

Killer whale ecotypes: is there a global model?

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ABSTRACT

Killer whales, *Orcinus orca*, are top predators occupying key ecological roles in a variety of ecosystems and are one of the most widely distributed mammals on the planet. In consequence, there has been significant interest in understanding their basic biology and ecology. Long-term studies of Northern Hemisphere killer whales, particularly in the eastern North Pacific (ENP), have identified three ecologically distinct communities or ecotypes in that region. The success of these prominent ENP studies has led to similar efforts at clarifying the role of killer whale ecology in other regions, including Antarctica. In the Southern Hemisphere, killer whales present a range of behavioural, social and morphological characteristics to biologists, who often interpret this as evidence to categorize individuals or groups, and draw general

ecological conclusions about these super-predators. Morphologically distinct forms (Type A, B, C, and D) occur in the Southern Ocean and studies of these different forms are often presented in conjunction with evidence for specialised ecology and behaviours. Here we review current knowledge of killer whale ecology and ecotyping globally and present a synthesis of existing knowledge. In particular, we highlight the complexity of killer whale ecology in the Southern Hemisphere and examine this in the context of comparatively well-studied Northern Hemisphere populations. We suggest that assigning erroneous or prefatory ecotypic status in the Southern Hemisphere could be detrimental to subsequent killer whale studies, because unsubstantiated characteristics may be assumed as a result of such classification. On this basis, we also recommend that ecotypic status classification for Southern Ocean killer whale morphotypes be reserved until more evidence-based ecological and taxonomic data are obtained.

Key words: killer whale, *Orcinus orca*, Southern Ocean, Antarctica, sub-Antarctic, eastern North Pacific, North Atlantic.

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I. INTRODUCTION

Large predators play key roles in both terrestrial (Berger *et al.*, 2001; Terborgh *et al.*, 2001; Sinclair, Mduma & Brashares, 2003; Owen-Smith & Mills, 2008) and aquatic ecosystems (Myers *et al.*, 2007; Estes *et al.*, 2009). One of the most cosmopolitan top predators, the killer whale *Orcinus orca*, has a charismatic status globally and recognition of its ecological importance as a top predator is reflected by several long-term studies (e.g. Lopez & Lopez, 1985; Bigg *et al.*, 1990; Similä, Holst & Christensen, 1996; Dahlheim, Ellifrit & Swenson, 1997; Matkin *et al.*, 1999). The

precise mechanisms of lower trophic level regulation by top predators like killer whales can only be understood if their role within the ecosystem is established.

Globally, killer whales are recognised as super-predators capable of adapting their behaviour (both social and hunting) to prey species availability (Jefferson, Stacey & Baird, 1991). This ability has resulted in killer whales, as a group, preying upon virtually all prey species available to them within an ecosystem. The broad regional success of the group appears linked to intra-species variation in hunting techniques, which seem to have become restricted to families or clans specialising on different prey types. The development of clan-specific behaviour may be attributable to the investment required for learning and remembering prey distribution as well as the specialised behaviours required to hunt those prey efficiently (Yurk *et al.*, 2002). These behavioural specialisations have in turn resulted in local behavioural and genetic differentiation among sympatric groups due to the matrifocal social structure of killer whale assemblages (Hoelzel, Dahlheim & Stern, 1998). As top predators, the impacts of killer whales in ecosystem functioning cannot be underestimated and as such, detailed studies of different killer whale groups are important for broad-scale ecosystem conservation and management.

Recently, the role of killer whales in ecosystem food-web dynamics has received much attention owing to debates surrounding the proposed sequential megafaunal collapse induced by killer whales in the eastern North Pacific (ENP) (e.g. Springer *et al.*, 2003, 2008; DeMaster *et al.*, 2006; Wade *et al.*, 2007; Estes *et al.*, 2009; Kuker & Barrett-Lennard, 2010). In the ENP, three distinct, sympatrically occurring ecotypes have been described (Bigg *et al.*, 1987; Ford, Ellis & Balcomb, 2000; Dahlheim *et al.*, 2008): transient, resident and offshore. Each ecotype specializes on certain prey, with

specific patterns of movement, behaviour and social system adaptations/ specialisations that are linked to this dietary specialisation (Heimlich-Boran, 1988; Bigg *et al.*, 1990; Baird, Abrams & Dill, 1992; Baird & Dill, 1995; Ford *et al.*, 1998; Baird & Whitehead, 2000). Killer whale populations from the North-west Pacific (NWP) (e.g. Kamchatka) have shown similar delineations to the ENP (Tarasyan *et al.*, 2005; Burdin *et al.*, 2004, 2007) and two ecotypes in the North Atlantic populations have been proposed although not confirmed (Foote *et al.*, 2009, 2011c).

Findings from killer whale research in the ENP have encouraged similar studies on other Northern and Southern Hemisphere populations. Indications of morphological and ecological differences among Southern Hemisphere killer whales were first apparent from observations and specimens collected by the Soviet Antarctic whaling fleets during the 1960s, 1970s and early 1980s (Budylenko, 1981; Mikhalev *et al.*, 1981; Evans, Yablokov & Bowles, 1982; Berzin & Vladimirov, 1983). More recently, three different morphological forms (morphotypes) of killer whales were identified in Antarctic waters (Pitman & Ensor, 2003), with differences in the suggested ecological specialisations possibly being even more pronounced than those reported for ENP ecotypes (Pitman & Ensor, 2003). Pitman *et al.* (2010) and Pitman (2011) expanded on their earlier findings and described five killer whale morphotypes in the waters around the Antarctic continent. In these latter studies, each morphotype is considered to be a distinct ecotype [Types A, B (two forms), C and recently, sub-Antarctic Type D] with their own physiological, morphological and social adaptations. Some authors have suggested that these ecotypes are sufficiently different to warrant full species status (e.g. Pitman *et al.*, 2007; Le Duc, Robertson & Pitman, 2008; Morin *et al.*, 2010; Pitman, 2011).

Studies at other lower latitude Southern Hemisphere localities also contribute to our knowledge of killer whales across the region. These include: Peninsula Valdez, Argentina (e.g. Lopez & Lopez, 1985; Hoelzel, 1991); sub-Antarctic Îles Crozet (e.g. Guinet, 1991; Poncelet, Barbraud & Guinet, 2010; Guinet & Tixier, 2011); sub-Antarctic Marion Island (Condy, van Aarde & Bester, 1978; Keith *et al.*, 2001; Pistorius *et al.*, 2002; Tosh, de Bruyn & Bester, 2008; Reisinger, de Bruyn & Bester, 2011*a, b*; Reisinger *et al.*, 2011*c*); Macquarie Island (Morrice, 2004); New Zealand (Visser, 1999*a*, Visser & Mäkeläinen, 2000; Visser, 2000); and southern Africa (Williams *et al.*, 2009; Best, Meyer & Lockyer, 2010). These studies have focussed on the photo-identification of individuals, observations of hunting behaviour and diet, and establishing abundance trends; but few have investigated social and movement behaviours.

Genetic differentiation of killer whale populations appears linked to differences in feeding habits, which are ultimately driven by the surrounding ecosystems. In this respect, the Northern Hemisphere environment is vastly different to the Southern Hemisphere. The Northern Hemisphere has a higher land to sea ratio than the Southern Hemisphere [1:1.5 (Northern Hemisphere) *versus* 1:4 (Southern Hemisphere)] and the Arctic Ocean is joined to the North Pacific and the North Atlantic *via* relatively narrow straits (Grémillet & Le Maho, 2003). By contrast, the Southern Ocean surrounds the Antarctic continent, providing complete and uninterrupted connectivity. These important differences are probably one of the key elements driving the reproductive isolation and/or ecological divergence of populations and ultimately the clarity of the ecotype delineation.

In the Northern Hemisphere, continental landmasses and the Arctic ice sheet are effective barriers to mixing of recognised sub-populations like those in the ENP and those in the North Atlantic. Even though some studies suggest that there has been gene flow between some of these physically separated populations (e.g. Hoelzel *et al.*, 2007; Pilot, Dahlheim & Hoelzel, 2010), there are considerably more physical barriers to mixing of populations there compared to the Southern Hemisphere. Such landmasses, and the increased productivity associated with them, also often provide more reliable access to prey (e.g. see salmon example below) and this is also likely to result in less mixing between populations that are not separated by physical barriers (e.g. the ENP and Kamchatka populations). Clear links have been identified, particularly in the ENP, among killer whale habitats, the main prey consumed and differences in ecology between ecotypes (Ford *et al.*, 1998). A good example of this is the reliance of the resident ecotype on salmon (*Oncorhynchus* spp.) in the ENP and the associated behavioural changes related to foraging on different salmonid species [e.g. coho salmon *O. kisutch* (Saulitis *et al.*, 2000) *versus* chinook salmon *O. tshawytscha* (Ford *et al.*, 1998)]. The lack of connectivity among distinct groups has allowed the long-term study of discrete populations, which is largely responsible for the better consensus on ecotype classification, particularly in the ENP. Even though the ENP population is considered one of the better understood, in several areas it is still considered data deficient as most studies focus on behaviour linked to seasonal prey availability (Ford *et al.*, 1998; Baird, Bradley Hanson & Dill, 2005). That there is still data deficiency after several decades reinforces the difficulty in gathering enough data to delineate definitive classifications, or reach consensus on ecological characteristics and the links between them.

In almost complete contrast, the Southern Ocean that dominates the Southern Hemisphere is a vast and varied environment with the Antarctic continent at its centre. Seasonal sea-ice surrounds the continent and the margins of this zone represent one of the most productive systems on Earth (Arrigo *et al.*, 1998). However, perhaps even more productive and richer in biomass are the surrounding pelagic ecosystems (Arrigo *et al.*, 1998; Knox, 2007). The Southern Ocean connects all three major oceans and the Antarctic circumpolar current (ACC) transports cold nutrient-rich waters from the south to the north. The sub-Antarctic zone is defined as the area between the Subtropical convergence zone in the north and the Antarctic Polar Front in the south and is interspersed with several island archipelagos. Killer whale research in this sector has been mostly restricted to land-based studies from these island groups. These small, isolated terrestrial refuges are the seasonal breeding sites for thousands of southern elephant seals *Mirounga leonina*, albatrosses and millions of fur seals and penguins (Goldsworthy *et al.*, 2001; Weimerskirch *et al.*, 2003; Ryan & Bester, 2008). These breeding colonies form high-prey-density foci for predators such as killer whales (e.g. Guinet, 1991; Reisinger *et al.*, 2011c). Being chiefly terrestrially or inshore based, observers at these sites encounter killer whales attracted to the specific prey types associated with these locations (Reisinger *et al.*, 2011b). Pelagic killer whale communities and/or activities are largely unknown, although observations of killer whales depredating fish from fishing vessels provide some ecological insight to these offshore areas (e.g. Kock, Purves & Duhamel, 2006; Moir-Clark & Agnew, 2010).

As the broader ecology of killer whales is inextricably linked to these differences in the physical nature of the environment and associated resources, we focus on a suite of ecological aspects that are observed in each hemisphere. This suite of ecological

aspects is consistent with criteria that are required to define ecotypes. We hypothesise that differences between the two hemispheres, and to a lesser extent within them, preclude the development of a global model for defining killer whale ecotypes. We begin with an assessment of knowledge gaps, and in so doing we consider in detail the ecology of the differentiated Northern Hemisphere killer whales. We then summarise killer whale literature from across the Southern Hemisphere (south of 30°), thereby acknowledging the observed ecological interconnectedness of the region. We evaluate published literature and present previously unpublished data from Southern Ocean killer whale populations, highlighting possible overlaps between Antarctic and sub-Antarctic populations/clans. Finally we ask whether, using similar models and criteria to those used in the Northern Hemisphere, there is sufficient information to classify Southern Ocean killer whales into ecotypes. We conclude by outlining potential future research directions for Southern Hemisphere killer whale studies that may enhance our understanding of the role that killer whales play in the ecology of the Southern Ocean region, and provide a sound, evidence-based framework for the management and conservation of groups and populations therein.

II. THE CONCEPT OF ECOTYPING

Turesson (1922) first proposed the term ‘ecotype’ as an “*ecological unit to cover the product arising as a result of the genotypical response of an ecospecies to a particular habitat*”. This definition does not distinguish between taxonomically and ecologically separated groups (Turrill, 1946) although the distinction between them is important. More recently, ecotypes have been defined as con-specific individuals or groups of individuals, with similar ecological adaptations regardless of genealogical relationship, and are usually designated based on ecological

and not phylogenetic criteria (Cronin & Mech, 2009). In consequence, although they are not taxonomic units, ecotypic descriptions may aid in the ultimate understanding of speciation (Thorpe, Reardon & Malhotra *et al.*, 2005). However, the use of the term varies across the literature, and there are inconsistencies in criteria used to confer ecotypic status.

Ecotypic variation may result in speciation if the divergence in morphology, physiology and behaviour is great enough to result in reproductive isolation and allow room for evolution by natural selection. Understanding the role of ecological factors in shaping ecotypes within a species is not only important in understanding the biology of an organism but also for the conservation and management of the species or species-complex. In this context, care needs to be taken in the assignation of ecotypic status to a species, and such designations made only when comprehensive knowledge of the different ecological factors shaping an organism have been obtained. In the case of killer whales, these key ecological characteristics can be encapsulated by five main categories: foraging and diet, movements, social structure, morphology, and genetics and kinship. Understanding them, and their interactions with each other, is a key element in any ecological assessment.

III. NORTHERN HEMISPHERE KILLER WHALES

(1) Study sites

High-latitude Northern Hemisphere killer whale research sites include the eastern North Pacific (ENP - spanning much of the central west coast of North America); the north-west Pacific (NWP - largely concentrated around the eastern Russian coastal province of Kamchatka and the Commander Islands) and the North Atlantic (bordered

Table 1. Northern Hemisphere ecotypes, proposed common names, diet and distribution as defined by Ford (2011) and Foote (2011). ENP, eastern North Pacific.

Ecotype	Proposed common name	Morphology	Diet	Distribution
Resident (ENP)	Resident killer whale	Tall dorsal fin, may be forward slanted, often has very open saddle, dorsal fin rounded on top	Fish and squid	ENP - spanning much of the central west coast of North America
Transient (ENP)	Bigg's killer whale	Typically pointed dorsal fin, eyepatch slants slightly downward towards the rear, closed saddle, often extends past midline of dorsal fin	Cetaceans and pinnipeds	
Offshore (ENP)	Offshore killer whales	Faint saddle patch, often rounded dorsal fin at tip, often with nicks in dorsal fin	Bony and cartilaginous fishes	
Type 1 Eastern North Atlantic		Conspicuous saddle patch, relatively large eyepatch	Mainly fish but some pinnipeds	North Atlantic (bordered in the south by Norway and Iceland)
Type 2 Eastern North Atlantic		Faint saddle, patch often slants towards rear	Mainly cetaceans	

in the south by Norway and Iceland) (Fig. 1A). At lower latitude, studies include those from Hawaii and Mexico. Research on ENP killer whales was pioneered by the late Dr Michael Bigg and colleagues in the early 1970s. Those early studies formed the foundation of numerous studies that have clearly and successfully elucidated much

Fig. 1. (A) Location of Northern Hemisphere study sites with references.

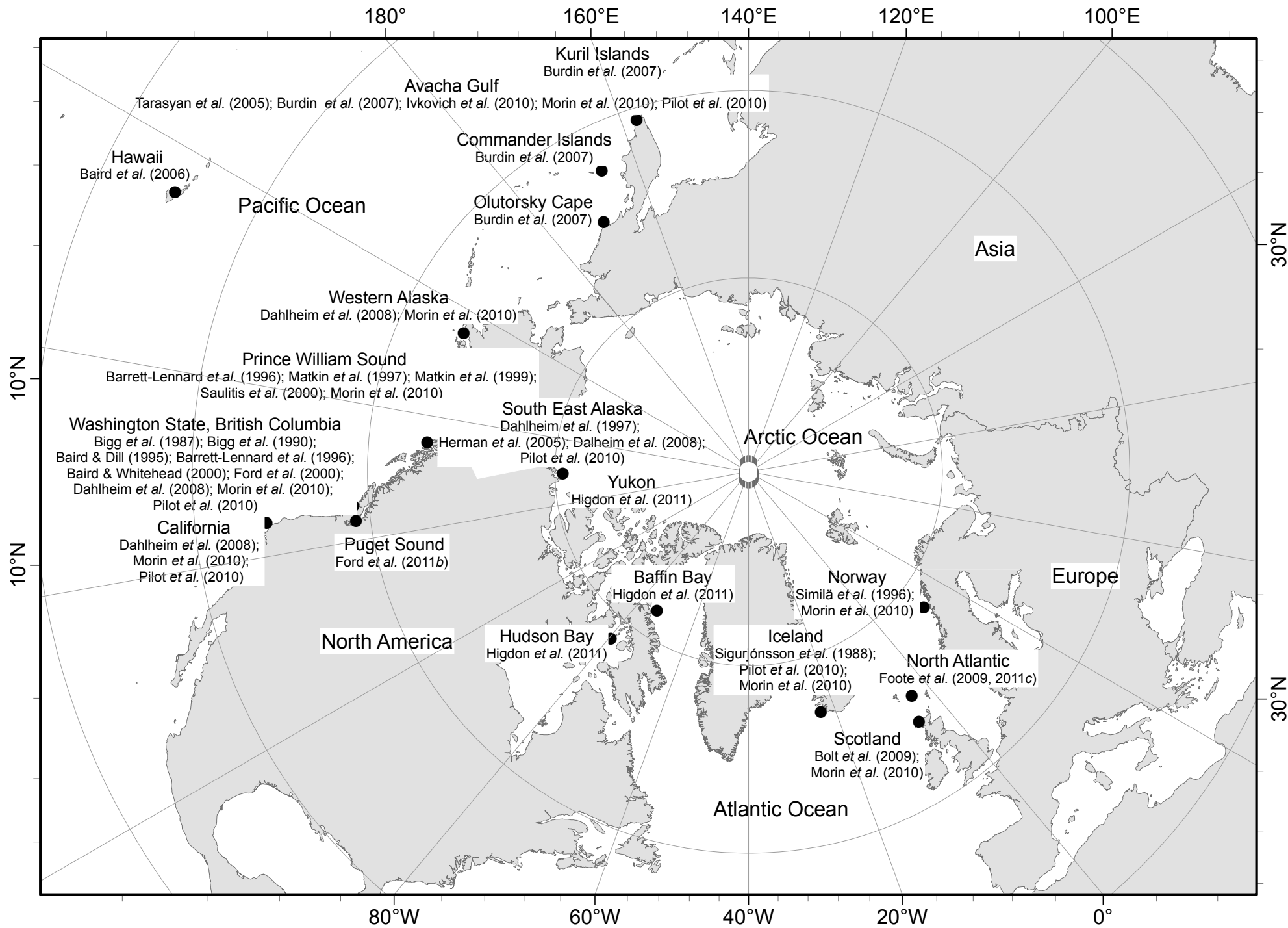
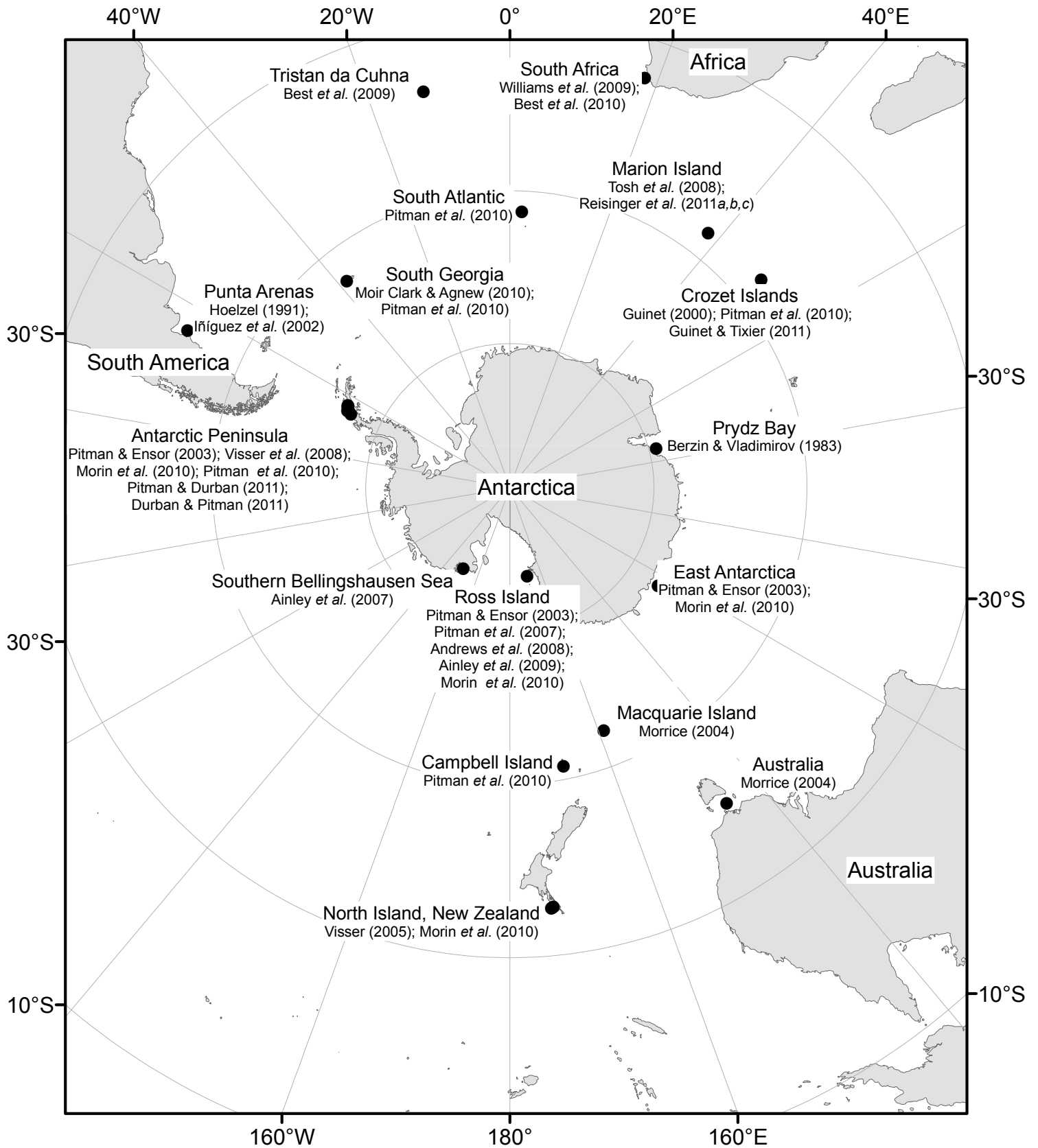


Fig. 1b.



of the ecology and status of the distinct ecotypes in the region (for a summary of this history, see Ford, 2011). A summary of the Northern Hemisphere ecotypes and their characteristics is provided in Table 1.

(2) Foraging and diet

In the ENP, different populations of killer whales display specialised diets (either fish-eating, or mammal-eating) that are associated with differences in social and acoustic behaviour, schooling and morphology. Transient killer whales feed mainly on marine mammals (both cetaceans and pinnipeds) but also prey on seabirds. Resident killer whales feed exclusively on fish and squid (Ford *et al.*, 1998; Saulitis *et al.*, 2000; Ford & Ellis, 2006). The exclusivity of the resident diet is such that a recent study has shown that chinook salmon exerts bottom-up regulation of the long-term demographics of this ecotype (Ford *et al.*, 2010). The diet of offshore killer whales is less well known, but likely comprises mainly bony and cartilaginous fishes (Herman *et al.*, 2005; Dahlheim *et al.*, 2008). Predation observations and tooth-wear evidence for this type suggest that sharks (elasmobranchs) are particularly important in the offshores' diet, thereby differentiating them from the salmonid-dominated resident type (Ford *et al.*, 2011a). Fish-eating resident killer whales along the Kamchatka coast feed mainly on Atka mackerel *Pleurogrammus monopterygius* and various salmonids *Oncorhynchus* spp. (Burdin *et al.*, 2007), whilst a less well-known population of mammal-eating killer whales have been reported to predate on largha seals *Phoca largha* and northern fur seals *Callorhinus ursinus* in far eastern Russia (Burdin *et al.*, 2007).

Similar levels of dietary specialisation are not seen for other Northern Hemisphere populations. They either do not adhere to equally strict diets, or the level of

specialisation in their diets remains unclear (e.g. Bolt *et al.*, 2009; Foote *et al.*, 2010). Studies in the North Atlantic (including the waters off Iceland, northern Scotland and northern Norway) suggest two ecotypes, a generalist (Type 1) and a specialist (Type 2) (Foote *et al.*, 2009). Type 1 killer whales have been documented feeding on herring *Clupea harengus* and mackerel *Scomber scombrus*, although isotopic and observational evidence indicates additional persistent predation on seals (Foote *et al.*, 2010). The specialist designation of Type 2 individuals is based on what is thought to be a more restricted diet that includes baleen whales. However, this is based on a very small sample size (Foote *et al.*, 2009) and further data are needed to clarify the diets of this group. Other studies in the region have reported predation events on marine mammals, seabirds and fish, but unfortunately the ‘type’ (Foote *et al.*, 2009) was not identified (Bolt *et al.*, 2009 and references therein). There is observational evidence that marine mammals dominate the diet of killer whales in the east Canadian Arctic (Higdon, Hauser & Ferguson, 2012; Ferguson, Kingsley & Higdon, 2012), although stomach samples of killer whales from adjacent areas (west Greenland) include fish and cephalopods (Higdon *et al.*, 2012 and references therein). Such findings highlight the difficulty in assessing the level of dietary specialisation in killer whale groups, particularly in the absence of individual identification.

Killer whales from the Hawaiian region feed on both humpback whales *Megaptera novaeangliae* and cephalopods; however, there is little evidence for two specialist populations (Baird *et al.*, 2006). A similarly generalist diet was reported from the Mexican Pacific, where killer whales were observed feeding on cetaceans, pinnipeds, turtles, and fish (Guerrero-Ruiz *et al.*, 2002).

(3) Movements

Photo-identification studies have also enabled researchers to track the movements of individual killer whales and their associated groups, pods and/or clans. For example, resident killer whales were shown to range widely within the ENP with pods from different geographic areas overlapping and potentially coming into frequent contact (Matkin *et al.*, 1997). Baird & Dill (1995, 1996) also showed that, contrary to their common name, many transient killer whales appear to be reasonably philopatric. When compared with wide-ranging offshore killer whales in the ENP, transients and residents have more localised movement patterns (Dahlheim *et al.*, 2008). Most of these data have been obtained during the main study season (July – August) and more data are needed to clarify the extent of the year-round geographic range. However, salmon resources are available year round in British Columbia (Ford *et al.*, 1998) and the Prince William Sound (Saulitis *et al.*, 2000), and perhaps at least resident killer whales remain close to salmon stocks, thus alluding to their distribution and movement patterns. The movements of NWP killer whales also seem to occur in relation to their main prey sources (Burdin *et al.*, 2007). Most fish-eating residents have been observed in the Avacha Gulf; however, some have been recorded as far south as 38°N (Burdin *et al.*, 2007). Transient mammal eaters have been reported predated on grey whales *Eschrichtius robustus* in the Chukchi Sea, just south of the Arctic Ocean, but it is likely their southerly distribution also extends to 38° N (Burdin *et al.*, 2007).

Killer whales in the east Canadian Arctic adjacent to the Northwest Passage are presumed to move away from the region in winter (Higdon *et al.*, 2012), probably to avoid heavy pack ice (Matthews *et al.*, 2011). Long-distance movement between the

east Canadian Arctic and the northern Atlantic complicate assessment of distributional limits of these killer whale populations (Matthews *et al.*, 2011). North Atlantic killer whales display both local and long-distance movements. Recent evidence links the long-distance movements of North Atlantic killer whales to the movement and seasonality of herring stocks (Simon, McGregor & Ugarte, 2007; Foote *et al.*, 2010) and grey seals *Halichoerus grypus* (Bolt *et al.*, 2009) between Iceland and the northern British Isles. Norwegian killer whales track the spring-spawning herring stocks (Stenersen & Similä, 2004) and do not seem to migrate between food sources. Little is known about the movements of killer whales in relation to prey such as baleen whales.

(4) Social organisation

The three ENP ecotypes display markedly different social organisation patterns, which likely evolved due to their foraging specializations (Baird & Whitehead, 2000; Riesch *et al.*, 2012). The piscivorous-specialist resident society is arranged into a number of groupings based principally on maternal genealogy (the matriline) (Bigg *et al.*, 1990). The bonds among members of the matriline are stable throughout life and no permanent dispersal of individuals has been observed. The pod is a grouping of related matrilineal members that associate with each other for at least 50% of the time (Bigg *et al.*, 1990). Pod sizes can be large (average = 18; range = 10–50); the strong matrilineal bonds and the longevity of killer whales allow several generations of a matriarch's offspring to become established within a matriline, that then associate in pods (Bigg *et al.*, 1990; Ford *et al.*, 2000). Conversely, transient pod sizes tend to be small (average = 2.4; range = 2–10), they likely display fission-fusion behaviour (Baird & Whitehead, 2000) and dispersal from the matriline is more common (Baird & Dill, 1996; Baird & Whitehead, 2000) although data on dispersal are few.

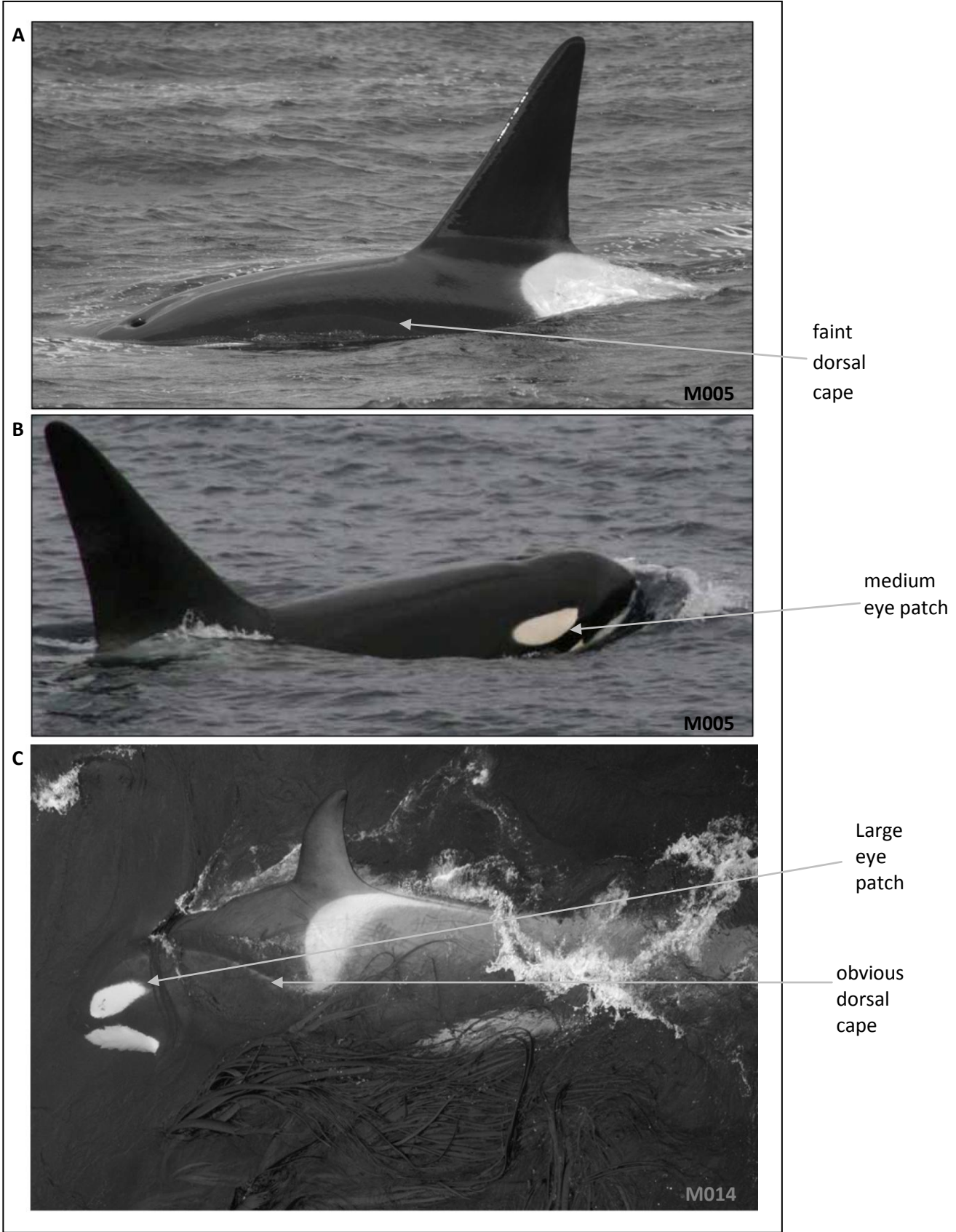
Differences in group size may be a consequence of the prey species targeted, with larger groups of fish-eating residents not being constrained by within-group competition for prey intake (Hoelzel, 1993). Optimal group size for mammal-hunting killer whales is thought to be three individuals although observed group sizes are often larger due to social factors or factors related to prey size (Baird & Dill, 1996). Although the social structure of the offshore ecotype in the ENP is not well known, Dahlheim *et al.* (2008) reported very large group sizes (75–100 individuals), comparable to multi-pod (clan) associations in residents.

Clans (the level of organisation above the pod) are defined by their acoustic repertoires. Acoustically, resident, transient and offshore ecotypes are differentiated, and again this differentiation is largely attributed to the prey with which each is associated (Barrett-Lennard, Ford & Heise, 1996; Deecke, Ford & Slater, 2005; Foote & Nystuen, 2008). In northern Norway, the acoustics of predominantly herring-eating killer whales (\approx Type 1 of Foote *et al.*, 2009) are reasonably well studied (see Simon *et al.*, 2007 and references therein). These piscivorous groups appear acoustically different from ENP piscivorous residents displaying a degree of social heterogeneity only made possible by divergent learning experiences in response to the different hearing abilities and behaviour of their prey [e.g. in this comparison salmon *versus* herring (Simon *et al.*, 2007), see also discussion in Riesch *et al.* (2012)].

(5) Morphology

Using photographs of killer whales from both hemispheres, Evans *et al.* (1982) found that six of 14 colour/shape features provided measures of geographical differentiation. The three most useful features were the pigmentation and shape of the dorsal patch, post-ocular patch size and position, and the presence or absence of a dorsal cape (Fig.

Fig. 2. Marion Island killer whales showing different morphological characteristics often used to delineate the Antarctic ecotypes. Note that male M005 has characteristics consistent with both Type A (medium sized eyepatch) and Type B (dorsal cape) ecotypes. (A) Male killer whale (M005) – note the faint dorsal cape. (B) Male killer whale (M005) – note the medium sized eyepatch. (C) Female killer whale (M014) – note the dorsal cape and medium to large eyepatch.



2). While variations in these features can allow individuals to be identified (Bigg *et al.*, 1987; Visser & Mäkeläinen, 2000), often there are insufficient differences to differentiate reliably among some ecotypes.

In the ENP, only saddle patch pigmentation differed significantly between transients and residents, with some residents having a black intrusion into the grey of the saddle patch unlike the transients (Baird & Stacey, 1988). Other studies in the ENP have described morphological characteristics of killer whales qualitatively (Bigg *et al.*, 1987; Dahlheim *et al.*, 2008) and used features like size, dorsal fin-tip orientation, dorsal patch size and patterning and body size to differentiate among ecotypes.

However the qualitative nature of these observations and their subjectivity make it difficult to rely on them for definitive ecotype descriptions. In a study of killer whales around the Alaskan Peninsula and Aleutian islands, Zerbini *et al.* (2007) distinguished between offshore and transient types based on the dorsal fin shape and saddle patch pigmentation, and suggested that the ecotypes identified using these characteristics were validated by molecular techniques. Putative North Atlantic Ocean ecotypes are best differentiated by body size. The Type 1 dietary generalists are smaller (up to 6.6 m in length) while the Type 2 specialists, which included whales in their diet, are typically larger (up to 8.5 m in length) (Foote *et al.*, 2009).

(6) Genetics and kinship

Killer whales from the ENP and the North Atlantic display a complex genetic structure that is often unique to specific populations (Hoelzel *et al.*, 2007; Foote *et al.*, 2011*b, c*) but may provide broader insights into the development of different ecotypes and the degree of separation observed between populations today. A common factor is the importance of matrifocal philopatry and reproductive isolation, due to resource

specialisation, in determining genetic diversity within populations (Hoelzel *et al.*, 2007; Pilot *et al.*, 2010; Foote *et al.*, 2011*a, b, c*). Whilst matrilineal philopatry may account for low levels of mitochondrial DNA (mtDNA) variation within populations, it does not explain low levels of mtDNA variation observed among populations worldwide (Hoelzel *et al.*, 2002).

Low levels of mtDNA variation observed worldwide and shared haplotypes amongst populations may be an indication of a bottleneck event occurring during a glacial maximum approximately 200 000 years ago (Hoelzel *et al.*, 2002, Foote *et al.*, 2011*b*). This may have resulted in the redistribution of populations and thus genetic variation around the world at a similar time (Hoelzel *et al.*, 2002, Foote *et al.*, 2011*b*). Some studies have suggested that the highly variable mtDNA control region (as used in Hoelzel *et al.*, 2002) may not be the best predictor of phylogeny (e.g. Duchene *et al.*, 2011); and these authors suggest that the inclusion of other coding genes, which evolve in a more clock-like manner, is likely to result in better estimates of bottleneck events or divergence. Using similar Bayesian methods to Duchene *et al.* (2011), Morin *et al.* (2010) suggest a bottleneck event at 700 000 years ago, but this does not preclude a second, more recent, bottleneck event at 200 000 years before present. The post-glacial history of the species and contrasting genetic evidence from mitochondrial and nuclear DNA analysis (Pilot *et al.*, 2010; Foote *et al.*, 2011*c*) complicates the interpretation of data from extant populations. For example, mammal-eating transient killer whales show the greatest mitogenome divergence from other Northern Hemisphere killer whale types (Morin *et al.*, 2010; Pilot *et al.*, 2010) but nuclear DNA analysis groups transient whales with offshore ecotypes (Pilot *et al.*, 2010). Atlantic killer whale populations also show clearly delineated populations

based on mtDNA differences but nuclear DNA markers provide less resolution (Foote *et al.*, 2011c).

The consideration of social structure when interpreting genetic results highlights the importance of maternal philopatry and resource specialisation in shaping population structure in this species (Hoelzel *et al.*, 2007; Foote *et al.*, 2011c). The importance of founding events in shaping distinct populations has been postulated for the Pacific Ocean killer whale populations (Hoelzel *et al.*, 2007; Pilot *et al.*, 2010) and for Atlantic Ocean killer whales (Foote *et al.*, 2011c). Although allopatric speciation may account for the differences observed among populations in the different ocean basins (Foote *et al.*, 2011b) it is unlikely that different populations within ocean basins diverged in this manner; perhaps reflecting the increased opportunity for ongoing gene flow among groups within an ocean basin. Importantly, reproductive isolation between populations has not been confirmed (but see discussion in Riesch *et al.*, 2012) and gene flow may occur between isolated populations through intermediate populations (Hoelzel *et al.*, 2007; Pilot *et al.*, 2010; Foote *et al.*, 2011c). Gene flow between pods is thought to occur by interaction of pods, either due to overlapping resources (Pilot *et al.*, 2010; Foote *et al.*, 2011c) or for specific social purposes (Filatova *et al.*, 2009). There is evidence that some populations have not experienced male-mediated gene flow from neighbouring populations (e.g. southern residents, Ford *et al.*, 2011b), suggesting highly insular mating behaviour. By contrast, Hoelzel *et al.* (2007) and Pilot *et al.* (2010) suggest there is evidence for male-mediated gene flow into the southern resident population from neighbouring groups. Despite the use of similar analytical techniques and software, these contrasting conclusions [Pilot *et al.* (2010) *versus* Ford *et al.* (2011b)] reinforce the difficulties in reaching consensus on the interpretation of some molecular studies. East Canadian Arctic killer whales

adjacent to the Northwest Passage that are geographically intermediate between North Pacific and North Atlantic populations have not yet been included in global genetic studies (Higdon *et al.*, 2012), but analyses of these individuals may shed some light on the broader patterns of gene flow in the region.

IV. SOUTHERN HEMISPHERE KILLER WHALES

Killer whales occur throughout the Southern Hemisphere, from the Antarctic continent to the equator. The high-latitude Antarctic killer whales have received considerable research attention with their divergent morphologies (Pitman & Ensor, 2003) and specialised hunting techniques (Pitman & Durban, 2010) making them the focus of evolutionary biologists and taxonomists worldwide (Le Duc *et al.*, 2008; Foote *et al.*, 2011a). The recent work of Dr Robert Pitman and colleagues dominates the Antarctic killer whale literature and they have contributed significantly to the underlying knowledge base of Southern Ocean killer whale ecology.

Currently five killer whale ecotypes have been proposed: four in Antarctic waters (south of 60°S) (Pitman *et al.*, 2007; Pitman, 2011) and one that has only been observed in the sub-Antarctic (Pitman, 2011). This classification is mainly based on the size, shape and orientation of the eyepatch and the presence or absence of a dorsal cape (Pitman & Ensor, 2003; Pitman, 2011). Observations of diet, hunting behaviour and other ecological aspects (Pitman & Ensor, 2003; Pitman *et al.*, 2010; Pitman, 2011) raise the possibility of ecological divergence within the species. While we suggest that these are currently more accurately described as morphotypes (Pitman & Ensor, 2003), due to their ubiquitous use as ecotypes in the literature to date we have retained the nomenclature and summarised their characteristics (as described by those authors) in Table 2.

Table 2. Southern Hemisphere ecotypes, proposed common names, diet and distribution as defined by Pitman & Ensor (2003), Pitman *et al.* (2010), Pitman (2011) and Pitman & Durban (2012).

Ecotype	Proposed common name	Morphology	Diet	Distribution
Type A	Antarctic killer whale	All black, large killer whale, medium-sized eye-patch parallel to body, females occasionally have slightly open saddle, size range 7-9m	Cetaceans and seals	Open water right around Antarctica in summer; winter distribution unknown
Type B (big)	Pack ice killer whale	Two-tone grey, large grey dorsal cape, eyepatch variable but larger than other whales, often yellow with diatoms	Pinnipeds	Pack ice in summer; unknown in winter
Type B (small)	Gerlache killer whale	As above but half the size	Penguins	Pack ice in summer, largely Antarctic Peninsula; winter tropical
Type C	Ross Sea killer whale	Two-tone grey and white, smallest reaching only 6 m in length, eyepatch angled at 45° to body	Fish	Antarctic pack ice; winter unknown, possibly remain all year round
Type D	Sub-Antarctic killer whale	Extremely small eyepatch and bulbous head	Unknown	Sub-Antarctic and temperate waters

(1) Study sites

The lack of land and connectedness of the Southern Hemisphere through the circumpolar Southern Ocean somewhat confounds its categorisation into discrete study units in a similar manner to the Northern Hemisphere. Nevertheless, broad regional areas and studies around islands or island groups serve a similar function (Fig. 1B). The main regions of study for which there are data include: South Africa, Australia, New Zealand, South America, some Antarctic regions, and several sub-Antarctic islands, including Marion Island, Macquarie Island and Îles Crozet.

(2) Foraging and diet

Observations of killer whales obtained from the Soviet Antarctic whaling vessel *Yuri Dolgorukiy* (Budylenko, 1981), and data resulting from specimens collected over a period of 15 years (1960–1975) provided the first insights into the dietary habits of Southern Ocean killer whales [Shevchenko (1975) and Doroshenko (1978) cited in Budylenko (1981)]. Stomach samples collected in the Atlantic sector of the Southern Ocean (see online Supporting information, Fig. S1) indicated killer whale diets consisted of dolphins and fish in more northern temperate waters, and minke whales *Balaenoptera acutorostrata* and pinnipeds in higher latitude waters [Shevchenko (1975) and Doroshenko (1978) cited in Budylenko (1981)]. Close agreement between minke and killer whale distribution mirrored the finding that the former constituted 85% of the killer whale diet (Budylenko, 1981). Dietary specialisation in Southern Ocean killer whales was first reported by Berzin & Vladimirov (1983) from samples collected in 1979/80 in Prydz Bay, Antarctica (69° 22' S, 76° 23' E – see online Supporting information, Fig. S1). The smaller (yellow, '*O. glacialis*', $N = 629$) killer whales had predominantly fish (98.5%) and negligible amounts of marine mammals

and squid in their stomachs. By contrast, the large (white, '*O. orca*', $N = 156$) killer whales ate mostly marine mammals (89.7%).

More recently, Pitman & Ensor (2003), and several subsequent studies (e.g. Krahn *et al.*, 2008; Ainley & Blight, 2009; Pitman & Durban, 2010, 2012; Pitman *et al.*, 2010; Pitman, 2011) also suggest there is dietary specialisation among the different forms of killer whales in the Southern Ocean (Table 2). These studies suggest that Type A feed mainly on Antarctic minke whales, Type B seem to specialise on pinniped prey but may also take minke, humpback whales and penguins, Type C is thought to feed on fish, particularly Antarctic toothfish, *Dissostichus mawsonii*, and Type D is suspected also to include fish in its diet (Pitman & Ensor, 2003; Lauriano, Fortuna & Vacchi, 2007; Pitman & Durban, 2010, 2012; Pitman *et al.*, 2010; Guinet & Tixier, 2011).

Some studies have observed killer whales (tentatively identified as Type C) displaying hunting behaviour around penguins, but have been cautious about drawing conclusions, suggesting that it is often difficult to distinguish between 'play' behaviour and actual predation (e.g. Ballard & Ainley, 2005). Recently we observed putative Type C killer whales displaying hunting behaviour around emperor penguins *Aptenodytes forsteri* in the Ross Sea (see online Supporting information, Fig. S2, and in this case there appeared to be actual predation, as evidenced by a penguin falling off the ice and killer whales converging and thrashing about in the immediate vicinity. There is also considerable evidence (presented in detail below) from other locations in the Southern Ocean to suggest more generalist diets of all Antarctic ecotypes.

Evidence also suggests that there may be as yet undescribed, or intermediary types of killer whales exhibiting varied morphological characteristics not consistent with existing ecotype descriptions (as described in Table 2), that also confound our dietary understanding of Southern Ocean killer whales.

The fact that Antarctic killer whales are known to move seasonally into more temperate waters (e.g. Mikhalev *et al.*, 1981; Pitman & Ensor, 2003; Moir-Clark & Agnew, 2010; Durban & Pitman, 2012) together with their known ability to travel long distances (Visser 1999c; Durban & Pitman, 2012), the absence of physical barriers to movement, and attempts to classify killer whales sighted as far north as the South African, Angolan and south-east Australian coasts as Antarctic ecotypes (Donnelly & Morrice, 2009; Williams *et al.*, 2009; Weir *et al.*, 2010) provide impetus for a broader discussion on the diet of the species elsewhere in this region.

At sub-Antarctic Marion Island (46°46'S, 37°51'E) killer whales have been observed feeding on southern elephant seals, king penguins *Aptenodytes patagonicus* and rockhopper penguins *Eudyptes chrysocome* close inshore (Condy *et al.*, 1978). Recent observations also indicate that Macaroni penguins *Eudyptes chrysolophus* and sub-Antarctic fur seals *Arctocephalus tropicalis* are included in killer whale diet there (Reisinger *et al.*, 2011c). Killer whales have been observed depredating from toothfish longliners in the vicinity of the island (Kock *et al.*, 2006), but whether these are the same individuals present inshore is unknown. Just under half of the killer whales at Marion Island (12 of 37 currently identified) exhibit morphological characteristics of both Type A and Type B Antarctic ecotypes (see Section IV.5), confounding simple categorisation of individuals on this basis and suggesting that the dietary preferences of these categories may not be quite so easily defined. At Macquarie Island putative Type A individuals have been observed predated on both seals and penguins (Morrice, 2004), providing further support for a more generalist diet.

At the Îles Crozet (~46°24'S, 51°46'E), photo-identified individual Type A killer whales have been reported attacking whales, pinnipeds, penguins and fish (Guinet, 1991, 1992, 2000; Guinet & Tixier, 2011). Actual feeding on whales, pinnipeds and king penguins inshore (Guinet, 2000), and depredation from toothfish longliners offshore by the same killer whales has been confirmed (Tixier *et al.*, 2010a). At other localities in the Southern Ocean some evidence of killer whale diet has also been provided. Putative Type B killer whales have been observed to depredate heavily off longliners around South Georgia (54°15'S, 36°45'W) migrating specifically for depredation activities during the austral winter between May and August (Moir-Clark & Agnew, 2010).

Off the coast of South America, killer whales are known to hunt pinnipeds at Peninsula Valdéz (42°30'S 63°56'W) (Hoelzel, 1991; Vila *et al.*, 2008). Individual killer whales, photo-identified to be regular pinniped hunters, have also been seen predated on seven gill sharks *Notorhynchus cepedianus* off the Patagonian coast, Argentina (Reyes & García-Borboroglu, 2004). In the same region, Iñiguez, Tossenberger & Gasparrou (2002) reported a more generalist diet for killer whales that included penguins and fish. Stomach content and feeding observations support the idea that killer whales off the South African coast are opportunistic hunters and a variety of cetaceans (at least six species), at least one pinniped species, fish (several unidentified species), large squid and seabirds contribute to their diet (Best *et al.*, 2010).

Killer whales in New Zealand waters are thought to feed primarily on elasmobranch fish, but also marine mammals (Visser, 1999b, 2000, 2005; Visser *et al.*, 2010).

Antarctic Type A individuals were observed in New Zealand waters consuming both

elasmobranch fish and pinnipeds in the same feeding frenzy (this study, Suppl. Mat. Fig. S3). In Australian waters Antarctic Type A killer whales have been reported feeding on whales, seals, dugongs, pelagic fish and depredated fish off lines (Morrice, 2004). There is limited knowledge of the spatial and temporal extent of killer whale movements throughout the region and this complicates in-depth assessments of dietary specialisation (Williams *et al.*, 2009; Pitman & Durban, 2012; Reisinger *et al.*, 2011c).

(3) Movements

Aside from the speculation on broad-scale movements by Mikhalev *et al.* (1981), studies of killer whale movement in the Southern Ocean are restricted to relatively infrequent matching of photo-identified individuals between distant localities (e.g. Visser, 1999c). To date only two published satellite-linked telemetry studies report on movements in the region (Andrews, Pitman & Ballance, 2008; Durban & Pitman, 2012). These studies describe the movements of Type B and Type C individuals and illustrate localised Antarctic movements as well as some longer journeys into subtropical waters. Other unpublished data were shown by Durban & Deecke (2011) to illustrate the movement of an Antarctic Type A individual around the West Antarctic Peninsula coast.

Some studies suggest that putative Type C killer whales are probably resident in the pack-ice of Antarctica (Pitman & Ensor, 2003; Ainley *et al.*, 2005) and Gill & Thiele (1997) recorded killer whales utilising leads deep in the sea ice during the winter months. Andrews *et al.* (2008) suggest that movement comparisons between their Type C and B individuals ($N = 4$ and $N = 1$, respectively) also support the premise that Type C animals remain in the pack ice, but the small sample size and limited

seasonal range preclude definitive conclusions. Photographs of Antarctic Type C individuals in south-east Australian waters suggest that this ecotype is not wholly restricted to the pack ice in winter (Donnelly & Morrice, 2009) and other photographs from New Zealand waters also support this interpretation (Pitman, 2011). Similarly, observations of ‘pack-ice’ Antarctic Type B killer whales in subtropical waters away from the continent recently have been confirmed (Durban & Pitman, 2012).

At Macquarie Island, killer whale sightings are highest in November and December, coinciding with the weaning of tens of thousands of elephant seal pups (Morrice, 2004). The increase in these months (tenfold from winter sightings) suggests that these Antarctic Type A killer whales are only visiting Macquarie Island to take advantage of this seasonal, abundant food resource. While evidence in support of seasonal philopatry exists for some populations, the year-round movements of virtually all populations of Southern Hemisphere killer whales remain unclear. One exception comes from the Indian Ocean where a combination of photo-identification work from the French Economic Exclusive Zone (EEZ) and Marion Island has shown that individuals range between Marion Island, Îles Crozet and the Kerguelen Archipelago, covering distances of almost 3000 km (Guinet & Tixier, 2011). In addition to the expansion and ongoing collection of images for photographic databases, the long-term movements of killer whales are also likely to be clarified by the increasing use of biotelemetry methods.

(4) Social organisation

Unlike the ENP populations, where differences in social characteristics underpin their ecotyping, relatively little is known about social organisation in the Southern Hemisphere. Photo-identification studies over several years at Peninsula Valdéz and

Îles Crozet show philopatry and long-term associations between individuals (Hoelzel, 1991; Guinet, 1992; Guinet & Tixier, 2011) and an unpublished catalogue of Îles Crozet individuals provides some information on pod delineation in the region (Tixier *et al.*, 2010b).

Preliminary results from a Marion Island photo-identification study provide evidence of associations between individuals, but the findings did not allow conclusive pod delineations (Tosh *et al.*, 2008). That study proposed that the observed social characteristics had aspects in common with both the ENP transients (e.g. small group size) and residents (e.g. high degree of philopatry), but cautioned that a longer dataset is required to assess this conclusively (Tosh *et al.*, 2008).

The social dynamics of killer whales in New Zealand waters can be broadly classified into two geographical groups (north and south) with individuals inhabiting both a social and a geographical transition area where the two groups overlap (Visser, 2000). At Macquarie Island, a long-term photo-identification study suggests that mean pod size is four individuals with a typical group composition of a single adult male with three females/older juveniles (Morrice, 2004).

Vocalisation is a key aspect of cetacean social behaviour and acoustic studies have been used to differentiate killer whale clans and ecotypes in the Northern Hemisphere (see Section III.4). Acoustic studies in the Southern Hemisphere have provided some evidence for broad-scale differences between Southern and Northern Hemisphere populations (e.g. Ross Sea killer whales compared to ENP populations - Jehl *et al.*, 1980; Thomas *et al.*, 1981). Richlen & Thomas (2008) provided perhaps the most detailed assessment of killer whale vocalisations and acoustics in the Ross Sea, and assigned these results to Type C killer whales. To date, no other acoustic studies have

been published on other Antarctic ecotypes. Guinet (1992) described the acoustic behaviour associated with foraging activities of killer whales at Îles Crozet (presumably Type A; Guinet & Tixier, 2011), but it is not known how these differ from other populations in the Southern Ocean.

Specialised foraging strategies also reflect an aspect of social behaviour. Foraging strategies including food sharing, co-operative hunting and the teaching of predatory behaviours have been reported from Peninsula Valdéz (Lopez & Lopez, 1985; Hoelzel, 1991), Îles Crozet (Guinet, 1992; Guinet & Bouvier, 1995), northern Patagonia (Iñíguez *et al.*, 2002) and Macquarie Island (Morrice, 2004). Working cooperatively to dislodge prey items from ice floes, using a ‘wave-washing’ technique has been described in both hemispheres (Visser *et al.*, 2008; Durban & Pitman, 2012; Pitman, 2011; Higdon *et al.*, 2012). Other specialised behaviours like intentional beaching to predate on seals, have been recorded independently from at least six different localities: Peninsula Valdez, Îles Crozet, Northern Patagonia, Macquarie Island, Marion Island and Tristan da Cunha (Hoelzel, 1991; Guinet, 1992; Best *et al.*, 2009; Iñíguez *et al.*, 2002).

(5) Morphology

The complexity of differentiating Southern Hemisphere killer whales on the basis of their morphology was recognised by some of the first studies using photo-identification (Evans *et al.*, 1982). The first documented morphological differences between the large black-and-white morphotype in the Southern Ocean and a smaller morphotype within the same geographic range comes from Soviet whaling vessel data from the 1970s and 1980s (Mikhalev *et al.*, 1981; Berzin & Vladimorov, 1983). These two studies independently quantified various morphometric observations of a smaller

‘variety’ captured during whaling expeditions, and from their different samples each proposed new species, *O. nanus* (Mikhalev *et al.*, 1981) and *O. glacialis* (Berzin & Vladimirov, 1983). More recently, Pitman *et al.* (2007) proposed that these two ‘species’ probably described the smaller morphotype (*viz.* Type C), but the holotype specimens no longer exist to resolve this issue. Further quantitative evidence of size differences comes from aerial photogrammetric assessments of Type C whales in the Ross Sea, where smaller body size has been confirmed (Pitman *et al.*, 2007).

Differences in the dorsal cape and eyepatch size and orientation were used by Pitman & Ensor (2003) and Pitman (2011) to delineate Antarctic ecotypes [Pitman & Ensor (2003) do not use the term ‘ecotype’ but rather ‘morphotype’; however, later studies imply such use from the prior study and themselves use the term ‘ecotype’. For simplicity here we use ‘ecotype’ as based on current literature] (see Table 2). Pitman *et al.* (2010) recently described an additional ecotype from photographic samples of killer whales distributed in the sub-Antarctic region 40°S to 60°S ($N = 7$). Type D individuals possess a distinctively small eyepatch orientated parallel to the long body axis and are to date the most readily identifiable morphotype. Although no ecological data exist for this type (Guinet & Tixier, 2011), both Pitman *et al.* (2010) and Pitman (2011) suggest that they are restricted to the sub-Antarctic region and propose the common name “sub-Antarctic killer whale”. Many morphologically dissimilar individuals have been recorded from this region, some of which may be resident (Guinet, 2000; Visser, 2000; Visser & Mäkeläinen, 2000; Tosh *et al.*, 2008; Reisinger *et al.*, 2011c) or whose movements may be restricted to the sub-Antarctic.

From over 13 000 photographs taken at Marion Island (2006–2011), 37 individual killer whales have been identified (Reisinger *et al.*, 2011a) and some preliminary

social associations described (Tosh *et al.*, 2008). Of the 37 identified individuals, 18 possess an identifiable dorsal cape, while for the remainder no cape can be discerned (despite at least 50 photographs per individual). Around 12 individuals had physical characteristics or associations that overlap at least two of the ecotype descriptions in Table 2. For example, one male (M005) has a faint dorsal cape (*viz.* Type B), and a medium eyepatch (*viz.* Type A) (Fig. 2A, B). Tosh *et al.* (2008) showed that this male regularly associated with a female (M014) whose eyepatch size is relatively large and who also has a very clear dorsal cape (*viz.* Type B) (Fig. 2C). The same male also associates closely with another female M002 (Fig. 3A) who displays a dorsal cape, and she in turn associates closely with female M012 (Fig. 3B) who does not have a dorsal cape; both females have large eyepatches (Fig. 3). Importantly, in line with current literature of morphological descriptors for the region's whales, the above descriptions exemplify the complexity associated with observer assignment of Type-specific morphology. Variation in morphological features is not restricted to Marion Island. Type C killer whales in the Antarctic Peninsula have also been recorded with eyepatches of varying size, both with and without a prominent dorsal cape (Fig. 4). The lack of adequate quantification of these features throughout the region impedes confident objective classification.

(6) Genetics and kinship

Despite worldwide genetic diversity in the killer whale being very low, some Antarctic (notably Types B and C) killer whales are genetically distinct from their Northern Hemisphere counterparts (Hoelzel *et al.*, 2002; Le Duc *et al.*, 2008; Morin *et al.*, 2010). Within the Antarctic, genetic studies using mtDNA control region sequences found that Type A killer whales represented a paraphyletic group, with one

Fig 3. Marion Island female killer whales known to associate with each other. Both show large eyepatches. A is with prominent dorsal cape and B is without dorsal cape.

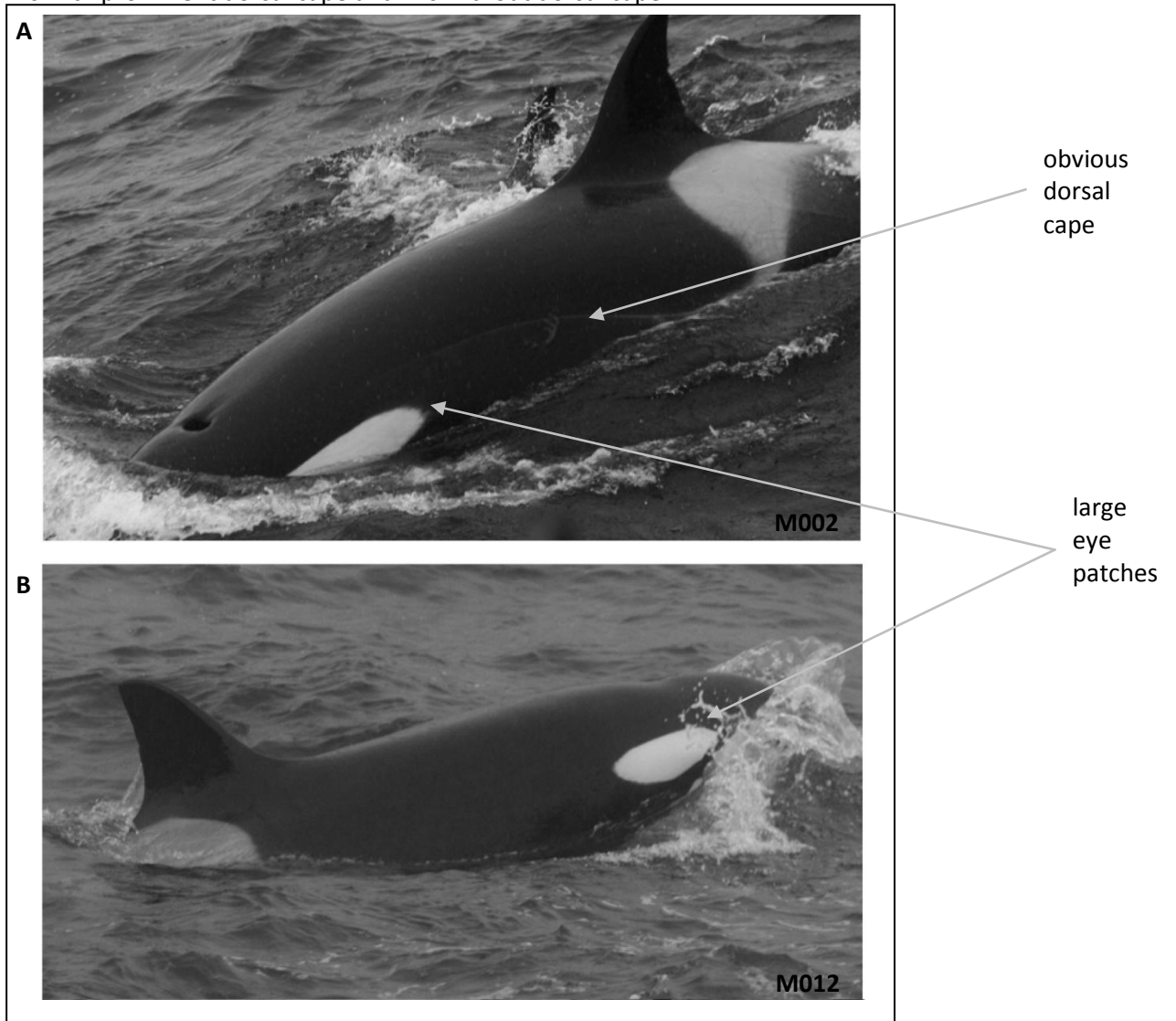


Fig. 4. Type C killer whales in McMurdo Sound, Ross Sea showing variation in morphological features. Both have the angled eyepatches characteristic of the type; however A has a large eyepatch and no obvious dorsal cape, while B has a considerably smaller eyepatch and a prominent dorsal cape.



group more closely related to the Type B and Type C killer whales from Antarctica, and the other more closely related to the ENP transients (Le Duc *et al.*, 2008). Types B and C represent a single monophyletic group that separate from Type A killer whales (Le Duc *et al.*, 2008). According to Morin *et al.* (2010) full mtDNA sequences support the separation of Types B and C killer whales into not only different ecotypes, but different species. However, as the mtDNA genome is a single maternally inherited locus, nuclear markers are required from multiple loci and from male and female components for conclusive identification of separate lineages and species divergence.

Using only mtDNA, species-level differences are only supported under the phylogenetic species concept. Foote *et al.* (2011a) contend that positive selection of amino acid changes in opposite directions in the mitogenome of Types B and C indicate strong directional selection in each providing support to Morin *et al.* (2010). Further genetic analyses using paternally inherited genetic markers are needed to provide conclusive evidence of reproductive isolation (Le Duc *et al.*, 2008). Presently no social or ecological information is available to put these genetic studies into context (Le Duc *et al.*, 2008).

V. IS THERE A GLOBAL MODEL OF ECOTYPING?

One of the clearest outcomes to emerge from our review and synthesis of killer whale ecology is the difference between the Northern and Southern Hemispheres. Some insight into these differences can be obtained from examining the historical progression of the ecological data collected. In the Northern Hemisphere, social organisation provided some of the first clues that there were separate groups, followed by dietary information, and behavioural differences. Focus on the morphological differences came later and finally molecular techniques were used to distinguish

groups further. In Antarctica we see a much different, shorter and less intensive research timeline. Morphological differences were noted first, and studies into diet and behaviours are at a much earlier stage compared to those in the Northern Hemisphere. Genetics studies and their interpretation have also produced some lucid results, but there is a clear lack of consensus in some areas. This is also true for some Northern Hemisphere molecular studies. The different sequence of ecological observations likely reflects the underlying processes, with non-heritable behavioural traits being the greatest phenotypic differences in the ENP, while in the interconnected Southern Hemisphere, the phenotypic traits that differ most clearly between the Antarctic types are heritable morphological traits that may reflect a slower divergence with some long-term level of gene flow. In an attempt to clarify these differences further, our comprehensive global synthesis of the current state of knowledge describes those areas for which there are good data and those where there are significant knowledge gaps. We now discuss more specific confounding issues associated with this knowledge, and how it relates to classification of groups and our overriding question: is there a global model of killer whale ecotypes?

Regional habitat differences notwithstanding, due to differences in access to individuals, the baseline dataset of Southern Hemisphere killer whales lags far behind that of their northern counterparts. Despite the existing knowledge base, the level of ecotypic differentiation between some Northern Hemisphere populations is still not absolutely clear (e.g. Dahlheim *et al.*, 2008; Foote *et al.*, 2010; Higdon *et al.*, 2012). Most of this uncertainty arises from a lack of evidence for dietary specialisation, indications of resource overlap among groups and lack of evidence for reproductive isolation.

Whilst resource specialisation is well supported for a killer whale population in the ENP and similar levels of resource specialisation exist for some North Atlantic populations, strict adherence to specific resources has not been documented for any population in the Southern Hemisphere. Much of our current understanding of Southern Ocean killer whale diets is based on studies that took place three decades ago (Budylenko, 1981; Mikhalev *et al.*, 1981; Berzin & Vladimirov, 1983). It is conceivable that the diet and hunting behaviours of killer whales may have changed since this time for a variety or combination of reasons including: the removal of a large number of individuals from the population (e.g. Ainley *et al.*, 2010), concurrent broad-scale ecosystem changes due to the large-scale removal of cetaceans, seals and fish (Ainley *et al.*, 2007, 2010; Ainley & Blight, 2009; Ainley, Ballard & Olmastroni, 2009) or the marked ecosystem changes observed in the last three decades due to combinations of the above factors with a changing climate (as has been demonstrated for other species - e.g. Weimerskirch *et al.*, 2003; Rolland, Barbraud & Weimerskirch, 2008; Ainley & Blight, 2009). A marked increase in killer whale observations in the Canadian Arctic during the last decade, for example, has been tentatively attributed to climatic changes, with significant consequences for the ecology of the species in the broader region (Higdon *et al.*, 2012).

As predators with high energetic demands (Reisinger *et al.*, 2011*b*) it is plausible that killer whales will maximise their energetic intake by using specialised hunting techniques in order to capitalise on seasonally available energy-rich food resources [e.g. southern elephant seals (Morrice, 2004; Reisinger *et al.*, 2011*b*) or Weddell seals *Leptonychotes weddellii* (Visser *et al.*, 2008; Pitman & Durban, 2012)]. It is also plausible that killer whales in the Southern Ocean follow prey resources, and often when observed are typically focussed on a specific prey resource. On this basis, more

generalist feeding behaviour cannot be excluded from the ecology of Southern Ocean killer whales (Section III.2, e.g. Krahn *et al.*, 2008), including the Antarctic ecotypes.

The close link between dietary specialisation and the evolution of killer whale ecotypes in the ENP cannot be ignored. While the model of transient, resident and offshore ecotypes is not appropriate for all killer whale populations, similarities do exist within specific groups that suggest differences among populations. In the ENP, such differences are largely behavioural and ecological. In the North Atlantic, herring-feeding killer whales around Norway display behavioural and ecological specialisations associated with their choice of prey (Stenersen & Similä, 2004), unlike other populations in that region which seem to interact in response to movement of common food resources (Foote *et al.*, 2011c; Beck *et al.*, 2012). In the Southern Hemisphere, differences are ostensibly morphological and studies investigating the behavioural and ecological differences among morphotypes are underway and ongoing. In both the Northern and the Southern Hemispheres scientists have looked to genetic studies to provide clarity on the status of these populations.

Genetic studies in the Northern Hemisphere have done much to clarify the population structure of killer whales in the region. In the ENP, genetically distinct populations are often related to different ecotypes. However, even in these well-studied populations, there is a clear lack of consensus on the best molecular methods to use, particularly in relation to phylogenetic studies (e.g. Pilot *et al.*, 2010; Morin *et al.*, 2010; Duchene *et al.*, 2011; Ford *et al.*, 2011b). Although structured populations exist in the North Atlantic, the ecological separation of populations is not as clear (Foote *et al.*, 2011c). Matrifocal philopatry and resource specialisation have been identified as factors driving the structure of populations in both the ENP and the North Atlantic.

These factors also tend to confound the degree of taxonomic differentiation among populations, causing discontinuities between results obtained from nuclear DNA and mtDNA analyses (Pilot *et al.*, 2010, Foote *et al.*, 2011c). As a result, reproductive isolation cannot be confirmed thus precluding the idea of speciation as proposed by Morin *et al.* (2010) The idea of ecological speciation in killer whales was recently reviewed by Riesch *et al.* (2012). While recognising the lack of certainty regarding the strength of reproductive isolation, these authors presented evidence to suggest that ecological speciation was a key driving force behind global killer whale diversity. However, they were not able to find a genetic mechanism that linked divergent selection to reproductive isolation and also suggested alternative mechanisms for ecological divergence (Riesch *et al.*, 2012).

The importance of social structure must also be considered when analysing genetic results, as the highly matrifocal social structure in the ENP pods clearly shows. This is particularly true at higher latitudes (Hoelzel *et al.*, 2007; Foote *et al.*, 2011c), where low levels of genetic diversity are explained by females remaining in maternal groups. The paucity of data on killer whale social organisation in locations other than the ENP is one of the key limiting factors in the clear delineation of ecotypes in both the North Atlantic and the Southern Hemisphere. Clarifying aspects of social organisation is largely confounded by the vast distances that killer whales are presumed to travel in the Southern Ocean, presumably attributable to the temporal instability of many of their preferred food sources. It is further confounded by the difficulty in observing killer whales in the Southern Ocean, particularly at higher latitudes in the winter months. Studies at Marion Island, Îles Crozet and New Zealand are beginning to reveal some social patterns; however, at other locations with varying levels of access to individuals and/or with more transient populations, this is proving difficult.

As has been demonstrated in the Northern Hemisphere, particularly the ENP, successful classification of killer whales into different ecotypes requires in-depth knowledge of social, behavioural, morphological and genetic characteristics of the different groups. Of particular importance is the close link between dietary specialisation and successful assignment of ecotypes in the ENP (e.g. see Riesch *et al.*, 2012), and the fact that this link does not appear as strong in the Southern Hemisphere may be at least in part responsible for the difficulty in easily assigning definitive ecotypes.

VI. THE FUTURE OF ECOTYPING KILLER WHALES

When distinct morphological differences between Southern Ocean killer whales are identified, researchers tend to speculate intuitively on levels of ecological specialisation and ultimately the possibility of new species. As we describe above, a different sequence of delineation occurred in the Northern Hemisphere, and groups were only refined on the basis of external morphology and colour patterns after different ecotypes were identified. The sheer size of the Southern Ocean, absence of physical barriers, varied prey resources, lack of consensus on molecular data (and ongoing debate over its interpretation) and the ability to travel great distances (often resulting in overlapping ranges and even encounters at certain localities) precludes researchers from drawing definitive conclusions about ‘ecotypic’ or species status. However, the recognition of the conservation benefits in assigning designations to groups of animals below species level provides considerable impetus to do so. While the ability to distinguish between conservation units is important for focussing conservation actions and identifying important information gaps, assigning or using

terms that imply certain knowledge of such groups may mask data gaps and give rise to erroneous assumptions about the ecological conditions affecting these groups.

The difficulties in assigning or categorising ecotypic status can be overcome with a clear definition of the sub-unit, and in our case, the ecotype can fairly simply be defined as a sub-unit of the population that has a different ecology to another sub-unit. In the case of the Southern Hemisphere killer whales, by looking at a range of ecological traits we have provided considerable evidence that the ecotypes described in Table 2, and currently in common use in the literature, may not be so clearly delineated, and in fact would be better described as morphotypes. Even so, morphological differences among groups need to be consistent and well quantified to clarify the different appearances of groups of killer whales and gain a measure of variation within groups. By using techniques similar to that employed by Visser & Mäkeläinen (2000) and Durban & Parsons (2006), reliable quantification of morphological characters should be achievable.

While photo-identification has been used successfully with killer whales in both the Northern and Southern Hemispheres (Visser, 2002; Durban & Parsons, 2006; Tosh *et al.*, 2008), the relative paucity of structured photographic identification studies in conjunction with the lack of movement and distributional data mean that there is no broad social organisation assessment of Southern Ocean killer whale populations. The sub-Antarctic social organisation studies are preliminary, but present stimulating results that can augment diet, movement, morphological and genetic studies and potentially provide valuable insight into broader ecological differences. Photo-identification studies are also becoming more common in Antarctic waters (e.g. Pitman *et al.*, 2007; Pitman, 2011), and as they continue, increasing identification of

individuals should allow further insights. Combining these types of studies with molecular studies could facilitate progress towards the definition of meaningful ecotypes. To date, genetic studies, often based on prior assumptions of ecotypic definitiveness of killer whales in the Antarctic region and without social information, have provided provocative, yet inconclusive results. Nevertheless, while recognising that authoritative phylogenetic evidence of differentiation will not in itself be sufficient for ecotypic classification, there is little doubt that future molecular work has an important role to play in the differentiation of killer whale groups in the Southern Ocean.

VII. CONCLUSIONS

(1) There does not appear to be a clear global model for the categorization of killer whales into ecotypes. The ecotypes in the ENP are reasonably well substantiated by social behaviour, diet, morphology and molecular data, but such clear-cut delineations are not possible for other Northern Hemisphere populations or those in the Southern Hemisphere.

(2) Good discriminatory morphological evidence for Antarctic Type C (Pitman & Ensor, 2003) and Antarctic Type D (Pitman *et al.*, 2010) killer whales is sufficient for their classification as different morphotypes. Despite some genetic evidence, the classification of Antarctic Type A killer whales into a separate group is confounded by variable morphological and ecological data. Quantification of these morphological features is required, and the potential for intermediary forms of killer whales (some perhaps yet to be observed) needs to be considered. This is particularly important in light of the absence of distributional data, which in itself should be augmented by photo-identification and satellite-tracking analysis. Inconclusive and disparate

ecological, behavioural and genetic data for the Southern Hemisphere suggest that ecotype classification of any groups of killer whales in the region is premature.

(3) Our intention here is to highlight the complexity of killer whale ecology. Although conservation efforts may be more effective when intra-species groups can be defined as a sub-species or even a new species (Cronin, 2006), premature classification may lead to erroneous assumptions about the status of a species.

(4) Ecotypes are invariably associated with inherent assumptions about the ecological role of a species in an ecosystem. Unless substantiated, such assumptions are not useful and indeed may negatively impact on the broader management and conservation of species (or species sub-units) because the most vulnerable parts of the population are not correctly defined.

(5) In contrast to the definitive ecotype designation of the ENP killer whales, in reality very little conclusive knowledge exists for other killer whale populations and the ecological role they play. As such the ENP model or variations thereof may not be appropriate. Studies should begin from first principles and if these populations turn out to be similarly differentiated (e.g. as in the ENP), this should be independently established.

(6) Only by conducting dedicated sampling over sufficient temporal (relative to killer whale longevity – Olesiuk, Bigg & Ellis, 1990) and relevant spatial scales will a clearer picture of killer whale life history in each region emerge. Photo-identification efforts should form the basis of killer whale studies allowing for accurate correlation of ecological data with individuals whose kin and social organisation are known (Whitehead, 1995). Possibly then will we begin to understand the true ecological role

of this important predator and eventually be in a confident position to classify them according to ecotype convention.

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X. SUPPORTING INFORMATION

Additional supporting information

Fig. S1. Map of *Orcinus orca* harvest (bycatch) data collected by Mikhalev *et al.*, (1981) (based on their Fig. 12). Numbers of animals caught per 10° grid cell are indicated (see boxed legend). Incidental killer whale catch around the South African coast (Best *et al.*, 2010) is shown. The dedicated killer whale catch (N=906) at Prydz Bay, Antarctica (○) (Berzin & Vladimirov, 1983) is also indicated.

Fig. S2. A pod of Type C killer whales (~14 individuals) hunting emperor penguins in McMurdo Sound, Ross Sea.

Fig. S3. A single pod (~25 Type A individuals) observed hunting both elasmobranch fish and seals in waters between the Chatham Islands and the South Island of New Zealand. Note the seal in the jaws of the female in A.

Fig. S1.

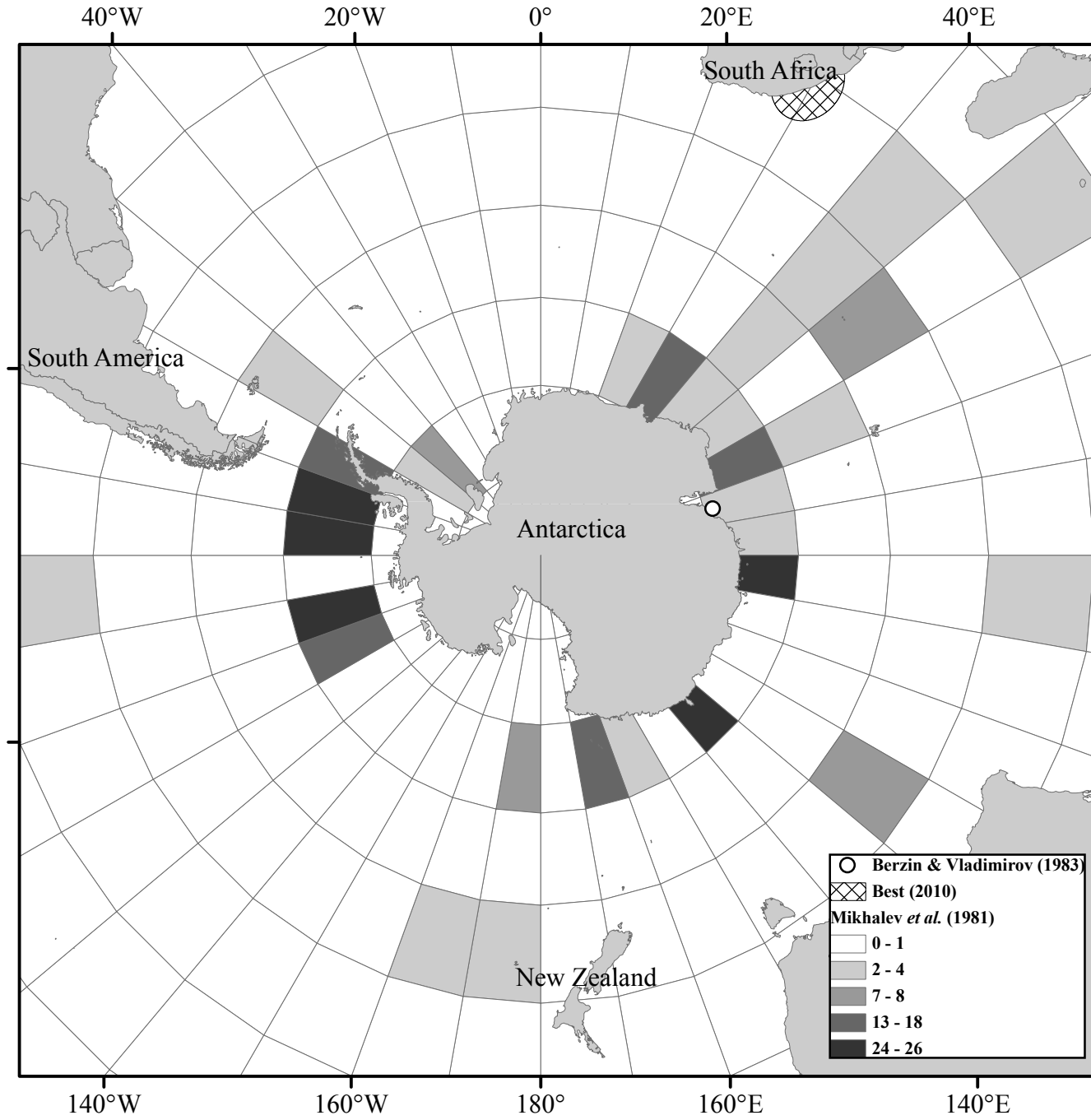


Fig. S2



Fig. S3.

