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REVIEW ARTICLE

Marine Mammal Science

Best practices for collecting and preserving marine mammal biological samples in the 'omics era

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Abstract

The recent rise of 'omics and other molecular research technologies alongside improved techniques for tissue preservation have broadened the scope of marine mammal research. Collecting biological samples from wild marine

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mammals is both logistically challenging and expensive. To enhance the power of marine mammal research, great effort has been made in both the field and the laboratory to ensure the scientific integrity of samples from collection through processing, supporting the long-term use of precious samples across a broad range of studies. However, identifying the best methods of sample preservation can be challenging, especially as this technological toolkit continues to evolve and expand. Standardizing best practices could maximize the scientific value of biological samples, foster multi-institutional collaborative efforts across fields, and improve the quality of individual studies by removing potential sources of error from the collection, handling, and preservation processes. With these aims in mind, we summarize relevant literature, share current expert knowledge, and suggest best practices for sample collection and preservation. This manuscript is intended as a reference resource for scientists interested in exploring collaborative studies and preserving samples in a suitable manner for a broad spectrum of analyses, emphasizing support for 'omics technologies.

KEYWORDS
archival, best practices, biomarkers, cetacean, field sampling, genomics, pinniped, preservation, sterile techniques

1 | INTRODUCTION

The field of marine mammal biology has seen recent dramatic growth in the use of biological samples—primarily tissue, blow, and feces—for emerging 'omics technologies (e.g., genomics, metagenomics, metabarcoding, transcriptomics, proteomics, metabolomics and epigenomics) and the analysis of exogenous and endogenous elements (pollutants, toxins, stable isotopes, and hormones; Cammen et al., 2016; Mancia, 2018; Nelms et al., 2021; Figure 1). This growth has advanced our capability to address evolutionary (Apprill et al., 2020; Foote et al., 2019; Gui et al., 2013; McGowen, Tsagkogeorga, Álvarez, et al., 2020; McGowen, Tsagkogeorga, Williamson, et al., 2020), ecological (Arregui et al., 2018; Hooper et al., 2018; Polanowski et al., 2014), health (Jepson et al., 1999; Lawson et al., 2020), and conservation (Apprill et al., 2017; Nelms et al., 2021) questions that were previously left largely unaddressed for nonmodel organisms. Concurrent advances in archival techniques, supporting the preservation of samples for long periods of time with little degradation, inspire new opportunities to maximize the scientific potential of tissue samples and biological collections.

One of the major limitations to studies relying on marine mammal biological samples is the logistical difficulty and expense associated with field sampling, which can severely limit sample size (Bowen & Iverson, 2013; Dantzer et al., 2014; Deyarmin et al., 2019; Khudyakov et al., 2017). Marine mammals often inhabit remote environments, resulting in costly transportation to sampling locations and shipping restrictions. Further, extreme weather conditions, elusive behavior of the study species, and the expertise required for remote sample collection methods all serve to limit sample numbers. The often remote or resource-limited

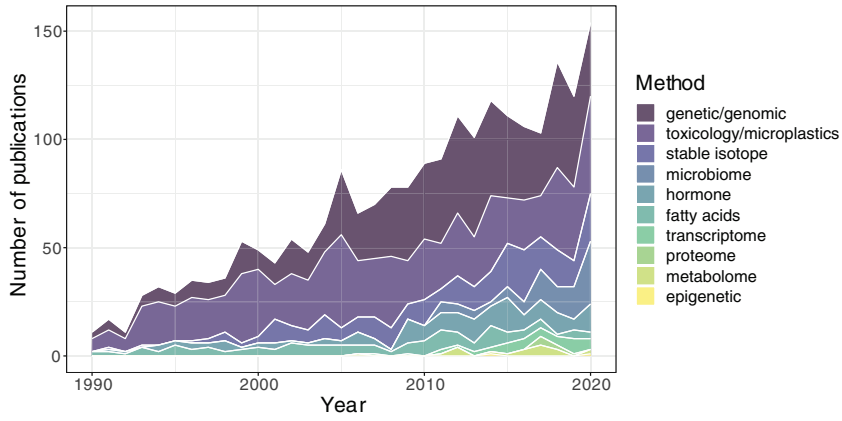

FIGURE 1 The number of studies relying on marine mammal biological samples published annually since 1990, stratified by primary study methodology. Counts were based on a Google Scholar search for "marine mammal" and the keyword listed in the legend, including permutations where appropriate to allow for inevitable variability in the way keywords are entered into databases (e.g., genom*, microbiom*, metabolom*). Each of these searches was then manually filtered based on study title to ensure extraneous or tangential studies were removed.

field sites challenge sample handling, processing, and preservation. Overall, these challenges and costs amplify the inherent value of every sample, especially in instances where the target species or population is on the verge of extinction.

Across the scientific research community, there is a strong desire to maximize the use of biological samples due to the logistical and financial costs associated with sampling marine mammals, and to establish a conservative sampling approach out of consideration for the health and welfare of study species. Project leads often go to great lengths to maximize the use of individual biological samples, by sampling and subsampling tissues to support multiple chemical and molecular studies (e.g., Bechmann et al., 2021). Many such studies require the collaboration of several institutions, both national and international, to achieve the sample size, geographic coverage, and/or taxonomic breadth needed to be successful (e.g., Apprill et al., 2020; Baker et al., 2013; Bik et al., 2016; Dudek et al., 2022; Herman et al., 2008; Krahn et al., 2007; Morin, Archer, et al., 2021; Morin, Forester, et al., 2021; Parsons et al., 2013; Van Cise et al., 2019). Further, interdisciplinary approaches are increasingly preferred to address research questions (e.g., population structure, evolution, individual or population health and fitness; Bahamonde et al., 2016), as ensemble methods are often better suited to address function, mechanism and/or causation (Hasin et al., 2017). As methods advance, and novel approaches are conceived to address new questions, the development of a set of best practices for the collection, processing, and long-term storage of marine mammal biological samples will allow scientists to capitalize on these developments to address complex questions and incorporate samples from long-term studies into future analyses to increase the scale and relevance of marine mammal research.

In the field, multiple considerations are routinely evaluated during sample handling, and the increasing sensitivity of 'omics approaches warrant particular consideration to protect sample integrity and avoid sample contamination (Kühn et al., 2020; Sepulveda et al., 2020; Taberlet et al., 1999). Wherever possible, following a set of best practices for sample collection, processing, and storage will increase the breadth of sample utility and support sample longevity; however, it is important to note that the best sample collection protocols and preservation methods are not uniform across all analysis types, and specific project objectives and consideration of future potential and/or collaborative efforts across multiple studies will drive collection and preservation options. This review summarizes contemporary information from current literature and ongoing or unpublished studies on best practices for handling and storing specimens collected from marine mammals for use in 'omics and other studies. In many cases, quantitative

published data are not available to guide recommendations for best practices. To address this issue, we aggregate expert opinions of our many coauthors, who collectively represent expertise in collecting, processing, storing, and analyzing biological samples using all analytical methods discussed in the paper, as well as the authors of studies cited in this paper. The best practices recommended herein are not intended to be prescriptive, but rather allow research scientists to make informed decisions based on the best available data to support short-term research objectives and maximize the potential use of these samples in future research. Finally, it is important to acknowledge that recommended best practices will likely evolve over time, as new preservatives become available and additional research is published that directly tests the effects of various collection and preservation methods on traditional and emerging analytical approaches.

2 | GENERAL CONSIDERATIONS

Samples collected from live marine mammals most commonly include blood and other biofluids, tissue (i.e., skin and blubber), feces, and keratin structures (e.g., whiskers, fur, baleen). While additional types of biospecimens (e.g., bones and teeth) are often collected from carcasses, the review and suggested guidelines herein will focus primarily on specimens typically collected from live animals using minimally invasive research procedures, i.e., biopsy sampling, collection of biofluids (e.g., blood, urine), or fecal sample collection. In the field, potential sources of sample contamination include the marine environment, human handlers, processing location, as well as cross-contamination from other samples that may be collected concurrently. The protocols for collecting, processing, and storing samples may differ according to the type of biological material as well as intended sample use. However, many best practice techniques for sterilizing collection equipment, preserving samples, and storing samples until archiving can be generalized across most types of biological samples and most research methods. In this section we provide a general overview of the best practice techniques for collecting and processing samples in the field, as well as long-term sample preservation and archiving, in an effort to contribute to the standardization of these techniques across the field of marine mammal research.

Many institutions will have IACUC (Institutional Animal Care and Use Committee) guidelines detailing approaches that should be followed for sampling instruments or equipment that will penetrate the body of a research animal. These protocols should be reviewed and followed when available. In addition to these protocols, which were created with the aim of protecting the health of the animals being studied, separate but complementary protocols are necessary to protect the samples, to ensure that samples are collected and processed in a way that avoids contamination by exogenous materials such as DNA or RNA, microbes, or other cross-contaminants.

2.1 | Best practice recommendations: an overview

The value of sterile techniques (defined here as methods intended to prevent the contamination of biological samples with exogenous DNA or RNA, microbes, environmental or other cross-contaminants) should be emphasized during each step of sample collection and processing (Khan et al., 2021; Weiss et al., 2014; Wong et al., 2012). Establishing minimum requirements for sampling, handling, and cleaning of reusable sampling equipment (e.g., tissue biopsy darts) is key for protecting sample integrity and documenting potential analytical limitations. 'Omics tools are rapidly increasing in sensitivity with technological advances, and the ability to generate millions of genomic sequences for each sample simultaneously increases the power to detect contamination and confound downstream analyses. Developing protocols that adopt a conservative approach to equipment sterilization and sample handling in the field and in the laboratory, and adhering to these protocols across field projects, will decrease downstream

errors, increase opportunities for collaboration and support our future efforts as we strive to adopt new methods and technologies.

2.1.1 | Sample collection

Prior to sample collection, standard protocols for sterile collection of samples should be reviewed or established, ideally including protocols for tracking sample nomenclature and metadata. Sampling equipment should be thoroughly cleaned and sterilized at the lab, prior to shipping to the field site. When preparing reusable field equipment for use (e.g., stainless steel biopsy tips or forceps), all devices should be sterilized using the best available techniques. It is generally recommended that reusable, metal sampling devices are sterilized using gas or heat sterilization (i.e., autoclaving), following instrument and/or institutional standards, when possible, prior to field deployment. During field sampling, all devices should be thoroughly cleaned and resterilized between use. Because autoclaves are not typically available in many field locations, field sterilization of reusable equipment relies on chemicals rather than heat/pressure. Here we outline one method for sterilizing reusable equipment in the field, which will hereafter be referred to as the *bleach and ethanol clean method*. First, all equipment should be thoroughly scrubbed using a small brush, hot water and detergent (or enzymatic cleaners) - paying particular attention to internal threads, barbs and cavities to remove all visible debris, dirt and tissue remnants -, and thoroughly rinsed with potable freshwater (e.g., tap, distilled, or deionized water). Following the cleaning step, sampling devices should be sterilized (e.g., Sinclair et al., 2015) by (1) soaking for 10 min in a 10% commercial bleach solution[1] (Prince & Andrus, 1992), (2) rinsing with potable water, (3) rinsing with 70%–95% ethanol (World Health Organization, 2014) to kill microbes and remove any corrosive material remaining from the use of bleach, and finally (4) allowing items to air dry before using or packaging in a clean, sterile container for future use. If 70%–95% ethanol is unavailable, isopropanol (isopropyl alcohol) can be used, but is less effective than ethanol. Other surface decontaminants, such as DNA AWAY or RNase AWAY, will remove target compounds (i.e., nucleic acids) but may not be sufficient to remove all exogenous biological material and completely sterilize equipment because their intended use is limited to the elimination of DNA or RNA molecules (Thermo Fisher Scientific, 2023). Alternatively, if bleach and ethanol are not available, stainless steel equipment (e.g., biopsy tips) can be boiled for 20 min in distilled water after scrubbing and washing and before storing (Krützen et al., 2002). Sample collection equipment can be stored in sterile, single-use Whirl-Pak[2] bags, which can double as a sterile barrier between ungloved hands and the sampling equipment. To address concerns regarding exposure to plastics and plasticizer compounds, e.g., when samples may be used for microplastics studies or chemical contaminant studies, sampling equipment (e.g., biopsy tips) can be wrapped in small pieces of clean aluminum foil or stored in Teflon bags or glass jars with Teflon-lined caps. In the case of single-use collection equipment, e.g., stainless steel blades that are often used to subset samples, nonlab grade or nonsurgical grade equipment may have residuals of industrial chemicals that should be removed prior to use to avoid contamination of downstream analyses. This can be achieved in the field by wiping the blades individually with bleach and ethanol prior to use, ensuring that the bleach and ethanol are completely wiped off and dried before use.

Limiting the number of people involved in sample collection will facilitate tracking of possible sources of contamination during collection. Sample handlers should wear disposable gloves and surgical masks to protect both the person and the sample, particularly during the collection of blow samples, and both work surfaces and

[1]Note that bleach is a corrosive chemical, and extensive or repeated exposure of metals, including common corrosion-resistant stainless steel metals used in scientific equipment, can cause corrosion/rust damage (Hollands & Postlewaite, 2014) over cumulative exposure periods of days to weeks. Because of this, equipment that is regularly exposed to bleach will need to be replaced periodically. Following Hollands and Postlewaite (2014), corrosion-resistant stainless steel equipment may begin to show signs of corrosion after approximately 576 10 min exposures to 10% commercial bleach solutions (four cumulative days of exposure).

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

sample handling tools (e.g., forceps, scalpel handles, biopsy darts) should be sterilized between samples (e.g., autoclaving or bleach and ethanol clean method; Bykowski & Stevenson, 2020). If field conditions prevent the use of gloves or other personal protective equipment, care should be taken to avoid touching equipment that contacts the sample, and to ensure sampling equipment does not come in contact with any nonsterile field equipment. Once collected, biological samples should be stored in a sterile vessel (e.g., Whirl-Pak, Falcon tube, glass vials with Teflon-lined caps, cell-free blood collection tubes) as appropriate for intended sample use and preserved as quickly as possible.

Biological samples intended for 'omics studies should be maintained in a stasis that reflects the moment of sampling as accurately as possible (except those intended for tissue culture; see below). Limiting the degradation of DNA, RNA, and proteins; growth or shifting of microbial communities; and alteration of proteins or metabolites in sampled tissues is critical to minimize downstream errors and ensure the sample accurately reflects the time of sampling. Rapid preservation of biological samples immediately after collection is vital to downstream data analyses and may be of equal or greater value to selecting the most appropriate preservation method (Michaud & Foran, 2011).

The best available practice is to store biological samples in a portable dewar or dry shipper containing liquid nitrogen (LN_2) immediately upon collection, until they can be transferred to a long-term archive at or below −80°C. A secondary option is to store samples on ice or in a − 20°C freezer until they can be transferred to long-term archival conditions. However, common household freezers (which support cooling to −20°C) equipped with automatic defrost cycles are not appropriate: subjecting samples to multiple freeze–thaw cycles may degrade their quality or skew the resulting data (Cardona et al., 2012; Koopman et al., 2002; Trana et al., 2015). Additional options, including liquid preservatives, can be useful in preserving samples for specific study methods without immediate freezing (Figure 2, Tables S1 and S2). The most commonly used liquid preservatives include RNA*later* (Invitrogen), salt-saturated 20% dimethyl sulfoxide solution (hereafter DMSO solution; Amos 1997, Amos & Hoelzel 1991), 95% ethanol (hereafter EtOH; King & Porter, 2004), and DESS (an aqueous solution containing 20% dimethyl sulfoxide (DMSO), 0.25 M ethylenediaminetetraacetic acid (EDTA) and saturated sodium chloride (NaCl; Seutin et al., 1991). Samples stored initially in liquid preservative may later be transferred to a long-term archive at −80°C, although researchers should check manufacturer specifications before doing so. When using liquid preservatives, it is valuable (e.g., particularly for microbiome studies) to simultaneously collect and store a negative control of the liquid preservative to detect potential contamination from the reagent itself (Pollock et al., 2018; Salter et al., 2014). The preservative of choice may dictate acceptable long-term storage temperatures, and preservative specifications should be referenced prior to freezing.

Samples stored frozen in LN_2 or at −80°C can be used for most currently available analytical methods, with the exception of specimens destined for tissue culture, which should be placed in tissue culture medium immediately upon collection and stored at 4°C (in a refrigerator). Tissue cultures require specialized fresh tissue handling and preservation, plus long-term specialized live cell culture and storage facilities that makes the collection and preservation of these samples a substantial investment that may be outside the reach of some research groups. While not a viable method for large sample collections, tissue culture is increasingly called for to preserve and expand ultrahigh-quality DNA and RNA genomics and to contribute to future conservation applications (see, e.g., Fritts, 2022; Morin et al., 2020; Morin, Forester, et al., 2021). It is also worth noting that sample-specific processing must occur before freezing samples for metabolomics (such as separating plasma from whole blood; see 3.3 Metabolomics below).

2.1.2 | Sample processing

After collection, most samples will undergo additional processing or subsampling to prepare them for one or multiple downstream analyses. In most sampling scenarios, especially on small boats, it is not always logistically possible or advisable to set up a sterile field for subsampling onsite, therefore the sample may need to be processed at a later time. It is generally preferable to conduct tissue sample processing and subsampling in a sterile laboratory setting. However, in some cases biological samples may require additional subsampling or processing immediately after collection, i.e., while still on the boat or at the field station, before they are transported to their archival locations. In

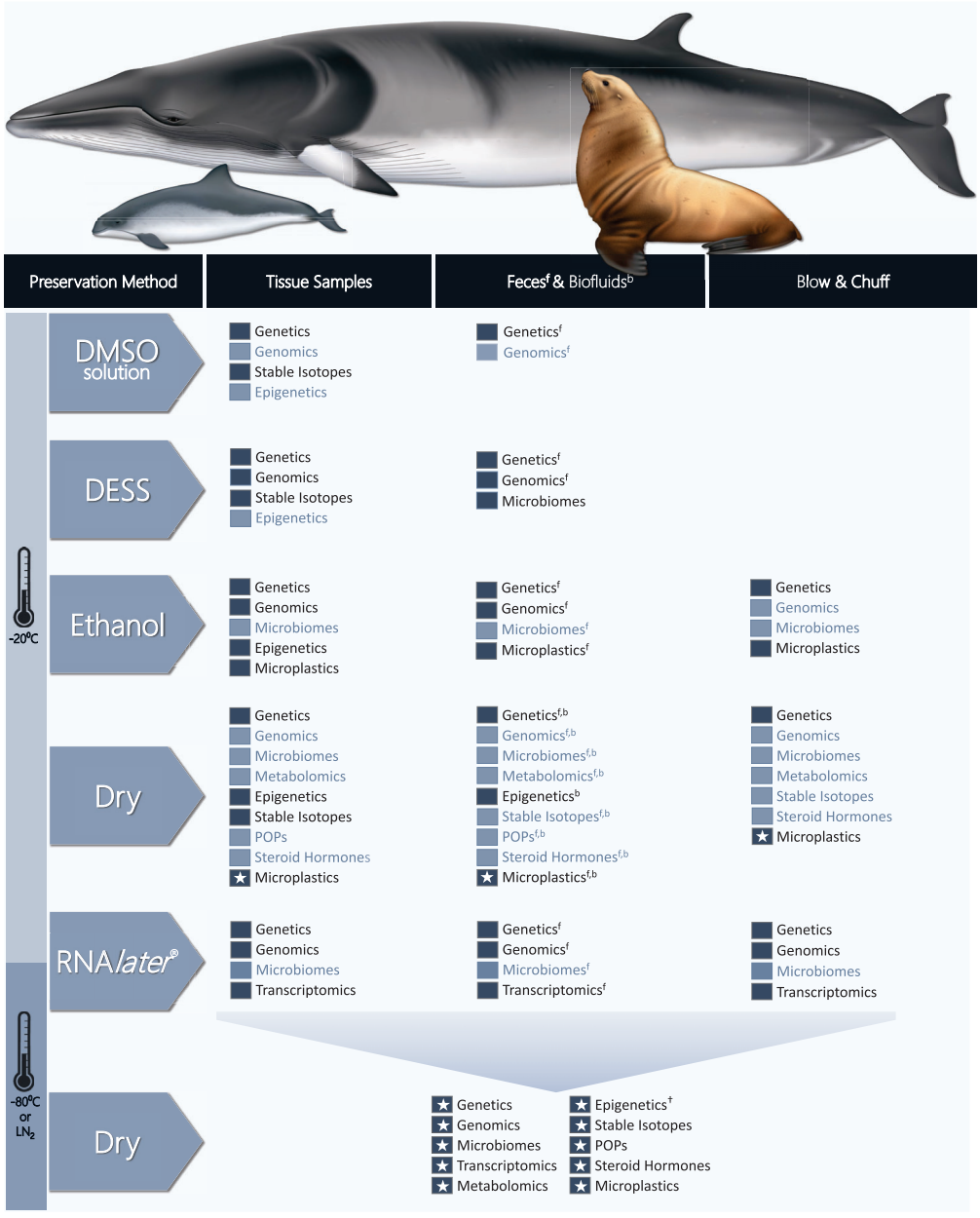

FIGURE 2 A schematic representation of common types of biospecimens collected from marine mammals and common sample preservation methods suitable for a suite of analytical approaches. Color scheme represents the suitability of each preservation method for each analytical approach covered in this manuscript: gray boxes and text indicate preservation methods that are suitable; dark blue boxes and black text indicate preservation methods that are considered to work well for a given analytical approach; a star indicates preservation methods that are strongly recommended based on existing data. In the feces and biofluids column, superscripts refer to whether the preservation method is suited to (f) feces or (b) biofluids, respectively. Suitability rankings in this figure reflect the guidelines outlined for each approach in the body of this paper and referenced literature can be found in the appropriate section for each analytical approach. Preservation methods that were identified as being unsuitable for a given sample type and analytical approach, or were lacking sufficient data to evaluate suitability (noted as "0" or "?" in Table S2), are not listed. †Epigenetic studies have not been conducted using feces, biofluids, or blow/chuff, therefore suitability here reflects only tissue samples.

these cases, samples should be removed from the freezer or chosen preservative for the minimum amount of time needed for subsampling and subsampled on ice whenever possible. Sample processing in the field should also follow best practices for sterile techniques. This includes thoroughly cleaning the workspace and all reusable equipment before processing begins using, at minimum, the bleach and ethanol clean method. If available, an autoclave should also be used to sterilize reusable equipment before use. If multiple samples are being processed, individual sterile fields should be prepared for each sample (e.g., by cleaning individual pieces of aluminum foil with bleach and EtOH, or by using sterile, single use working surfaces such as disposable weigh boats). Sterilization and sample processing should be performed wearing disposable gloves. For microbiome samples, a mask should be worn when feasible. Equipment used to process samples (e.g., forceps or razor blades) may be reused if resterilized between samples using the bleach and ethanol clean method or autoclave if available. All subsamples should be transferred to labeled sterile containers appropriate to the intended use of the sample and returned to the freezer (or chosen preservation method) as soon as possible to minimize sample degradation. If pathogens or other potential health conditions are suspected or known to be present, users should minimize their exposure by performing all handling and processing in a biosafety level 2 cabinet in a laboratory setting.

2.1.3 | Sample archiving and curation

Many factors will influence the choice of long-term sample archiving methods and ultimately impact both the success of sample preservation and the potential for downstream analyses. Variables including sample age and tissue type, field conditions and available facilities, storage conditions, handling, and transport all may impact preservation of valuable biological samples and therefore factor into the decision of how best to preserve those samples (Keighley et al., 2021). Long-term storage methods should account for potential contamination of a sample by its immediate storage environment (e.g., chemical contamination or adulteration of sample due to vial type) or by environmental factors specific to the archive (Waller, 1994).

The gold standard for sample preservation for analytical approaches included in this review is ultracold storage, i.e., −80°C or colder, or cryopreservation, i.e., −153°C or colder (e.g., liquid nitrogen, LN_2). This can be achieved by immediately flash-freezing the tissue sample in LN_2 or nitrogen vapor in a Dewar or other suitable LN_2 storage device, followed by long-term storage at −80°C or colder (Salehi & Najafi, 2014; Wong et al., 2012). Figure 2 illustrates a full breakdown of recommended preservation methods by tissue and analysis type. Ultracold storage or cryopreservation is considered to be the most efficient method for preserving genomic material and other biomolecules as all chemical and biological processes are halted and enzymes that result in degradation (e.g., RNase, DNase, proteinase) are inactivated by flash-freezing in LN_2 (Nagy, 2010; Shabihkhani et al., 2014; Wong et al., 2012). Ideally, long-term sample archives will preserve tissue samples dry, in ultracold (−80°C or below) or cryogenic conditions, as fluid preservatives can contribute to unanticipated complications in the preservation and analytical processes (e.g., De Wit et al., 2012; Gamble, 2014; Kotrba & Schilling, 2017; Nagy, 2010). Some sample types may experience RNA degradation during long-term storage (>7 years) at −80°C (Chu et al., 2002), so preserving subsamples in LN_2 specifically for future potential analyses of gene expression may be prudent where possible (Babel et al., 2020 and see Transcriptomics section). In general, extracting biomolecules (e.g., DNA, RNA, proteins) from tissue and storing them in a molecule-specific buffer at −80°C will protect them from enzymatic activity, oxidative damage, and hydrolysis, increasing the chance of retaining high quality molecules (Fordyce et al., 2013; Oosting et al., 2020). Extracting DNA/RNA from samples prior to long-term archiving can also minimize the potential degrading effects of repeated freeze/thaw cycles over time (Fan et al., 2019) and is beneficial for many, but not all, potential analyses (e.g., chromatin-based genomic mapping, ultralong read sequencing; Dahn et al., 2022).

Where ultracold or cryogenic storage is not feasible due to cost, logistical challenges, lack of facilities, and/or shipping restrictions, short-term storage in liquid preservative followed by long-term archiving at −20°C is recommended, leaving the tissues in the liquid preservative to minimize sample handling. Liquid preservatives such as lab-grade EtOH, DMSO solution, DESS, or RNA*later* have been used successfully and may be appropriate for

long-term archiving of samples for some types of studies (Amos, 1997; Blom, 2021; Kilpatrick, 2002; Moustafa, 2021; Oosting et al., 2020; Seutin et al., 1991; Zimkus et al., 2018); several of these preservatives can be stored at −20°C or − 80°C for additional sample protection (see manufacturer specifications for more details). For ethanol storage, we recommend storing samples in 95% EtOH. Note that denatured alcohol is not appropriate for sample storage, 100% ethanol will often include benzene stabilizers, and lower concentrations of ethanol (<95%) are generally not recommended for sample preservation as samples stored in lower concentrations of ethanol have been shown to exhibit significant degradation after periods as short as a year (King & Porter, 2004). When using liquid preservatives, it is important to consider that not all preservatives are compatible with all downstream applications (Figure 2, Table S2), and that the order in which preservation actions are taken is critical. For example, improperly adding high-salt RNA/DNA preservatives (e.g., RNA*later*) to already frozen specimens will leave the specimen surrounded by, rather than preserved by, fluid (De Wit et al., 2012; Gamble, 2014). Similarly, the dehydrating effect of EtOH causes the release of water from the specimen, diluting the fluid preservative which can have detrimental results if the fluid is not replaced with fresh EtOH one to two days after initial preservation (Gamble, 2014; Nagy, 2010). Regardless of the preservative of choice, the sample-to-preservative ratio is of key importance when preserving biological samples in liquid preservatives. In general, sample preservation should allow for at least five times the volume of liquid to tissue, particularly for very dense tissues or those with very high water content (Nagy, 2010). For some applications, samples may be stored dry at −20°C (see Figure 2), although some studies suggest that storing samples dry at −20°C may be less effective than storing samples in a liquid preservative at −20°C (Rodriguez-Ezpeleta et al., 2013); liquid preservative is generally recommended in addition to storage at −20°C.

The currently available published literature does not provide clear recommendations on the best liquid preservative for use in long-term storage of biological samples when ultracold storage is not available. Most studies directly examining DNA quality are limited to samples stored for <2 years (Dawson et al., 1998; Kilpatrick, 2002; Michaud & Foran, 2011; Moustafa, 2021; Oosting et al., 2020; Seutin et al., 1991). In most of these studies, samples were additionally frozen (e.g., −20°C) and ultracold storage (−70°C or − 80°C) was used as the control treatment for comparison. These studies broadly concur that storage in ethanol, DMSO solution, and DESS for periods ranging from several weeks up to 28 months did not significantly alter the quantity of amplifiable DNA in a sample as compared to ultracold storage, with DESS outperforming the others when it was included in the study. One comparison of fish tissues stored in a range of liquid preservatives highlighted that ethanol (95%–99%), RNA*later*, and DESS preserved the DNA concentration equally well in tissues stored for up to 60 days, although DNA purity was higher for those stored in ethanol versus DESS (Rodriguez-Ezpeleta et al., 2013). DESS is most commonly used at a pH of 7.5–8 (Seutin et al., 1991), but recent studies have shown that EDTA, the active preservation agent in DESS (Sharpe et al., 2020), may be more effective at higher pH (8–10) in the storage of samples for 9–12 months (DeSanctis et al., 2023). Generally, the relatively short time frames of these studies make it challenging to interpolate their applicability to sample archives housing tissues stored over multiple decades.

Preservation solutions most frequently cited in marine mammal studies reference DMSO solution without EDTA (e.g., Morin et al., 2018; O'Corry-Crowe et al., 1997; Torres et al., 2003; Valsecchi & Amos, 1996), largely following an early recommendation from Amos and Hoelzel (1991). Since then, numerous marine mammal genetics and genomics studies have successfully generated sequence data from tissue samples stored long-term using various preservation methods including DMSO solution and − 20°C storage (e.g., Brown Gladden et al., 1997; Leslie & Morin, 2016; O'Corry-Crowe et al., 2018; Parsons et al., 2002; Quérouil et al., 2007; Viricel & Rosel, 2014); however, the rate of sample loss associated with various preservatives and preservation time periods is infrequently reported, making data-based evaluations of long-term storage efficacy difficult. The limited data that are published (Quérouil et al., 2007) suggest that sequencing success may be lower for samples stored for multiple years (or decades) in liquid preservative (e.g., DMSO solution, DESS, or 100% ethanol) without ultracold freezing. One study of cetacean skin samples stored long-term in DMSO solution or 100% ethanol detected amplifiable host DNA in the storage solutions themselves, suggesting that tissue degradation and cell lysis may occur in tissues stored in either of the two liquid preservatives for prolonged periods (2–18 years at −20°C; Robertson et al., 2013).

Researchers should consider again at the archival stage that biospecimen quality (e.g., protein and DNA stability) may be significantly degraded when the sample is thawed, and limiting the number of times a sample is thawed throughout long-term archiving can be beneficial for preserving sample integrity. This may be accomplished by dividing samples into smaller aliquots so that only a portion is thawed for a given experiment (Shabihkhani et al., 2014). Samples preserved in liquid preservatives before freezing are partly protected against DNA/RNA degradation occurring during freeze–thaw cycles (Nagy, 2010). Specific freeze–thaw protective media (e.g., RNA*later*-ICE) may reduce detrimental effects of thawing, but impacts on long-term storage of samples after treatment with these media are unknown. As in the case of short-term storage, commercially available freezers equipped with freeze/thaw cycles are not appropriate for long-term sample storage (Cardona et al., 2012; Koopman et al., 2002; Trana et al., 2015).

2.1.4 | A note on sample metadata

The importance of sample metadata is increasingly recognized as curated tissue collections have grown. Ensuring the integrity of sample metadata, including sampling protocols and deviations from standardized protocols, preserves the sample-metadata connection, supporting downstream analyses and holistic sample sharing agreements across institutions. At a minimum, metadata should include a detailed description of the field conditions and sample collection location, including the date, time, sample number, latitude, longitude, field conditions that might affect the collection of biological samples (e.g., sea state and wind speed), species, sex (if known), age class (if known), anatomical sample site, and collection method. Metadata collection should also include details such as time from collection to preservation, in-field processing techniques (noting deviations from standard techniques), field storage method and duration, number of freeze/thaw cycles before archiving, location and method for long-term archiving, and the number of freeze–thaw cycles a sample has undergone after archiving as it is used in various research projects. It is highly recommended to record collection metadata on a data sheet, notebook or digital platform, rather than (or in addition to) directly onto the sample label as text on sample labels can often become lost or distorted through time and use. When sampling from carcasses, note the amount of time that has passed since death (if known) and degree of composition, as this will affect data quality and downstream interpretability of molecular results from these samples. Noting unavoidable deviations from sample handling protocols in sample metadata is valuable for reference during downstream troubleshooting and interpretation of data/sample anomalies.

Mislabeled samples and incorrect metadata collection can be a source of significant error in studies involving sample collection (Frasier et al., 2009; Stevick et al., 2001). It is worthwhile to consider training all sample handlers in accurate sample labeling and metadata collection techniques, ensuring protocols exist that are up-to-date, and having a second person review the labels and metadata collected to minimize these types of error. Further, when multiple data types are being collected on the same project (e.g., biological samples and photographs, videos, or acoustic data), ensuring clear communication among data streams is recommended.

3 | 'OMICS: SAMPLE PRESERVATION FOR SEQUENCING AND OTHER 'OMIC ANALYSES

3.1 | Genetics/genomics

Sanger sequencing, or first-generation sequencing (Sanger et al., 1977), has been the bedrock of marine mammal genetics for over three decades for species identification, phylogenetics and population genetics. Sanger sequencing is a flexible and somewhat forgiving technique that allows high quality genetic sequences up to about 1,000 base pairs (bp; Crossley et al., 2020) to be generated from marine mammal tissue and body parts that are degraded and/or

stored in a variety of media. While a sterile environment is not required for sample preservation if processing is limited to Sanger sequencing, a clean workspace and specific protocols should be in place to minimize contamination between samples and maximize future potential for tissue samples and extracted DNA. For short term preservation (8–12 hr), samples intended for Sanger sequencing can be preserved dry in sterile vials, or sterile vials with liquid preservative (e.g., EtOH, DMSO solution, or DESS), and stored temporarily in a cooler on wet or dry ice (Michaud & Foran, 2011; Mulcahy et al., 2016). For long term preservation, if ultracold or cryogenic freezer storage is unavailable, samples should be preserved in liquid preservative at −20°C, following the general preservation guidelines outlined in 2.1.3 Sample archiving and curation above.

DNA used in next generation sequencing studies, e.g., mitogenome sequencing and whole genome sequencing, is often more sensitive to reduced DNA quality than traditional Sanger sequencing (Lutz et al., 2011; Mayjonade et al., 2016; Nishii et al., 2023) due to the exponential increase in sensitivity and sequencing depth. Sterile sampling and processing techniques are particularly important for molecular genetic or genomic approaches involving next generation sequencing to avoid contamination. GTseq, RADseq, and mitogenome sequencing have been successfully performed using tissue stored long-term in both EtOH and DMSO solution, as well as tissues stored frozen at −80°C without preservative (e.g., Albertson et al., 2022; Batley et al., 2019; Morin, Forester, et al., 2021). However, protocols such as RADseq that rely on restriction enzymes to cut DNA at very specific places in the genome may be affected by degradation of tissues that are not stored at −80°C or lower (Graham et al., 2015), but published studies are lacking to compare across preservation methods. Preliminary assessment of archived samples to assess DNA quality (i.e., evaluation of DNA degradation) may be useful for ensuring downstream data quality in all next generation and genomic sequencing applications.

Standards for reference genome assemblies have evolved rapidly as technologies for long-read sequencing - e.g., PacBio and Nanopore sequencing and chromatin linkage methods (Hi-C; Burton et al., 2013), optical mapping (Weissensteiner et al., 2017) - have allowed highly contiguous, complete chromosome-length assemblies (Rhie et al., 2021; Whibley, 2021; Whibley et al., 2021). These methods all require very high-quality tissue samples to yield the ultrahigh-quality DNA and chromatin structure, as well as RNA (preferably from multiple tissues) that can be sequenced to improve annotation of genes, and live tissue cultures are quickly becoming the platinum standard tissue used to generate complete and error-free genome sequences from mammalian species (e.g., Rhie et al., 2021). Current best practices still call for cryopreserved fresh tissues, stored in LN_2 or ultracold freezers without thawing until extraction, or cultured cells (Blom, 2021; Dahn et al., 2022; Morin, Archer, et al., 2021). However, as large genome consortia strive to generate reference genomes from more species, multiple preservation methods have shown promise for at least short-term preservation of ultrahigh-quality DNA, in particular liquid preservatives with simple refrigeration for initial storage and transport, though DNA quantity and quality can vary by tissue type and storage conditions (Dahn et al., 2022). In a comparative study of preservation methods conducted by the Vertebrate Genome Project, storage temperature was found to be the strongest predictor of ultrahigh molecular weight fragment lengths. Immediate flash-freezing remains the sample preservation gold standard, however samples preserved in 95% EtOH or DESS showed little degradation when stored at 4°C for 6 hr and still yielded adequate amounts of ultrahigh molecular weight DNA for up to one week (Dahn et al., 2022). Commercial preservatives such as Allprotect (Qiagen), RNA*later*, and DNAgard (Sigma-Aldrich) performed less well, and DNAgard is not suitable for use with Hi-C library preparation, but these preservatives may be preferable in some cases to provide greater ease of use and transport (Dahn et al., 2022).

3.2 | Transcriptomics

Gene expression and high throughput sequencing of the transcriptome can be used to reveal gene activity at a particular moment in time; additionally, transcriptomics provides an extensive genomic resource for biomarker discovery (e.g., Hoffman, 2011; Humble et al., 2016; Jung et al., 2011; Khudyakov et al., 2015). While DNA can remain relatively stable in tissue following sample collection without any preservation, RNA is prone to rapid degradation after

tissue sampling and appropriate sample preservation is critical to preserve integrity. In addition, gene expression continues in isolated tissues until preservation, and preserving the tissue as soon as possible is essential for capturing the transcriptomic profile at the moment of collection. The greatest variability in RNA quality is introduced at the preanalytical stage immediately after tissue collection. Temperature during transport, time elapsed between collection and stabilization in a buffer or transfer to ultralow temperatures are all important factors affecting RNA integrity (Caixeiro et al., 2016; Choi et al., 2016; Vincek et al., 2003). In general, tissues that are flash-frozen immediately after collection, with or without stabilization buffer, are shown to yield the highest quality RNA (Choi et al., 2016; Wong et al., 2012); however, some studies indicate that preserving tissue in preservatives such as RNA*later* or Allprotect before long-term cryogenic or ultracold freezing may result in higher quantities of RNA (Sherker et al., 2013; Wolfe et al., 2014). RNA quality and gene expression profiles have been shown to be stable for up to 16 hr postcollection, as long as the unpreserved tissue is kept on ice (Micke et al., 2006). The application of EtOH to living cells has been shown to alter the expression of some genes related to stress; the effects of using EtOH to store biological samples for gene expression studies has not been directly tested and is unknown (Li et al., 2005).

Collection and preservation methods resulting in high-quality RNA in sufficient quantities have been challenging due to limitations commonly associated with fieldwork conditions (Camacho-Sanchez et al., 2013; Gallego Romero et al., 2014). When flash-freezing in the field isn't available, a number of commercially available RNA stabilizing buffers may provide adequate or improved preservation, including RNA*later*, PAXgene Blood RNA Tubes (BD Biosciences), Allprotect tissue reagent and DNA/RNA Shield (Zymo Research), the latter two with capabilities to preserve multiple molecular components. According to the manufacturer's protocols, RNA*later* stabilizes RNA at room temperature (25°C) for 1 week and at refrigerator temperatures (4°C) for 1 month. PAXgene Blood RNA system allows stabilization of RNA for up to 3 days at room temperature (18°C–25°C), and for up to 5 days at refrigerated conditions (2°C–8°C). Allprotect tissue reagent stabilizes RNA and protein at room temperature (15°C–25°C) for 1 week and at refrigerator temperatures (2°C–8°C) for 12 months, however, it is relatively expensive and harder to work with due to its viscosity (Salehi & Najafi, 2014). On the other hand, DNA/RNA Shield stabilizes RNA at ambient temperatures (4°C–25°C) for at least 1 month. Additionally, all these preservatives can be used for long-term storage of the tissue at −20°C or colder. In particular, RNA*later* has revolutionized field collection of tissue samples by enabling RNA preservation at ambient temperatures often much longer than recommended by the manufacturer (Caixeiro et al., 2016; Camacho-Sanchez et al., 2013; Gayral et al., 2011; Mutter et al., 2004). RNA*later*-ICE (Ambion), which enables transitioning of previously frozen tissue into an RNA*later* preserved state, has also been successfully utilized (Van Dolah et al., 2015). However, one study suggests that RNA*later* may elicit a physiological response resulting in a bias in transcriptome profiles in the form of enrichment for functional categories that are involved in RNA processing when compared with flash-frozen samples (Passow et al., 2019).

The selection of a preservation buffer also depends on tissue type. Both RNA*later* and PAXgene Blood RNA Tubes have been successfully utilized in cetacean gene expression and transcriptomic studies including blood (Chen et al., 2015; Foote et al., 2015; Mancia et al., 2010; Morey et al., 2016; Unal et al., 2021) and skin (Neely et al., 2017; Trego et al., 2019; Unal et al., 2018; Van Dolah et al., 2015; Wang et al., 2021). RNA*later* has also been utilized to preserve cetacean blow samples (Rhodes et al., 2022; Richard et al., 2022). However, technical guidance from ThermoFisher Scientific suggested that RNA*later* solution density may reduce or prevent effective precipitation of cells in suspension. Alternatively, DNA/RNA Shield allows precipitation of the cells while inactivating infectious agents, and samples that stay in suspension can be processed without reagent removal. DNA/RNA Shield has successfully been utilized for sample preservation for blow collections from belugas resulting in generation of multiyear gene expression data (E.U., unpublished data).

3.3 | Metabolomics

Metabolomics assesses the small-molecule ($\lesssim$1,500 Da) chemical intermediates of metabolic reactions, i.e., metabolites (Liu & Locasale, 2017). Relative to the other primary 'omic fields (genomics, transcriptomics, and proteomics), metabolomics lies nearest to the biological phenotype (Wishart, 2019) and has been used in a variety of

marine mammal applications, including characterizing metabolic changes following food restriction (Houser et al., 2021; Olmstead et al., 2017), responses to environmental perturbation/disturbance (Pasamontes et al., 2017), and discovering biomarkers of health status (Borras et al., 2017). Metabolomic samples collected from marine mammals most commonly include blood and other biofluids, tissue, and feces. The critical aspect in metabolomics studies is consistency—each sample should be collected, processed, and stored in an identical manner to minimize the effect of postsampling alterations—generally processing samples and freezing them as rapidly as possible to minimize any changes postsampling (e.g., continued metabolism).

Several biofluids, including blow, whole blood and serum, can be used in metabolomic studies, but blood plasma (collected in EDTA vacutainers) is the most common sample type (Kennedy et al., 2021). Care is needed to keep blood samples cool, but unfrozen, to prevent lysing of erythrocytes by avoiding direct contact of ice with the walls of the vacutainer. Delayed separation of hematocytes from plasma affects the measured metabolome (Jain et al., 2017), so samples must be centrifuged promptly ($\lesssim$2 hr), in the field if possible. Other biofluid samples (e.g., urine, milk, and respiratory blow) must be collected into clean (nonsterile is acceptable) containers compatible with metabolite analyses (e.g., clean polypropylene or glass vials Giskeødegård et al., 2019). Best practice is to rapidly freeze plasma and other biofluid samples immediately on dry ice or in a LN_2 dewar or dry shipper and store frozen at $-80^{\circ}C$ until subsequent analyses (Smith et al., 2020). Ideally, samples should be shipped overnight on dry ice to a metabolomics facility for final processing, however, a recent study found that freeze–thaw cycles and extended thawing at 4°C had little effect on plasma metabolite levels (Kennedy et al., 2021).

For skin, blubber, and muscle tissues destined for metabolomic analyses, sterile, disposable biopsy tools should be used, but properly cleaned instruments (refer to 2 General considerations above) would be appropriate in many circumstances (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists, 2016). Target tissue samples are frequently "contaminated" with surrounding tissue at the time of extraction (e.g., blood, connective tissue); as with other methods such as transcriptomic and proteomics, it may be best to perform a rough cleaning of the sample tissue using dissection tools or rinsing in physiological saline before transferring to cryosafe vials (e.g., polypropylene tubes). This handling protocol should be consistent across all samples within the study and standard collection protocols should be used. Tissue samples are highly metabolically active and flash-freezing in LN_2 (preferred) or on dry ice and storing samples at $-80^{\circ}C$ until analysis is necessary to stop cell metabolism.

A variety of fecal collection and storage methods have been used in metabolomic studies of nonmarine mammals, with varying influences on metabolomic measurements (Karu et al., 2018). Marine mammal fecal collection is often opportunistic and generally occurs under varying field conditions. The method of fecal sample collection and processing (e.g., endoscopically sampled versus ex vivo sampling; processing in the field versus in the lab) can affect the measured metabolome, so consistent collection methods are important across a study (Couch et al., 2013). To the extent possible, entire fecal samples should be collected using clean (nonsterile is acceptable) collection equipment free of contamination from previous samples and stored in a clean container. Fecal samples can be heterogeneous, so collecting a partial fecal sample may not be representative of the entire sample; after collecting a fecal sample, the entire bolus should be homogenized to avoid within-sample variance (Santiago et al., 2014), and subsample(s) transferred to a storage vial (e.g., clean polypropylene or glass vials). Samples can be stored in EtOH at room temperature (Karu et al. 2018 recommend a 1:5 feces:EtOH ratio), or at $\lesssim -10^{\circ}C$ if available; the important factor is that all samples in a study be stored consistently. Samples can then be transported for analysis on dry ice (see figs. 1 and S1 in Karu et al. 2018). To our knowledge, metabolomics has not yet been performed on marine mammal fur, vibrissae, or other keratin compounds. Few specific sample collection demands would be required, but substantial development of appropriate washing and extraction techniques would be needed.

3.4 | Microbiomes and metagenomics

A growing body of research highlights the value of examining microbial communities (microbiomes) associated with marine mammals, and their functional potential (metagenomes), to infer relationships between

microorganisms, animal health and ecology (Apprill, 2017; Bik et al., 2016; Dudek et al., 2017; Nelson et al., 2015; Sanders et al., 2015; Van Cise et al., 2020). Adhering to best practices, including attention to sterile or aseptic technique, is essential for microbiome analysis, to prevent sample contamination from the marine environment (e.g., from seawater and sand), human handlers (e.g., from skin or exhalates), processing location, and other samples collected concurrently.

Careful study design is important in microbiome and metagenomics studies due to a greater number of potential sources of bias and variation. Study design will include a precise definition of the sample site, as subtle differences in body biogeography may influence microbial community composition (Costello et al., 2009; Donaldson et al., 2016; Jones et al., 2018; Proctor et al., 2018; Simón-Soro et al., 2013), or recoverable microbial biomass which affects susceptibility to contamination (Eisenhofer et al., 2019; Quince et al., 2017). Host species is also an important consideration to meet study objectives; whereas feces (frozen without preservative) has been successfully used to characterize the fecal metagenome of baleen whales (Sanders et al., 2015), similar attempts in sea otters were instead reflective of the host's diet, at least in some cases (Dudek et al., 2022). Furthermore, collection methods as well as sampling approaches can influence the microbial community. For example, although significant differences in microbial community structure have been documented between fecal or mucus samples and the surrounding seawater (Bik et al., 2016; Raverty et al., 2017; Rhodes et al., 2022), fecal samples collected from seawater will contain some seawater-associated microbiota, and swabs collected from dead, anesthetized or captive animals may have altered community composition (Garber et al., 2020; Roy et al., 2021; Serbanescu et al., 2019; Wang et al., 2019).

To minimize sample contamination and protect sample integrity for microbiome analyses, sample handlers should wear disposable gloves and face masks (where possible) and sterilize sampling surfaces and equipment between samples (Bykowski & Stevenson, 2020); e.g., using the bleach and ethanol clean method if an autoclave or Bunsen burners are not available. In addition to sterilizing equipment using the bleach and ethanol clean method, laboratory-based microbiome analyses require an additional UV sterilization step in which equipment is exposed to UVC light for 30 minutes or more to fully eradicate any microbes on the surface (Kowalski, 2009). UVC at 254 nm is effective for eliminating microbes as well as free DNA/RNA from laboratory or field equipment; the amount of time equipment should be exposed to UVC radiation will depend on the tissue type (Gefrides et al., 2010; Gršković et al., 2013).

During sampling campaigns, negative sampling controls are valuable for detecting exogenous microbial contamination (Apprill, 2017; Apprill et al., 2014; Eisenhofer et al., 2019). For example, collecting samples from adjacent seawater and dietary items can facilitate microbial source-tracking downstream (Apprill et al., 2014; Bik et al., 2016; Sanders et al., 2015). Laboratory negatives, in which no sample is present but otherwise all reagents and handling protocols are followed, should ideally be incorporated throughout sample processing and downstream lab procedures as they may also help account for reagent or other lab-based bacterial contamination that can affect microbiome datasets and can be otherwise difficult to discern, especially in low-biomass samples.

The gold standard for preserving community structure for microbiome studies is immediate cryopreservation (e.g., LN_2) without preservative, followed by storage at −80°C or lower (Choo et al., 2015; Goodrich et al., 2014; Rissanen et al., 2010). Freezing at −20°C will yield similar results (Bundgaard-Nielsen et al., 2018), but care should be taken to minimize the number of freeze–thaw cycles, as this can alter microbial community composition and degrade DNA (Sergeant et al., 2012). If necessary, samples may be held frozen on dry or wet ice and transferred to a freezer immediately upon return to the lab (Apprill et al., 2014; Bik et al., 2016). Short-term refrigeration of samples (72 hr) has been shown to yield comparable results to flash-freezing (Choo et al., 2015); however, a recent study suggested that refrigeration may alter community structure (Poulsen et al., 2021). Immediate processing of fresh samples, while considered by some as another best-practice technique, is not a practical option for most marine mammal researchers, so freezing (−20°C or − 80°C) prior to DNA extraction is recommended to promote comparability between studies (Poulsen et al., 2021).

While liquid preservative buffers may be used to stabilize the samples chemically at room temperature, there may be undesired side effects such as altering microbial community composition and inhibiting potential future metabolomic analyses (Goodrich et al., 2014; Gorzelak et al., 2015). Kit-based OMNIgene-Gut is an appropriate

alternative to flash-freezing for metagenomic studies (Anderson et al., 2016; Ilett et al., 2019), although the Copan FLOQSwab-ADT method produced more robust results (Pribyl et al., 2021). RNA*later* performed well for short-term storage at room temperature but lost stability after two weeks (Song et al., 2016) and has been shown to result in reduced microbial DNA yields in fecal samples (Gorzelak et al., 2015). Long-term preservation in EtOH is an acceptable and cost-efficient option but may result in reduced DNA yield. DMSO solution has also been used in one microbiome study, but its effect on microbial DNA has not been tested (Toro et al., 2021). One recent study that developed the use of DESS for fecal microbiome wipes found that this preservation method was effective over periods up to 8 weeks (Hua et al., 2022). For fecal samples, fecal occult blood test cards (FOBT) are also an acceptable and accessible option (Byrd et al., 2020). Regardless of the chosen preservation approach, all samples should be treated in a consistent manner.

3.5 | Epigenetics

The study of how cells control gene activity without altering the genetic sequence, epigenetics, is a growing field providing insight into the effects of both environmental and behavioral stressors. Although still an emerging field in marine organisms, epigenetic analyses in marine mammals can extend our understanding of phenotypic plasticity or health and disease, and provide useful biomarkers of age and stress (Barratclough et al., 2021; Beal et al., 2019; Bors et al., 2021; Crossman et al., 2021; Horvath, 2013; Maegawa et al., 2010; Polanowski et al., 2014; Tanabe et al., 2020; Weaver et al., 2004).

The various carriers of epigenetic information include DNA methylation, histone modifications and noncoding RNAs, and best practices for sample handling and processing depend upon marker selection. DNA methylation refers to the addition of a methyl group to a cytosine residue in DNA that occurs almost exclusively at CpG dinucleotides (i.e., a cytosine located 5′ of a guanine). This strong covalent carbon-to-carbon bond is stable and relatively robust to degradation, and best practices for sampling are the same as those for genomic DNA (see Genetics/Genomics section). In humans, DNA methylation has been shown to be stable in genomic DNA isolated from decades-old dried blood spots (Staunstrup et al., 2016), up to 30-year old formalin-fixed paraffin-embedded (FFPE) tissues (Kristensen et al., 2009) and in human placental tissue at room temp for up to 24 hr (Vilahur et al., 2013). However, it should be noted that for some genome-wide approaches, DNA methylation quantification can be affected by DNA quality (Vilahur et al., 2013) and should be evaluated prior to use in epigenomic applications. While DNA methylation has been measured in skin tissues preserved in DMSO solution (Bors et al., 2021), the effects of DMSO solution on tissue methylation profiles is currently unknown and warrants further examination. Histone modifications are chemical tags attached to histone proteins and are evaluated using chromatin immunoprecipitation combined with high-throughput sequencing (ChIP-Seq). ChIP-Seq approaches have been applied in marine mammals (Villar et al., 2015), but studies are sparse. It is considered best practice to crosslink freshly sampled tissues, although protocols have been developed for performing ChIP-Seq on FFPE samples (Cejas et al., 2016). As such, field sampling for histone modification analysis without laboratory support remains technically challenging as tissue samples must be processed prior to freezing or storing; processing these samples requires a multistep, sterile protocol that is best performed in a laboratory setting (Schmidt et al., 2009). Noncoding RNAs (ncRNAs) play a role in modulating gene expression and can be isolated from tissues that have been preserved following best practices for sterile sampling (to avoid contamination) and processing of total RNAs (see 3.2 Transcriptomics above). In addition, total RNA that has been stored according to best practices (see 3.2 Transcriptomics above) can also be processed to analyze ncRNAs.

3.6 | Proteomics

Proteomics provides a tissue-specific, proteome-wide survey of translated proteins in a sample, and is the study of protein "expression" to provide insight into an organism's health and physiology at the time of sampling. Minimally

invasive sampling from living tissue can limit the hypotheses tested with this technology, but researchers have successfully applied proteomics in marine mammals to investigate, for example, health impacts of disease (e.g., Nelly et al., 2018), the impacts of captivity on physiology (e.g., Tian et al., 2020), and the impact of physical activity on physiology (e.g., Miller et al., 2017). Since proteins are the molecules that directly influence phenotypic change, proteomics is a powerful tool for better understanding marine mammal physiology.

Acquiring samples for proteomics from marine mammals, especially wild specimens, requires careful consideration of available tissues and how their analysis can support scientific inquiry. Similar to metabolomics, transcriptomics, and epigenomics, proteomic profiles are tissue-specific since each tissue has its own specific function supporting the whole organism, and care must be taken to sample only the tissue of interest, avoiding contamination from other tissues. For most wild marine mammals, this narrows the tissues available for analysis to skin (Neely et al., 2018), blubber (Deyarmin et al., 2019; Kershaw et al., 2018; Khudyakov et al., 2018; Neely et al., 2018), chuff (Bergfelt et al., 2018), or urine/feces (Neely et al., 2018). For a very small number of species/populations with intensive health monitoring programs, muscle (Shero et al., 2019; Voisinet et al., 2015), blood/serum (Desoubeaux et al., 2019; Lazensky et al., 2021; Miller et al., 2017; Neely et al., 2013, 2018; Sobolesky, Harrell, et al., 2016; Sobolesky, Parry, et al., 2016; Tian et al., 2020), and cerebrospinal fluid (Neely et al., 2015) provide additional sample types suitable for proteomics. Recently deceased animals can be sampled for proteomics (Kershaw et al., 2018), but proteins rapidly degrade in dead and dying tissue and may not provide a high quality or accurate dataset. Similar to other methods, tools used to remove tissue samples for proteomics must be thoroughly cleaned and disinfected using the bleach and ethanol clean method or autoclaved between samples.

To preserve the proteome in its closest state to in vivo function, tissue specimens should be immediately flash-frozen in LN_2 or in an EtOH/dry ice slurry and then transferred to a −80°C freezer for long-term storage. Many ex vivo proteins degrade quickly, altering the proteome from its natural, functioning state, and inhibiting accurate interpretation of the specimen's physiological status. Protease inhibitors can be added to the tissue to decrease protein degradation rates. Alternatively, recent work in mammals and plants suggests that incubation in RNA*later* at room temperature prior to freezing at −80°C has minimal impact on the proteome (e.g., Bae et al., 2019; Bennike et al., 2016; Kruse et al., 2017; Zhu et al., 2019). Tissue storage at −20°C has been successful in some marine mammal proteomics studies (Desoubeaux et al., 2019; Kershaw et al., 2018; Neely et al., 2018), but −80°C is the biomedical standard and storage at warmer temperatures measurably alters the proteome (Lee et al., 2010). Repeated freeze–thaw cycles can lead to sample degradation, but long-term storage, at least for up to four years, does not appear to impact proteome profiles in mammal serum (Mitchell et al., 2005) and proteomic profiles seem to be unimpacted for up to 30 years in formalin-fixed and paraffin-embedded human tissue (Balgley et al., 2009).

4 | BEYOND 'OMICS: SAMPLE PRESERVATION FOR CHEMICAL, MICROPARTICLE, AND SMALL MOLECULE ANALYSES

4.1 | Hormones

Most endocrine investigations of free-ranging marine mammals have focused on the relatively stable steroid class of hormones that are derived from cholesterol, including sex steroids (progesterone, androgens, estrogens) and corticosteroids (e.g., cortisol, corticosterone, aldosterone; Champagne et al., 2018; Kellar et al., 2009, 2015; Mello et al., 2017; Mingramm et al., 2019). These lipophilic molecules are frequently studied in blubber (Kellar et al., 2015) but are also detectable in numerous alternative sample types, including feces (Hunt et al., 2019; Rolland et al., 2012), skin (Bechmann et al., 2021), respiratory blow (Burgess et al., 2016, 2018), claws (Karpovich et al., 2020), and vibrissae (Keogh et al., 2021), and can be collected from deceased subjects or museum specimens in baleen (Hunt et al., 2014, 2017), earplugs (Trumble et al., 2018), and teeth and bone (Charapata et al., 2018; Hudson et al., 2021). For brevity, this section will focus primarily on the collection and storage of blubber samples, currently the most common bio-sample used for hormone analyses.

Anatomical sample site should be noted at the time of collection as variance can affect expected blubber hormone concentrations (Aguilar & Borrell, 1990; Deslypere et al., 1985; Kershaw et al., 2017; Koopman et al., 1996). Hormone concentrations in blubber reflect an average over the previous tens of minutes to tens of hours depending on the species and conditions associated with the individual prior to sampling (Beaulieu-McCoy et al., 2017; Champagne et al., 2018; Kellar et al., 2006). It is worth noting that, particularly with stress-related hormones (e.g., cortisol), sampling activities can alter the detected hormone levels if samples are not collected rapidly, e.g., within 60 min or less of the initiation of the stress event (see example study in bottlenose dolphins (Champagne et al., 2018).

Blubber and fecal samples should be collected in clean (sterility is not required) collection jars or vials and placed immediately on dry ice or in a LN_2 dewar or dry shipper (Kley & Rick, 1984; Toone et al., 2013). If this is not possible, samples may be stored at temperatures below 0°C for up to 8 hr (e.g., in coolers with reusable ice packs), the duration of which will depend on the ambient temperature (Lemos et al., 2020). Respiratory hormones are best detected when blow is collected in polystyrene dishes and rinsed with EtOH before storing cold and later transferring to long-term storage at −20°C or − 80°C (Burgess et al., 2016, 2018). To minimize problems associated with sample thawing and seeping of lipids, tissue biopsy subsampling is best conducted in a laboratory setting where tissues can be subsampled on a cold surface (4°C). If it is imperative that sample processing occur in the field where a laboratory setting is not available, the sample should be processed on a surface that has been prechilled and remains on ice during processing; however, processing these samples in the field is not a recommended practice. Steroid hormone measurements are likely less sensitive to common contamination processes compared to other 'omics techniques described above (do Rego & Vaudry, 2016; Fang et al., 2016). Nonetheless, it is recommended to follow best practices to minimize sample contamination as there are common anthropogenic compounds that can bind to steroid receptors (Lilienthal et al., 2006).

The relative stability of steroid hormones allows some flexibility across a range of sample storage conditions (Bolelli et al., 1995; Hunt et al., 2017; Kellar et al., 2006). For interim storage and long-term archiving, blubber samples should be maintained at −80°C or below, although several studies have demonstrated usability of samples stored at −20°C for multiple years particularly for applications targeting large differences in hormone concentration (Kellar et al., 2006, 2009; Kley & Rick, 1984; Toone et al., 2013). Less is understood about the suitability of samples stored in liquid preservatives and as such they are not recommended as these solutions may pull target hormones away from the tissue (Sheridan, 2004).

4.2 | Stable isotopes

Stable isotopic analyses are a powerful means to examine trophic ecology, inferring dietary preferences and trophic shifts predictably reflected in the ratio of stable isotopes in a consumer's tissues (Fry, 2006). Carbon stable isotope ratios (i.e., $^{13}C/^{12}C$ or $\delta^{13}C$), for example, change very little between diet and consumer, which makes this ratio a convenient tracer of habitats the consumer moved through. In contrast, nitrogen stable isotope ratios (i.e., $^{15}N/^{14}N$ or $\delta^{15}N$) become more enriched at each trophic level making it suitable for estimating a consumer's trophic position (Post, 2002). Recent advances in compound specific (i.e., amino and fatty acids) stable isotope analyses are further improving the understanding of metabolic processes and trophic relationships, providing increased resolution for specific amino acids (Dale et al., 2011).

Samples intended for stable isotope analyses should follow sterile handling techniques (see General Considerations) to avoid cross contamination among individuals or tissues (in the case when multiple tissue types are collected, e.g., blubber, organs, etc., from the same individual). Sterile handling techniques should also be used when subsampling and homogenizing tissue for stable isotope analysis, and modified to include rinsing all working surfaces and equipment with acetone prior to processing (Gates et al., 2020). To prevent tissue degradation during subsampling, thawing should be minimized by working on one sample at a time, on an ice block covered by acetone-rinsed aluminum foil, and returned immediately to a −80°C freezer for a minimum of 1 hr prior to lyophilization, or for long-term storage (Gates et al., 2020).

Tissues collected for stable isotopic analyses are best stored frozen (Busquets-Vass et al., 2017; Kaehler & Pakhomov, 2001; Newsome et al., 2010). Burrows et al. (2014) reported that stable isotope values of killer whale skin remained stable for up to 14 days at 4°C or lower, and values were stable for at least a year when skin and blubber samples were stored at −20°C or − 80°C; although only minor advantages were reported when storing samples at −80°C rather than −20°C, −80°C is recommended for long-term storage when possible. For animal carcasses, confidence in stable isotope values will be low without a known time of death or visual evidence indicating little or no postmortem tissue decay, as decomposition has been observed to significantly change $\delta^{15}N$ within 3 days (Burrows et al., 2014). Slight differences in stable isotope values were reported for lipids extracted from cetacean skin samples when comparing samples that were frozen without preservative to those preserved in a DMSO solution and stored either frozen or at room temperature (Burrows et al., 2014; Lesage et al., 2010), including samples preserved in DMSO for multiple decades (Newsome et al., 2018). However, subtle effects due to storage differences have the potential to mask isotopic differences among population groups or species (Burrows et al., 2014; Ruiz-Cooley et al., 2011).

4.3 | Toxic contaminants

Analysis of contaminants in marine mammal tissues is routinely conducted for legacy contaminants such as polychlorinated biphenyls (PCBs), polybrominated diphenyl ethers (PBDEs) and organochlorine pesticides (Krahn et al., 2007; Montie et al., 2010; O'Hara et al., 1999; Ylitalo et al., 2001). In recent years, interest has increased in other types of pollutants such as perfluorinated compounds, often referred to as contaminants of emerging concern (CEC). The primary concern in tissue sampling and storage for contaminant analysis is preventing degradation of pollutant molecules by enzymatic and nonenzymatic pathways. This is best achieved by freezing samples as soon as possible after collection. Short-term (several months) storage at −20°C is usually acceptable, with longer term (>2 years) storage at −80°C most desirable (Muir & Sverko, 2006). If a sample cannot be immediately frozen upon collection (−80°C or LN_2), temporary storage in a 1°C cooler for up to 8 hr is acceptable. In general, the use of preservative solutions such as formalin or RNA*later* should be avoided as they may leach or structurally alter analytes from the tissue (Muir & Sverko, 2006).

Additional considerations during both sample collection and sample storage include the composition of the storage container, preventing contamination, and ensuring uniformity and representativeness of the sample. Contamination can occur from deposition of airborne particulates and leaching of chemicals from the storage container. The latter can be prevented by using a storage container made of an appropriate material (e.g., Teflon) and thoroughly rinsing and cleaning all sampling and processing equipment prior to use with methanol (or acetone, if methanol is unavailable). Aluminum foil is frequently used to wrap solid tissue samples because it is easily rinsed with solvent (e.g., methanol or acetone) and can be baked at 450°C for several hours prior to use. All commercially purchased tubes or other sampling supplies should be rinsed with solvent and oven baked at 450°C (if possible) prior to coming in contact with the sample.

The distribution of contaminants within a tissue is typically heterogeneous (e.g., Aguilar, 1985; Tilbury et al., 1997; but see Calambokidis & Barlow, 1991; Granby & Kinze, 1991); therefore, consideration of the sample representativeness is warranted and careful documentation of sampling location relative to the animal's body is key to ensure consistency with past and ongoing sampling efforts. If study resources permit, collecting multiple samples from different regions of a large animal is helpful to assess the overall pattern of contaminant distribution among tissues.

4.4 | Microplastics

The ingestion of microplastics (plastic particles <5 mm in size) has been heavily documented in a wide range of marine species, from the base of the food chain to top predators (Cole et al., 2013; Maes et al., 2020; Nelms, Barnett,

et al., 2019; Setälä et al., 2014). Recent methodological advances allow microplastics analysis to be seamlessly integrated with fecal prey metabarcoding to investigate the relationship between microplastic ingestion, diet, and trophic transfer, better informing our understanding of trophic level interactions (Nelms, Perry, et al., 2019).

Collecting fecal samples or gut contents (during postmortem processing) for microplastics analyses requires strict contamination control protocols to ensure accurate results and avoid particle contamination in the field or laboratory. Key sampling practices to support the isolation of microplastic particles include (1) using nonplastic sampling equipment (e.g., glass or metal) and ensuring all sampling equipment is free of both microplastics and biological contaminants that may affect metabarcoding, and thoroughly rinsed with prefiltered Milli-Q water, (2) limiting possible exogenous microplastic contamination during sample collection and/or accounting for it with field collection of negative controls, (3) sampling upwind of potential sources of contamination (e.g., clothing) and monitoring airborne contamination by exposing damp filter paper to sample collection conditions, (4) processing samples in a laboratory setting with a positive pressure laminar flow hood, and finally (5) storing scat or gut contents at −20°C or below for metabarcoding purposes (see Zantis et al., 2021 for a comprehensive review). In cases where plastics cannot be avoided, e.g., plastic lids on collection vials, protocols incorporating sampling controls can be used to identify, and account for, potential sources of exogenous microplastic contamination (e.g., Miller et al., 2021). Field scientists collecting samples intended for microplastic analysis should avoid wearing clothing with plastics or synthetic fibers to the extent possible during sample collection to limit sources of field contamination (Gwinnett & Miller, 2021). Generating a reference library of synthetic materials and clothing worn during sample collection may help to identify microparticle contamination downstream. Nelms, Parry, et al. (2019) provide a practical framework for parallel isolation of microplastics and DNA for prey metabarcoding, demonstrating the potential value of extending the use of fecal samples collected from wild marine mammals beyond 'omics.

Analysis of archived fecal samples can be challenging if protocols to avoid exogenous contamination were not adopted at the time of sample collection. However, archived and opportunistically collected samples represent valuable opportunities to examine temporal and spatial changes in microplastic particle exposure and consumption. Acknowledging potential sources of field contamination, maximizing sample numbers to minimize sampling artifacts and capitalizing on opportunities for collecting contemporary samples using comparable methods that also incorporate field/lab controls provide avenues for minimizing the effects of contamination while generating valuable data on microplastics consumption by marine mammals.

5 | DISCUSSION

Technological advances in the lab allow scientists to derive ever greater amounts of information from the diverse array of biological samples collected from marine species. These advances consistently trend toward improved sensitivity and resolution, promising enhanced ability to address previously intractable questions relevant to the conservation, management, and health of wildlife populations. Concomitantly, this increased sensitivity exacerbates the risk of contamination during the sample handling and processing steps that can introduce irrevocable bias into a data set. Adhering to and documenting sterile methods, both in the field and in the laboratory, goes a long way to ensure that sample quality is not compromised, and that sample use can be maximized in current or future studies without fear of bias. Here, we summarize the best practice methods for preserving and archiving marine mammal biospecimens used in some of the most common or innovative molecular methods. However, this list is by no means comprehensive and analytical approaches not listed here (e.g., targeted gene expression and fatty acid analysis) may require specific considerations for sample collection and preservation. Further, many preservation methods have not yet been rigorously validated for all analytical approaches; as the 'omics fields continue to evolve, so does the body of literature evaluating suitability of various preservatives for long-term tissue storage.

In the field, the use of sterile collection equipment is key both for the safety of the animal as well as to avoid contamination from other sources. Similarly, equipment used to process samples in the field should be sterilized with both bleach and EtOH (not one or the other) using the bleach and ethanol clean method before processing begins,

and between each sample. The sterile techniques section above outlines an accessible procedure for sterilizing equipment prior to use, and method-specific recommendations are included in each methodological overview section. Personal protective equipment, such as disposable gloves, should be worn on both hands while working with samples to avoid contaminating the samples, and special consideration is warranted to protect the integrity of samples at high risk for contamination, such as samples used in microbiome or metabolomics studies.

Although tissue samples are most often collected via biopsy, scientists performing necropsies often have the opportunity to collect a much larger amount of tissue. For 'omics and other molecular analyses, we recommend collecting 2–3 replicate samples (~1 cm^3) of each tissue type and storing these in separate vials appropriate for the analysis methods of interest. This approach allows one sample replicate to be subsampled and preserved using various methods appropriate for each analytical approach, and the remaining replicate sample(s) can remain archived, eliminating repeated freeze/thaw cycles. Similarly, with forethought and planning, even small tissue biopsies can be subsampled into multiple sections to maximize their utility for various projects. For example, skin microbiomes are best studied using the thin epidermal layer of the tissue sample, while genetic, genomic and stable isotopes are best generated from the full depth of the dermis down to the blubber. Similarly, with sufficient mass, blubber can often be subsampled for fatty acid profiling, contaminants and/or hormone analyses.

Decisions regarding short-term storage and long-term archiving of samples each carry their own set of challenges and considerations. Short-term preservation is often limited to cooler-based storage on a boat or remote field location followed by temporary storage in a freezer at the field site, or storage in a dry shipper charged with LN_2. When deciding how to store samples in the short-term, scientists should consider both availability of preservatives and potential restrictions for transferring samples to the final location (e.g., hazardous materials when shipping or hand-carrying samples on commercial airlines). When choosing long-term storage methods, there is always a balance between considerations of freezer stability, freeze/thaw cycles and long-term cost and maintenance needs. In many cases, it may not be feasible or recommendable for smaller organizations to invest in −80°C freezers; rather, these organizations can achieve an optimal standard of preservation by partnering with academic institutions, national archives (e.g., museums, government agencies), or zoological societies. Many of these types of institutions often have stable archiving facilities onsite and are similarly equipped to properly manage and curate archived samples. Such partnerships and centralization of resources can support a high standard of sample preservation without the unsustainable burden of investing in additional equipment and maintenance needs.

For most end-point methods, freezing samples without preservatives is recommended nearly universally (see Figure 2 and Table S2 for additional detail). Under ideal conditions, samples are frozen using LN_2 or a − 80°C freezer immediately upon collection and removed as briefly as possible for processing and subsampling. Recent efforts have begun to examine the effects of contamination due to sample collection methods, but additional studies would be beneficial to understand the effects and limitations of samples stored for long periods of time (>20 years) in liquid preservatives. Such studies could be conducted in parallel with targeted 'omics analyses and would provide invaluable information to scientists aiming to maximize the use of long-term, archived biological samples. In the meantime, although accessibility to dewars/dry shippers and sources of LN_2 are increasing, remote field sites, limited research budgets, and long-term field deployments often limit access to such resources. If immediate freezing is not possible, many analytical approaches are still possible using samples that are stored for short periods of time at −20°C and/or in liquid preservative (see method-specific sections for further details). Preserving segments of unprocessed samples in appropriate liquid preservatives may support a suite of future analyses for samples archived at room temperature (see Figure 2 and method-specific sections for more details).

These best practice recommendations are based on a comprehensive literature review as well as the expert opinions of researchers who have worked in their fields for decades, involved in both sample collection and preservation as well as leveraging long-term archives of marine mammal samples. In the absence of direct citations in this review paper, statements made reflect the consensus opinion of the coauthors, due to the lack of published research on the specific topic in question. There are relatively few studies directly evaluating preservation media and processes for samples archived for more than a couple of years (but see, e.g., Amos & Hoelzel, 1991; Seutin et al., 1991, and other references cited throughout this manuscript). We suggest that conducting additional such studies

would provide valuable and much needed information to our research community. Due to the paucity of peer-reviewed research testing various sample preservation methods, the majority of these protocols result from historical practices passed down by word of mouth and developed based on logistical and/or financial considerations (e.g., Simmons, 2014). The longest-duration preservation experiment using marine mammal tissue to date was conducted over a 9-year period (Kiszka et al., 2014), which pales in comparison to the decades some samples have been stored at many long-term archival storage collection facilities (e.g., Marine Mammal and Sea Turtle Research (MMaSTR) Collection at Southwest Fisheries Science Center, La Jolla, California, was established in 1989). Long-term evaluations are needed to understand how preservation decisions (e.g., ultracold storage, liquid preservatives, preservative percentages, etc.) impact various 'omics and non-'omics analysis methods, although initial explorations have been made in some fields (Amos & Hoelzel, 1991; Castellini et al., 1992; Dahn et al., 2022; Geraci & Medway, 1974; Lesage et al., 2010; McCormack et al., 2020; Moore et al., 2015) for particular sample types (e.g., epidermal, microbial, blubber, muscle, blood).

In addition to identifying a need for more studies assessing the long-term effects of various collection and preservation methods, and until these studies can be successfully conducted and published, the authors of this study recommend that future 'omics and related publications include data indicating the success/failure and data quality (e.g., sequence quality score for genomic data) of each sample, along with comprehensive metadata on how the sample was collected and preserved. Gathering this information from a variety of studies will make it easier to assess preservation methods going forward.

Through collaborative research and the standardization of sample archiving methods, the marine mammal research community can capitalize on technological developments that promise to increase the breadth and depth of marine mammal research. Proactive consideration of sample collection and preservation methods is especially important for critically endangered marine mammal species and populations where sampling efforts are increasingly difficult and time is limited. Furthermore, explicit consideration of funding needs for sample handling and archiving during early project planning stages is key for supporting the future scientific value of the samples. Considering the substantial investment in time and resources involved in marine mammal fieldwork, maximizing the use of biospecimens is most often a key consideration for research centers maintaining sample archives, and working towards standardized documentation including collection and processing protocols supports these goals, promising generalizable results and increasing opportunities for collaborative and interdisciplinary efforts.

A robust system for tracking samples, methods, and metadata, while not immediately related to sterile sampling techniques, is equally important in facilitating the use of samples in future studies, as there are many factors that can affect downstream data quality. For example, samples collected from beached or bycaught animals may have undergone significant decomposition prior to sampling, which may negatively impact data quality to a greater degree than any issues arising from sample handling or preservation methods. Many marine mammal studies make use of dozens if not hundreds of samples contributed by multiple collaborating research organizations (e.g., Apprill et al., 2020; Baker et al., 2013; Bik et al., 2016; Dudek et al., 2022; Krahn et al., 2007; Morin, Forester, et al., 2021; Van Cise et al., 2019; Vendl et al., 2020). Integrating disparate sample sets and associated metadata can be challenging, and equally important to standardized sample collection (Kolker et al., 2014; Rajesh et al., 2021). Ideally, sample metadata will include all of the information listed in the metadata section of this paper and will be included as supplementary material in any peer-reviewed publication using those samples.

In addition to collecting metadata on sample collection and storage, it will be important to collect and report metadata on laboratory processing of samples. In particular, we strongly recommend recording data on which samples were successfully processed for analyses and which samples dropped out at each step of the laboratory processing protocol (e.g., extraction, amplification, or sequencing) due to either low quantity or poor quality. Including these metadata as a supplement in peer-review publications will be an extremely valuable contribution to the body of information that will inform future decisions regarding best practices for long-term storage. Such information is especially important to report for pioneering studies that utilize marine mammal tissues for novel 'omics techniques in order to guide future attempts and avoid unnecessary waste of resources and/or valuable samples.

Capitalizing on sampling investments by collecting samples in a way that is compatible with new and emerging 'omics technologies offer numerous avenues for expanding ongoing research studies and increasing resolution

through interdisciplinary efforts. Rapid developments in molecular and chemical assays offer new insights into marine mammal health and physiology and, through direct integration with 'omics data, support a holistic approach to conservation and management goals. By highlighting the opportunities and limitations associated with specific techniques across the spectrum of 'omics and small molecule analyses, we hope to support the growing breadth of research projects, highlight the potential future value of archived samples, and contribute to the development of best practices for the collection, processing, and archiving of biospecimens in the marine mammal community.

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