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Worldwide variation in shape and size of orca (Orcinus orca) saddle patches

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Funding information

dodoland (Orca EUGY); Global Orca Charity; Natural Sciences and Engineering Research Council of Canada; OceanX; Orca Research Trust; Patreon supporters; Suomalainen Konkordia-liitto

Abstract

The global distribution of Orcinus orca (orcas/killer whales) encompasses populations which differ from each other. Saddle patch shapes and sizes were compared for nearly 4,000 individuals, in 48 geographically or ecologically divided groups/populations/ecotypes (GP/E), in four Ocean Basins. Some Antarctic GP/E had five shapes, contrary to previous studies, which found only one shape in these Southern GP/E. Pacific Resident ecotypes had the highest variation in saddle patch shapes. Globally, the most common shape was the 'Smooth' category. Saddle patch sizes were measured using a ratio of the width of the saddle patch compared to the width of the dorsal fin base and averaged within each GP/E. The narrowest saddle patches were observed in New Zealand waters. The widest saddle patches were observed at the Crozet Islands and the Falkland Islands (Islas Malvinas). Globally, we found that the shape and size of saddle patches helped to define various GP/E, reinforcing earlier predictions that this pigmentation may be indicative population divisions. Our findings with describing poorly defined or undescribed ecotypes. Such results may therefore aid assessments by management authorities/policy makers and provide levels of guidance in the creation of conservation or recovery plans.

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KEYWORDS

coloration, ecotype, geographic variation, killer whale, orca, Orcinus orca, pigmentation, saddle patch

1 | INTRODUCTION

Phenotypic and genetic traits of practically all organisms, from plants to mollusks through to mammals, vary over species' geographic ranges (e.g., Crisp & Weston, 1993; Jefferson & Van Waerebeek, 2004; Parsons, 1997). Within the infraorder of Cetacea, many species have a range of features that may be variable across geographic locations, including body size, dorsal fin shape, number of teeth and vertebra (Perrin, 2018), skull morphology (Jefferson & Van Waerebeek, 2004; Yoshida et al., 1995), and pigmentation (Evans & Yablokov, 1978). For the latter variation, examples include spinner dolphins (Stenella longirostris), which exhibit a range of ventral field patterns across the Eastern Pacific (Perrin et al., 1991); striped dolphins (Stenella coeruleoalba), which have pigmentation variations on their flanks and shoulders in the north-western Mediterranean (Rosso et al., 2008); and in humpback whales (Megaptera novaeangliae), there is variation in the ventral fluke pigmentation (Rosenbaum et al., 1995) and lateral flank pigmentation (Kaufman et al., 1987) for various populations throughout their range.

Orcas (*Orcinus orca*, killer whales) have been documented with pigmentation variation which may extend over the whole body (e.g., Evans & Yablokov, 1978; Evans et al., 1982; Visser, 1999, 2002), or be localized to specific features such as the orientation/size and shape of the eye patches (Visser & Mäkeläinen, 2000; Yablokov, 1963) or tail flukes (Visser et al., 2022). Another area of variable pigmentation on orcas is the "saddle patch"—a gray area behind the dorsal fin, which usually develops in the early life stages of an individual (Bigg, 1982). Once formed, typically the pattern does not change (Bigg, 1982), unless there is trauma (e.g., from boat strike as described in Visser et al., 2021). Saddle patches can help to distinguish ecologically divided populations/ecotypes and assist in individual orca identification (e.g., Bigg et al., 1976; Evans & Yablokov, 1978; Martinez & Klinghammer, 1978; Sugarman, 1984).

The saddle patch was recognized as a distinctive feature early in the process of describing the species and then later when developing identification methods for individuals. For example, as early as the 1830s, Regis (1831) described this species as having pigmentation including "the saddle-like mark on each side [of] the back is of a silvery grey." Variation of the saddle patches from illustrations sourced from six authors spanning 1912–1955 were compiled by Yablokov (1963, their fig. 6). By the mid-1970s, saddle patches were described or illustrated at both a population and individual level (e.g., Bigg et al., 1976; Martinez & Klinghammer, 1978), with Evans and Yablokov (1978) illustrating 16 variations in saddle patch shape (their fig. 2N).

As sample sizes increased and the recognition, as well as monitoring, of individuals became more conventional (e.g., Bigg, 1982), authors began publishing in detail about saddle patches. For example, Sugarman (1984) produced a field guide for orca found in the Puget Sound (USA) and southern British Columbia (Canada), which included detailed analysis of saddle patches of more than 100 individuals. His methods involved five "areas" within any given saddle patch (his figs. 3 and 4) as well as five variations of the "upper saddle patch line" creating five "shapes" (his figs. 4–9). Baird and Stacey (1988) used the latter method of Sugarman's five saddle patch shapes in their peer-reviewed paper to compare 471 individuals from populations of orcas in the Pacific Northwest. They also suggested that analyzing saddle patch shapes may be useful when determining orca ecotypes (which are frequently delimited by their geographic distribution and their food type). Baird and Stacey (1988) as well as Ford et al., (1994) noted that although one ecotype, known as Residents, had various amounts of black pigmentation within their gray saddle patches (often termed "open," e.g., see Bigg, 1982; Ford et al., 2000), a sympatric ecotype, known as Transients, did not.

Up to this point, most publications focused on Northern Hemisphere orca populations/ecotypes. However, Evans et al. (1982) described saddle patches found on 109 orcas from the Northern Hemisphere, but also 115 from the Southern Hemisphere. Of these, 99 orcas were photographed in Antarctic waters and an additional 216 taken by

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the Soviet Antarctic whaling fleet from Antarctic waters. Notwithstanding this relatively large sample size, only three saddle patch shapes are illustrated (their figs. 1–14) and only one of these shapes was identified from Antarctic waters. Despite this, they hypothesized that the pigmentation patterns of orcas were geographically variable and that they possibly could be used to characterize different regional populations. In the Southern Hemisphere, saddle patch variations have now been illustrated in various identification catalogs, e.g., Argentina (Punta Norte Orca Research, 2023), Falkland Islands (Islas Malvinas; Sanvito & Galimberti, 2023), and New Zealand (Visser & Cooper, 2020) and detailed descriptions of saddle patches have been compiled for orcas in New Zealand waters (Mäkeläinen, 1999; Visser & Cooper, 2020). Since Regis (1831), and during the development of these various methods/descriptions, five saddle patch shapes have consistently reoccurred in the various descriptions/illustrations (see Material & Methods for more details).

Other than shape, the size of the saddle patch may vary too. However, we could only find generic descriptions such as "Individual whales were identified from a combination of characteristic dorsal fin size and shape, saddle patch size and shape...." (Balcomb & Goebel, 1976) and generalized comparisons of saddle patch sizes between ecotypes, e.g., Ford et al. (1994) stated that the Offshore ecotype "...saddle patch is roughly the same relative size as that of Residents." and the Transient ecotype "...saddle patch [is] typically quite large compared to Residents and Offshores." As such we could find no examples in the peer-reviewed literature where physical measurements and/or comparative ratio measurements of saddle patches have been applied to individual orcas or to geographic populations/ecotypes (hereafter referred to as 'GP/E').

The main goals of our research were to determine (1) if the five saddle patch shapes which are consistently reoccurring in the literature were still applicable, given that we had an increased data set (in both numbers and locations); (2) how differentiated orca saddle patch shapes and sizes are among, as well as between, orca GP/E around the world; and (3) whether there was a cline for average saddle patch size among orca GP/E.

Anecdotally, based on our prior field and literature research (e.g., Mäkeläinen, 1999; Visser, 2000), we speculated that a large proportion of the saddle patches would fall into these reoccurring five shapes. Knowing that the saddle patch shape/size is specific to each individual orca, if the variations observed are driven by social and geographical factors then we could hypothesize that; (1) there would be Ocean-specific saddle patch shapes

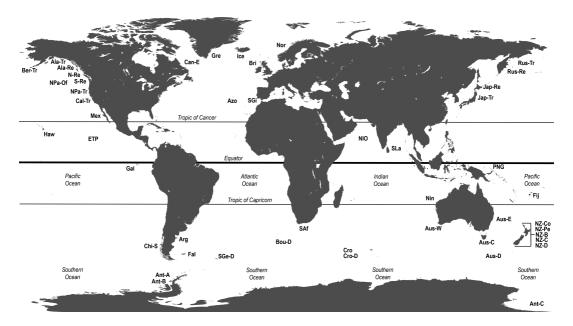


FIGURE 1 Map showing the geographic populations/ecotypes (GP/E) used in this study. See Table 1 for abbreviations.

and (2) saddle patch size would show gradients among Oceans and GP/E. If our hypotheses were well-founded, our overall prediction was that saddle patch pigmentation (i.e., both shape and size) may help us delimit geographic populations and/or ecotypes outside of the already well-described differences for Resident, Transient (also known as Bigg's), and Offshore ecotypes. A closer look at any patterns of shape and/or size would therefore provide non-invasive methods to perhaps identify undescribed ecotypes, more clearly differentiate sympatric ecotypes, or help in describing specific populations. Such results would help with assessments of this species for Management Authorities and policy makers in the creation of recovery or conservation plans.

2 | MATERIAL & METHODS

2.1 | Data sets

We collated photographs of orcas that were taken during a period encompassing 1975–2020 from two sources: (1) preedited data (by other researchers) from peer-reviewed scientific articles and/or orca identification catalogs from the Pacific Ocean (Black et al., 1997; Burdin et al., 2006; Denkinger & Alarcon, 2017; Ford & Ellis, 1999; Ford et al., 1994, 2000, Matkin et al., 1999; Olson & Gerrodette, 2008); North Atlantic Ocean (Mäkeläinen et al., 2014; Mrusczok, 2017); northern Indian Ocean (Gemmell & Northern Indian Ocean Killer Whale Alliance, 2016), and Southern Hemisphere (Donnelly et al., 2018; Häussermann et al., 2013; Sanvito & Galimberti, 2018; Tixier et al., 2009, 2014; Visser & Cooper, 2020; Wellard & Erbe, 2018) and (2) raw data from research centers, field researchers, citizen scientists, NGOs, whale watching companies (see Acknowledgments for details), and from the authors (T.E.C., P.H.M., I.N.V.) own collections and archival images in the Orca Research Trust database. From the latter we also included images collected during a 1955 stranding on the New Zealand coastline. We recognize that there are potentially other GP/E of orcas which we have not included, however, at the time of analysis these were not available to us.

For each photograph we classified the individuals into an age class (adult, nonadult) and sex (male [M], female plus unknown sex [F+]). We acknowledge that subadult male orcas at some stages of their development can appear to be the same size as adult females and therefore, where possible, we used individuals of known sex (e.g., identified as such in a catalog or known by researchers). Where the sex of an adult female-sized individual was not known, but the animal was accompanied in the photograph by a calf/juvenile, we have classified it as female. We only used photographs of juveniles (i.e., those individuals who were approximately 25%–50% the size of an adult female orca), when there were less than eight individuals available for that population of orcas. We did not use photographs of calves as new-born orcas do not have clearly defined saddle patches for the early months of their life.

We edited the photographs to select the best quality for each orca, using both sides where available. Each photograph was assessed for (1) cropping of the saddle patch/ front of the dorsal fin (either by the photographer, or by the angle of the animal as it reentered the water) and if cropped it was not used; (2) focus; and (3) angle to the camera (with 90° the optimum). However, only one side of any given individual was used to eliminate duplicate sampling and potentially skewing the data set, although we recognize that saddle patches exhibit bilateral asymmetry (Mäkeläinen et al., 2013). Preference was arbitrarily given to the left side, using right-side saddle patches when needed (i.e., if no left side photographs were available for those individuals).

Note that due to the opportunistic nature of the data collection and availability of photographs, there were varying numbers of individuals from each area/ecotype and therefore the number of individuals analyzed for each location/ecotype does not necessarily reflect actual population sizes.

2.2 | Ocean, geographic region, and ecotype

The orcas were categorized into four main groups according to their oceanographic distribution: (1) Atlantic Ocean (North and mid), (2) Pacific Ocean (North and mid), (3) Indian Ocean (North and mid), and (4) Southern

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Hemisphere (including Antarctic and subantarctic waters, South Atlantic Ocean, and the South Pacific Ocean). Although the Galápagos Islands straddle the equator, because of their proximity to other Pacific Ocean GP/E (Figure 1) we have included them as part of the Northern Hemisphere for analysis comparing hemispheres. The Southern Hemisphere was designated as an entity based on the theory of "open access" to each Ocean Basin, when considering the circumpolar regions. Within each of those four groups, we separated the individuals into geographic regions based on the localized distribution of the orca and by their ecotype if known. For example, we geographically divided the Pacific Transient/Bigg's orca into six GP/E: Alaska, Bering Sea, California, North Pacific, Russian Far East and Japan. Where there was overlap in different GP/E (i.e., sympatric populations), we relied on the local researchers' designation of an individual into a GP/E. Where an individual was entered into multiple catalogs, or documented by multiple researchers, or in multiple locations, the earliest entry was used to designate it into a geographic region for this research.

A total of 48 GP/E were designated and are listed in Table 1, with their locations illustrated in Figure 1. Details of the number of individuals from each GP/E are reported in Tables 1 and S1.

2.3 | Shape and size of saddle patches

We categorized each of the saddle patches into a shape based on the five variations proposed by Sugarman (1984) and used by Baird and Stacey (1988), i.e., "Smooth," "Bump," "Horizontal notch," "Vertical notch," and "Hook" (Figure 2a-e), collectively referred to herein as "SBS-5." We added a sixth variation we termed "Other" (Figure 2f), collectively referred to herein as "SBS-5+1." This Other category included individuals where the saddle patch was (1) not present, (2) could not be clearly discerned, (3) opaque, or (4) not one of the SBS-5 categories, such as the "Arabesque" shape described by Sasaki et al. (2015). To compare the degree of variation of saddle patch shapes, we created two clusters of complexity: Low complexity = Smooth + Bump (these saddle patches are closed in their shape) and the High complexity = Horizontal notch + Vertical notch + Hook (these saddle patches are open in their shape; Table S2). We did not include Other in this analysis due to the indeterminant shape and/or lack of saddle patch for several of the individuals in this category. To characterize the diversity of saddle patch shapes within each GP/E, we used the Simpson diversity index that estimates the probability of two individuals, taken randomly, belonging to the same shape. This index then allowed us to compare the diversity of each GP/E in relation to the other GP/E.

To categorize and compare the size of the saddle patches, we developed a ratio calculation of saddle patch width (at widest) compared to the dorsal fin width (widest at the base) (Figure 3a). This allowed for scaling of the animal while maintaining the proportional integrity of the saddle patch. When calculating the ratio size of the saddle patches, we only used images which were perpendicular to the camera to remove any potential distortion biases. We specified the ratio sizes into categories of "narrow" (<0.50), "medium" (0.50–0.70), and "wide" (>0.70; Figure 3b-d). We compared saddle patch size ratios between all individuals as well as between GP/E, where an average of the GP/E was calculated. We then compared the size ratio between Ocean Basins and between sexes (see details under Data analysis).

2.4 | Data analysis

Comparisons of saddle patch shape abundance of the six categories (SBS-5+1), and within or between GP/E, were done using nonparametric permutational multivariate analysis of variance (PERMANOVA with 9,999 permutations [Anderson et al., 2008], with Euclidian distance matrices). Data were standardized by the total in each GP/E prior to analysis. This allowed comparisons of the proportion (percent) between each saddle patch shape category, regardless of the total number of individuals. We tested the dispersion (multivariate variance) of data using PERMDISP for each of the categories (Anderson et al., 2008). The differences in saddle patch shape abundance of

TABLE 1 List of geographic populations/ecotypes (GP/E) names, abbreviation codes and number of individual orcas assessed in each. Ocean Basin categories: Atlantic Ocean = ATL, Indian Ocean = IO, Pacific Ocean = PAC and Southern Hemisphere = SH. Number (#) of photographs analyzed for shape and size ratio are given.

Ocean	GP/E	Code	# of photos, shape	# of photos, ratio
ATL	Azores Islands	Azo	59	54
ATL	British Isles	Bri	86	72
ATL	Canadian Arctic Atlantic	Can-E	18	16
ATL	Denmark Greenland	Gre	14	13
ATL	Iceland	Ice	287	258
ATL	Norway	Nor	551	426
ATL	Strait of Gibraltar (Iberian)	SGi	36	31
Ю	Northern Indian Ocean	NIO	13	5
Ю	Sri Lanka	SLa	28	22
PAC	Eastern Tropical Pacific	ETP	189	69
PAC	Galápagos Islands	Gal	52	19
PAC	Japan Residents	Jap-Re	136	132
PAC	Japan Transients	Jap-Tr	57	57
PAC	Mexico Pacific	Mex	44	31
PAC	North Pacific Offshores	NPa-Of	33	33
PAC	North Pacific Transients	NPa-Tr	176	133
PAC	Northern Residents	N-Re	257	214
PAC	Russian Far East Transients	Rus-Tr	34	25
PAC	Russia Kamchatka Residents	Rus-Re	141	90
PAC	Southern Residents	S-Re	125	87
PAC	USA Alaskan Transients	Ala-Tr	94	35
PAC	USA Bering Sea Transients	Ber-Tr	26	19
PAC	USA Californian Transients	Cal-Tr	106	91
PAC	USA Hawaiʻi	Haw	6	5
PAC	USA Southern Alaskan Residents	Ala-Re	359	323
SH	Antarctic Type A	Ant-A	44	39
SH	Antarctic Type B	Ant-B	26	31
SH	Antarctic Type B in New Zealand	NZ-B	9	8
SH	Antarctic Type C	Ant-C	201	178
SH	Antarctic Type C in Australia	Aus-C	14	14
SH	Antarctic Type C in New Zealand	NZ-C	67	48
SH	Argentina Punta Norte	Arg	31	30
SH	Australia East	Aus-E	65	59
SH	Australia Ningaloo	Nin	21	18
SH	Australia West	Aus-W	94	77
SH	Chilean Patagonia	Chi-S	41	22
SH	Crozet Islands	Cro	93	78
SH	Falkland Islands (Islas Malvinas)	Fal	37	29
SH	Fiji, Republic of	Fij	5	_

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TABLE 1 (Continued)

Ocean	GP/E	Code	# of photos, shape	# of photos, ratio
SH	New Zealand Coastal	NZ-Co	103	59
SH	New Zealand Pelagic	NZ-Pe	36	33
SH	Papua New Guinea	PNG	10	6
SH	South Africa	SAf	20	19
SH	Sub-Antarctic Type D in Australia	Aus-D	7	5
SH	Sub-Antarctic Type D at Bouvet Island	Bou-D	13	11
SH	Sub-Antarctic Type D at Crozet Islands	Cro-D	32	32
SH	Sub-Antarctic Type D in New Zealand	NZ-D	5	5
SH	Sub-Antarctic Type D in South Georgia	SGe-D	8	5
	Total number of individuals, globally		3,909	3,066

the six categories of each GP/E were visualized using nonmetric multidimensional scaling plots (nMDS). We evaluated the percentage contribution of each of the six categories to the observed Euclidian distances among categories using a similarity percentage analysis (SIMPER; Clarke et al., 2014). This latter method helps to identify more precisely which shape category is the most responsible for the differences between tested categories (e.g., Ocean Basin, GP/E).

We used similar nonparametric permutational analysis of variance to compare averages of saddle patch size ratio between Ocean Basins and between sex (M and F+). Analyses and ordinations plots were done using PRIMER+PERMANOVA v.7 (Anderson et al., 2008; Clarke et al., 2014). A significance level of $\alpha=0.05$ was used for all statistical tests. For ratios, comparison across GP/E were plotted using 95% confidence intervals to identify potential average differences.

3 | RESULTS

3.1 | Saddle patch shape

We classified saddle patch shape for 3,909 individuals (Table 1), with (n = 3,428) left saddle patches and (n = 481) right saddle patches. The orcas were distributed in 48 GP/E. There were 25 GP/E in the Northern Hemisphere (Figure 1) distributed as follows; Atlantic Ocean (n = 7), Indian Ocean (n = 2), and Pacific Ocean (n = 16), with a subtotal of 2,927 orcas (Table S1). There were 23 GP/E in the Southern Hemisphere (Figure 1), which were all considered as one Ocean Basin (see Material & Methods for details), with a subtotal of 982 orcas (Table S1).

Only the Pacific Ocean Basin had examples of GP/E that had SBS-5 + 1 saddle patch shapes (n = 2), i.e., Southern Residents and Japan Residents (Figures 4 and 5). SBS-5 saddle patch shapes were found in both Hemispheres (Figures 4 and 5) and in the Pacific, Atlantic and Southern Ocean Basins. The number of GP/E which exhibited all five SBS-5 saddle patch shapes was highest in the Pacific Ocean (n = 7), compared to any other ocean. Only two GP/E; the Antarctic Type A in Antarctic waters and the Antarctic Type C in New Zealand waters exhibited all five SBS-5 saddle patch shapes in the Southern Hemisphere (Figure 4). The number of GP/E which had three and four saddle patch shapes was similar in both the Northern (three shapes n = 6; four shapes n = 3) and Southern (three shapes n = 7; four shapes n = 3) Hemispheres (Figure 4).

Globally, the SBS-5 saddle patch shapes accounted for 97.6%, i.e., the remaining 2.4% was classified as Other. Of these combined SBS-5+1 saddle patch shapes, the most frequent in the global data set was the Smooth (74.9%), followed by Bump (10.4%), Horizontal notch (6.2%), Vertical notch (3.7%), Hook (2.5%), and Other (2.4%) (Figure 4). Orcas without saddle patches, or with saddle patches that were barely discernible, were only found north of 20° S.

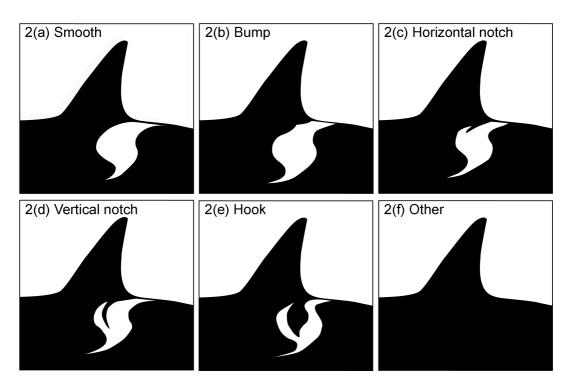


FIGURE 2 Shape of saddle patches: Saddle patches were categorized into six shape variations 2(a–f), collectively referred to as SBS-5+1 (after Sugarman (1984) and Baird & Stacey (1988)); where Other included if the saddle patch was (1) not present, (2) could not be clearly discerned, (3) opaque, or (4) not one of the SBS-5 categories. (Drawings P. H. Mäkeläinen & S. Remes, modified from Sugarman, 1984).

Out of the 48 GP/E, eight (Antarctic Type B in New Zealand, Australia Ningaloo, USA Bering Strait Transients, USA Hawai'i, Japan Transients, Sub-Antarctic Type D at Bouvet, Sub-Antarctic Type D in Australia and Sub-Antarctic Type D in New Zealand) had only one saddle patch shape and all those were Smooth (Figure 4). Although an additional three GP/E (Galápagos Islands, northern Indian Ocean, Papua New Guinea) had only Smooth shape saddles, they also had individuals within their group where the saddle patch areas were not visible (i.e., these individuals would be classified as Other). In contrast, nine GP/E (Antarctic Type A, Antarctic Type C, Iceland, Japan Residents, Russia Kamchatka Residents, Northern Residents, Norway, Southern Residents and USA South Alaskan Residents) had all five SBS-5 saddle patch shapes. The remaining 30 GP/E all had two or more saddle patch shapes (Figure 4). All saddle patches in the Republic of Fiji GP/E belonged to the Other category as there were either no saddle patch shapes or they were indefinable (Visser et al., in press). The Simpson diversity index (which equals zero if only one saddle patch shape is present in a given GP/E) was zero for nine of our GP/E and the highest for the Southern Residents and the Japan Residents (Table S1).

Although visually there does appear to be a weak global pattern of the distribution of saddle patch shapes, e.g., there seems to be a cluster of Southern Hemisphere datapoints in Figure 5(a), when zoomed in (Figure 5b) this is no longer apparent. Rather, the distribution of the SBS-5+1 saddle patch shapes within each GP/E was not significantly different among the four Ocean Basins (pseudo- $F_{3,44} = 1.15$, p = .2808; Figure 5a-d). Yet in contrast, the five Residents and six Transient groups (all found within the Pacific Ocean) showed significant differences between the two ecotypes (pseudo- $F_{1,9} = 39.2$, p = .0019; Figure 5e) in saddle patch shapes. Moreover, the five Residents GP/E showed more variation within these GP/E than the six Transients GP/E (average \pm SE: 21.8 \pm 4.3 and 5.7 \pm 0.8, respectively; t = 4.08, p = .0026; Figure 5e).

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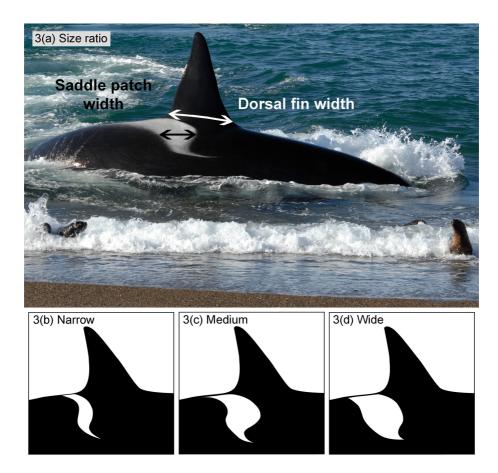


FIGURE 3 Size of saddle patches. (a) Ratio of saddle patch width (black double-headed arrow) to dorsal fin width (white double-headed arrow). (b) Saddle patches were grouped into three sizes: narrow (ratio <0.50), medium (0.50–0.70), and wide (>0.70). (Photograph of an adult male orca at Punta Norte, Argentina, I. N. Visser. Drawings P. H. Mäkeläinen & S. Remes).

Based on the potential for greater mobility within the Southern Hemisphere oceans due to their circumpolar nature, one would expect for example that the three geographically distinct Antarctic Type C GP/E (Figure 1), would be clustered together when plotted. However, we found no clearly discernible patterns as the Antarctic Type C documented in Antarctic waters was positioned in the plot near several other GP/E and was distant from Antarctic Type C in Australia and Antarctic Type C in New Zealand (Figure 5f).

When examining the complexity of the saddle patches for Residents, we observed 84% Low complexity in the Northern Resident GP/E compared to only 26% in the Southern Residents (Table S2). Further examination of the GP/E in the Pacific Ocean illustrated that the Japan Transients and the Bering Sea Transients each had 100% Low complexity (Table S2) while other GP/E within the Transients, also from the Pacific Ocean have few individuals (3% to 4%) with High complexity (Table S2). In the Southern Hemisphere, there were six Antarctic GP/E which had 100% Low complexity of saddle patches (Table S2), however, Antarctic Type C in New Zealand reached 34% of High complexity (Table S2).

3.2 | Saddle patch size ratios

We assessed 3,066 individuals for saddle patch size ratio (Table 1), which were in 47 GP/E (we excluded the Fijian orcas from the size analysis as no animal from this population had a saddle patch that could be measured). When

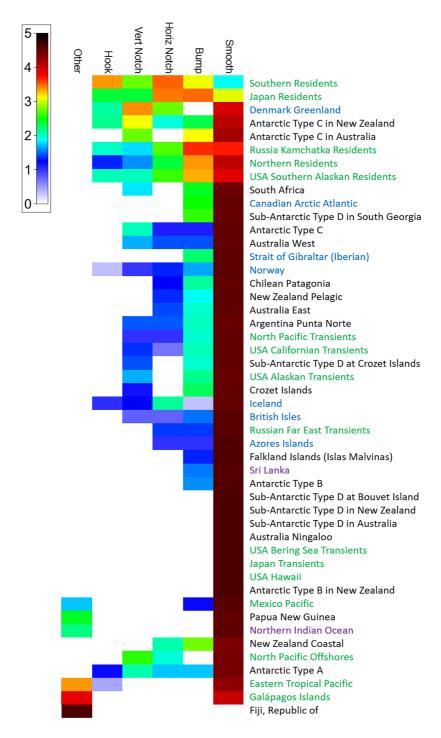


FIGURE 4 Percentage occurrence (log scale, standardized by total occurrence) of saddle patch shape in each geographic populations/ecotypes (GP/E) ordered by a cluster analysis (group average cluster mode). The Ocean Basins are indicated by the color of the GP/E names, with those from the Atlantic Ocean in blue, the Indian Ocean in purple, the Pacific Ocean in green and the Southern Hemisphere in black. See Figure 2 for saddle patch shapes. The original five categories proposed by Sugarman (1984) accounted for 97.6% of the saddle patches, with all the remaining (including no saddle patches) falling into our Other category.

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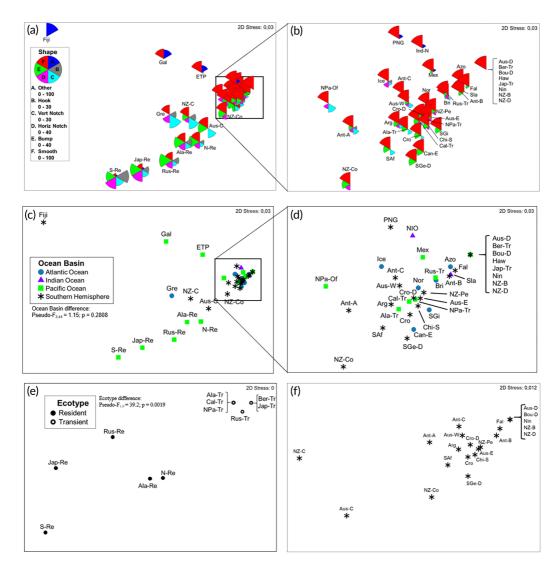
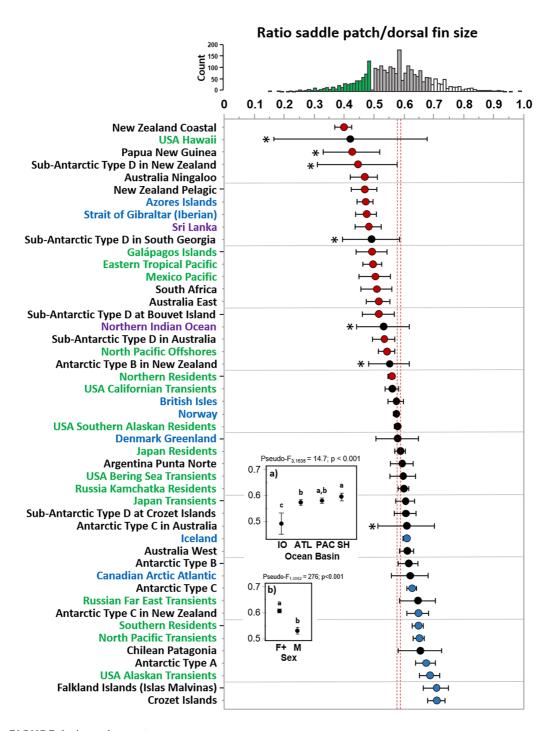


FIGURE 5 Nonmetric multidimensional scaling plots showing the difference in saddle patch abundance of each shape within the six categories (SBS-5+1) and within or between geographic populations/ecotypes (GP/E) (See Table 1 for abbreviations and Figure 2 for saddle patch shapes). Multiple bubble plots showing proportion of pattern in each shape (a) with inset (b) showing the expanded tight cluster. The same distribution, by Ocean Basin, is illustrated in (c) with inset (d) showing the expanded tight cluster. Plots for Pacific Resident and Transient ecotypes are shown in (e) and Southern Hemisphere GP/E in (f).

comparing individual saddle patch ratios to the global data set, the narrowest ratio was found on a male from the NZ Coastal ecotype, with the widest on a female from the Crozet Islands, i.e., both were in the Southern Hemisphere. There were 1,420 individuals who had saddle patches that were equal to or narrower than the global average (0.57, indicated by the red double dotted line in Figure 6) and 1,648 that were wider (Figure 6).

The most common saddle patch size ratio was narrow (65.8%), while 20% and 14.2% were medium and wide, respectively (Table 2). Globally, narrow ratio sizes were found most frequently (44.4%) on orcas from the Indian Ocean, while medium ratio sizes were found most frequently (71%) on orcas from the Atlantic Ocean and wide ratio sizes were found most frequently (21.2%) on orcas in the Southern Hemisphere (Table 2). When using 95% confidence intervals, 17 GP/E (indicated by red point averages in Figure 6) were below the global average size ratio

and nine GP/E (indicated by blue point averages in Figure 6) were above the global average size ratio. An additional seven (indicated by asterisks in Figure 6) had small sample sizes (n < 8) and had larger interval brackets. Those GP/E where the confidence interval did not bracket each other can be considered as different (at a significance level of α close to 0.05). The narrowest saddle patches were observed in New Zealand, Hawai'i, and Papua New Guinea



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Ocean Basin	Narrow	Medium	Wide
Atlantic Ocean	19.5%	71.0%	9.4%
Indian Ocean	44.4%	55.6%	0.0%
Pacific Ocean	19.2%	67.4%	13.4%
Southern Hemisphere	21.0%	57.8%	21.2%
Subtotals	65.8%	20.0%	14.2%

TABLE 2 Average percentage of narrow, medium and wide ratio category in each Ocean Basin.

(Figure 6) with the latter two having small sample sizes. The widest saddle patches were observed at the Crozet Islands and the Falkland Islands (Islas Malvinas; Figure 6).

We found significant variation in saddle patch size ratios (pseudo- $F_{3,1,535} = 14.7$, p < .001) among the four Ocean Basins. The Southern hemisphere had the highest ratios and the Indian Ocean the lowest (inset graph, Figure 6a). The Atlantic Ocean and Southern Hemisphere showed significant differences, but we failed to find significant differences between the Pacific Ocean and either the Atlantic Ocean or Southern Hemisphere Ocean Basins. The F+ group showed significantly (pseudo- $F_{1,3,062} = 276$, p < .001) higher ratios than the male group (inset graph, Figure 6b). We observed the latter trend within all Ocean Basins except in the Indian Ocean where the data set was limited.

4 | DISCUSSION

Using what we believe to currently be the largest data set of orca saddle patches on a global scale (in both numbers and locations), our observations confirmed that the vast majority of these saddle patches could be classified into the SBS-5 model, i.e., the five shapes proposed by Sugarman (1984) and investigated further by Baird and Stacey (1988), despite our data set being more than eight-fold the size of the latest study. Therefore, our hypothesis that the SBS-5 classifications were still applicable and relevant contemporaneously was supported. However, as five saddle patch shapes were found in all but one Ocean Basin, we were not able to support our hypothesis that there would be Ocean-specific saddle patch shapes. We recognize that for some of the GP/E the data sets were small, and this may have influenced the outcomes or created biases. Clearly, increased data from these populations would be welcome and we encourage researchers from those areas to create publicly available photo-identification catalogs which may help address the paucity of data.

Although oceans are separated overall by landmasses, orcas could pass from one to another (primarily via the Southern Ocean) and as such rapid global radiation of the species and high mobility with interoceanic and interhemispheric movement has been suggested (Morin et al., 2015). Notwithstanding the wide distribution and differentiation of orca ecotypes, the genetic diversity and differentiation of the species on a global level is relatively low (Hoelzel et al., 2002; Morin et al., 2010). It could be speculated that the low genetic variability of orcas on a

FIGURE 6 Average (\pm 95%CI) ratio of saddle patch width to dorsal fin width for each geographic population/ ecotype (GP/E). The double red dotted bracket line indicates the \pm 95%CI of the global average. GP/E with red or blue point average show ratio values below and above (respectively) the overall global average. Inset graphs: (a) the average ratio size among Ocean Basins, where different letters above average show significant differences (p < .05). Similarly, inset graph (b) illustrates the average ratio between sexes (M and F+). Points marked with asterisks, have a small sample size ($n \le 8$). The count distribution is shown at the top of the figure; categories are narrow (<0.50, green bars) medium (0.50–0.70, gray bars), and wide (>0.70, white bars). The Ocean Basins are indicated by color, with the GP/E from the Atlantic Ocean in blue, the Indian Ocean in purple, the Pacific Ocean in green and the Southern Hemisphere in black.

global scale may partly explain the Smooth saddle patch shape being documented in 47 of the 48 orca GP/E examined herein. And, although the global genetic diversity is low, the genetic differences between North Pacific GP/E are clear (Barrett-Lennard, 2000; Parsons et al., 2013) and similarly our study demonstrated that the saddle patch shape on orcas varied between the Pacific ecotypes more than other GP/E around the world. Furthermore, the genetic diversity of the Pacific Transients/Bigg's orca is known to be significantly greater than the genetic diversity of the Residents (Barrett-Lennard, 2000; Morin et al., 2010) and genetically the most divergent of all orca GP/E (Morin et al., 2010). Yet, we found the variation of saddle patch shape was almost four times lower in the Transient/ Bigg's than in the Residents (Figure 5e). It is not clear what might be driving such a contradiction, but it may warrant further investigation. Conversely, the Southern Residents and Japan Residents showed the greatest diversity in saddle patch shapes of the 47 GP/E (see Simpson diversity index values in Table S1).

We found most of the Southern Hemisphere GP/E had predominantly Low complexity of saddle patches (95%–100%). Evans et al., (1982) described only one saddle patch shape (equivalent to the Sugarman, 1984, "Smooth") in the Southern Hemisphere. In contrast to Evans et al. (1982), we found all SBS-5 (but not Other) in the Antarctic ecotypes, in both Antarctic and New Zealand waters and three saddle patch shapes in the NZ Coastal ecotype.

Building on the methodologies of previous authors, who categorized orca saddle patches by shape, we developed a ratio measurement to be able to assess saddle patch size and applied that across a global data set for individuals and as GP/E averages. Interestingly, both the narrowest and the widest saddle patches of any individual orca were found within the Southern Hemisphere. However, when the GP/E averages were plotted there was a visible and statistically significant gradient difference from one end of the scale to the other, supporting our second hypothesis that there would be a cline of average saddle patch size between orca GP/E. The difference that we documented between the M and F+ sex groups may be an artefact of the sexually dimorphic dorsal fins of the males. However, investigating that potential artefact was outside the scope of this current study.

Morin et al. (2015) suggested that long-range dispersing orcas colonized and established new populations and, in some cases mixed, with existing lineages for example in the Eastern Tropical Pacific. Existence of narrow saddle patches in Pacific GP/E could be explained by such proposed migrations and common ancestors. In comparison, we found that the NZ Coastal orcas had, on average, the narrowest saddle patches suggesting that if pigmentation is indeed linked to genetics, this population of orca may be more reproductively isolated than others.

Although we recognize that sympatric GP/E of orcas with similar saddle patch shapes and/or size ratios may not be easily discernible using saddle patch pigmentation alone, our findings support the prediction that at least for geographically separated populations/ecotypes saddle patch pigmentation may help us delimit those. These noninvasive methods would therefore be helpful describing specific populations, such as the Punta Norte ecotype, which are arguably one of the most publicly recognizable orca populations due to their unique behavior of intentionally stranding to hunt pinnipeds on the beaches of Argentina. Despite this, they remain in a state of uncertainty in terms of official recognition, as many international scientists as well as local management authorities, have yet to formally acknowledge this population (Copello et al., 2021). Naturally, the methods described herein would be of value in identifying as yet undescribed ecotypes.

Given the local and global crisis for orcas at individual and population levels (Desforges et al., 2018; Visser et al., 2021), any methods which can be added to the toolbox to help with assessments for management authorities and policy makers, as well as aid in the creation of recovery or conservation plans, would be of value. We believe the findings presented here, which illustrate that at least 48 geographic groups/ecotypes of orcas can be distinguished based on saddle patch shape and size, along with the new method for measuring saddle patch size ratios, contribute significantly to that framework.

ACKNOWLEDGMENTS

We would like to thank all our colleagues for their assistance through providing access to their photographic data sets; Robin Baird, Ken Balcomb and the Center for Whale Research team, Lance Barrett-Lennard, Nancy Black, Alexander Burdin, Jorge Cazenave, Juan M. Copello and the Punta Norte Orca Research team, David Cothran, Graeme Ellis, Ruth Esteban, Chris and Monique Fallows, Steve Ferguson, Andy Foote, John Ford, Christophe Guinet,

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Sanna Kuningas, Craig Matkin, Julius Nielsen, Filipa Samarra, Hal Sato, Alisa Schulman-Janiger, Tatiana Shulezhko, Tiu Similä, and Renaud de Stephanis.

We also acknowledge and thank those researchers who have published identification catalogs, as well as those who included photographs of individual orcas in their publications. Hannu Pietiäinen provided useful advice for the early studies by PHM on saddle patches. We thank the two anonymous reviewers and Dr Felix Marx for their helpful comments, which improved the manuscript. S. Remes kindly assisted with the drawings for Figure 3 and Scout Trom helped with editing. PHM received a travel grant from Suomalainen Konkordia-liitto to collect materials for her PhD studies from which a proportion of this data set was collated. This work was also partially supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grants (RGPIN-2017-05525) to MC. INV & TEC acknowledge the support of the Orca Research Trust for access to the New Zealand, Southern Hemisphere and South Pacific photographic data sets. The authors and Orca Research Trust acknowledges the Māori as tangata whenua and Treaty of Waitangi partners in Aotearoa New Zealand. The Orca Research Trust also thanks dodoland (Orca EUGY) and Uber Ultrafast Broadband and Yamaha Motors for their sponsorship of the work conducted by the Trust. INV also thanks her Patreon supporters for their financial assistance during the preparation of this publication and she extends a special thanks to OceanX for their philanthropic support of her work and that of the Orca Research Trust, through the Global Orca Charity. The authors have no conflict of interest.

AUTHOR CONTRIBUTIONS

Pirjo Helena Mäkeläinen: Conceptualization; data curation; formal analysis; investigation; methodology; resources; visualization; writing – original draft; writing – review and editing. **Ingrid Natasha Visser:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; validation; visualization; writing – original draft; writing – review and editing. **Tracy E Cooper:** Data curation; investigation; methodology; validation; writing – review and editing. **Mathieu Cusson:** Data curation; formal analysis; funding acquisition; methodology; validation; visualization; writing – original draft; writing – review and editing.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Mäkeläinen, P. H., Visser, I. N., Cooper, T. E., & Cusson, M. (2024). Worldwide variation in shape and size of orca (*Orcinus orca*) saddle patches. *Marine Mammal Science*, e13171. https://doi.org/10.1111/mms.13171

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Supplementary materials

Table S1. Detail of number of individuals (#) by shapes; 'Smooth' (S), 'Bump' (B), 'Horizontal notch' (HN), 'Vertical notch' (VN), 'Hook' (H) and 'Other' (O) in each geographic group/ecotype (listed by Ocean Basin, see Table 1 for details). The results for the Simpson Diversity index values from the distribution of the saddle patch shape within each geographical group/ecotype are listed (where zero = no diversity) and their magnitudes are illustrated with blue bars on the right side of the table.

Geographic region/ecotype	#	S	В	HN	VN	Н	О	Simpson diversity
group names	70		1					·
Azores Islands	59	57	1	1	-			0,067
British Isles	86	81	3	1	1			0,113
Canadian Arctic Atlantic	18	16	2	2	4	1		0,209
Denmark Greenland	14	7		2	4	1		0,692
Iceland	287	253	1	21	7	5		0,217
Norway	551	502	23	15	9	2		0,167
Strait of Gibraltar	36	33	3				- 1	0,157
Northern Indian Ocean	13	12	1				1	0,154
Sri Lanka	28	27	1			1		0,071
Eastern Tropical Pacific	189	135				1	53	0,413
Galápagos Islands	52	28	42	41	10	0	24	0,507
Japan Residents	136	27	43	41	12	9	4	0,762
Japan Transients	57	57	1			1		0,000
Mexico Pacific	44	41	1		4		2	0,132
North Pacific Offshores	33	27	11	2	4			0,322
North Pacific Transients	176	159	11	3	3			0,180
Northern Residents	257	144	72 52	24	10	7		0,599
Russia Kamchatka Residents	141	54		19	7	9		0,698
Russian Far East Transients	34	32	1	1	1.77	22		0,116
Southern Residents	125	7	26	40	17	33	2	0,769
USA Alaskan Transients	94	83	7		4			0,215
USA Bering Sea Transients	26	26	7	1	2			0,000
USA Californian Transients	106	95	7	1	3			0,193
USA Hawaii	6	172	02	1.0	22	24		0,000
USA Southern Alaskan Residents	359	173	93	46	23	24		0,678
Antarctic Type A	44 26	36	1	2	3	1		0,329
Antarctic Type B	9	25 9	1					0,077
Antarctic Type B in New Zealand Antarctic Type C	201	180	4	4	13			0,000
	14	9	3	4	2			0,194
Antarctic Type C in Australia	67		6	4	14	5		
Antarctic Type C in New Zealand Argentina Punta Norte	31	38 27	2	1	14	3		0,627 0,243
Australia East	65	59	4	2	1			0,243
Australia Pingaloo	21		4					0,174
Australia Ningaloo Australia West	94	21 84	3	3	1			0,000
Chilean Patagonia	41	37	3	1	4			0,200
Crozet Islands	93	83	8	1	2			0,184
Falkland Islands (Islas Malvinas)	37	36	1					0,198
Fiji, Republic of	5	30	1				5	0,034
New Zealand Coastal	103	81	15	7			<u> </u>	0,359
New Zealand Coastal New Zealand Pelagic	36	33	2	1				0,339
Papua New Guinea	10	9		1			1	0,160
South Africa	20	17	2		1		1	0,200
Sub-Antarctic Type D in Australia	7	7			1			0,279
Sub-Antarctic Type D in Australia Sub-Antarctic Type D at Bouvet Island	13	13						0,000
Sub-Antarctic Type D at Bouvet Island Sub-Antarctic Type D at Crozet Islands	32		2		1			0,000
Sub-Antarctic Type D at Crozet Islands Sub-Antarctic Type D in New Zealand	5	29 5			1			0,179
Sub-Antarctic Type D in New Zealand Sub-Antarctic Type D in South Georgia	8	7	1					0,000

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Table S2. Numbers and percentages of individuals according to the degree of saddle patch complexity in each geographic group/ecotype (listed by Ocean Basin). *Low complexity* includes 'Smooth' and 'Bump' shapes while *High complexity* includes 'Horizontal notch', 'Vertical notch' and 'Hook' shapes. The category 'Other' is not included in this analysis. # = categorised number of individuals.

	SHAPE	5		5 5	4	
	Total #	Low comp	lexity	High complexity		
Geographical group/ecotype		#	%	#	%	
Residents Pacific Ocean						
Japan Residents	132	70	53%	62	47%	
Northern Residents	257	216	84%	41	16%	
Russia Kamchatka Residents	141	106	75%	35	25%	
Southern Residents	124	33	26%	91	73%	
USA Southern Alaska	359	266	74%	93	26%	
Residents						
Total	1020	691	68%	329	32%	
Transients Pacific Ocean						
USA Alaskan Transients	94	90	96%	4	4%	
USA Californian Transients	106	102	96%	4	4%	
Japan Transients	57	57	100%	0	0%	
North Pacific Transients	176	170	97%	6	3%	
Russian Far East Transients	34	33	97%	1	3%	
USA Bering Sea Transients	26	26	100%	0	0%	
Total	493	478	97%	15	3%	
Others Pacific Ocean						
Eastern tropical Pacific	136	135	99%	1	1%	
Galápagos Islands	28	28	100%	0	0%	
Hawaii	6	6	100%	0	0%	
Mexico Pacific	42	42	100%	0	0%	
North Pacific Offshore	33	27	82%	6	18%	
Total	245	238	97%	7	3%	
Atlantic Ocean						
Azores Islands	59	58	98%	1	2%	
British Isles	86	84	98%	2	2%	
Canadian Arctic Atlantic	18	18	100%	0	0%	
Denmark Greenland	14	7	50%	7	50%	
Iceland	287	254	89%	33	12%	
Norway	551	525	95%	26	5%	

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Strait of Gibraltar	36	36	100%	0	0%
Total	1051	982	93%	69	7%
Indian Ocean					
Northern Indian Ocean	12	12	100%	0	0%
Sri Lanka	28	28	100%	0	0%
Total	40	40	100%	0	0%
Southern Hemisphere					
Argentina Punta Norte	31	29	94%	2	6%
Australia East	65	63	97%	2	3%
Australia Ningaloo	21	21	100%	0	0%
Australia West	94	87	93%	7	7%
Chilean Patagonia	41	40	98%	1	2%
Crozet Islands	93	91	98%	2	2%
Falkland Islands (Islas	37	27	100%	0	0%
Malvinas)	3/	37	100%	0	0%
New Zealand Coastal	103	96	93%	7	7%
New Zealand Pelagic	36	35	97%	1	3%
Papua New Guinea	9	9	100%	0	0%
South Africa	20	19	95%	1	5%
Antarctic Type A	44	38	86%	6	14%
Antarctic Type B	26	26	100%	0	0%
Antarctic Type B in NZ	9	9	100%	0	0%
Antarctic Type C	201	184	92%	17	8%
Antarctic Type C in Australia	14	12	86%	2	14%
Antarctic Type C in NZ	67	44	66%	23	34%
Sub-Antarctic Type D in	7	7	100%	0	0%
Australia	/	/	10070	U	070
Sub-Antarctic Type D at	13	13	100%	0	0%
Bouvet Is.	13	13	10070	U	070
Sub-Antarctic Type D at	32	31	97%	1	3%
Crozet	32	31	9/70	1	370
Sub-Antarctic Type D in NZ	5	5	100%	0	0%
Sub-Antarctic Type D in S.	8	8	100%	0	0%
Georgia	o	o	100/0	U	U70
Total	976	904	93%	72	7%