 1006-1016. doi: 10.1111/2041-210X.12968.

Bidle, K.D. (2016). Programmed Cell Death in Unicellular Phytoplankton. *Curr Biol* 26(13), R594-R607. doi: 10.1016/j.cub.2016.05.056.

Bilgmann, K., Griffiths, O.J., Allen, S.J., and Möller, L.M. (2007a). A Biopsy Pole System for Bow-Riding Dolphins: Sampling Success, Behavioral Responses, and Test for Sampling Bias. *Mar. Mamm. Sci.* 23(1), 218-225. doi: 10.1111/j.1748-7692.2006.00099.x.

Bilgmann, K., Möller, L.M., Harcourt, R.G., Gales, R., and Beheregaray, L.B. (2008). Common dolphins subject to fisheries impacts in Southern Australia are genetically differentiated: implications for conservation. *Anim. Conserv.* 11(6), 518-528. doi: 10.1111/j.1469-1795.2008.00213.x.

Bilgmann, K., Möller, L.M., Harcourt, R.G., Gibbs, S.E., and Beheregaray, L. (2007b). Genetic differentiation in bottlenose dolphins from South Australia: association with local oceanography and coastal geography. *Mar. Ecol. Prog. Ser.* 341, 265–276. doi: 10.3354/meps341265.

Bilgmann, K., Parra, G.J., Holmes, L., Peters, K.J., Jonsen, I.D., and Moller, L.M. (2019). Abundance estimates and habitat preferences of bottlenose dolphins reveal the importance of two gulfs in South Australia. *Sci Rep* 9(1), 8044. doi: 10.1038/s41598-019-44310-3.

Bilgmann, K., Parra, G.J., and Möller, L.M. (2018). Occurrence, distribution and abundance of cetaceans off the western Eyre Peninsula in the Great Australian Bight. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 157-158, 134-145. doi: 10.1016/j.dsr2.2017.11.006.

Bilgmann, K., Parra, G.J., Zanardo, N., Beheregaray, L.B., and Möller, L.M. (2014). Multiple management units of short-beaked common dolphins subject to fisheries bycatch off southern and southeastern Australia. *Mar. Ecol. Prog. Ser.* 500, 265-279. doi: 10.3354/meps10649.

Bird, E. (2005). "Australia, Coastal Geomorphology", in: *Encyclopedia of Coastal Science. Encyclopedia of Earth Science Series.* (ed.) S. M.L.: Springer, Dordrecht).

Blanchet, F.G., Legendre, P., and Borcard, D. (2008). Forward selection of explanatory variables. *Ecology* 89, 2623–2632.

Blower, D.C., Pandolfi, J.M., Bruce, B.D., Gomez-Cabrera, M., and Ovenden, J.R. (2012). Population genetics of Australian white sharks reveals fine-scale spatial structure, transoceanic dispersal events and low effective population sizes. *Marine Ecology Progress Series* 455, 229-244. doi: 10.3354/meps09659.

Bonte, D., and Bafort, Q. (2019). The importance and adaptive value of life-history evolution for metapopulation dynamics. *J Anim Ecol* 88(1), 24-34. doi: 10.1111/1365-2656.12928.

Boonanuntanasarn, S., Nakharuthai, C., Schrama, D., Duangkaew, R., and Rodrigues, P.M. (2019). Effects of dietary lipid sources on hepatic nutritive contents, fatty acid composition and proteome of Nile tilapia (*Oreochromis niloticus*). *J Proteomics* 192, 208-222. doi: 10.1016/j.jprot.2018.09.003.

Boso, D., Rampazzo, E., Zanon, C., Bresolin, S., Maule, F., Porcu, E., et al. (2019). HIF-1alpha/Wnt signaling-dependent control of gene transcription regulates neuronal differentiation of glioblastoma stem cells. *Theranostics* 9(17), 4860-4877. doi: 10.7150/thno.35882.

Bossart, G.D. (2011). Marine mammals as sentinel species for oceans and human health. *Vet Pathol* 48(3), 676-690. doi: 10.1177/0300985810388525.

Bourman, R.P., Murray-Wallace, C.V., and Harvey, N. (2016). *Coastal Landscapes of South Australia.* Adelaide: University of Adelaide Press.

Bradburd, G.S., Coop, G.M., and Ralph, P.L. (2018). Inferring Continuous and Discrete Population Genetic Structure Across Space. *Genetics* 210(1), 33-52. doi: 10.1534/genetics.118.301333.

Bradbury, I.R., Hubert, S., Higgins, B., Borza, T., Bowman, S., Paterson, I.G., et al. (2010). Parallel adaptive evolution of Atlantic cod on both sides of the Atlantic Ocean in response to temperature. *Proc Biol Sci* 277(1701), 3725-3734. doi: 10.1098/rspb.2010.0985.

Brauer, C.J., Hammer, M.P., and Beheregaray, L.B. (2016). Riverscape genomics of a threatened fish across a hydroclimatically heterogeneous river basin. *Mol Ecol* 25(20), 5093-5113. doi: 10.1111/mec.13830.

Brauer, C.J., Unmack, P.J., Smith, S., Bernatchez, L., and Beheregaray, L.B. (2018). On the roles of landscape heterogeneity and environmental variation in determining population genomic structure in a dendritic system. *Mol Ecol* 27(17), 3484-3497. doi: 10.1111/mec.14808.

Breed, M.F., Harrison, P.A., Blyth, C., Byrne, M., Gaget, V., Gellie, N.J.C., et al. (2019). The potential of genomics for restoring ecosystems and biodiversity. *Nat. Rev. Genet.* 20(10), 615-628. doi: 10.1038/s41576-019-0152-0.

Breves, J.P., Fujimoto, C.K., Phipps-Costin, S.K., Einarsdottir, I.E., Bjornsson, B.T., and McCormick, S.D. (2017). Variation in branchial expression among insulin-like growth-factor binding proteins (igfbps) during Atlantic salmon smoltification and seawater exposure. *BMC Physiol* 17(1), 2. doi: 10.1186/s12899-017-0028-5.

Brooke, B.P., Harris, P.T., Nichol, S.L., Sexton, J., Arthur, W.C., Haese, R.R., et al. (2012). "Living on the edge – waterfront views," in *A geology of Australia.* (Canberra: Geoscience Australia and ANU E Press), 276-331.

Brooke, B.P., Nichol, S.L., Huang, Z., and Beaman, R.J. (2017). Palaeoshorelines on the Australian continental shelf: Morphology, sea-level relationship and applications to environmental management and archaeology. *Continental Shelf Research* 134, 26-38. doi: 10.1016/j.csr.2016.12.012.

Caballero, S., Islas-Villanueva, V., Tezanos-Pinto, G., Duchene, S., Delgado-Estrella, A., Sanchez-Okrucky, R., et al. (2012). Phylogeography, genetic diversity and population structure of common bottlenose dolphins in the Wider Caribbean inferred from analyses of mitochondrial DNA control region sequences and microsatellite loci: conservation and management implications. *Anim. Conserv.* 15(1), 95-112. doi: 10.1111/j.1469-1795.2011.00493.x.

Calò, A., Muñoz, I., Pérez-Ruzafa, Á., Vergara-Chen, C., and García-Charton, J.A. (2016). Spatial genetic structure in the saddled sea bream (*Oblada melanura* [Linnaeus, 1758]) suggests multi-scaled patterns of connectivity between protected and unprotected areas in the Western Mediterranean Sea. *Fish. Res.* 176, 30-38. doi: 10.1016/j.fishres.2015.12.001.

Cammen, K.M., Andrews, K.R., Carroll, E.L., Foote, A.D., Humble, E., Khudyakov, J.I., et al. (2016). Genomic Methods Take the Plunge: Recent Advances in High-Throughput Sequencing of Marine Mammals. *J. Hered.* 107(6), 481-495. doi: 10.1093/jhered/esw044.

Cammen, K.M., Schultz, T.F., Rosel, P.E., Wells, R.S., and Read, A.J. (2015). Genomewide investigation of adaptation to harmful algal blooms in common bottlenose dolphins (Tursiops truncatus). *Mol Ecol* 24(18), 4697-4710. doi: 10.1111/mec.13350.

Capblancq, T., Luu, K., Blum, M.G.B., and Bazin, E. (2018). Evaluation of redundancy analysis to identify signatures of local adaptation. *Molecular Ecology Resources* 18(6), 1223-1233. doi: 10.1111/1755-0998.12906.

Cassens, I., Van Waerebeek, K., Best, P.B., Tzika, A., Van Helden, A.L., Crespo, E.A., et al. (2005). Evidence for male dispersal along the coasts but no migration in pelagic waters in dusky dolphins (Lagenorhynchus obscurus). *Mol Ecol* 14(1), 107-121. doi: 10.1111/j.1365-294X.2004.02407.x.

Castro-Tavares, D., Moura, J.F., Acevedo-Trejos, E., and Merico, A. (2019). Traits Shared by Marine Megafauna and Their Relationships With Ecosystem Functions and Services. *Frontiers in Marine Science* 6. doi: 10.3389/fmars.2019.00262.

Catchen, J., Hohenlohe, P.A., Bassham, S., Amores, A., and Cresko, W.A. (2013). Stacks: an analysis tool set for population genomics. *Mol. Ecol.* 22(11), 3124-3140. doi: 10.1111/mec.12354.

Catchen, J.M., Amores, A., Hohenlohe, P., Cresko, W., and Postlethwait, J.H. (2011). Stacks: building and genotyping Loci de novo from short-read sequences. *G3 (Bethesda)* 1(3), 171-182. doi: 10.1534/g3.111.000240.

Charlesworth, D., Barton, N.H., and Charlesworth, B. (2017). The sources of adaptive variation. *Proc Biol Sci* 284(1855). doi: 10.1098/rspb.2016.2864.

Charlton-Robb, K., Gershwin, L.A., Thompson, R., Austin, J., Owen, K., and McKechnie, S. (2011). A new dolphin species, the Burrunan Dolphin *Tursiops australis* sp. nov., endemic to southern Australian coastal waters. *PLoS One* 6(9), e24047. doi: 10.1371/journal.pone.0024047.

Chen, I.H., Chou, L.S., Chou, S.J., Wang, J.H., Stott, J., Blanchard, M., et al. (2015). Selection of suitable reference genes for normalization of quantitative RT-PCR in peripheral blood samples of bottlenose dolphins (Tursiops truncatus). *Sci Rep* 5, 15425. doi: 10.1038/srep15425.

Chen, I.H., Wang, J.H., Chou, S.J., Wu, Y.H., Li, T.H., Leu, M.Y., et al. (2016). Selection of reference genes for RT-qPCR studies in blood of beluga whales (Delphinapterus leucas). *PeerJ* 4, e1810. doi: 10.7717/peerj.1810.

Chiswell, S.M., Bostock, H.C., Sutton, P.J.H., and Williams, M.J.M. (2015). Physical oceanography of the deep seas around New Zealand: a review. *N. Z. J. Mar. Freswhater Res.* 49(2), 286-317. doi: 10.1080/00288330.2014.992918.

Cingolani, P., Platts, A., Wang le, L., Coon, M., Nguyen, T., Wang, L., et al. (2012). A program for annotating and predicting the effects of single nucleotide polymorphisms, SnpEff: SNPs in the genome of *Drosophila melanogaster* strain w1118; iso-2; iso-3. *Fly* 6(2), 80-92. doi: 10.4161/fly.19695.

Cirillo, A., Di Salle, A., Petillo, O., Melone, M.A., Grimaldi, G., Bellotti, A., et al. (2014). High grade glioblastoma is associated with aberrant expression of ZFP57, a protein involved in gene imprinting, and of CPT1A and CPT1C that regulate fatty acid metabolism. *Cancer Biol Ther* 15(6), 735-741. doi: 10.4161/cbt.28408.

Clement, M., Snell, Q., Walker, P., Posada, D., and Crandall, K. (2002). "TCS: Estimating Gene Genealogies", in: *Proc. 16th Int. Parallel Distrib. Process Symp. 2.*).

CMS (2020). *Convention on the Conservation of Migratory Species of Wild Animals (CMS) . Bonn Convention* [Online]. CMS Secretariat, Bonn, Germany Available at: cms.int. [Accessed 29/05/2020 2020].

Colton, M.A., and Swearer, S.E. (2012). Locating faunal breaks in the nearshore fish assemblage of Victoria, Australia. *Marine and Freshwater Research* 63(3). doi: 10.1071/mf10322.

CommitteeonTaxonomy (2017). *List of marine mammal species and subspecies* [Online]. Available at: Society for Marine Mammalogy marinemammalscience.org. [Accessed 16/010/2017 and 12/02/2021 2017 and 2021].

Compton, B.W., McGarigal, K., Cushman, S.A., and Gamble, L.R. (2007). A resistant-kernel model of connectivity for amphibians that breed in vernal pools. *Conserv. Biol.* 21(3), 788-799. doi: 10.1111/j.1523-1739.2007.00674.x.

Condie, S.A., Mansbridge, J.V., and Cahill, M.L. (2011). Contrasting local retention and cross-shore transports of the East Australian Current and the Leeuwin Current and their relative influences on the life histories of small pelagic fishes. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 58(5), 606-615. doi: 10.1016/j.dsr2.2010.06.003.

Condie, S.A., Waring, J., Mansbridge, J.V., and Cahill, M.L. (2005). Marine connectivity patterns around the Australian continent. *Environmental Modelling & Software* 20(9), 1149-1157. doi: 10.1016/j.envsoft.2004.07.005.

Conti, F.J., Monkley, S.J., Wood, M.R., Critchley, D.R., and Muller, U. (2009). Talin 1 and 2 are required for myoblast fusion, sarcomere assembly and the maintenance of myotendinous junctions. *Development* 136(21), 3597-3606. doi: 10.1242/dev.035857.

Costello, M.J., Tsai, P., Wong, P.S., Cheung, A.K.L., Basher, Z., and Chaudhary, C. (2017). Marine biogeographic realms and species endemicity. *Nat. Commun.* 8(1), 1057. doi: 10.1038/s41467-017-01121-2.

Crow, J.F., and Kimura, M. (1970). *Introduction to population genetics theory.* New York: Harper and Row.

Cumming, R.A., Nikula, R., Spencer, H.G., and Waters, J.M. (2016). Trans-Tasman genetic connectivity in the intertidal air-breathing slug *Onchidella nigricans*. *Mar. Ecol. Prog. Ser.* 562, 93-100. doi: 10.3354/meps11926.

Cunha, H.A., de Castro, R.L., Secchi, E.R., Crespo, E.A., Lailson-Brito, J., Azevedo, A.F., et al. (2015). Molecular and Morphological Differentiation of Common Dolphins (Delphinus sp.) in the Southwestern Atlantic: Testing the Two Species Hypothesis in Sympatry. *PLoS One* 10(11), e0140251. doi: 10.1371/journal.pone.0140251.

Currie, D.R., McClatchie, S., Middleton, J.F., and Nayar, S. (2012). Biophysical factors affecting the distribution of demersal fish around the head of a Submarine Canyon off the Bonney Coast, South Australia. *PLoS One* 7(1), e30138. doi: 10.1371/journal.pone.0030138.

D'Aloia, C.C., Andres, J.A., Bogdanowicz, S.M., McCune, A.R., Harrison, R.G., and Buston, P.M. (2020). Unraveling hierarchical genetic structure in a marine metapopulation: A comparison of three high-throughput genotyping approaches. *Mol Ecol* 29(12), 2189-2203. doi: 10.1111/mec.15405.

Dalongeville, A., Benestan, L., Mouillot, D., Lobreaux, S., and Manel, S. (2018). Combining six genome scan methods to detect candidate genes to salinity in the Mediterranean striped red mullet (Mullus surmuletus). *BMC Genomics* 19(1), 217. doi: 10.1186/s12864-018-4579-z.

Danecek, P., Auton, A., Abecasis, G., Albers, C.A., Banks, E., DePristo, M.A., et al. (2011). The variant call format and VCFtools. *Bioinformatics* 27(15), 2156-2158. doi: 10.1093/bioinformatics/btr330.

Daskalov, G.M. (2002). Overfishing drives a trophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.* 225, 53-63. doi: 10.3354/meps225053.

Dawson, M.N., Cieciel, K., Decker, M.B., Hays, G.C., Lucas, C.H., and Pitt, K.A. (2014). Population-level perspectives on global change: genetic and demographic analyses indicate various scales, timing, and causes of *scyphozoan* jellyfish blooms. *Biol. Invasions* 17(3), 851-867. doi: 10.1007/s10530-014-0732-z.

deBruijn, S.E., Verbakel, S.K., de Vrieze, E., Kremer, H., Cremers, F.P.M., Hoyng, C.B., et al. (2018). Homozygous variants in KIAA1549, encoding a ciliary protein, are associated with autosomal recessive retinitis pigmentosa. *J Med Genet* 55(10), 705-712. doi: 10.1136/jmedgenet-2018-105364.

Derville, S., Constantine, R., Baker, C.S., Oremus, M., and Torres, L.G. (2016). Environmental correlates of nearshore habitat distribution by the Critically Endangered Maūi dolphin. *Marine Ecology Progress Series* 551, 261-275. doi: 10.3354/meps11736.

Derville, S., Torres, L.G., Albertson, R., Andrews, O., Baker, C.S., Carzon, P., et al. (2019). Whales in warming water: Assessing breeding habitat diversity and adaptability in Oceania's changing climate. *Glob Chang Biol*. doi: 10.1111/gcb.14563.

Desert, C., Baeza, E., Aite, M., Boutin, M., Le Cam, A., Montfort, J., et al. (2018). Multi-tissue transcriptomic study reveals the main role of liver in the chicken adaptive response to a switch in dietary energy source through the transcriptional regulation of lipogenesis. *BMC Genomics* 19(1), 187. doi: 10.1186/s12864-018-4520-5.

DiBattista, J.D., Travers, M.J., Moore, G.I., Evans, R.D., Newman, S.J., Feng, M., et al. (2017). Seascape genomics reveals fine-scale patterns of dispersal for a reef fish along the ecologically divergent coast of Northwestern Australia. *Mol. Ecol.* 26(22), 6206-6223. doi: 10.1111/mec.14352.

Dineshram, R., Q, Q., Sharma, R., Chandramouli, K., Yalamanchili, H.K., Chu, I., et al. (2015). Comparative and quantitative proteomics reveal the adaptive strategies of oyster larvae to ocean acidification. *Proteomics* 15(23-24), 4120-4134. doi: 10.1002/pmic.201500198.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., et al. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36(1), 27-46. doi: 10.1111/j.1600-0587.2012.07348.x.

Draheim, H.M., Moore, J.A., Winterstein, S.R., and Scribner, K.T. (2020). Spatial genetic structure and landscape connectivity in black bears: Investigating the significance of using different land cover datasets and classifications in landscape genetics analyses. *Ecol Evol* 11(2), 978-989. doi: 10.1002/ece3.7111.

Dunn, D.C., Harrison, A.L., Curtice, C., DeLand, S., Donnelly, B., Fujioka, E., et al. (2019). The importance of migratory connectivity for global ocean policy. *Proc. Biol. Sci.* 286(1911), 20191472. doi: 10.1098/rspb.2019.1472.

Dwyer, S.L., Pawley, M.D.M., Clement, D.M., and Stockin, K.A. (2020). Modelling habitat use suggests static spatial exclusion zones are a non-optimal management tool for a highly mobile marine mammal. *Mar. Biol.* 167(5). doi: 10.1007/s00227-020-3664-4.

Emami, N.K., Jung, U., Voy, B., and Dridi, S. (2020). Radical Response: Effects of Heat Stress-Induced Oxidative Stress on Lipid Metabolism in the Avian Liver. *Antioxidants (Basel)* 10(1). doi: 10.3390/antiox10010035.

Emlen, J.M. (1966). The role of time and energy in food preference. *Am. Nat.* 100(916), 611–617. doi: 10.1086/282455.

Eriksen, R.S., Davies, C.H., Bonham, P., Coman, F.E., Edgar, S., McEnnulty, F.R., et al. (2019). Australia's Long-Term Plankton Observations: The Integrated Marine Observing System National Reference Station Network. *Frontiers in Marine Science* 6. doi: 10.3389/fmars.2019.00161.

Excoffier, L., and Lischer, H.E. (2010). Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* 10(3), 564-567. doi: 10.1111/j.1755-0998.2010.02847.x.

Fick, S.E., and Hijmans, R.J. (2017). WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12), 4302-4315.

Filby, N.E., Bossley, M., Sanderson, K.J., Martinez, E., and Stockin, K.A. (2010). Distribution and Population Demographics of Common Dolphins (*Delphinus delphis*) in the Gulf St. Vincent, South Australia. *Aquat. Mamm.* 36(1), 33-45. doi: 10.1578/am.36.1.2010.33.

Filby, N.E., Bossley, M., and Stockin, K.A. (2013). Behaviour of free-ranging short-beaked common dolphins (*Delphinus delphis*) in Gulf St Vincent, South Australia. *Aust. J. Zool.* 61(4). doi: 10.1071/zo12033.

Fisher, R. (1930). *The genetical theory of natural selection.* New York available at: archive.org/details/geneticaltheoryo00fishuoft: Clarendon Press, Dover Publications.

Flynn, A.J., Kloser, R.J., and Sutton, C. (2018). Micronekton assemblages and bioregional setting of the Great Australian Bight: A temperate northern boundary current system. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 157-158, 58-77. doi: 10.1016/j.dsr2.2018.08.006.

Foll, M., and Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics* 180(2)**,** 977-993. doi: 10.1534/genetics.108.092221.

Foo, D., Hindell, M., McMahon, C., Goldsworthy, S., and Bailleul, F. (2020). Environmental drivers of oceanic foraging site fidelity in central place foragers. *Marine Biology* 167(6). doi: 10.1007/s00227-020-03685-y.

Foote, A.D., Martin, M.D., Louis, M., Pacheco, G., Robertson, K.M., Sinding, M.S., et al. (2019). Killer whale genomes reveal a complex history of recurrent admixture and vicariance. *Mol Ecol* 28(14)**,** 3427-3444. doi: 10.1111/mec.15099.

Foote, A.D., Vijay, N., Avila-Arcos, M.C., Baird, R.W., Durban, J.W., Fumagalli, M., et al. (2016). Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nat. Commun.* 7**,** 11693. doi: 10.1038/ncomms11693.

Forester, B.R., Lasky, J.R., Wagner, H.H., and Urban, D.L. (2018). Comparing methods for detecting multilocus adaptation with multivariate genotype-environment associations. *Molecular Ecology* 27(9)**,** 2215-2233. doi: 10.1111/mec.14584.

Frankham, R., Ballou, J.D., and Briscoe, D.A. (2010). *Introduction to Conservation Genetics.* Cambridge University Press.

Frankham, R., Ballou, J.D., Ralls, K., Eldridge, M., Dudash, M.R., Fenster, C.B., et al. (2017).

Fruet, P., Secchi, E.R., Daura-Jorge, F., Vermeulen, E., Flores, P.A.C., Simões-Lopes, P.C., et al. (2014). Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. *Conserv. Genet.* 15**,** 879-895. doi: 10.1007/s10592-014-0586-z).

Fuentes, J., Brinca, L., Guerreiro, P.M., and Power, D.M. (2010). PRL and GH synthesis and release from the sea bream (Sparus auratus L.) pituitary gland in vitro in response to osmotic challenge. *Gen Comp Endocrinol* 168(1)**,** 95-102. doi: 10.1016/j.ygcen.2010.04.005.

Fullard, K.J., Early, G., Heide-Jorgensen, M.P., Bloch, D., Rosing-Asvid, S.A., and Amos, W. (2000). Population structure of long-finned pilot whales in the North Atlantic: a correlation with sea surface temperature? *Mol. Ecol.* 9**,** 949-958.

Funk, W.C., Forester, B.R., Converse, S.J., Darst, C., and Morey, S. (2019). Improving conservation policy with genomics: a guide to integrating adaptive potential into U.S. Endangered Species Act decisions for conservation practitioners and geneticists. *Conservation Genetics* 20(1)**,** 115-134. doi: 10.1007/s10592-018-1096-1.

Funk, W.C., McKay, J.K., Hohenlohe, P.A., and Allendorf, F.W. (2012). Harnessing genomics for delineating conservation units. *Trends Ecol. Evol.* 27(9)**,** 489-496. doi: 10.1016/j.tree.2012.05.012.

Gagnaire, P.A., Broquet, T., Aurelle, D., Viard, F., Souissi, A., Bonhomme, F., et al. (2015). Using neutral, selected, and hitchhiker loci to assess connectivity of marine populations in the genomic era. *Evol Appl* 8(8)**,** 769-786. doi: 10.1111/eva.12288.

Galpern, P., Peres-Neto, P.R., Polfus, J., Manseau, M., and Pybus, O. (2014). MEMGENE: Spatial pattern detection in genetic distance data. *Methods in Ecology and Evolution* 5(10)**,** 1116-1120. doi: 10.1111/2041-210x.12240.

Gardner, B., Hoban, S., and Luikart, G. (2020). IUCN Red List and the value of integrating genetics. *Conserv. Genet.* doi: 10.1007/s10592-020-01301-6.

Gaspari, S., Holcer, D., Mackelworth, P., Fortuna, C., Frantzis, A., Genov, T., et al. (2015a). Population genetic structure of common bottlenose dolphins (*Tursiops truncatu*s) in the Adriatic Sea and contiguous regions: implications for international conservation. *Aquatic Conserv. Mar. Freshw. Ecosyst.* 25(2)**,** 212-222. doi: 10.1002/aqc.2415.

Gaspari, S., Scheinin, A., Holcer, D., Fortuna, C., Natali, C., Genov, T., et al. (2015b). Drivers of Population Structure of the Bottlenose Dolphin (*Tursiops truncatus*) in the Eastern Mediterranean Sea. *Evol. Biol.* 42(2)**,** 177-190. doi: 10.1007/s11692-015-9309-8.

Gatesy, J., Geisler, J.H., Chang, J., Buell, C., Berta, A., Meredith, R.W., et al. (2013). A phylogenetic blueprint for a modern whale. *Mol Phylogenet Evol* 66(2), 479-506. doi: 10.1016/j.ympev.2012.10.012.

Gene Ontology, C. (2015). Gene Ontology Consortium: going forward. *Nucleic Acids Res* 43(Database issue), D1049-1056. doi: 10.1093/nar/gku1179.

Genov, T., Bearzi, G., Bonizzoni, S., and Tempesta, M. (2012). Long-distance movement of a lone short-beaked common dolphin *Delphinus delphis* in the central Mediterranean Sea. *Mar. Biodivers. Rec.* 5. doi: 10.1017/s1755267211001163.

Genov, T., Kotnjek, P., and Centrih, T. (2020). Occurrence of common dolphins (*Delphinus delphis*) in the Gulf of Trieste and the northern Adriatic Sea. *Aquatic Conserv. Mar. Freshw. Ecosyst.* . doi: 10.1002/aqc.3407.

Genoves, R.C., Fruet, P.F., Botta, S., Beheregaray, L.B., Möller, L.M., and Secchi, E.R. (2020). Fine-scale genetic structure in Lahille's bottlenose dolphins (*Tursiops truncatus gephyreus*) is associated with social structure and feeding ecology. *Marine Biology* 167(3). doi: 10.1007/s00227-019-3638-6.

Gkafas, G.A., Exadactylos, A., Rogan, E., Raga, J.A., Reid, R., and Hoelzel, A.R. (2017). Biogeography and temporal progression during the evolution of striped dolphin population structure in European waters. *Journal of Biogeography*. doi: 10.1111/jbi.13079.

Goldsworthy, S.D., Bailleul, F., NurseyBray, M., Mackay, A., Oxley, A., Reinhold, S.-L., et al. (2019a). "Assessment of the impacts of seal populations on the seafood industry in South Australia", (ed.) A. South Australian Research and Development Institute (Aquatic Sciences). (Adelaide, June).

Goldsworthy, S.D., Ferguson, G.J., and Ward, T.M. (2019b). "Assessment of dolphin interactions, effectiveness of Code of Practice and fishing behaviour in the South Australian Sardine Fishery: 2018-19. ", (ed.) A. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences). (F2010/000726-10. SARDI Research Report Series No. 1041. 36pp.).

Goldsworthy, S.D., Page, B., Rogers, P.J., Bulman, C., Wiebkin, A., McLeay, L.J., et al. (2013). Trophodynamics of the eastern Great Australian Bight ecosystem: Ecological change associated with the growth of Australia's largest fishery. *Ecological Modelling* 255, 38-57. doi: 10.1016/j.ecolmodel.2013.01.006.

Grummer, J.A., Beheregaray, L.B., Bernatchez, L., Hand, B.K., Luikart, G., Narum, S.R., et al. (2019). Aquatic Landscape Genomics and Environmental Effects on Genetic Variation. *Trends Ecol. Evol.* 34(7), 641-654. doi: 10.1016/j.tree.2019.02.013.

Halden, J.B.S. (1957). The cost of natural selection. *J. Genet.* 55, 511-524.

Hamer, D.J., Ward, T.M., and McGarvey, R. (2008). Measurement, management and mitigation of operational interactions between the South Australian Sardine Fishery and short-beaked common dolphins (*Delphinus delphis*). *Biol. Conserv.* 141(11), 2865-2878. doi: 10.1016/j.biocon.2008.08.024.

Hamilton, S., and Baker, G.B. (2019). Technical mitigation to reduce marine mammal bycatch and entanglement in commercial fishing gear: lessons learnt and future directions. *Rev. Fish Biol.* 29(2), 223-247. doi: 10.1007/s11160-019-09550-6.

Hammond, P.S., Bearzi, G., Bjørge, A., Forney, K., Karczmarski, L., Kasuya, T., et al. (2008). *Delphinus delphis* [Online]. The IUCN Red List of Threatened Species 2008. [Accessed 2017].

Hanski, I. (1998). Metapopulation dynamics. *Nature* 396(6706), 41-49. doi: 10.1038/23876.

Hanski, I. (1999). *Metapopulation ecology* Oxford ; New York: Oxford University Press.

Hanski, I., and Saccheri, I. (2006). Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biol* 4(5), e129. doi: 10.1371/journal.pbio.0040129.

Hanson, J.O., Rhodes, J.R., Riginos, C., and Fuller, R.A. (2017). Environmental and geographic variables are effective surrogates for genetic variation in conservation planning. *Proc Natl Acad Sci U S A* 114(48), 12755-12760. doi: 10.1073/pnas.1711009114.

Havird, J.C., Mitchell, R.T., Henry, R.P., and Santos, S.R. (2016). Salinity-induced changes in gene expression from anterior and posterior gills of *Callinectes sapidus* (Crustacea: Portunidae) with implications for crustacean ecological genomics. *Comp Biochem Physiol Part D Genomics Proteomics* 19**,** 34-44. doi: 10.1016/j.cbd.2016.06.002.

Heimeier, D., Alexander, A., Hamner, R.M., Pichler, F., and Baker, C.S. (2018). The Influence of Selection on MHC DQA and DQB Haplotypes in the Endemic New Zealand Hector's and Maui Dolphins. *J. Hered.* 109(7)**,** 744-756. doi: 10.1093/jhered/esy050.

Hendricks, S., Anderson, E.C., Antao, T., Bernatchez, L., Forester, B.R., Garner, B., et al. (2018). Recent advances in conservation and population genomics data analysis. *Evol. Appl.* 11(8)**,** 1197-1211. doi: 10.1111/eva.12659.

Hindle, A.G. (2020). Diving deep: understanding the genetic components of hypoxia tolerance in marine mammals. *J Appl Physiol (1985)* 128(5)**,** 1439-1446. doi: 10.1152/japplphysiol.00846.2019.

Hoban, S., Kelley, J.L., Lotterhos, K.E., Antolin, M.F., Bradburd, G., Lowry, D.B., et al. (2016). Finding the Genomic Basis of Local Adaptation: Pitfalls, Practical Solutions, and Future Directions. *American Naturalist* 188(4)**,** 379-397. doi: 10.1086/688018.

Hobday, A.J., and Lough, J.M. (2011). Projected climate change in Australian marine and freshwater environments. *CSIRO Marine and Freshwater Research* 62**,** 1000-1014. doi: 10.1071/MF10302.

Hoelzel, A.R. (1994). GENETICS AND ECOLOGY OF WHALES AND DOLPHINS. *Annu. Rev. Ecol. Syst.* 25**,** 377-399.

Hoelzel, A.R. (1998). Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: implications for conservation policy. *J. Hered.* 89(5)**,** 451-458. doi: 10.1093/jhered/89.5.451.

Hoelzel, A.R., Bruford, M.W., and Fleischer, R.C. (2019). Conservation of adaptive potential and functional diversity. *Conservation Genetics* 20(1)**,** 1-5. doi: 10.1007/s10592-019-01151-x.

Hoelzel, A.R., Hey, J., Dahlheim, M.E., Nicholson, C., Burkanov, V., and Black, N. (2007). Evolution of population structure in a highly social top predator, the killer whale. *Mol. Biol. Evol.* 24(6)**,** 1407-1415. doi: 10.1093/molbev/msm063.

Holderegger, R., Schmidt, B.R., Grünig, C., Meier, R., Csencsics, D., Gassner, M., et al. (2020). Ready-to-use workflows for the implementation of genetic tools in conservation management. *Conserv. Genet. Resour.* doi: 10.1007/s12686-020-01165-5.

Holland, L.P., Jenkins, T.L., and Stevens, J.R. (2017). Contrasting patterns of population structure and gene flow facilitate exploration of connectivity in two widely distributed temperate octocorals. *J. Hered.* 119(1)**,** 35-48. doi: 10.1038/hdy.2017.14.

Horio, N., Yoshida, R., Yasumatsu, K., Yanagawa, Y., Ishimaru, Y., Matsunami, H., et al. (2011). Sour taste responses in mice lacking PKD channels. *PLoS One* 6(5)**,** e20007. doi: 10.1371/journal.pone.0020007.

Hupman, K. (2016). *Photo-identification and its application to gregarious delphinids: Common dolphins (Delphinus sp.) in the Hauraki Gulf, New Zealand.* Doctor of Philosophy, Massey University.

Hupman, K., Stockin, K.A., Pollock, K., Pawley, M.D.M., Dwyer, S.L., Lea, C., et al. (2018). Challenges of implementing Mark-recapture studies on poorly marked gregarious delphinids. *PLoS One* 13(7)**,** e0198167. doi: 10.1371/journal.pone.0198167.

Ikeda, D., Ono, Y., Hirano, S., Kan-no, N., and Watabe, S. (2013). Lampreys have a single gene cluster for the fast skeletal myosin heavy chain gene family. *PLoS One* 8(12)**,** e85500. doi: 10.1371/journal.pone.0085500.

Irwin, R.E., Thursby, S.J., Ondicova, M., Pentieva, K., McNulty, H., Richmond, R.C., et al. (2019). A randomized controlled trial of folic acid intervention in pregnancy highlights a putative methylation-regulated control element at ZFP57. *Clin Epigenetics* 11(1)**,** 31. doi: 10.1186/s13148-019-0618-0.

Jasper, M., Schmidt, T.L., Ahmad, N.W., Sinkins, S.P., and Hoffmann, A.A. (2019). A genomic approach to inferring kinship reveals limited intergenerational dispersal in the yellow fever mosquito. *Mol. Ecol. Resour.* 19(5), 1254-1264. doi: 10.1111/1755-0998.13043.

Jeong, B.C., Kang, I.H., and Koh, J.T. (2014). MicroRNA-302a inhibits adipogenesis by suppressing peroxisome proliferator-activated receptor gamma expression. *FEBS Lett* 588(18), 3427-3434. doi: 10.1016/j.febslet.2014.07.035.

Jombart, T. (2008). adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 24(11), 1403-1405. doi: 10.1093/bioinformatics/btn129.

Jombart, T., and Ahmed, I. (2011). adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics* 27(21), 3070-3071. doi: 10.1093/bioinformatics/btr521.

Jombart, T., and Collins, C. (2015). "A tutorial for discriminant analysis of principal components (DAPC) using adegenet 2.0.0". (available at: adegenet.r-forge.r-project.org/files/tutorial-dapc.pdf).

Jones, F.C., Grabherr, M.G., Chan, Y.F., Russell, P., Mauceli, E., Johnson, J., et al. (2012). The genomic basis of adaptive evolution in threespine sticklebacks. *Nature* 484(7392), 55-61. doi: 10.1038/nature10944.

Jordan, F.F.J., Murphy, S., Martinez, E., Amiot, C., van Helden, A., and Stockin, K.A. (2015). Criteria for assessing maturity of skulls in the common dolphin,Delphinussp., from New Zealand waters. *Marine Mammal Science* 31(3), 1077-1097. doi: 10.1111/mms.12229.

Kämpf, J. (2010). On preconditioning of coastal upwelling in the eastern Great Australian Bight. *Journal of Geophysical Research* 115(C12). doi: 10.1029/2010jc006294.

Kämpf, J. (2015). Phytoplankton blooms on the western shelf of Tasmania: evidence of a highly productive ecosystem. *Ocean Sci.* 11(1), 1-11. doi: 10.5194/os-11-1-2015.

Kämpf, J., and Bell, D. (2014). "The Murray/Coorong Estuary: Meeting of the Waters?," in *Estuaries of Australia in 2050 and beyond,* ed. E. Wolanski. (Springer Dordrecht Heidelberg New York London: Springer), 31-47.

Kämpf, J., and Chapman, P. (2016). *Upwelling Systems of the World: A Scientific Journey to the Most Productive Marine Ecosystems.* Switzerland: Springer Nature.

Keane, J.P., and Neira, F.J. (2008). Larval fish assemblages along the south-eastern Australian shelf: linking mesoscale non-depth-discriminate structure and water masses. *Fisheries Oceanography* 17(4), 263-280. doi: 10.1111/j.1365-2419.2008.00478.x.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., et al. (2012). Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28(12), 1647-1649. doi: 10.1093/bioinformatics/bts199.

Kelley, J.L., Brown, A.P., Therkildsen, N.O., and Foote, A.D. (2016). The life aquatic: advances in marine vertebrate genomics. *Nat Rev Genet* 17(9), 523-534. doi: 10.1038/nrg.2016.66.

Kemper, C., Pemberton, D., Cawthorn, M., Heinrich, S., Mann, J., Würsig, B., et al. (2003). "Aquaculture and marine mammals : Co-existence or conflict?," in *Marine mammals: Fisheries, tourism and management issues,* ed. H.M.K. R. (Melbourne, Australia: CSIRO Publishing), 208–226.

Kemper, C.M., Tomo, I., Bingham, J., Bastianello, S.S., Wang, J., Gibbs, S.E., et al. (2016). Morbillivirus-associated unusual mortality event in South Australian bottlenose dolphins is largest reported for the Southern Hemisphere. *R Soc Open Sci* 3(12), 160838. doi: 10.1098/rsos.160838.

Kent, C.S., Bouchet, P., Wellard, R., Parnum, I., Fouda, L., and Erbe, C. (2020). Seasonal productivity drives aggregations of killer whales and other cetaceans over submarine canyons of the Bremer Sub-Basin, south-western Australia. *Australian Mammalogy*. doi: 10.1071/am19058.

Kimura, M. (1968). Genetic variability maintained in a finite population due to mutational production of neutral and nearly neutral isoalleles. *Genet Res* 11(3), 247-269. doi: 10.1017/s0016672300011459.

Kool, J.T., Huang, Z., and Nichol, S.L. (2015). Simulated larval connectivity among Australia's southwest submarine canyons. *Marine Ecology Progress Series* 539, 77-91. doi: 10.3354/meps11477.

Koslow, J.A., Pesant, S., Feng, M., Pearce, A., Fearns, P., Moore, T., et al. (2008). The effect of the Leeuwin Current on phytoplankton biomass and production off Southwestern Australia. *Journal of Geophysical Research* 113(C7). doi: 10.1029/2007jc004102.

Kritzer, J.P., and Sale, P.F. (2004). Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5, 131-140. doi: doi.org/10.1111/j.1467-2979.2004.00131.x.

Krutzen, M., Barre, L., Möller, L.M., Heithaus, M.R., Simms, C., and Sherwin, W.B. (2002). A Biopsy System for small ceteceans: darting success and wound healing in *Tursiops* spp. *Mar. Mamm. Sci.* 18(4), 863-878. doi: doi:10.1111/j.1748-7692.2002.tb01078.x.

Krutzen, M., and Sherwin, W.B. (2004). Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: Bottlenose dolphins (Tursiops Sp.) in Shark Bay Western Australia. *Mar. Mamm. Sci.* 20(1), 28-47. doi: 10.1111/j.1748-7692.2004.tb01139.x.

Lal, M.M., Southgate, P.C., Jerry, D.R., Bosserelle, C., and Zenger, K.R. (2017). Swept away: ocean currents and seascape features influence genetic structure across the 18,000 Km Indo-Pacific distribution of a marine invertebrate, the black-lip pearl oyster *Pinctada margaritifera*. *BMC Genomics* 18(1), 66. doi: 10.1186/s12864-016-3410-y.

Langmead, B., and Salzberg, S.L. (2012). Fast gapped-read alignment with Bowtie 2. *Nat. Methods* 9, 357. doi: 10.1038/nmeth.1923.

Larson, J., Drew, K.L., Folkow, L.P., Milton, S.L., and Park, T.J. (2014). No oxygen? No problem! Intrinsic brain tolerance to hypoxia in vertebrates. *J Exp Biol* 217(Pt 7), 1024-1039. doi: 10.1242/jeb.085381.

Lazzarotto, V. (2016). *Consequences of long-term feeding trout with plant-based diets on the regulation of energy and lipid metabolism: special focus on trans-generational effects and early stages.*, L' Universite de Pau et des Pay Del'Adour.

Legendre, P., Oksanen, J., and ter Braak, C.J.F. (2011). Testing the significance of canonical axes in redundancy analysis. *Methods in Ecology and Evolution* 2(3), 269-277. doi: 10.1111/j.2041-210X.2010.00078.x.

Leitwein, M., Duranton, M., Rougemont, Q., Gagnaire, P.A., and Bernatchez, L. (2020). Using Haplotype Information for Conservation Genomics. *Trends Ecol. Evol.* 35(3), 245-258. doi: 10.1016/j.tree.2019.10.012.

Leslie, M.S., and Morin, P.A. (2016). Using Genome-Wide SNPs to Detect Structure in High-Diversity and Low-Divergence Populations of Severely Impacted Eastern Tropical Pacific Spinner (*Stenella longirostris*) and Pantropical Spotted Dolphins (*S. attenuata*). *Front. Mar. Sci.* 3. doi: 10.3389/fmars.2016.00253.

Leslie, M.S., and Morin, P.A. (2018). Structure and phylogeography of two tropical predators, spinner (*Stenella longirostris*) and pantropical spotted (*S. attenuata*) dolphins, from SNP data. *R. Soc. Open Sci.* 5(4), 171615. doi: 10.1098/rsos.171615.

Levins, R. (1969). Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bull. Entomol. Soc. of Am.* 15(3(1)), 237-240. doi: 10.1093/besa/15.3.237.

Li, L., Xie, X., Qin, J., Jeha, G.S., Saha, P.K., Yan, J., et al. (2009). The nuclear orphan receptor COUP-TFII plays an essential role in adipogenesis, glucose homeostasis, and energy metabolism. *Cell Metab* 9(1), 77-87. doi: 10.1016/j.cmet.2008.12.002.

Li, S., Mi, L., Yu, L., Yu, Q., Liu, T., Wang, G.X., et al. (2017). Zbtb7b engages the long noncoding RNA Blnc1 to drive brown and beige fat development and thermogenesis. *Proc Natl Acad Sci U S A* 114(34), E7111-E7120. doi: 10.1073/pnas.1703494114.

Li, Y.L., Xue, D.X., Zhang, B.D., and Liu, J.X. (2019). Population Genomic Signatures of Genetic Structure and Environmental Selection in the Catadromous Roughskin Sculpin *Trachidermus fasciatus*. *Genome Biol Evol* 11(7), 1751-1764. doi: 10.1093/gbe/evz118.

Lim, Y.K., Cheung, K., Dang, X., Roberts, S.B., Wang, X., and Thiyagarajan, V. (2020). DNA methylation changes in response to ocean acidification at the time of larval metamorphosis in the edible oyster, *Crassostrea hongkongensis*. *Mar Environ Res* 163, 105214. doi: 10.1016/j.marenvres.2020.105214.

Linck, E., and Battey, C.J. (2018). Minor allele frequency thresholds strongly a↵ect population structure inference with genomic datasets. doi: 10.1101/188623.

Linnaeus, C. (1758). *Per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentiis, synonymis, locis.* Edito decima, reformatta, Tomus I. Systema Naturae: 824.

Liu, S., Lorenzen, E.D., Fumagalli, M., Li, B., Harris, K., Xiong, Z., et al. (2014). Population genomics reveal recent speciation and rapid evolutionary adaptation in polar bears. *Cell* 157(4), 785-794. doi: 10.1016/j.cell.2014.03.054.

Lotterhos, K.E., and Whitlock, M.C. (2014). Evaluation of demographic history and neutral parameterization on the performance of FST outlier tests. *Mol Ecol* 23(9), 2178-2192. doi: 10.1111/mec.12725.

Lotterhos, K.E., and Whitlock, M.C. (2015). The relative power of genome scans to detect local adaptation depends on sampling design and statistical method. *Mol Ecol* 24(5), 1031-1046. doi: 10.1111/mec.13100.

Louis, M., Fontaine, M.C., Spitz, J., Schlund, E., Dabin, W., Deaville, R., et al. (2014a). Ecological opportunities and specializations shaped genetic divergence in a highly mobile marine top predator. *Proceedings in Biological Science Royal Society* 281(1795). doi: 10.1098/rspb.2014.1558.

Louis, M., Viricel, A., Lucas, T., Peltier, H., Alfonsi, E., Berrow, S., et al. (2014b). Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. *Mol. Ecol.* 23(4), 857-874. doi: 10.1111/mec.12653.

Lourey, M.J., Dunn, J.R., and Waring, J. (2006). A mixed-layer nutrient climatology of Leeuwin Current and Western Australian shelf waters: Seasonal nutrient dynamics and biomass. *Journal of Marine Systems* 59(1-2), 25-51. doi: 10.1016/j.jmarsys.2005.10.001.

Luikart, G., England, P.R., Tallmon, D., Jordan, S., and Taberlet, P. (2003). The power and promise of population genomics: from genotyping to genome typing. *Nat. Rev. Genet.* 4(12), 981-994. doi: 10.1038/nrg1226.

Luo, W., Hu, H., Chang, R., Zhong, J., Knabel, M., O'Meally, R., et al. (2011). Pyruvate kinase M2 is a PHD3-stimulated coactivator for hypoxia-inducible factor 1. *Cell* 145(5), 732-744. doi: 10.1016/j.cell.2011.03.054.

Lynch, T.P., Morello, E.B., Evans, K., Richardson, A.J., Rochester, W., Steinberg, C.R., et al. (2014). IMOS National Reference Stations: a continental-wide physical, chemical and biological coastal observing system. *PLoS One* 9(12), e113652. doi: 10.1371/journal.pone.0113652.

MacArthur, R.H., and Pianka, E.R. (1966). On the optimal use of a patchy environment. *Am. Nat.* 100, 603–609. doi: 10.1086/282454.

MacArthur, R.H., and Wilson, E.O. (1967). *The Theory of Island Biogeography.* Princeton, NJ: Princeton University Press.

Mackay, A.I., Bailleul, F., Carroll, E.L., Andrews-Goff, V., Baker, C.S., Bannister, J., et al. (2020). Satellite derived offshore migratory movements of southern right whales (Eubalaena australis) from Australian and New Zealand wintering grounds. *PLoS One* 15(5), e0231577. doi: 10.1371/journal.pone.0231577.

Mackay, A.I., and Goldsworthy, S.D. (2017). "Mitigating operational interactions with short-beaked common dolphin (*Delphinus delphis*): application of the South Australian Sardine Fishery industry Code of Practice 2016-17", (ed.) R.t.P.F.a. Aquaculture.

(South Australian Research and Development Institute (Aquatic Sciences), Adelaide.: SARDI).

Mackay, A.I., Goldsworthy, S.D., and Harrison, P. (2016). "Critical knowledge gaps: estimating potential maximum cumulative anthropogenic mortality limits of key marine mammal species to inform management in the Small Pelagic Fishery area", (ed.) S.A.R.a.D.I.A. Sciences). (Adelaide, 2016).

Manel, S., and Holderegger, R. (2013). Ten years of landscape genetics. *Trends Ecol Evol* 28(10), 614-621. doi: 10.1016/j.tree.2013.05.012.

Manel, S., Joost, S., Epperson, B.K., Holderegger, R., Storfer, A., Rosenberg, M.S., et al. (2010). Perspectives on the use of landscape genetics to detect genetic adaptive variation in the field. *Mol Ecol* 19(17), 3760-3772. doi: 10.1111/j.1365-294X.2010.04717.x.

Manel, S., Loiseau, N., Andrello, M., Fietz, K., Goni, R., Forcada, A., et al. (2019). Long-Distance Benefits of Marine Reserves: Myth or Reality? *Trends. Ecol. Evol.* 34(4), 342-354. doi: 10.1016/j.tree.2019.01.002.

Manel, S., Perrier, C., Pratlong, M., Abi-Rached, L., Paganini, J., Pontarotti, P., et al. (2016). Genomic resources and their influence on the detection of the signal of positive selection in genome scans. *Mol Ecol* 25(1), 170-184. doi: 10.1111/mec.13468.

Manel, S., Schwartz, M.K., Luikart, G., and Taberlet, P. (2003). Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution* 18(4), 189-197. doi: 10.1016/s0169-5347(03)00008-9.

Mantel, N. (1967). The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Res.* 27(2), 209-220.

Marra, N.J., Stanhope, M.J., Jue, N.K., Wang, M., Sun, Q., Pavinski Bitar, P., et al. (2019). White shark genome reveals ancient elasmobranch adaptations associated with wound healing and the maintenance of genome stability. *Proc Natl Acad Sci U S A* 116(10), 4446-4455. doi: 10.1073/pnas.1819778116.

Mason, S., Salgado Kent, C., Donnelly, D., Weir, J., and Bilgmann, K. (2016). Atypical residency of short-beaked common dolphins (*Delphinus delphis*) to a shallow, urbanized embayment in south-eastern Australia. *R. Soc. Open Sci.* 3(9), 160478. doi: 10.1098/rsos.160478.

Mateo-Sánchez, M.C., Balkenhol, N., Cushman, S., Pérez, T., Domínguez, A., and Saura, S. (2015). Estimating effective landscape distances and movement corridors: comparison of habitat and genetic data. *Ecosphere* 6(4), 1-16. doi: 10.1890/es14-00387.1.

Matthews, J.M., and Sunde, M. (2002). Zinc Fingers—Folds for Many Occasions. *Life* 54, 351–355. doi: 10.1080/15216540290114711.

McClatchie, S., Middleton, J.F., and Ward, T.M. (2006). Water mass analysis and alongshore variation in upwelling intensity in the eastern Great Australian Bight. *Journal of Geophysical Research* 111(C8). doi: 10.1029/2004jc002699.

McGowen, M.R., Gatesy, J., and Wildman, D.E. (2014). Molecular evolution tracks macroevolutionary transitions in Cetacea. *Trends Ecol Evol* 29(6), 336-346. doi: 10.1016/j.tree.2014.04.001.

McGowen, M.R., Grossman, L.I., and Wildman, D.E. (2012). Dolphin genome provides evidence for adaptive evolution of nervous system genes and a molecular rate slowdown. *Proc Biol Sci* 279(1743), 3643-3651. doi: 10.1098/rspb.2012.0869.

McGowen, M.R., Spaulding, M., and Gatesy, J. (2009). Divergence date estimation and a comprehensive molecular tree of extant cetaceans. *Mol Phylogenet Evol* 53(3), 891-906. doi: 10.1016/j.ympev.2009.08.018.

McGowen, M.R., Tsagkogeorga, G., Williamson, J., Morin, P.A., and Rossiter, S.J. (2020). Positive selection and inactivation in the vision and hearing genes of cetaceans. *Mol Biol Evol*. doi: 10.1093/molbev/msaa070.

Meirmans, P.G., and Van Tienderen, P.H. (2004). GENOTYPE and GENODIVE: two programs for the analysis of genetic diversity of asexual organisms. *Mol. Ecol. Not.* 4(4), 792-794. doi: 10.1111/j.1471-8286.2004.00770.x.

Meissner, A.M., Christiansen, F., Martinez, E., Pawley, M.D., Orams, M.B., and Stockin, K.A. (2015). Behavioural effects of tourism on oceanic common dolphins, *Delphinus* sp., in New Zealand: the effects of Markov analysis variations and current tour operator compliance with regulations. *PLoS One* 10(1), e0116962. doi: 10.1371/journal.pone.0116962.

Mendez, M., Rosenbaum, H.C., and Bordino, P. (2008). Conservation genetics of the franciscana dolphin in Northern Argentina: population structure, by-catch impacts, and management implications. *Conserv. Genet.* 9(2), 419-435. doi: 10.1007/s10592-007-9354-7.

Mendez, M., Rosenbaum, H.C., Subramaniam, A., Yackulic, C., and Bordino, P. (2010). Isolation by environmental distance in mobile marine species: molecular ecology of franciscana dolphins at their southern range. *Mol Ecol* 19(11), 2212-2228. doi: 10.1111/j.1365-294X.2010.04647.x.

Mendez, M., Subramaniam, A., Collins, T., Minton, G., Baldwin, R., Berggren, P., et al. (2011). Molecular ecology meets remote sensing: environmental drivers to population structure of humpback dolphins in the Western Indian Ocean. *Heredity (Edinb)* 107(4), 349-361. doi: 10.1038/hdy.2011.21.

Meynier, L., Stockin, K.A., Bando, M.K.H., and Duignan, P.J. (2008). Stomach contents of common dolphin (*Delphinus* sp.) from New Zealand waters. *N. Z. J. Mar. Freswhater Res.* 42(2), 257-268. doi: 10.1080/00288330809509952.

Middleton, J.F., and Bye, J.A.T. (2007). A review of the shelf-slope circulation along Australia's southern shelves: Cape Leeuwin to Portland. *Progress in Oceanography* 75(1), 1-41. doi: 10.1016/j.pocean.2007.07.001.

Mirimin, L., Westgate, A., Rogan, E., Rosel, P.E., Read, A., Coughlan, J., et al. (2009). Population structure of short-beaked common dolphins (*Delphinus delphis*) in the North Atlantic Ocean as revealed by mitochondrial and nuclear genetic markers. *Mar. Biol.* 156(5), 821-834. doi: 10.1007/s00227-008-1120-y.

Möller, L., and Beheregaray, L. (2001). Coastal Bottlenose dolphins from Southeastern Australia are *Tursiops Aduncus* according to sequences of the mitochondrial DNA control region. *Mar. Mamm. Sci.* 17(2), 249-263.

Möller, L.M. (2011). Sociogenetic structure, kin associations and bonding in delphinids. *Mol. Ecol.* 21(3), 745-764. doi: 10.1111/j.1365-294X.2011.05405.x.

Möller, L.M., Attard, C.R.M., Bilgmann, K., Andrews-Goff, V., Jonsen, I., Paton, D., et al. (2020). Movements and behaviour of blue whales satellite tagged in an Australian upwelling system. *Sci Rep* 10(1), 21165. doi: 10.1038/s41598-020-78143-2.

Möller, L.M., and Beheregaray, L.B. (2004). Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Mol. Ecol.* 13(6), 1607-1612. doi: 10.1111/j.1365-294X.2004.02137.x.

Möller, L.M., Beheregaray, L.B., Harcourt, R.G., and Krutzen, M. (2001). Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Proc. Biol. Sci.* 268(1479), 1941-1947. doi: 10.1098/rspb.2001.1756.

Möller, L.M., Valdez, F.P., Allen, S., Bilgmann, K., Corrigan, S., and Beheregaray, L.B. (2011). Fine-scale genetic structure in short-beaked common dolphins (*Delphinus delphis*) along the East Australian Current. *Mar. Biol.* 158(1), 113-126. doi: 10.1007/s00227-010-1546-x.

Möller, L.M., Wiszniewski, J., Allen, S., and Beheregaray, L. (2007). Habitat type promotes rapid and extremely localised genetic differentiation in dolphins. *Mar. Freshwater Res.* 58(7), 640-648. doi: 10.1071/MF06218.

Morin, P.A., Forester, B., Hancock- Hanser, B.L., Baird, R.W., Taylor, L., Forney, K.A., et al. (2021). Population structure in a continuously distributed coastal marine species, the harbor porpoise, based on microhaplotypes derived from poor quality samples. *Molecular Ecology*. doi: 10.1111/mec.15827.

Morin, P.A., Parsons, K.M., Archer, F.I., Avila-Arcos, M.C., Barrett-Lennard, L.G., Dalla Rosa, L., et al. (2015). Geographic and temporal dynamics of a global radiation and diversification in the killer whale. *Mol Ecol* 24(15), 3964-3979. doi: 10.1111/mec.13284.

Moura, A.E., Natoli, A., Rogan, E., and Hoelzel, A.R. (2013a). Atypical panmixia in a European dolphin species (*Delphinus delphis*): implications for the evolution of diversity across oceanic boundaries. *J. Evol. Biol.* 26(1), 63-75. doi: 10.1111/jeb.12032.

Moura, A.E., Natoli, A., Rogan, E., and Hoelzel, A.R. (2013b). Evolution of Functional Genes in Cetaceans Driven by Natural Selection on a Phylogenetic and Population Level. *Evolution Biology* 40, 341-354. doi: 10.1007/s11692-012-9215-2.

MPI (2019). "Aquatic Environment and Biodiversity Annual Review 2018". (Ministry for Primary Industries. Compiled by the Fisheries Science Team, Ministry for Primary Industries, Wellington New Zealand).

Murphy, S., Evans, P.G.H., Pinn, E., and Pierce, G.J. (2019). Conservation management of common dolphins: Lessons learned from the North-East Atlantic. *Aquatic Conserv. Mar. Freshw. Ecosyst.*, 1-30. doi: 10.1002/aqc.3212.

Murphy, S., Pinn, E.H., and Jepson, P.D. (2013). The short beaked common dolphin (*Delphinus delphis*) in the north- east atlantic: distribution, ecology, managmenet and conservation status. *Oceanogr. Mar. Biol.* 51, 193-280.

Nam, K., Lee, K.W., Chung, O., Yim, H.S., Cha, S.S., Lee, S.W., et al. (2017). Analysis of the FGF gene family provides insights into aquatic adaptation in cetaceans. *Sci Rep* 7, 40233. doi: 10.1038/srep40233.

Narum, S.R., and Hess, J.E. (2011). Comparison of F(ST) outlier tests for SNP loci under selection. *Mol Ecol Resour* 11 Suppl 1, 184-194. doi: 10.1111/j.1755-0998.2011.02987.x.

Nations, F.a.A.O.o.t.U. (1995). "Code of Conduct for Responsible Fisheries". (Food and Agriculture Organization of the United Nations (FAO), Rome).

Natoli, A., Birkun, A., Aguilar, A., Lopez, A., and Hoelzel, A.R. (2005). Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proc. Biol. Sci.* 272(1569), 1217-1226. doi: 10.1098/rspb.2005.3076.

Natoli, A., Canadas, A., Peddemors, V.M., Aguilar, A., Vaquero, C., Fernandez-Piqueras, P., et al. (2006). Phylogeography and alpha taxonomy of the common dolphin (*Delphinus* sp.). *J. Evol. Biol.* 19(3), 943-954. doi: 10.1111/j.1420-9101.2005.01033.x.

Natoli, A., Cañadas, A., Vaquero, C., Politi, E., Fernandez-Navarro, P., and Hoelzel, A.R. (2008). Conservation genetics of the short-beaked common dolphin (*Delphinus delphis*) in the Mediterranean Sea and in the eastern North Atlantic Ocean. *Conserv. Biol.* 9(6), 1479-1487. doi: 10.1007/s10592-007-9481-1.

NCBI (2020). "BLAST Command Line Applications User Manual".).

Nery, M.F., Gonzalez, D.J., and Opazo, J.C. (2013). How to Make a Dolphin: Molecular Signature of Positive Selection in Cetacean Genome. *PLoS One* 8(6), e65491. doi: 10.1371/journal.pone.0065491.

Neumann, D.R. (2001). Seasonal movements of short-beaked common dolphins(Delphinus delphis)in the north-western Bay of Plenty, New Zealand: Influence of sea surface temperature and El Niño/La Niña. *New Zealand Journal of Marine and Freshwater Research* 35(2), 371-374. doi: 10.1080/00288330.2001.9517007.

Neumann, D.R., and Orams, M.B. (2003). Feeding behaviours of short-beaked common dolphins, *Delphinus delphis* , in New Zealand. *Aquat. Mamm.* 29, 137-149. doi: 10.1578/016754203101023997.

Niedergang, F., and Chavrier, P. (2004). Signaling and membrane dynamics during phagocytosis: many roads lead to the phagos(R)ome. *Curr Opin Cell Biol* 16(4), 422-428. doi: 10.1016/j.ceb.2004.06.006.

Nykanen, M., Dillane, E., Englund, A., Foote, A.D., Ingram, S.N., Louis, M., et al. (2018). Quantifying dispersal between marine protected areas by a highly mobile species, the bottlenose dolphin, *Tursiops truncatus*. *Ecol. Evol.* 8(18), 9241-9258. doi: 10.1002/ece3.4343.

O'brien, R.M. (2007). A Caution Regarding Rules of Thumb for Variance Inflation Factors. *Quality & Quantity* 41(5), 673-690. doi: 10.1007/s11135-006-9018-6.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., et al. (2019). "Community Ecology Package". 2.5-6 ed.).

Oleksiak, M.F., and Rajora, O.P. (2020). *Population Genomics: Marine Organisms.* Switzerland AG: Springer Nature.

Oremus, M., Poole, M.D., and Baker, C.S. (2007). Isolation and interchange among insular spinner dolphin communities in the South Pacific revealed by individual identification and genetic diversity. *Mar. Ecol. Prog. Ser.* 336, 275-289. doi: 10.3354/meps336275.

Paetkau, D., Slade, R., Burden, M., and Estoup, A. (2004). Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Mol. Ecol.* 13, 55-65. doi: 10.1046/j.1365-294X.2003.02008.x.

Palacios, D.M., Baumgartner, M.F., Laidre, K.L., and Gregr, E.J. (2013). Beyond correlation: integrating environmentally and behaviourally mediated processes in models of marine mammal distributions. *Endangered Species Research* 22(3), 191-203. doi: 10.3354/esr00558.

Palumbi, S.R. (1994). Genetic divergence reproductive isolation and marine speciation. *Annual Review of Ecology and Systematics* 25, 547-572. doi: 10.1146/annurev.es.25.110194.002555.

Palumbi, S.R. (2003). Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13(1), S146-S158. doi: 10.1890/1051-0761(2003)013[0146:PGDCAT]2.0.CO;2.

Pang, G., Xie, J., Chen, Q., and Hu, Z. (2014). Energy intake, metabolic homeostasis, and human health. *Food Science and Human Wellness* 3(3-4), 89-103. doi: 10.1016/j.fshw.2015.01.001.

Papa, Y., Oosting, T., Valenza-Troubat, N., Wellenreuther, M., and Ritchie, P.A. (2020). Genetic stock structure of New Zealand fish and the use of genomics in fisheries management: an overview and outlook. *N. Z. J. Zool.*, 1-31. doi: 10.1080/03014223.2020.1788612.

Parra, G.J., Bilgmann, K., Peters, K., and Möller, L.M. (in review). Abundance and potential biological removal of common dolphins subject to fishery-impacts in South Australian waters. *Front. Mar. Sci.*

Parra, G.J., Cagnazzi, D., Jedensjö, M., Ackermann, C., Frere, C., Seddon, J., et al. (2018). Low genetic diversity, limited gene flow and widespread genetic bottleneck effects in a threatened dolphin species, the Australian humpback dolphin. *Biol. Conserv.* 220, 192-200. doi: 10.1016/j.biocon.2017.12.028.

Patterson, H., Williams, A., Woodhams, J., and Curtotti, R. (2019). "Fishery status reports 2019". (Australian Bureau of Agricultural and Resource Economics and Sciences (ABARES), Canberra. CC BY 4.0).

Pawley, M.D.M., Hupman, K.E., Stockin, K.A., and Gilman, A. (2018). Examining the viability of dorsal fin pigmentation for individual identification of poorly-marked delphinids. *Sci. Rep.* 8(1), 12593. doi: 10.1038/s41598-018-30842-7.

Perrin, W.F. (2021). *World Cetacea Database* [Online]. marinespecies.org/cetacea. [Accessed 2017-03-06 and 2021-02-09].

Perry, G.L.W., and Lee, F. (2019). How does temporal variation in habitat connectivity influence metapopulation dynamics? *Oikos*. doi: 10.1111/oik.06052.

Pespeni, M.H., Sanford, E., Gaylord, B., Hill, T.M., Hosfelt, J.D., Jaris, H.K., et al. (2013). Evolutionary change during experimental ocean acidification. *Proc Natl Acad Sci U S A* 110(17), 6937-6942. doi: 10.1073/pnas.1220673110.

Peters, K.J., Bury, S.J., Betty, E., Parra, G.J., Tezanos-Pinto, G., and Stockin, K.A. Insights into the foraging ecology of common dolphins (*Delphinus delphis*) revealed by stable isotope analysis. . *Mar. Ecol. Prog. Ser.*, in press.

Peters, K.J., Bury, S.J., Betty, E.L., Parra, G.J., Tezanos-Pinto, G., and Stockin, K.A. (2020). Foraging ecology of the common dolphin *Delphinus delphis* revealed by stable isotope analysis. *Marine Ecology Progress Series* 652**,** 173-186. doi: 10.3354/meps13482.

Peters, K.J., and Stockin, K.A. (2021). Cetacean sighting records in the New Caledonia Basin, Tasman Sea, New Zealand. *New Zealand Journal of Marine and Freshwater Research***,** 1-15. doi: 10.1080/00288330.2020.1867201.

Peterson, B.K., Weber, J.N., Kay, E.H., Fisher, H.S., and Hoekstra, H.E. (2012). Double digest RADseq: an inexpensive method for de novo SNP discovery and genotyping in model and non-model species. *PLoS One* 7(5)**,** e37135. doi: 10.1371/journal.pone.0037135.

Pianka, E.R. (2000). *Evolutionary Ecology.* Benjamin-Cummings, Addison-Wesley-Longman.

Pierre, J. (2019). "Associated Species Marine Mammals". (Ministry for Primary Industries and Department of Conservations Available at: openseas.org.nz/wp-content/uploads/2019/05/SDRMarineMammals2019.pdf).

Pietroluongo, G., Cipriano, G., Ashok, K., Antichi, S., Carlier, H., Miliou, A., et al. (2020). Density and Abundance of *Delphinus delphis* in Waters South of Samos Island, Greece (Eastern Mediterranean Sea). *Journal of Marine Science and Engineering* 8(3). doi: 10.3390/jmse8030218.

Piry, S., Alapetite, A., Cornuet, J.M., Paetkau, D., Baudouin, L., and Estoup, A. (2004). GENECLASS2: a software for genetic assignment and first-generation migrant detection. *J. Hered.* 95(6)**,** 536-539. doi: 10.1093/jhered/esh074.

Pitman, R.L., and Durban, J.W. (2012). Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. *Marine Mammal Science* 28(1)**,** 16-36. doi: 10.1111/j.1748-7692.2010.00453.x.

Pitt, K.A., and Kingsford, M.J. (2000). Geographic separation of stocks of the edible jellyfish *Catostylus mosaicus* (Rhizostomeae) in New South Wales, Australia. *Mar. Ecol. Prog. Ser.* 196**,** 143-155.

Pratt, E.A.L. (2020). *The Genomic Basis of Adaptation in Bottlenose Dolphins (genus Tursiops).* Doctor of Philosophy, Flinders University.

Pratt, E.A.L., Beheregaray, L.B., Bilgmann, K., Zanardo, N., Diaz-Aguirre, F., and Möller, L.M. (2018). Hierarchical metapopulation structure in a highly mobile marine predator: the southern Australian coastal bottlenose dolphin (*Tursiops* cf. *australis*). *Conserv. Genet.* 19(3)**,** 637-654. doi: 10.1007/s10592-017-1043-6.

Pritchard, J.K., Pickrell, J.K., and Coop, G. (2010). The Genetics of Human Adaptation: Hard Sweeps, Soft Sweeps, and Polygenic Adaptation. *Current Biology* 20(4)**,** R208-R215. doi: 10.1016/j.cub.2009.11.055.

Prunier, J.G., Colyn, M., Legendre, X., Nimon, K.F., and Flamand, M.C. (2015). Multicollinearity in spatial genetics: separating the wheat from the chaff using commonality analyses. *Mol Ecol* 24(2)**,** 263-283. doi: 10.1111/mec.13029.

Prunier, J.G., Colyn, M., Legendre, X., Nimon, K.F., and Flamand, M.C. (2017). Corrigendum Multicollinearity in spatial genetics: separating the wheat from the chaff using commonality analyses. *Mol Ecol* 26(21)**,** 6183. doi: 10.1111/mec.14283.

Puritz, J.B., Hollenbeck, C.M., and Gold, J.R. (2014). dDocent: a RADseq, variant-calling pipeline designed for population genomics of non-model organisms. *PeerJ* 2**,** e431. doi: 10.7717/peerj.431.

Qiu, J., Ni, Y.H., Gong, H.X., Fei, L., Pan, X.Q., Guo, M., et al. (2007). Identification of differentially expressed genes in omental adipose tissues of obese patients by suppression subtractive hybridization. *Biochem Biophys Res Commun* 352(2)**,** 469-478. doi: 10.1016/j.bbrc.2006.11.049.

Quérouil, S., Silva, M.A., Freitas, L., Prieto, R., Magalhães, S., Dinis, A., et al. (2007). High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conserv. Genet.* 8(6)**,** 1405-1419. doi: 10.1007/s10592-007-9291-5.

Rajora, O.P. (2019). *Population Genomics. Concepts, Approaches and Applications.* Springer.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., and Suchard, M.A. (2018). Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7. *Syst. Biol.* 67(5)**,** 901-904. doi: 10.1093/sysbio/syy032.

Rannala, B., and Mountain, J. (1997). Detecting immigration by using multilocus genotypes. *Proc. Natl. Acad. Sci. USA* 94.

Razgour, O., Forester, B., Taggart, J.B., Bekaert, M., Juste, J., Ibanez, C., et al. (2019). Considering adaptive genetic variation in climate change vulnerability assessment reduces species range loss projections. *Proc Natl Acad Sci U S A* 116(21)**,** 10418-10423. doi: 10.1073/pnas.1820663116.

Razgour, O., Taggart, J.B., Manel, S., Juste, J., Ibanez, C., Rebelo, H., et al. (2018). An integrated framework to identify wildlife populations under threat from climate change. *Mol Ecol Resour* 18(1)**,** 18-31. doi: 10.1111/1755-0998.12694.

RDevelopmentCoreTeam (2018). "R: a language and environment for statistical computing". (Vienna, Austria.: R Foundation for Statistical Computing).

Reed, J., Harcourt, R., New, L., and Bilgmann, K. (2020). Extreme Effects of Extreme Disturbances: A Simulation Approach to Assess Population Specific Responses. *Frontiers in Marine Science* 7. doi: 10.3389/fmars.2020.519845.

Rellstab, C., Gugerli, F., Eckert, A.J., Hancock, A.M., and Holderegger, R. (2015). A practical guide to environmental association analysis in landscape genomics. *Mol Ecol* 24(17)**,** 4348-4370. doi: 10.1111/mec.13322.

Richardson, A.J., Eriksen, R., Moltmann, T., Hodgson-Johnston, I., and Wallis, J.R. (2020). "State and Trends of Australia's Oceans", (ed.) IMOS. (Hobart: Integrated Marine Observing System).

Richardson, L.E., Kyser, T.K., James, N.P., and Bone, Y. (2009). Analysis of hydrographic and stable isotope data to determine water masses, circulation, and mixing in the eastern Great Australian Bight. *Journal of Geophysical Research* 114(C10). doi: 10.1029/2009jc005407.

Ridgway, K.R. (2004). The 5500-km-long boundary flow off western and southern Australia. *Journal of Geophysical Research* 109(C4). doi: 10.1029/2003jc001921.

Ridgway, K.R., and Godfrey, J.S. (2015). The source of the Leeuwin Current seasonality. *Journal of Geophysical Research: Oceans* 120(10)**,** 6843-6864. doi: 10.1002/2015jc011049.

Riginos, C., Crandall, E.D., Liggins, L., Bongaerts, P., and Treml, E.A. (2016). Navigating the currents of seascape genomics: how spatial analyses can augment population genomic studies. *Curr. Zool.* 62(6)**,** 581-601. doi: 10.1093/cz/zow067.

Riginos, C., Hock, K., Matias, A.M., Mumby, P.J., Oppen, M.J.H., and Lukoschek, V. (2019). Asymmetric dispersal is a critical element of concordance between biophysical dispersal models and spatial genetic structure in Great Barrier Reef corals. *Divers. Distrib.* 25(11)**,** 1684-1696. doi: 10.1111/ddi.12969.

Riginos, C., and Liggins, L. (2013). Seascape Genetics: Populations, Individuals, and Genes Marooned and Adrift. *Geography Compass* 7(3)**,** 197-216. doi: 10.1111/gec3.12032.

Robbins, W.D., Huveneers, C., Parra, G.J., Möller, L., and Gillanders, B.M. (2017). Anthropogenic threat assessment of marine-associated fauna in Spencer Gulf, South Australia. *Marine Policy* 81**,** 392-400. doi: 10.1016/j.marpol.2017.03.036.

Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., et al. (2017). Marine reserves can mitigate and promote adaptation to climate change. *Proc Natl Acad Sci U S A* 114(24)**,** 6167-6175. doi: 10.1073/pnas.1701262114.

Roca-Agujetas, V., de Dios, C., Leston, L., Mari, M., Morales, A., and Colell, A. (2019). Recent Insights into the Mitochondrial Role in Autophagy and Its Regulation by Oxidative Stress. *Oxid Med Cell Longev* 2019**,** 3809308. doi: 10.1155/2019/3809308.

Rodriguez-Zarate, C.J., Sandoval-Castillo, J., van Sebille, E., Keane, R.G., Rocha-Olivares, A., Urteaga, J., et al. (2018). Isolation by environment in the highly mobile olive ridley turtle (*Lepidochelys olivacea*) in the eastern Pacific. *Proc. Biol. Sci.* 285(1878). doi: 10.1098/rspb.2018.0264.

Rosel, P.E., Hansen, L., and Hohn, A.A. (2009). Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western North Atlantic. *Mol. Ecol.* 18(24), 5030-5045. doi: 10.1111/j.1365-294X.2009.04413.x.

Rosel, P.E., Taylor, B.L., Hancock-Hanser, B.L., Morin, P.A., Archer, F.I., Lang, A.R., et al. (2017). A review of molecular genetic markers and analytical approaches that have been used for delimiting marine mammal subspecies and species. *Mar. Mamm. Sci.* 33(S1), 56-75. doi: 10.1111/mms.12412.

Ross, P.M., Hogg, I.D., Pilditch, C.A., and Lundquist, C.J. (2009). Phylogeography of New Zealand's coastal benthos. *N. Z. J. Mar. Freswhater Res.* 43(5), 1009-1027. doi: 10.1080/00288330.2009.9626525.

Rowe, P.S. (2012). Regulation of bone-renal mineral and energy metabolism: the PHEX, FGF23, DMP1, MEPE ASARM pathway. *Crit Rev Eukaryot Gene Expr* 22(1), 61-86. doi: 10.1615/critreveukargeneexpr.v22.i1.50. .

Rowe, S.J. (2007). "A review of methodologies for mitigating incidental catch of protected marine mammals", (ed.) D.o. Conservation. (Wellington, New Zealand: Science & Technical Publishing Department of Conservation).

Ruan, R., Guo, A.H., Hao, Y.J., Zheng, J.S., and Wang, D. (2015). De novo assembly and characterization of narrow-ridged finless porpoise renal transcriptome and identification of candidate genes involved in osmoregulation. *Int J Mol Sci* 16(1), 2220-2238. doi: 10.3390/ijms16012220.

Saccheri, I., and Hanski, I. (2006). Natural selection and population dynamics. *Trends Ecol Evol* 21(6), 341-347. doi: 10.1016/j.tree.2006.03.018.

Sandoval-Castillo, J., Robinson, N.A., Hart, A.M., Strain, L.W.S., and Beheregaray, L.B. (2018). Seascape genomics reveals adaptive divergence in a connected and commercially important mollusc, the greenlip abalone (*Haliotis laevigata*), along a longitudinal environmental gradient. *Mol. Ecol.* 27(7), 1603-1620. doi: 10.1111/mec.14526.

Sandoval-Castillo, J., and Beheregaray, L.B. (2020). Oceanographic heterogeneity influences an ecological radiation in elasmobranchs. *J. Biogeography* 47(7), 1599-1611. doi: 10.1111/jbi.13865.

SASIA (2015). "Code of Practice for Mitigation of Interactions of the South Australian Sardine Fishery with Threatened, Endangered and Protected Species", (ed.) S.A.S.I.A. (SASIA). (Port Lincon).

Savolainen, O., Lascoux, M., and Merila, J. (2013). Ecological genomics of local adaptation. *Nat Rev Genet* 14(11), 807-820. doi: 10.1038/nrg3522.

Schumann, N., Gales, N.J., Harcourt, R.G., and Arnould, J.P.Y. (2013). Impacts of climate change on Australian marine mammals. *Australian Journal of Zoology* 61(2), 146. doi: 10.1071/zo12131.

Segura-Garcia, I., Gallo, J.P., Chivers, S., Diaz-Gamboa, R., and Hoelzel, A.R. (2016). Post-glacial habitat release and incipient speciation in the genus Delphinus. *Heredity (Edinb)* 117(6), 400-407. doi: 10.1038/hdy.2016.66.

Segura, I., Rocha-Olivares, A., Flores-Ramírez, S., and Rojas-Bracho, L. (2006). Conservation implications of the genetic and ecological distinction of Tursiops truncatus ecotypes in the Gulf of California. *Biological Conservation* 133(3), 336-346. doi: 10.1016/j.biocon.2006.06.017.

Selkoe, K.A., D’Aloia, C.C., Crandall, E.D., Iacchei, M., Liggins, L., Puritz, J.B., et al. (2016). A decade of seascape genetics: contributions to basic and applied marine connectivity. *Mar. Ecol. Prog. Ser.* 554, 1-19. doi: 10.3354/meps11792.

Selkoe, K.A., Henzler, C.M., and Gaines, S.D. (2008). Seascape genetics and the spatial ecology of marine populations. *Fish and Fisheries* 9, 366-377.

Selkoe, K.A., Watson, J.R., White, C., Horin, T.B., Iacchei, M., Mitarai, S., et al. (2010). Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Mol Ecol* 19(17), 3708-3726. doi: 10.1111/j.1365-294X.2010.04658.x.

Sha, Y., Wei, X., Ding, L., Ji, Z., Mei, L., Huang, X., et al. (2020). Biallelic mutations of CFAP74 may cause human primary ciliary dyskinesia and MMAF phenotype. *J Hum Genet* 65(11), 961-969. doi: 10.1038/s10038-020-0790-2.

Shafer, A.B., Wolf, J.B., Alves, P.C., Bergstrom, L., Bruford, M.W., Brannstrom, I., et al. (2015). Genomics and the challenging translation into conservation practice. *Trends Ecol. Evol.* 30(2), 78-87. doi: 10.1016/j.tree.2014.11.009.

Shao, M., Ishibashi, J., Kusminski, C.M., Wang, Q.A., Hepler, C., Vishvanath, L., et al. (2016). Zfp423 Maintains White Adipocyte Identity through Suppression of the Beige Cell Thermogenic Gene Program. *Cell Metab* 23(6), 1167-1184. doi: 10.1016/j.cmet.2016.04.023.

Short, A.D. (2020). *Australian Coastal Systems: Beaches, Barriers and Sediment Compartments.* Switzerland: Springer.

Slater, G.J., Price, S.A., Santini, F., and Alfaro, M.E. (2010). Diversity versus disparity and the radiation of modern cetaceans. *Proc Biol Sci* 277(1697), 3097-3104. doi: 10.1098/rspb.2010.0408.

Slatkin, M. (1987). Gene Flow and the Geographic Structure of Natural Populations. *Science* 236(4803), 787-792. doi: 10.1126/science.3576198.

Smith, S., Brauer, C.J., Sasaki, M., Unmack, P.J., Guillot, G., Laporte, M., et al. (2020). Latitudinal variation in climate-associated genes imperils range edge populations. *Mol Ecol*. doi: 10.1111/mec.15637.

Smith, S., and Morin, P.A. (2005). Optimal Storage Conditions for Highly Dilute DNA Samples: A Role for Trehalose as a Preserving Agent. *J. Forensic Sci.* (5), 1101-1108. doi: 10.1520/JFS2004411.

Sousa, A., Alves, F., Dinis, A., Bentz, J., Cruz, M.J., and Nunes, J.P. (2019). How vulnerable are cetaceans to climate change? Developing and testing a new index. *Ecol. Indic.* 98, 9-18. doi: 10.1016/j.ecolind.2018.10.046.

Spitz, J., Mourocq, E., Leauté, J.-P., Quéro, J.-C., and Ridoux, V. (2010). Prey selection by the common dolphin: Fulfilling high energy requirements with high quality food. *Journal of Experimental Marine Biology and Ecology* 390(2), 73-77. doi: 10.1016/j.jembe.2010.05.010.

Spitz, J., Trites, A.W., Becquet, V., Brind'Amour, A., Cherel, Y., Galois, R., et al. (2012). Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. *PLoS One* 7(11), e50096. doi: 10.1371/journal.pone.0050096.

Sproles, A.E., Oakley, C.A., Matthews, J.L., Peng, L., Owen, J.G., Grossman, A.R., et al. (2019). Proteomics quantifies protein expression changes in a model cnidarian colonised by a thermally tolerant but suboptimal symbiont. *The ISME Journal* 13(9), 2334-2345. doi: 10.1038/s41396-019-0437-5.

Stapley, J., Reger, J., Feulner, P.G., Smadja, C., Galindo, J., Ekblom, R., et al. (2010). Adaptation genomics: the next generation. *Trends Ecol Evol* 25(12), 705-712. doi: 10.1016/j.tree.2010.09.002.

Steeman, M.E., Hebsgaard, M.B., Fordyce, R.E., Ho, S.Y., Rabosky, D.L., Nielsen, R., et al. (2009). Radiation of extant cetaceans driven by restructuring of the oceans. *Syst Biol* 58(6), 573-585. doi: 10.1093/sysbio/syp060.

Stephenson, F., Goetz, K., Sharp, B.R., Mouton, T.L., Beets, F.L., Roberts, J., et al. (2020). Modelling the spatial distribution of cetaceans in New Zealand waters. *Diversity and Distributions* 26(4), 495-516. doi: 10.1111/ddi.13035.

Stockin, K.A. (2008). *The New Zealand common dolphin (Delphinus sp.) Identity, ecology and conservation.* Doctor of Philosophy in Zoology, Massey University.

Stockin, K.A., Amaral, A.R., Latimer, J., Lambert, D.M., and Natoli, A. (2014). Population genetic structure and taxonomy of the common dolphin (*Delphinus* sp.) at its southernmost range limit: New Zealand waters. *Mar. Mamm. Sci.* 30(1), 44-63. doi: 10.1111/mms.12027.

Stockin, K.A., Binedell, V., Wiseman, N., Brunton, D.H., and Orams, M.B. (2009a). Behavior of free-ranging common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. *Mar. Mamm. Sci.* 25(2)**,** 283-301. doi: 10.1111/j.1748-7692.2008.00262.x.

Stockin, K.A., Duignan, P.J., Alley, M., Roe, W.D., Meynier, L., and Fettermann, T. (2009b). Causes of mortality in stranded Common Dolphin (*Delphinus* sp.) from New Zealand waters between 1998 and 2008. *Pac. Conserv. Biol.* 15(217–227). doi: 10.1071/PC090217.

Stockin, K.A., and Orams, M.B. (2009). The status of common dolphins (*Delphinus delphis*) within New Zealand waters. *J. Cetacean Res. Manage.* SC/61/SM20**,** 1-13.

Stockin, K.A., Pierce, G.J., Binedell, V., Wiseman, N., and Orams, M.B. (2008). Factors Affecting the Occurrence and Demographics of Common Dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand. *Aquat. Mamm.* 34(2)**,** 200-211. doi: 10.1578/am.34.2.2008.200.

Strobel, J.S., Hack, N.L., Label, K.T., Cordova, K.L., Bersin, T.V., Journey, M.L., et al. (2020). Effects of food deprivation on plasma insulin-like growth factor-1 (Igf1) and Igf binding protein (Igfbp) gene transcription in juvenile cabezon (*Scorpaenichthys marmoratus*). *Gen Comp Endocrinol* 286**,** 113319. doi: 10.1016/j.ygcen.2019.113319.

Sunnucks, P., and Balkenhol, N. (2015). "Incorporationg Landscape Genetics into Road Ecology," in *Hanbook of Road Ecology,* eds. R. Van der Ree, D. Smith & C. Grilo. 1st ed: Jhon Wiley and Sons).

Sunnucks, P., and Hales, D.F. (1996). Numerous Transposed Sequences of Mitochondrial Cytochrome Oxidase I-II in Aphids of the Genus *Sitobion* (Hemiptera: Aphididae) *Mol. Biol. Evol.* 13(3)**,** 510-524.

Suthers, I.M., Young, J.W., Baird, M.E., Roughan, M., Everett, J.D., Brassington, G.B., et al. (2011). The strengthening East Australian Current, its eddies and biological effects — an introduction and overview. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 58(5)**,** 538-546. doi: 10.1016/j.dsr2.2010.09.029.

Tabangin, M.E., Woo, J.G., and Martin, L.J. (2009). The effect of minor allele frequency on the likelihood of obtaining false positives. *BMC Proc* 3 Suppl 7**,** S41. doi: 10.1186/1753-6561-3-S7-S41.

Tabata, E., Kashimura, A., Kikuchi, A., Masuda, H., Miyahara, R., Hiruma, Y., et al. (2018). Chitin digestibility is dependent on feeding behaviors, which determine acidic chitinase mRNA levels in mammalian and poultry stomachs. *Sci Rep* 8(1)**,** 1461. doi: 10.1038/s41598-018-19940-8.

Taft, H.R., McCoskey, D.N., Miller, J.M., Pearson, S.K., Coleman, M.A., Fletcher, N.K., et al. (2020). Research–management partnerships: An opportunity to integrate genetics in conservation actions. *Conserv. Sci. Pract.* doi: 10.1111/csp2.218.

Takeuchi, K., Xu, Y., Kitano, M., Chiyonobu, K., Abo, M., Ikegami, K., et al. (2020). Copy number variation in DRC1 is the major cause of primary ciliary dyskinesia in the Japanese population. *Mol Genet Genomic Med* 8(3)**,** e1137. doi: 10.1002/mgg3.1137.

Taylor, B.L., Archer, F.I., Martien, K.K., Rosel, P.E., Hancock-Hanser, B.L., Lang, A.R., et al. (2017). Guidelines and quantitative standards to improve consistency in cetacean subspecies and species delimitation relying on molecular genetic data. *Mar. Mamm. Sci.* 33(S1)**,** 132-155. doi: 10.1111/mms.12411.

Taylor, B.L., Chivers, S.J., Larese, J., and Perrin, W.F. (2007). "Generation length and percent mature estimates for IUCN assessments of cetaceans". (La Jolla, CA, Southwest Fisheries Science Center, 24pp: Southwest Fisheries Science Center Administrative Report).

Teske, P.R., Golla, T.R., Sandoval-Castillo, J., Emami-Khoyi, A., van der Lingen, C.D., von der Heyden, S., et al. (2018). Mitochondrial DNA is unsuitable to test for isolation by distance. *Sci. Rep.* 8(1)**,** 8448. doi: 10.1038/s41598-018-25138-9.

Teske, P.R., Sandoval-Castillo, J., Golla, T.R., Emami-Khoyi, A., Tine, M., von der Heyden, S., et al. (2019). Thermal selection as a driver of marine ecological speciation. *Proc Biol Sci* 286(1896)**,** 20182023. doi: 10.1098/rspb.2018.2023.

Teske, P.R., Sandoval-Castillo, J., van Sebille, E., Waters, J., and Beheregaray, L.B. (2015). On-shelf larval retention limits population connectivity in a coastal broadcast spawner. *Mar. Ecol. Prog. Ser.* 532**,** 1-12. doi: 10.3354/meps11362.

Teske, P.R., Sandoval-Castillo, J., van Sebille, E., Waters, J., and Beheregaray, L.B. (2016). Oceanography promotes self-recruitment in a planktonic larval disperser. *Sci. Rep.* 6**,** 34205. doi: 10.1038/srep34205.

Teske, P.R., Sandoval-Castillo, J., Waters, J., and Beheregaray, L.B. (2017). An overview of Australia's temperate marine phylogeography, with new evidence from high-dispersal gastropods. *J. Biogeography* 44(1)**,** 217-229. doi: 10.1111/jbi.12783.

Tetushkin, E.Y. (2013). Landscape and ecological genomics. *Russian Journal of Genetics* 49(10)**,** 985-998. doi: 10.1134/s1022795413090111.

Tezanos-Pinto, G., Baker, C.S., Russell, K., Martien, K., Baird, R.W., Hutt, A., et al. (2009). A worldwide perspective on the population structure and genetic diversity of bottlenose dolphins (*Tursiops truncatus*) in New Zealand. *J. Hered.* 100(1)**,** 11-24. doi: 10.1093/jhered/esn039.

Therkildsen, N.O., Hemmer-Hansen, J., Als, T.D., Swain, D.P., Morgan, M.J., Trippel, E.A., et al. (2013). Microevolution in time and space: SNP analysis of historical DNA reveals dynamic signatures of selection in Atlantic cod. *Mol Ecol* 22(9)**,** 2424-2440. doi: 10.1111/mec.12260.

Thewissen, J.G.M., and Williams, E.M. (2002). The Early Radiations of Cetacea (Mammalia): Evolutionary Pattern and Developmental Correlations. *Annual Review of Ecology and Systematics* 33(1)**,** 73-90. doi: 10.1146/annurev.ecolsys.33.020602.095426.

Thompson, F.N., Abraham, E.R., and Berkenbusch, K. (2013). Common dolphin (*Delphinus delphis*) bycatch in New Zealand commercial trawl fisheries. *PLoS One* 8(5)**,** e64438. doi: 10.1371/journal.pone.0064438.

Tivey, T.R., Parkinson, J.E., Mandelare, P.E., Adpressa, D.A., Peng, W., Dong, X., et al. (2020). N-Linked Surface Glycan Biosynthesis, Composition, Inhibition, and Function in Cnidarian-Dinoflagellate Symbiosis. *Microb Ecol* 80(1)**,** 223-236. doi: 10.1007/s00248-020-01487-9.

Tollis, M., Robbins, J., Webb, A.E., Kuderna, L.F.K., Caulin, A.F., Garcia, J.D., et al. (2019). Return to the Sea, Get Huge, Beat Cancer: An Analysis of Cetacean Genomes Including an Assembly for the Humpback Whale (Megaptera novaeangliae). *Mol Biol Evol* 36(8)**,** 1746-1763. doi: 10.1093/molbev/msz099.

Tukey, J.W. (1949). Comparing individual means in the analysis of variance. *Int. Biom. Soc.* 5(2)**,** 99-114. doi: 10.2307/3001913.

Tulloch, V., Pirotta, V., Grech, A., Crocetti, S., Double, M., How, J., et al. (2020). Long-term trends and a risk analysis of cetacean entanglements and bycatch in fisheries gear in Australian waters. *Biodivers. Conserv.* 29(1)**,** 251-282. doi: 10.1007/s10531-019-01881-x.

Turcot, V., Lu, Y., Highland, H.M., Schurmann, C., Justice, A.E., Fine, R.S., et al. (2018). Protein-altering variants associated with body mass index implicate pathways that control energy intake and expenditure in obesity. *Nat Genet* 50(1)**,** 26-41. doi: 10.1038/s41588-017-0011-x.

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., and De Clerck, O. (2012). Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography* 21(2)**,** 272-281. doi: 10.1111/j.1466-8238.2011.00656.x.

Ulman, A., Zengin, M., Demirel, N., and Pauly, D. (2020). The Lost Fish of Turkey: A Recent History of Disappeared Species and Commercial Fishery Extinctions for the Turkish Marmara and Black Seas. *Frontiers in Marine Science* 7. doi: 10.3389/fmars.2020.00650.

Vincent, B., Dionne, M., Kent, M.P., Lien, S., and Bernatchez, L. (2013). Landscape genomics in Atlantic salmon (Salmo salar): searching for gene-environment interactions driving local adaptation. *Evolution* 67(12), 3469-3487. doi: 10.1111/evo.12139.

Viricel, A., and Rosel, P.E. (2014). Hierarchical population structure and habitat differences in a highly mobile marine species: the Atlantic spotted dolphin. *Mol Ecol* 23(20), 5018-5035. doi: 10.1111/mec.12923.

Vu, N.T.T., Zenger, K.R., Guppy, J.L., Sellars, M.J., Silva, C.N.S., Kjeldsen, S.R., et al. (2020). Fine-scale population structure and evidence for local adaptation in Australian giant black tiger shrimp (*Penaeus monodon*) using SNP analysis. *BMC Genomics* 21(1), 669. doi: 10.1186/s12864-020-07084-x.

Wadi, L., Meyer, M., Weiser, J., Stein, L.D., and Reimand, J. (2016). Impact of outdated gene annotations on pathway enrichment analysis. *Nat Methods* 13(9), 705-706. doi: 10.1038/nmeth.3963.

Wang, J. (2007). Triadic IBD coefficients and applications to estimating pairwise relatedness. *Genet. Res.* 89(3), 135-153. doi: 10.1017/S0016672307008798.

Wang, J. (2011). COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Mol. Ecol. Resour.* 11(1), 141-145. doi: 10.1111/j.1755-0998.2010.02885.x.

Waples, R.S., and Gaggiotti, O. (2006). What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. *Mol. Ecol.* 15(6), 1419-1439. doi: 10.1111/j.1365-294X.2006.02890.x.

Ward, T.M., and Grammer, G.L. (2018). "Commonwealth Small Pelagic Fishery: Fishery Assessment Report 2017.", (ed.) A. Report to the Australian Fisheries Management Authority. South Australian Research and Development Institute (Aquatic Sciences). (SARDI Publication No. F2010/000270-9. SARDI Research Report Series No. 982. 114pp.).

Ward, T.M., McLeay, L.J., Dimmlich, W.F., Rogers, P.J., McClatchie, S.A.M., Matthews, R., et al. (2006). Pelagic ecology of a northern boundary current system: effects of upwelling on the production and distribution of sardine (Sardinops sagax), anchovy (*Engraulis australis*) and southern bluefin tuna (*Thunnus maccoyii*) in the Great Australian Bight. *Fisheries Oceanography* 15(3), 191-207. doi: 10.1111/j.1365-2419.2006.00353.x.

Ward, T.M., Smart, J., and Ivey, A. (2017). "Stock assessment of Australian Sardine (*Sardinops sagax*) off South Australia 2017", (ed.) A. Report to PIRSA Fisheries and Aquaculture. South Australian Research and Development Institute (Aquatic Sciences). (SARDI Publication No. F2007/000765-6. SARDI Research Report Series No. 971. 107pp.).

Waters, J.M. (2008). Marine biogeographical disjunction in temperate Australia: historical landbridge, contemporary currents, or both? *Divers. Distrib.* 14(4), 692-700. doi: 10.1111/j.1472-4642.2008.00481.x.

Waters, J.M., Emerson, B.C., Arribas, P., and McCulloch, G.A. (2020). Dispersal Reduction: Causes, Genomic Mechanisms, and Evolutionary Consequences. *Trends Ecol. Evol.* doi: 10.1016/j.tree.2020.01.012.

Waters, J.M., King, T.M., O'Loughlin, P.M., and Spencer, H.G. (2005). Phylogeographical disjunction in abundant high-dispersal littoral gastropods. *Mol Ecol* 14(9), 2789-2802. doi: 10.1111/j.1365-294X.2005.02635.x.

Waters, J.M., Wernberg, T., Connell, S.D., Thomsen, M.S., Zuccarello, G.C., Kraft, G.T., et al. (2010). Australia's marine biogeography revisited: Back to the future? *Austral Ecol.* 35(8), 988-992. doi: 10.1111/j.1442-9993.2010.02114.x.

Watson, J.R., Kendall, B.E., Siegel, D.A., and Mitarai, S. (2012). Changing seascapes, stochastic connectivity, and marine metapopulation dynamics. *American Naturalist* 180(1), 99-112. doi: 10.1086/665992.

Watson, R.A., Nowara, G.B., Tracey, S.R., Fulton, E.A., Bulman, C.M., Edgar, G.J., et al. (2013). Ecosystem model of Tasmanian waters explores impacts of climate-change induced changes in primary productivity. *Ecological Modelling* 264, 115-129. doi: 10.1016/j.ecolmodel.2012.05.008.

Weir, B.S., and Cockerham, C.C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution* 38(6), 1358-1370.

Wellenreuther, M., and Bernatchez, L. (2018). Eco-Evolutionary Genomics of Chromosomal Inversions. *Trends Ecol Evol* 33(6), 427-440. doi: 10.1016/j.tree.2018.04.002.

Wernberg, T., Russell, B.D., Moore, P.J., Ling, S.D., Smale, D.A., Campbell, A., et al. (2011). Impacts of climate change in a global hotspot for temperate marine biodiversity and ocean warming. *Journal of Experimental Marine Biology and Ecology* 400(1-2), 7-16. doi: 10.1016/j.jembe.2011.02.021.

Whitehead, H., McGill, B., and Worm, B. (2008). Diversity of deep-water cetaceans in relation to temperature: implications for ocean warming. *Ecol. Lett.* 11(11), 1198-1207. doi: 10.1111/j.1461-0248.2008.01234.x.

Whitlock, M., and McCauley, D. (1999). Indirect measures of gene flow and migration: FST81/(4Nm+1). *Heredity* 82, 117-225.

Whitlock, M.C., and Barton, N.H. (1997). The Effective Size of a Subdivided Population. *Genetics Society of America* 146, 427-441.

Whitmarsh, S.K., Huveneers, C., and Fairweather, P.G. (2020). Investigating the cumulative effects of multiple stressors on fish assemblages in a semi-enclosed bay. *Marine Biology* 167(11). doi: 10.1007/s00227-020-03784-w.

Wickham, H. (2016). "ggplot2: Elegant Graphics for Data Analysis", in: *Springer-Verlag New York.*).

Wild, S., Krutzen, M., Rankin, R.W., Hoppitt, W.J.E., Gerber, L., and Allen, S.J. (2019). Long-term decline in survival and reproduction of dolphins following a marine heatwave. *Curr Biol* 29(7), R239-R240. doi: 10.1016/j.cub.2019.02.047.

Wilder, A.P., Palumbi, S.R., Conover, D.O., and Therkildsen, N.O. (2019). Footprints of local adaptation span hundreds of linked genes in the Atlantic silverside genome. *Evol Lett* 4(5), 430-443. doi: 10.1002/evl3.189.

Wilson, G.A., and Rannala, B. (2003). Bayesian Inference of Recent Migration Rates Using Multilocus Genotypes. *Genetics* 163, 1177-1191.

Wiszniewski, J., Beheregaray, L.B., Allen, S.J., and Möller, L.M. (2009). Environmental and social influences on the genetic structure of bottlenose dolphins (*Tursiops aduncus*) in Southeastern Australia. *Conserv. Genet.* 11(4), 1405-1419. doi: 10.1007/s10592-009-9968-z.

Wright, S. (1931). Evolution in mendelian populations. *Genetics* 16(2), 97-159.

Wright, S. (1968). *Evolution and the Genetics of Populations.* University of Chicago Press.

Wu, P., Zhang, Z., Ma, G., Li, J., and Zhou, W. (2020). Transcriptomics and metabolomics reveal the cardioprotective effect of Compound Danshen tablet on isoproterenol-induced myocardial injury in high-fat-diet fed mice. *J Ethnopharmacol* 246, 112210. doi: 10.1016/j.jep.2019.112210.

Xing, S., Liu, R., Zhao, G., Liu, L., Groenen, M.A.M., Madsen, O., et al. (2020). RNA-Seq Analysis Reveals Hub Genes Involved in Chicken Intramuscular Fat and Abdominal Fat Deposition During Development. *Front Genet* 11, 1009. doi: 10.3389/fgene.2020.01009.

Xuereb, A., Benestan, L., Normandeau, E., Daigle, R.M., Curtis, J.M.R., Bernatchez, L., et al. (2018a). Asymmetric oceanographic processes mediate connectivity and population genetic structure, as revealed by RADseq, in a highly dispersive marine invertebrate (*Parastichopus californicus*). *Mol. Ecol.* 27(10), 2347-2364. doi: 10.1111/mec.14589.

Xuereb, A., D'Aloia, C.C., Andrello, M., Bernatchez, L., and Fortin, M.J. (2020). Incorporating putatively neutral and adaptive genomic data into marine conservation planning. *Conserv Biol*. doi: 10.1111/cobi.13609.

Xuereb, A., Kimber, C.M., Curtis, J.M.R., Bernatchez, L., and Fortin, M.J. (2018b). Putatively adaptive genetic variation in the giant California sea cucumber (*Parastichopus californicus*) as revealed by environmental association analysis of restriction-site associated DNA sequencing data. *Mol Ecol* 27(24), 5035-5048. doi: 10.1111/mec.14942.

Yau, S.W., Russo, V.C., Clarke, I.J., Dunshea, F.R., Werther, G.A., and Sabin, M.A. (2015). IGFBP-2 inhibits adipogenesis and lipogenesis in human visceral, but not subcutaneous, adipocytes. *Int J Obes (Lond)* 39(5), 770-781. doi: 10.1038/ijo.2014.192.

Yim, H.S., Cho, Y.S., Guang, X., Kang, S.G., Jeong, J.Y., Cha, S.S., et al. (2014). Minke whale genome and aquatic adaptation in cetaceans. *Nat Genet* 46(1), 88-92. doi: 10.1038/ng.2835.

Yiming, L., Siqi, W., Chaoyuan, C., Jiaqi, Z., Supen, W., Xianglei, H., et al. (2020). Latitudinal gradients in genetic diversity and natural selection at a highly adaptive gene in terrestrial mammals. *Ecography*. doi: 10.1111/ecog.05082.

York, K.L., Blacket, M.J., and Appleton, B.R. (2008). The Bassian Isthmus and the major ocean currents of southeast Australia influence the phylogeography and population structure of a southern Australian intertidal barnacle *Catomerus polymerus* (Darwin). *Mol. Ecol.* 17(8), 1948-1961. doi: 10.1111/j.1365-294X.2008.03735.x.

Youds, J.L., Mets, D.G., McIlwraith, M.J., Martin, J.S., Ward, J.D., ONeil, N.J., et al. (2010). RTEL-1 enforces meiotic crossover interference and homeostasis. *Science* 5(327), 1254-1258. doi: 10.1126/science.1183112.

Zanardo, N., Bilgmann, K., Parra, G.J., and Möller, L.M. (2016). Socio-genetic structure of short-beaked common dolphins in southern Australia. *J. Zool.* 299(2), 89-97. doi: 10.1111/jzo.12330.

Zanardo, N., Parra, G.J., Passadore, C., and Möller, L.M. (2017). Ensemble modelling of southern Australian bottlenose dolphin *Tursiops* sp. distribution reveals important habitats and their potential ecological function. *Mar. Ecol. Prog. Ser.* 569, 253-266. doi: 10.3354/meps12091.

Zealand, F.N. (2020). "Aquatic Environment and Biodiversity Annual Review 2019–20". (Fisheries Science and Information, Wellington New Zealand: Compiled by the Aquatic Environment Team, Fisheries New Zealand).

Zglejc, K., and Franczak, A. (2017). Peri-conceptional under-nutrition alters the expression of TRIM28 and ZFP57 in the endometrium and embryos during peri-implantation period in domestic pigs. *Reprod Domest Anim* 52(4), 542-550. doi: 10.1111/rda.12943.

Zhang, S., Cagatay, T., Amanai, M., Zhang, M., Kline, J., Castrillon, D.H., et al. (2007). Viable mice with compound mutations in the Wnt/Dvl pathway antagonists nkd1 and nkd2. *Mol Cell Biol* 27(12), 4454-4464. doi: 10.1128/MCB.00133-07.

Zhou, X., Guang, X., Sun, D., Xu, S., Li, M., Seim, I., et al. (2018a). Population genomics of finless porpoises reveal an incipient cetacean species adapted to freshwater. *Nat Commun* 9(1), 1276. doi: 10.1038/s41467-018-03722-x.

Zhou, X., Sun, D., Guang, X., Ma, S., Fang, X., Mariotti, M., et al. (2018b). Molecular Footprints of Aquatic Adaptation Including Bone Mass Changes in Cetaceans. *Genome Biol Evol* 10(3), 967-975. doi: 10.1093/gbe/evy062.

Zhou, X., Sun, F., Xu, S., Fan, G., Zhu, K., Liu, X., et al. (2013). Baiji genomes reveal low genetic variability and new insights into secondary aquatic adaptations. *Nat Commun* 4, 2708. doi: 10.1038/ncomms3708.

Zhu, K., Zhou, X., Xu, J., Sun, D., Ren, W., Zhou, K., et al. (2014). CandidategenesTasteCetaceans_Yang_BMCEB.pdf. *BMC Evolutionary Biology* 14(218). doi: 10.1186/s12862-014-0218-8.