Received: 15 September 2021 | Accepted: 21 January 2023

DOI: 10.1111/mms.13013

ARTICLE

Marine Mammal Science

# Color pattern complexity in dwarf minke whales (*Balaenoptera acutorostrata*) of the northern Great Barrier Reef of Australia

**Marissa J. Hutchings**[1,2] | **Mark Hamann**[1] | **Scott G. Smithers**[1] | **Emily N. Daley**[1,2] | **R. Alastair Birtles**[1,2]

[1]College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

[2]Minke Whale Project, James Cook University, Townsville, Queensland, Australia

**Correspondence**
Marissa J. Hutchings, 1 James Cook Drive, Douglas, Queensland 4814, Australia.
Email: marissa.hutchings@my.jcu.edu.au

## Abstract

Complex color patterning is a characteristic feature of dwarf minke whales (DMWs; *Balaenoptera* acutorostrata) which has been used to photographically identify (photo-ID) individuals and to research an aggregation on Australia's Great Barrier Reef (GBR). DMW color patterns have been described and applied in various studies, but a detailed and systematic analysis of their complexity is yet to be performed. Here, we applied a novel categorization tool to assess the variation, asymmetry, and association of several DMW color pattern elements, subelements, and their character states. Proportions, hierarchical clustering, and multiple correspondence analysis revealed a high level of asymmetric color pattern variation, with white markings dominant and associated on the right of the body. Our results will improve the citizen science driven photo-ID of this little-known cetacean as labor-intensive manual methods transition to more efficient automated approaches. Such advancement will be challenging, yet beneficial for broader research into the poorly understood areas of DMW life history, evolution, genetics, social structure, and feeding. This could also potentially allow investigation into the functional significance of their color patterns.

**KEYWORDS**

*Balaenoptera*, cetacean, color, dwarf minke whale, Great Barrier Reef, pattern, photo-identification, swim-with

## 1 | INTRODUCTION

Following observations of a diminutive and distinctively marked form off South Africa (Best, 1985) and Australia (Arnold et al., 1987), "dwarf" minke whales (DMWs) were proposed by Rice (1998) as a subspecies of the common minke whale (*Balaenoptera acutorostrata*). Although, their taxonomy remains unresolved (Risch et al., 2019), DMWs display several osteological, morphometric, and pigmentation differences to both the common and Antarctic minke whale (*Balaenoptera bonaerensis*; Arnold et al., 1987, 2005). Recent mitochondrial DNA evidence (Ramirez-Flores et al., 2019) has further highlighted genetic divergence within this species complex, but additional morphological and molecular evidence is needed for the DMW to receive formal subspecies designation (IWC, 2001).

DMWs are sporadically sighted throughout the Southern Hemisphere in locations including South America, South Africa, New Zealand, Vanuatu, and New Caledonia (Arnold, 1997). They have also been observed around western and eastern Australia more frequently in recent years (Risch et al., 2019). However, the only known predictable aggregation of DMWs occurs on the northern Great Barrier Reef (GBR) during the austral winter, when hundreds of individuals migrate up the eastern Australian coast from the Subantarctic (Birtles et al., 2015; Ramirez-Flores et al., 2019). Sightings are common between May and September, with 90% occurring in June and July (Birtles et al., 2014). Why this aggregation occurs remains unclear as no feeding, mating, or calving has been observed in the area (Birtles et al., 2002). Based on strong site fidelity, social behavior, and sightings of pre-established cow and calf pairs, it is suggested that these sheltered waters may be an important location for courtship and nursing (Birtles & Mangott, 2011).

DMWs within the GBR are highly inquisitive and willingly interact with vessels and snorkelers, which led to the establishment of a permit-based swim-with-DMW industry at the aggregation site in 1996 (Dunstan et al., 2007). In collaboration with this, the Minke Whale Project (MWP) at James Cook University has harnessed citizen science to investigate the biology and ecology of this little-known cetacean for over 30 years. This research has increased understanding on the interacting population's size (Sobtzick, 2010), demographics (Dunstan et al., 2007), behavior (Mangott, 2010), and movement (Birtles et al., 2015). Most importantly, it provides vital information for the sustainable management and conservation of GBR DMWs (Birtles et al., 2014; Curnock, 2010; Curnock et al., 2013; Valentine et al., 2004). Central to the MWP's work is a long-term photo-identification (photo-ID) study which uses temporally stable color patterning, along with scars and other natural markings, to accurately identify individuals repeatedly over space and time (Birtles et al., 2002).

DMWs are the second smallest and most highly patterned mysticete. Like many other surface foraging marine species, they are counter shaded for predator concealment (Caro et al., 2011; Thayer, 1909). Their lateral coloration is, however, more complex and may be comprised of several dark gray fields descending from the dorsum, a number of white blazes ascending from the ventrum, and a series of light gray patches, saddles, and streaks (Arnold et al., 2005). Each of these components can be defined as a distinct element (e.g., thorax patch) and/or subelement (e.g., anterior margin) of fixed position and hue that varies in character state (e.g., sinuous) depending on the occurrence and distribution of pigment (Figure 1). Therefore, whilst the color patterns of DMWs follow a general template, each individual displays a unique profile much like the spots of giraffes (Lee et al., 2018) or fingerprints of humans (Junaid Mir et al., 2014). Like the fin whale (*Balaenoptera physalus*; Methion & Díaz López, 2019), DMW coloration is consistently asymmetrical whereby markings on the right anterior third of the body are lighter than those on the left (Arnold et al., 2005). This is due to the co-occurrence of several white blazes across a single profile, particularly on the right. Together these sources of variation, asymmetry, and association produce differences both within and between individuals that are proven to persist over time (Birtles et al., 2002).

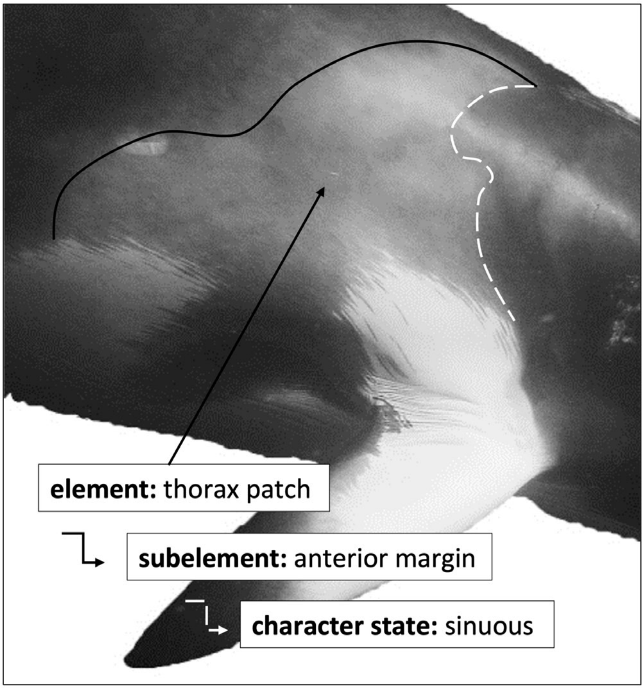

**FIGURE 1** This dwarf minke whale (DMW) has a thorax patch (element) anterior margin (subelement) which is sinuous (character state).

Various attempts have been made to define DMW color patterns due to their importance in photo-ID and broader research (Arnold et al., 2005; Birtles et al., 2001; Hasling, 2003; Sobtzick, 2010; Stephens et al., 2015; Watson, 2011). This has generated a multitude of context-specific terms which have been built upon over time to classify elements, subelements, and character states. However, given that their application has been entirely descriptive thus far, many of these lack definitive criteria. Furthermore, the variation, asymmetry, and association of DMW color patterns has not yet been investigated in a robust manner. With this in mind, Hutchings (2020) developed a suite of standardized descriptors that could be applied with greater certainty and consistency. These were refined through the visual assessment of several hundred individuals and agreement tests between multiple MWP members. In this study, we present the first application of this novel categorization tool in a detailed systematic analysis of DMW color pattern complexity. More specifically, we aimed to quantify the variation, asymmetry, and association of several elements, subelements, and character states.

## 2 | METHODS

Imagery for photo-ID was opportunistically collected by MWP members, passengers, and crew from swim-with-DMW industry vessels. This process involved maintaining a dedicated watch during daylight hours and attempting to photograph all individuals present for each in-water interaction. Trained assessors then manually collated, organized, and analyzed this imagery within hard drive directories, Microsoft Excel spreadsheets, and digital viewers. Photographs and videos were first graded using a five-point system based on image quality and information content so that they could be ordered from most to least useful (Sobtzick, 2010). All available imagery was then visually assessed to assign as many DMWs as possible with a unique, alphanumeric identity (ID). A complete ID was assigned where an individual's left-hand side (LHS) and right-hand side (RHS) were visible and connected in a top side shot. A partial ID was assigned when imagery only existed for one side of an individual's body or if two sides, thought to belong to the same animal, could not be connected by at least three distinguishing features. Multi-shot reference libraries of each ID were then validated by several MWP members to reduce the likelihood of LHS and RHS images being falsely classified as the same, or a different, whale.

A data set of 196 complete IDs and 2,078 images from the 2017 season was compiled for this study. This cohort represented the MWPs most comprehensive within-season photo-ID census to date (Daley, 2019). Partial IDs were deliberately excluded so that analysis could be performed across the entire body. A single, experienced assessor then used a recently developed DMW color pattern categorization tool (Figure S1) to record character state in 12 elements and subelements (Figure 2) of each individual's LHS and RHS. An exception to this was made for the nape streak dorsal portion which, given its anatomical position, was categorized by the same character state across both sides of the body. To ensure all the elements and subelements were equally represented, only individuals for which character states could be observed across the entire body were included in the analysis. This filtering removed 94 individuals, leaving 102 individuals for which full body color pattern profiles were compared.

Hierarchical clustering was performed separately for the LHS and RHS color pattern profiles in RStudio (Appendix S1). Gower's metric (Gower, 1971) was chosen to create the distance (dis)similarity matrices due to its ability to handle categorical variables (Huang, 1998). Divisive clustering (i.e., a top-down approach where all observations begin in one cluster then are split recursively down the hierarchy) was applied here as it is considered most accurate for larger data sets (Everitt, 2011). Optimum cluster number was determined from average silhouette width, a simple and popular validation index independent of assumptions (Batool & Hennig, 2021). Branch height was used as a measure of (dis)similarity and gauge of tree topology to reveal which attributes of the data (i.e., character states) were underlying certain nodes. Mean relative difference in branch height was also calculated to compare this across the LHS and RHS. Cophenetic correlation coefficients were computed both separately and together for these dendrograms. This evaluated how well each clustering result preserved its distance (dis)similarity matrix and how alike the two trees were in terms of branch height (Saraçli et al., 2013). A tanglegram of lowest possible entanglement was produced to display the dendrograms for each side of the body in parallel. This allowed visual comparisons to be made simultaneously across both the LHS and RHS.

Multiple correspondence analysis was carried out on the LHS and RHS color pattern profiles in RStudio as well (Appendix S2). Individual and variable coordinates, derived from chi-squared distances of the raw contingency tables, were mapped independently so that their results could be interpreted in turn. This generated a plot for each upon

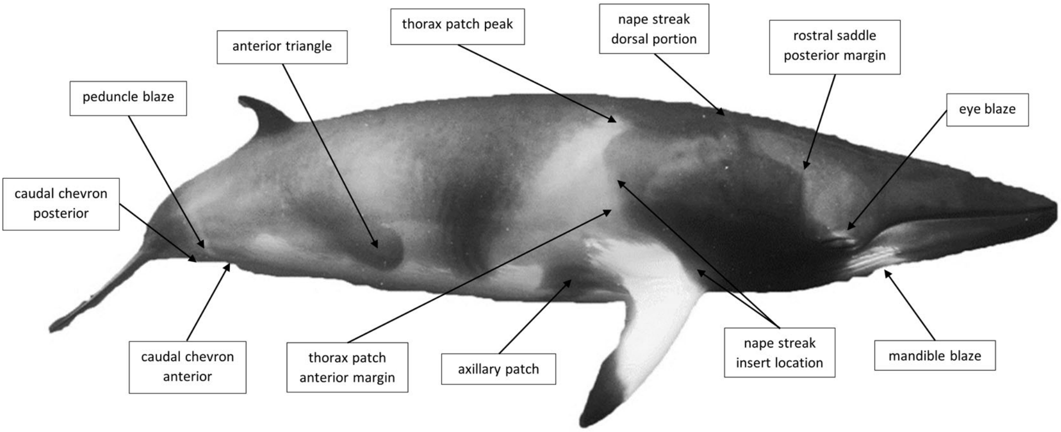

**FIGURE 2** The 12 dwarf minke whale (DMW) color pattern elements and subelements analyzed.

which the distance between points (i.e., individuals or character states) provided a graphic measure of their association (Abdi & Valentin, 2006). Eigenvalues were extracted to identify the proportion of variance retained by the first two dimensions. Axes contribution and squared cosine values were used to assess the definition and quality of representation for individuals and variables along both dimensions (Lê et al., 2008).

## 3 | RESULTS

Character state proportions differed within and between the elements and subelements (Figure 3) as well as across the sides of the body (Figure 4). Some features appeared largely asymmetric (e.g., MB = 94.12%) because they were well expressed on the RHS yet poorly defined on the LHS. For instance, eye and mandible blazes were usually

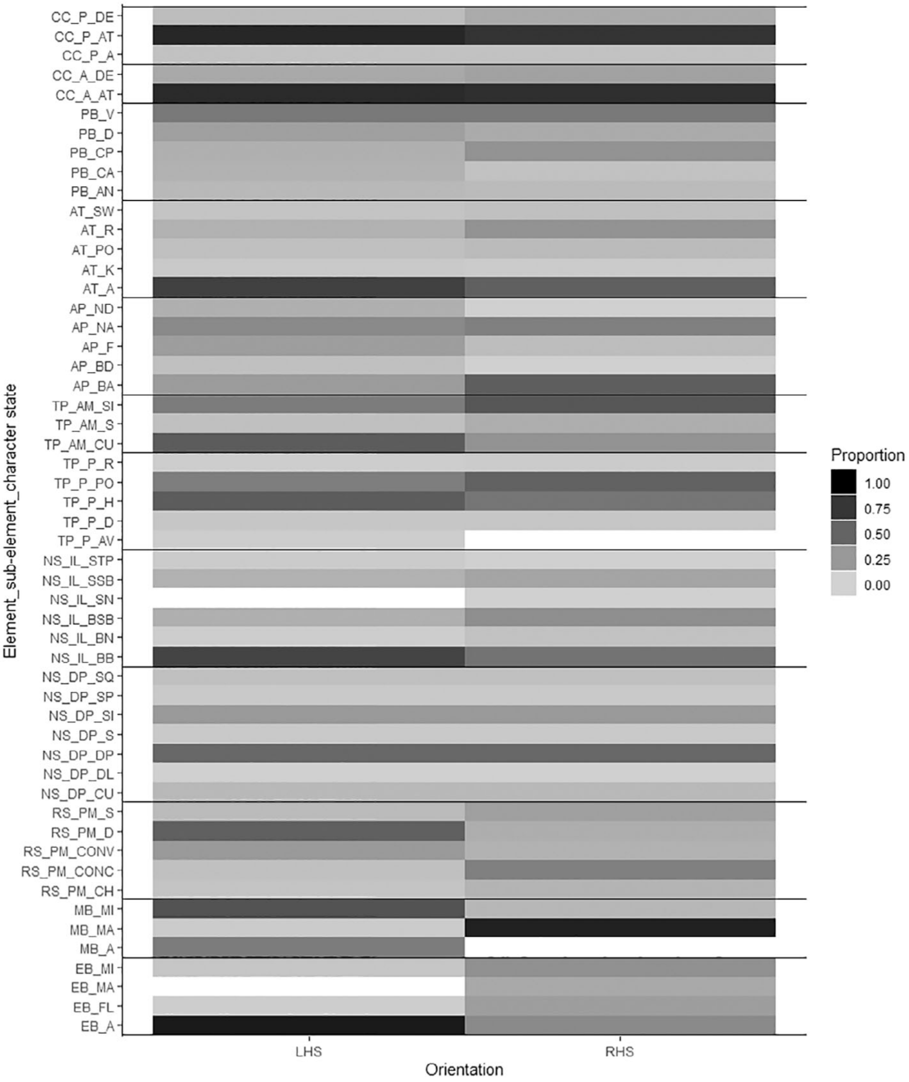

**FIGURE 3** Proportions of character states observed for each element and subelement across both the left-hand side (LHS) and right-hand side (RHS) of the 2017 cohort of dwarf minke whales (DMWs).

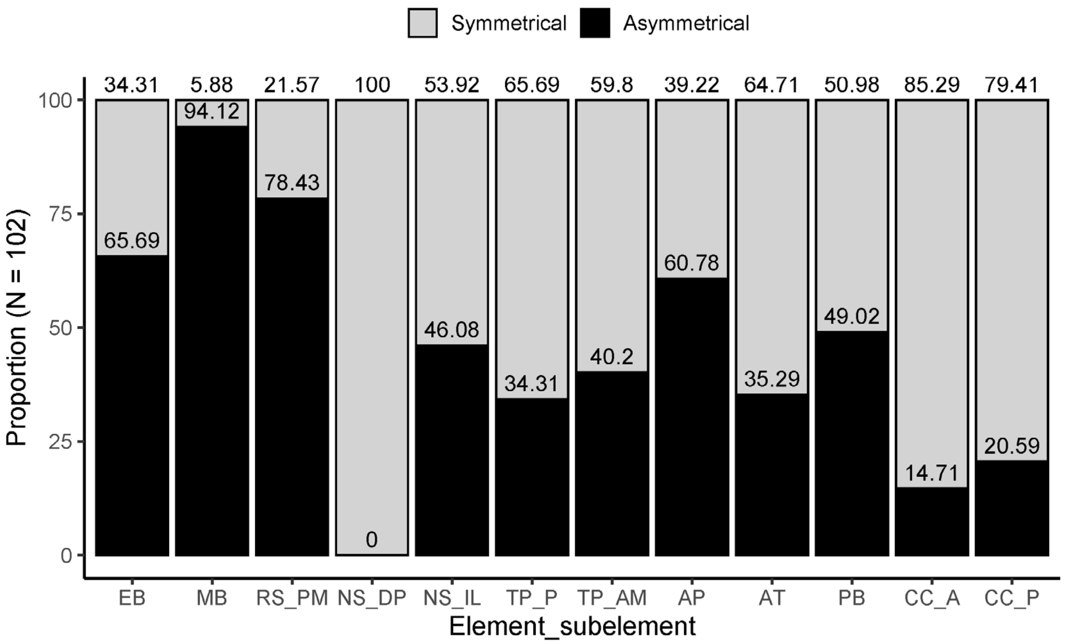

**FIGURE 4** Asymmetry in each element and subelement (see Supplementary Material 1(a-l) for abbreviations) for the 2017 cohort of dwarf minke whales (DMWs).

present on the RHS (e.g., MB_MA = 88.24%) and mostly absent on the LHS (e.g., EB_A = 93.14%). Similarly, the RHS rostral saddle posterior margin was often concave (36.27%), whilst that of the LHS was generally diffuse (51.96%). The axillary patch also appeared quite asymmetric with the RHS most frequently being broadly (52.94%) or narrowly attached (36.27%). In contrast, the most symmetric features (e.g., CC_A = 85.29%) were dominated by just one or two traits across the entire body. For example, the anterior and posterior caudal chevrons were attached on both the LHS (e.g., CC_P = 84.31%) and RHS (e.g., CC_P = 76.47%) for over three quarters of the individuals. Likewise, the thorax patch peak was hooked (e.g., LHS = 53.92%) or pointed (e.g., RHS = 50.98%) with a curved (e.g., LHS = 53.92%) or sinuous (e.g., RHS = 56.86%) anterior margin for most of the observed cohort. The anterior triangle also appeared relatively symmetrical given it was most frequently absent on both the LHS (68.63%) and RHS (51.96%). Other features, such as the nape streak insert location and peduncle blaze, were symmetric on occasion (e.g., PB = 50.98%). These elements displayed multiple character states, with more evenly distributed proportions, across each side of the body. The nape streak dorsal portion was typically double peak (48.04%) or sinuous (24.51%).

LHS and RHS color pattern profiles were each sorted into two hierarchical clusters (Figure 5). Across both sides of the body, these clusters diverged at branch heights of 0.92 and 0.83, respectively. For the LHS, cluster one contained 84 members and cluster two contained 18. Individuals in the first cluster were grouped by having an attached anterior caudal chevron, whereas those in the second cluster displayed the detached form of this feature. Beyond this, one pair (#27 and #95) shared the same LHS color pattern profile and another eight pairs differed by a single character state (e.g., #21 and #58). The former terminated on the same node and the latter diverged at a branch height of 0.08. For the RHS, cluster one contained 78 members and cluster two contained 24. Individuals were grouped depending on their combination of traits for the nape streak insert location, thorax patch peak and axillary patch. No pairs shared the same RHS color pattern profile and only three pairs differed by a single character state (e.g., #95 and #58). These also diverged at a branch height of 0.08. Across both sides of the body, the two individuals (#95 and #58) with the most similar color pattern profiles differed by three character states on the LHS and one on the RHS. The cophenetic correlation coefficient for the LHS was 0.53 and for the RHS was 0.50. Between these two

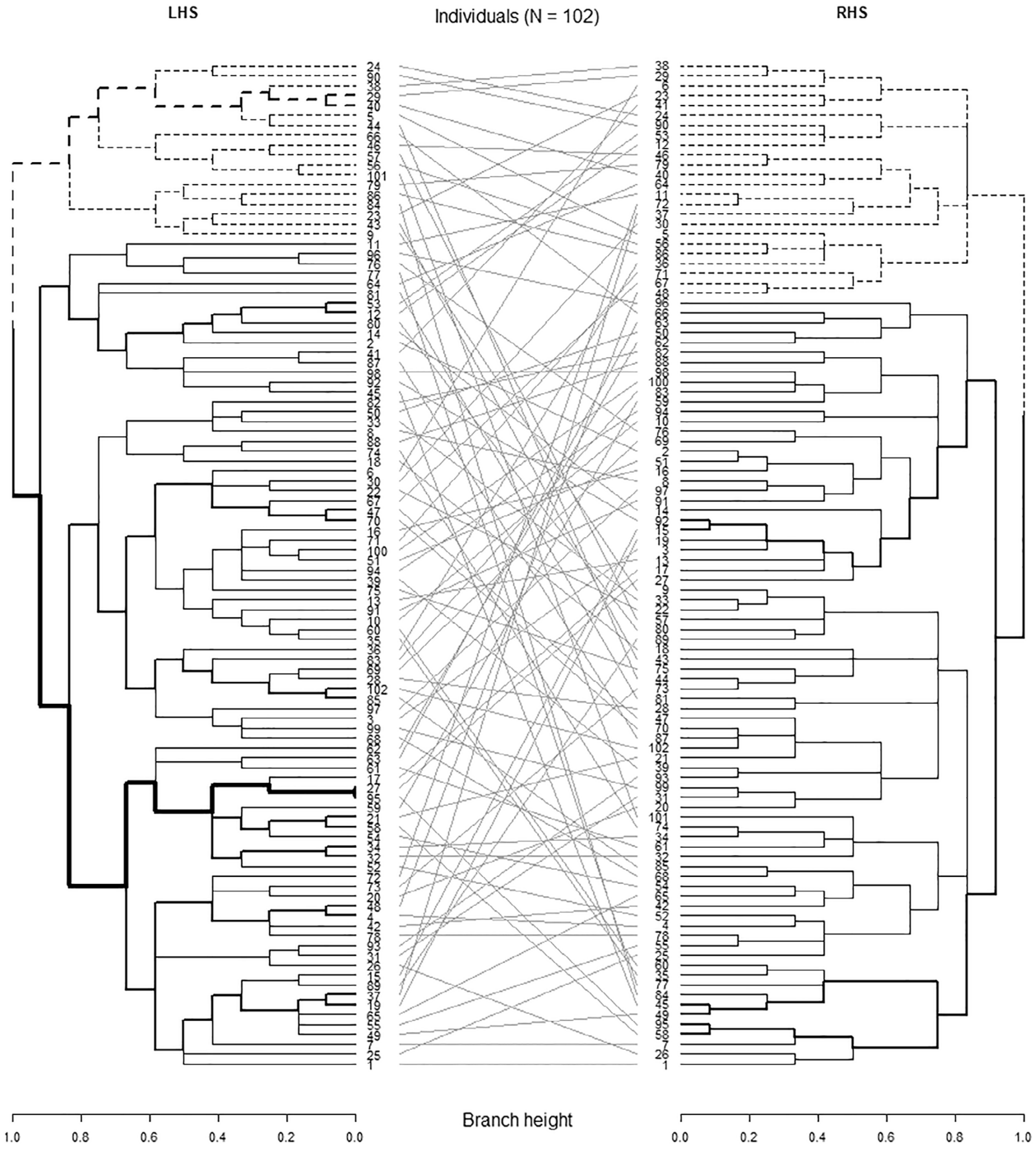

**FIGURE 5** Tanglegram of hierarchical cluster analysis showing left-hand side (LHS) and right-hand side (RHS) color pattern variation for the 2017 cohort of dwarf minke whales (DMWs). The shorter the height (Gower's metric) of a branch, the more similar the color pattern profile of individuals. Solid branches represent individuals belonging to cluster one. Dashed branches represent individuals belonging to cluster two. Thicker branches represent individuals that were either categorized by the same color pattern profile (e.g., the LHS of #27 and #95) or differed by only one character state (e.g., the RHS of #45 and #49).

dendrograms, the cophenetic correlation coefficient was 0.15, the mean relative difference in branch height was 0.23 and the lowest possible entanglement achieved was 0.29.

The cumulative proportions of variance retained by the first two dimensions of the individual (Figure 6) and variable (Figure 7) multiple correspondence analyses were 11.37% and 9.57%. For the individual plot, LHSs were closely positioned in the second and third quadrats with RHSs further dispersed among the second and fourth quadrats. RHSs predominately defined both axes (e.g., #86 = 2.4%) with just one LHS contributing in a similar extent to the

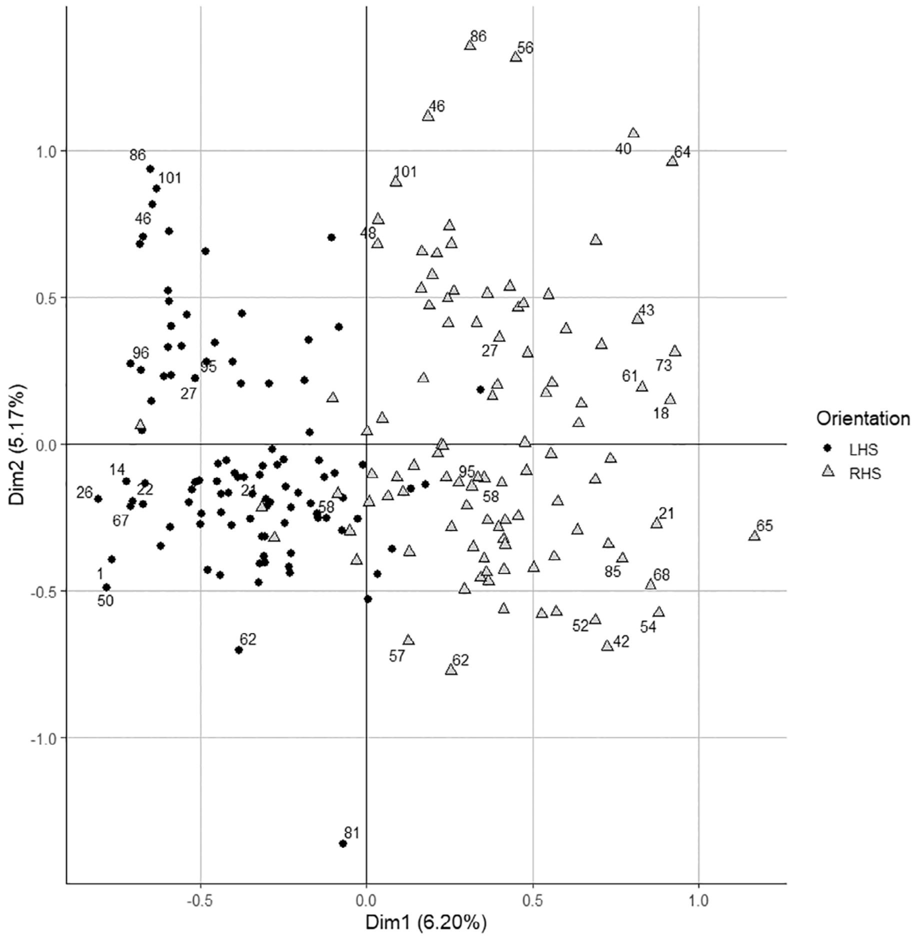

**FIGURE 6** Multiple correspondence analysis between the left-hand side (LHS) and right-hand side (RHS) color pattern profiles of each 2017 individual dwarf minke whale (DMW). The individuals which contributed most to the dimensional variance are labeled.

second dimension (#81 = 2.3%). On the contrary, element and subelement character states from both sides of the body contributed to axes definition for the variable plot (e.g., LHS_CC_A_DE = 4.5% and RHS_PB_D = 4.4%). Diffuse peduncle blazes as well as detached and absent caudal chevrons were closely paired by orientation and drawn out to the right of the *x*-axis. Nearby was also the RHS major eye blaze, narrowly attached, broadly detached, and narrowly detached axillary patches. Squared cosine values reflected that certain individuals and variables were moderately represented by these plots (e.g., #56 = 0.52 and RHS_CC_P_AT = 0.41).

## 4 | DISCUSSION

The 2017 cohort of DMWs demonstrated a high degree of color pattern complexity underpinned by several sources of variation, asymmetry, and association. The elements and subelements displayed certain character states which were common (e.g., a hooked thorax patch peak) and others that were rare (e.g., an anvil thorax patch peak). In addition, some of these features (e.g., the eye blaze) were highly asymmetric and expressed their traits in a consistent

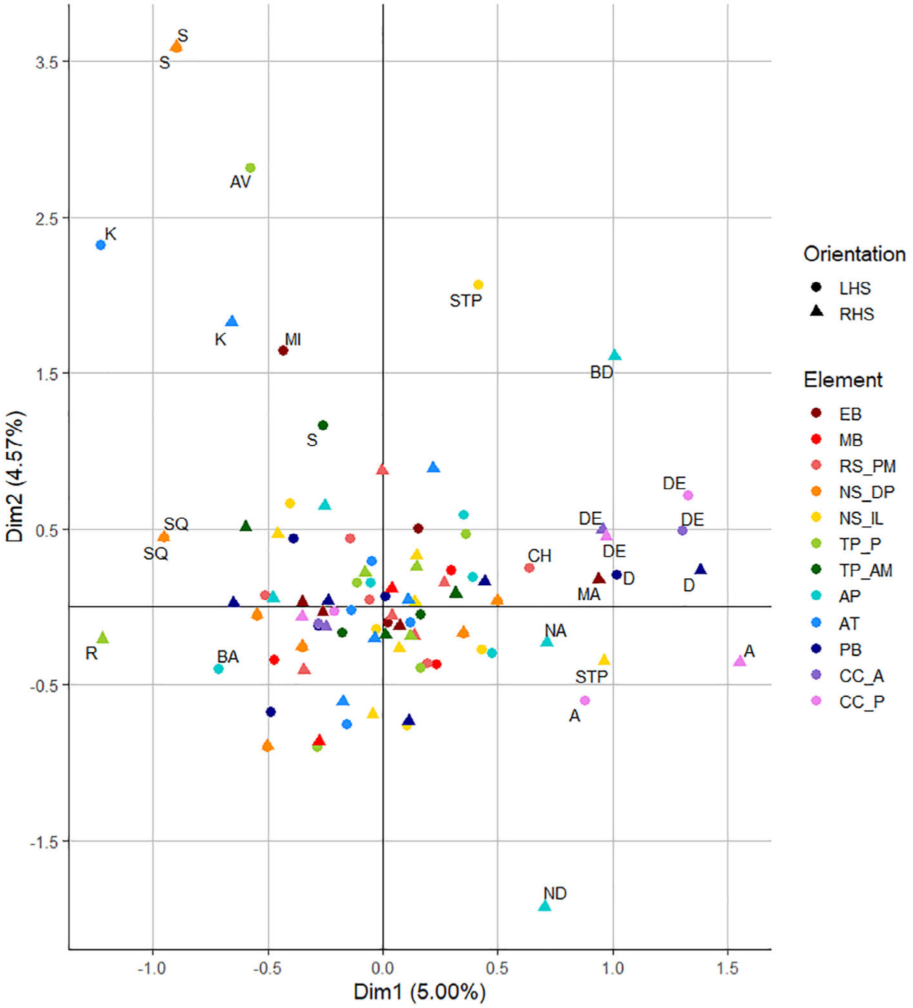

**FIGURE 7** Multiple correspondence analysis between the left-hand side (LHS) and right-hand side (RHS) character states of each element and subelement (see supplementary material for abbreviations) for the 2017 cohort of dwarf minke whales (DMWs). The character states which contributed most to the dimensional variance are labeled.

rather than a random manner. This was particularly evident on the right anterior third of the body where markings often appeared lighter than those on the left. Similarly, several white blazes were found to be associated across the entire length of the RHS. This result is notable considering it occurred despite proportions indicating that, overall, these character states (e.g., a diffuse peduncle blaze) were rarer. Color pattern profiles on the RHS of individuals were also more variable, with fewer similarities detected within the cohort through hierarchical clustering. Multiple correspondence analysis confirmed that the LHS color pattern profiles of individuals were in fact more like each other than they were to their own RHS and vice versa. These findings reinforce the many asymmetric differences that can exist both within and between unique DMWs.

Research on cetacean coloration has largely focused on the more distinctly marked odontocetes (Mercer, 1973; Mitchell, 2011). Several studies report geographic variation in the saddle patch, dorsal cape, and postocular patch of killer whales (*Orcinus orca*; Baird & Stacey, 1988; Evans et al., 1982; Visser & Mäkeläinen, 2000). Similarly, the color pattern components of white-beaked (*Lagenorhynchus albirostris*; Bertulli et al., 2016), spotted (*Stenella frontalis*;

Herzing, 1997), bottlenose (*Tursiops* sp.; Krzyszczyk & Mann, 2012), humpback (*Sousa chinensis*; Chen et al., 2018), and spinner (*Stenella longirostris*) dolphins (Perrin, 1972) have been shown to display ontogenetic differences. Sexual dichromatism has also been documented in the killer whale (Evans & Yablokov, 1978) and Fraser's dolphin (*Lagenodelphis hosei*; Azevedo et al., 2003). Furthermore, it is hypothesized that the distinct markings of some cetaceans may aid in disruptive coloration (Madsen & Herman, 1988), intraspecific communication (Yablokov, 1963) and prey disorientation. White markings upon the flanks (Würsig & Würsig, 1980), pectoral fins (Brodie, 1977), and mandible (Gaskin, 1967) are thought to be useful in corralling schools of invertebrates and fish. The asymmetrical anterior coloration of the fin whale (Methion & Díaz López, 2019), also shown here for the DMW, is an adaption that could allow individuals to startle, concentrate, and capture prey when lunging from one side (Tershy & Wiley, 1992). An examination of this hypothesis for the DMW was outside the scope of this study. However, our results demonstrate that DMW color pattern complexity rivals that of many odontocetes and functional significance related to crypsis, socialization, and foraging is certainly possible and worthy of further investigation (see also Arnold et al., 2005).

The limitations of this study should be borne in mind when interpreting these results. Firstly, imagery collection for photo-ID depends upon the voluntary approach of individuals to swim-with-DMW vessels (Birtles et al., 2001). Therefore, whilst there is no indication of unobserved animals on the periphery of most encounters (Mangott et al., 2011), the resulting data only represent the interacting population. Sampling of the study area also depends upon access made available by the tourism operators. Thus, it is neither random nor systematic, but opportunistic and reflective of industry site use (Curnock, 2010; Curnock et al., 2013). This is a common constraint in marine-based citizen science research. Although necessary, the sample size was further constrained to only those individuals which could be assigned full body color pattern profiles. Many of the elements and subelements (e.g., the nape streak insert location) were difficult to distinguish even in high quality imagery. This then raises the concern that more distinct character states (e.g., a swirled anterior triangle) may have been overrepresented given that they were easier to observe. The large number of categorical variables involved also somewhat confounded statistical analysis. For example, cophenetic correlation values were moderate suggesting that each clustering result only moderately preserved its distance (dis)similarity matrix. Likewise, MCA plots were based upon a small amount of dimensional variance for which many individuals and variables had low axes contribution and squared cosine values.

Lastly, though we used a single, experienced assessor and the most standardized DMW color pattern categorization tool available (Hutchings, 2020), the visual assignment of character states in this manner has the inherent potential to introduce bias. Moreover, defining color pattern in this way presents a predicament in and of itself given it simply cannot capture fine scale detail. For instance, the nape streak dorsal portion falsely appeared entirely symmetrical due to the way in which it was categorized. Whilst this novel tool is a significant advance on preceding approaches, its wider application in DMW photo-ID, particularly between multiple, inexperienced assessors, is yet to be thoroughly reviewed and considered best practice. However, there is potential for it to be implemented into automated processes as the quantity of imagery collected and the number of identified individuals grows beyond the ability of manual methods (Konovalov et al., 2020). For example, an algorithm could be trained to read and quantify DMW color pattern complexity based on the probabilities of variation, asymmetry, and association found for the several elements, subelements, and character states explored here. Automatic recognition software has increased the usability and efficiency of photo-ID for many taxa in recent years (Adams et al., 2006; Blount et al., 2022; Carvajal-Gámez et al., 2017; Hemingson et al., 2019). The employment of this in an accurate manner for DMWs will be made challenging by inconsistent image quality. Nonetheless, such advances have the potential to greatly accelerate species assessment and conservation management action (Blount et al., 2019).

This study represents the most detailed systematic analysis of DMW color pattern complexity to date and is the first of its kind undertaken for a mysticete species. We applied a novel categorization tool to confirm that a high level of asymmetric color pattern variation exists, with white markings dominant and associated on the right of the body. Future work should strive to increase understanding of DMW life history, evolution, genetics, social structure, and feeding in order to further investigate the functional significance of their distinctive markings. Similarly, there is a need to move towards automated approaches in DMW photo-ID as manual processes have become increasingly time-consuming. Although, training an algorithm to read and quantify such a complex color pattern, even in high-quality imagery, will be a difficult feat. Our results provide a foundation for this that will, in turn, benefit the citizen science driven photo-ID, broader research, and conservation management of this little-known cetacean.

## ACKNOWLEDGMENTS

This study would not have been possible without the extensive and long-standing support of the GBR swim-with-DMW industry. We thank the crew and passengers upon these "platforms of opportunity" for their assistance with our data collection. It is equally important to acknowledge the many MWP members, past and present, whose efforts in both data collection and photo-ID have provided the foundations for this study. We are particularly grateful for the contributions of Peter Arnold, Susan Sobtzick, Suzanne Hillcoat, Martha Kusetic, and Claire Barr. Similarly, we appreciate the editors and reviewers for their time and comments which have significantly improved this paper. Lastly, we must give thanks to the DMWs who allow us to study them with just as much curiosity as they have for us. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

## AUTHOR CONTRIBUTIONS

**Marissa Janet Hutchings:** Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing – original draft; writing – review and editing. **Mark Hamann:** Conceptualization; methodology; supervision; validation; writing – review and editing. **Scott G. Smithers:** Conceptualization; methodology; supervision; validation; writing – review and editing. **Emily N. Daley:** Data curation; investigation; writing – review and editing. **Robert Alastair Birtles:** Conceptualization; investigation; methodology; supervision; validation; writing – review and editing.

## ORCID

*Marissa J. Hutchings* https://orcid.org/0000-0001-5621-804X

## REFERENCES

Abdi, H., & Valentin, D. (2006). Multiple correspondence analysis. In E. J. Salkin (Ed.), *Encyclopedia of measurement and statistics* (Vol. 2, pp. 651–657). SAGE Publishing.

Adams, J., Speakman, T., Zolman, E., & Schwacke, L. H. (2006). Automating image matching, cataloging, and analysis for photo-identification research. *Aquatic Mammals*, *32*, 374–384. https://doi.org/10.1578/AM.32.3.2006.374

Arnold, P. W. (1997). Occurrence of dwarf minke whales (*Balaenoptera acutorostrata*) on the northern Great Barrier Reef, Australia. *Reports of the International Whaling Commission*, *47*, 419–424

Arnold, P. W., Birtles, A., Dunstan, A., Lukoschek, V., & Matthews, M. (2005). Colour patterns of the dwarf minke whale *Balaenoptera acutorostrata* sensu lato: description, cladistic analysis and taxonomic implications. *Memoirs of the Queensland Museum*, *51*(2), 277–307. https://researchonline.jcu.edu.au/4935/

Arnold, P. W., Marsh, H., & Heinsohn, G. (1987). The occurrence of two forms of minke whales in east Australian waters with a description of the external characters and skeleton of the diminutive or dwarf form. *Scientific Reports of the Whales Research Institute, Tokyo*, *38*, 1–46.

Azevedo, A., Lailson Brito, J., Siciliano, S., Cunha, H., & Fragoso, A. (2003). Colour pattern and external morphology of the Fraser's dolphin (*Lagenodelphis hosei*) in the Southwestern Atlantic. *Aquatic Mammals*, *29*, 411–416. https://doi.org/10.1578/016754203360736613

Baird, R. W., & Stacey, P. J. (1988). Variation in saddle patch pigmentation in populations of killer whales (*Orcinus orca*) from British Columbia, Alaska, and Washington State. *Canadian Journal of Zoology*, *66*(11), 2582–2585. https://doi.org/https://doi.org/10.1139/z88-380

Batool, F., & Hennig, C. (2021). Clustering with the Average Silhouette Width. *Computational Statistics & Data Analysis*, *158*, Article 107190. https://doi.org/10.1016/j.csda.2021.107190

Bertulli, C. G., Galatius, A., Kinze, C. C., Rasmussen, M. H., Keener, W., & Webber, M. A. (2016). Color patterns in white-beaked dolphins (*Lagenorhynchus albirostris*) from Iceland. *Marine Mammal Science*, *32*(3), 1072–1098. https://doi.org/https://doi.org/10.1111/mms.12312

Best, P. B. (1985). External characters of southern minke whales and the existence of a diminutive form. *Scientific Reports of the Whales Research Institute, Tokyo*, *36*, 1–33.

Birtles, A., Andrews, D. R., & Jenner, C. (2015). Spatial ecology, migratory paths and critical areas of habitat use of Australia's dwarf minke whales (Preliminary Report 2013/36). Australian Marine Mammal Centre, Townsville, Australia.

Birtles, A., Arnold, P., Curnock, M., Valentine, P., & Dunstan, A. (2001). *Developing ecologically sustainable dwarf minke whale tourism (1999–2001)* (Final Report to the Commonwealth Department of Environment and Heritage, Environment Australia). James Cook University, Townsville, Australia.

Birtles, A., Arnold, P. W., & Dunstan, A. (2002). Commercial swim programs with dwarf minke whales on the northern Great Barrier Reef, Australia: some characteristics of the encounters with management implications. *Australian Mammalogy*, *24*, 23–38. https://doi.org/10.1071/AM02023

Birtles, A., & Mangott, A. (2011). Highly interactive behaviour of inquisitive dwarf minke whales. In P. Brakes & M. P. Simmonds (Eds.), *Whales and dolphins: Cognition, culture, conservation and human perceptions*. Earthscan Publications.

Birtles, A., Valentine, P., Curnock, M., Mangott, A., Sobtzick, S., & Marsh, H. (2014). *Dwarf minke whale tourism monitoring program (2003–2008)* (Research Publication No. 122). Great Barrier Reef Marine Park Authority, Townsville, Australia. https://hdl.handle.net/11017/2908

Blount, D., Gero, S., Van Oast, J., Parham, J., Kingen, C., Scheiner, B., Stere, T., Fisher, M., Minton, G., Khan, C., Dulau, V., Thompson, J., Moskvyak, O., Berger-Wolf, T., Stewart, C. V., Holmberg, J., & Levenson, J. J. (2022). Flukebook: an open-source AI platform for cetacean photo identification. *Mammalian Biology*, *102*, 1005–1023. https://doi.org/10.1007/s42991-021-00221-3

Blount, D., Holmberg, J., Minton, G., & Khan, C. (2019). *Flukebook – Recent advances for cetacean photo identification and data archiving including automated fluke matching*. Paper SC/68A/SH07 presented to the Scientific Committee of the International Whaling Commission.

Brodie, P. F. (1977). Form, function and energetics of Cetacea: a discussion. In R. J. Harrison (Ed.), *Functional anatomy of marine mammals* (3rd ed., pp. 45–58). Academic Press.

Caro, T., Beeman, K., Stankowich, T., & Whitehead, H. (2011). The functional significance of colouration in cetaceans. *Evolutionary Ecology*, *25*(6), 1231–1245. https://doi.org/10.1007/s10682-011-9479-5

Carvajal-Gámez, B. E., Trejo-Salazar, D. B., Gendron, D., & Gallegos-Funes, F. J. (2017). Photo-id of blue whale by means of the dorsal fin using clustering algorithms and color local complexity estimation for mobile devices. *EURASIP Journal on Image and Video Processing*, *2017*(1), Article 6. https://doi.org/10.1186/s13640-016-0153-2

Chen, B., Jefferson, T. A., Wang, L., Gao, H., Zhang, H., Zhou, Y., Xu, X., & Yang, G. (2018). Geographic variation in pigmentation patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Chinese waters. *Journal of Mammalogy*, *99*(4), 915–922. https://doi.org/10.1093/jmammal/gyy068

Curnock, M. I. (2010). *Mechanisms for assessing the sustainability of swimming-with-whales tourism in the Great Barrier Reef* [Doctoral dissertation]. James Cook University. http://eprints.jcu.edu.au/24896/

Curnock, M. I., R. Birtles, A., & Valentine, P. S. (2013). Increased use levels, effort, and spatial distribution of tourists swimming with dwarf minke whales at the Great Barrier Reef. *Tourism in Marine Environments*, *9*(1–2), 5–17. https://doi.org/10.3727/154427313X13659574649867

Daley, E. N. (2019). *Dwarf minke whales in the northern Great Barrier Reef: a population-based cohort study of the world's only known aggregation* [Unpublished minor project dissertation]. James Cook University.

Dunstan, A., Sobtzick, S., Birtles, A., & Arnold, P. (2007). Use of videogrammetry to estimate length to provide population demographics of dwarf minke whales in the northern Great Barrier Reef. *Journal of Cetacean Research and Management*, *9*(3), 215–223. https://researchonline.jcu.edu.au/10509/

Evans, W. E., & Yablokov, A. V. (1978). Intraspecific variation of the color pattern of the killer whale (*Orcinus orca*). In V. E. Sokolov & A. V. Yablokov (Eds.), *Advances in studies of cetaceans and pinnipeds* (pp. 102–115). Nauka Publishing.

Evans, W. E., Yablokov, A. V., & Bowles, A. E. (1982). Geographic variation in the color pattern of killer whales (*Orcinus orca*). *Reports of the International Whaling Commission*, *32*, 687–694.

Everitt, B. (2011). *Cluster analysis* (5th ed.). Wiley.

Gaskin, D. E. (1967). Luminescence in a squid *Moroteuthis* sp. (probably *ingens* Smith) and a possible feeding mechanism in the sperm whale *Physeter catodon* L. *Tuatara*, *15*(2), 86–88.

Gower, J. C. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, *27*(4), 857–871. https://doi.org/10.2307/2528823

Hasling, J. C. (2003). *Meet the minkes: Developing effective interpretation for the swim-with-dwarf minke whale industry* [Unpublished Master's dissertation]. James Cook University.

Hemingson, C. R., Cowman, P. F., Hodge, J. R., & Bellwood, D. R. (2019). Colour pattern divergence in reef fish species is rapid and driven by both range overlap and symmetry. *Ecology Letters*, *22*, 190–199. https://doi.org/10.1111/ele.13180

Herzing, D. L. (1997). The life history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): Age classes, color phases, and female reproduction. *Marine Mammal Science*, *13*(4), 576–595. https://doi.org/10.1111/j.1748-7692.1997.tb00085.x

Huang, Z. (1998). Extensions to the k-means algorithm for clustering large data sets with categorical values. *Data Mining and Knowledge Discovery*, *2*(3), 283–304. https://doi.org/10.1023/A:1009769707641

Hutchings, M. (2020). *Dwarf minke whale colour pattern complexity: a broad and detailed systematic analysis inferring functional significance* [Unpublished Honours dissertation]. James Cook University.

IWC. (2001). Report of the International Whaling Commission Scientific Committee working group on nomenclature. *Journal of Cetacean Research and Management*, *3*, 363–365.

Junaid Mir, M., Malik, I., & Sharma, R. (2014). Finger-vein pattern matching for human identification. *International Journal of Engineering Research and Technology*, *3*(2), 1966–1972. https://doi.org/https://doi.org/10.17577/IJERTV3IS21119

Konovalov, D. A., Swinhoe, N., Efremova, D. B., Birtles, R. A., Kusetic, M., Hillcoat, S., Curnock, M. I., WIlliams, G., & Sheaves, M. (2020). Automatic sorting of dwarf minke whale underwater images. *Information*, *11*(4), Article 200. https://doi.org/10.3390/info11040200

Krzyszczyk, E., & Mann, J. (2012). Why become speckled? Ontogeny and function of speckling in Shark Bay bottlenose dolphins (*Tursiops* sp.). *Marine Mammal Science*, *28*(2), 295–307. https://doi.org/https://doi.org/10.1111/j.1748-7692.2011.00483.x

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, *25*, 1–18. https://doi.org/10.18637/jss.v025.i01

Lee, D. E., Cavener, D. R., & Bond, M. L. (2018). Seeing spots: quantifying mother-offspring similarity and assessing fitness consequences of coat pattern traits in a wild population of giraffes (*Giraffa camelopardalis*). *PeerJ*, *6*, *Article e5690*. https://doi.org/10.7717/peerj.5690, e5690

Madsen, C. J., & Herman, L. M. (1988). Social and ecological correlated of cetacean vision and visual appearance. In L. M. Herman (Ed.), *Cetacean behaviour: Mechanisms & functions* (pp. 101–148). Robert E. Krieger Publishing Company.

Mangott, A. H. (2010). *Behaviour of dwarf minke whales* (Balaenoptera acutorostrata subsp.) *associated with a swim-with industry in the northern Great Barrier Reef* [Doctoral dissertation]. James Cook University. http://eprints.jcu.edu.au/19001

Mangott, A. H., Birtles, R. A., & Marsh, H. (2011). Attraction of dwarf minke whales *Balaenoptera acutorostrata* to vessels and swimmers in the Great Barrier Reef World Heritage Area – the management challenges of an inquisitive whale. *Journal of Ecotourism*, *10*(1), 64–76. https://doi.org/10.1080/14724041003690468

Mercer, M. C. (1973). Observations on distribution and intraspecific variation in pigmentation patterns of odontocete Cetacea in the western North Atlantic. *Journal of the Fisheries Research Board of Canada*, *30*(8), 1111–1130. https://doi.org/10.1139/f73-182

Methion, S., & Díaz López, B. (2019). First record of atypical pigmentation pattern in fin whale *Balaenoptera physalus* in the Atlantic Ocean. *Diseases of Aquatic Organisms*, *135*, 121–125. https://doi.org/10.3354/dao03385

Mitchell, E. (2011). Pigmentation pattern evolution in delphinid cetaceans: An essay in adaptive coloration. *Canadian Journal of Zoology*, *48*, 717–740. https://doi.org/10.1139/z70-129

Perrin, W. F. (1972). Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific. *Fishery Bulletin*, *70*(3), 983–996.

Ramirez-Flores, O., Birtles, A., Pazmino, D., Zenger, K. R., & Van-Herwerden, L. (2019). Dwarf minke whales from the South Pacific share a matrilineal lineage distinct from *Balaenoptera acutorostrata acutorostrata* and *B. a. scammoni*. *Australian Mammalogy*, *41*(2), 231–240. https://doi.org/10.1071/AM18015

Rice, D. W. (1998). *Marine mammals of the world: Systematics and distribution*. Special Issue Number 4, The Society for Marine Mammalogy. https://www.marinemammalscience.org/wp-content/uploads/2014/09/MarineMammalsOfTheWorld.pdf

Risch, D., Norris, T., Curnock, M., & Friedlaender, A. (2019). Common and Antarctic minke whales: conservation status and future research directions. *Frontiers in Marine Science*, *6*, Article 247. https://doi.org/10.3389/fmars.2019.00247

Saraçli, S., Doğan, N., & Doğan, İ. (2013). Comparison of hierarchical cluster analysis methods by cophenetic correlation. *Journal of Inequalities and Applications*, *2013*(1), Article 203. https://doi.org/10.1186/1029-242X-2013-203

Sobtzick, S. (2010). *Dwarf minke whales in the northern Great Barrier Reef and implications for the sustainable management of the swim-with whales industry* [Doctoral dissertation]. James Cook University. http://eprints.jcu.edu.au/28199/

Stephens, T., Birtles, A., & Williams, G. (2015). *Photo-identification guide to the Great Barrier Reef dwarf minke whales satellite tagged in 2013 & 2014* [Unpublished student report]. Minke Whale Project, James Cook University, Townsville, Australia.

Tershy, B. R., & Wiley, D. N. (1992). Asymmetrical pigmentation in the fin whale: a test of two feeding related hypotheses. *Marine Mammal Science*, *8*(3), 315–318. https://doi.org/10.1111/j.1748-7692.1992.tb00416.x

Thayer, G. H. (1909). *Concealing-coloration in the animal kingdom: An exposition of the laws of disguise through color and pattern: Being a summary of Abbott H. Thayer's discoveries*. The Macmillan Co.

Valentine, P. S., Birtles, A., Curnock, M., Arnold, P., & Dunstan, A. (2004). Getting closer to whales—passenger expectations and experiences, and the management of swim with dwarf minke whale interactions in the Great Barrier Reef. *Tourism Management*, *25*(6), 647–655. https://doi.org/10.1016/j.tourman.2003.09.001

Visser, I. N., & Mäkeläinen, P. (2000). Variation in eye-patch shape of killer whales (*Orcinus orca*) in New Zealand waters. *Marine Mammal Science*, *16*(2), 459–469. https://doi.org/https://doi.org/10.1111/j.1748-7692.2000.tb00938.x

Watson, C. (2011). *Expanding photographic identification efforts in dwarf minke whale research* [Unpublished Graduate Diploma Report]. James Cook University.

Würsig, B., & Würsig, M. (1980). Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fishery Bulletin*, *77*(4), 871–890.

Yablokov, A. V. (1963). Types of colour of the Cetacea. *Bulletin of Moscow Society of Naturalists Biological Series*, *68*(6), 27–41.

## 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:** Hutchings, M. J., Hamann, M., Smithers, S. G., Daley, E. N., & Birtles, R. A. (2023). Color pattern complexity in dwarf minke whales (*Balaenoptera acutorostrata*) of the northern Great Barrier Reef of Australia. *Marine Mammal Science*, *39*(3), 780–793. https://doi.org/10.1111/mms.13013