THE DIP DELINEATION HANDBOOK: A GUIDE TO USING MULTIPLE LINES OF EVIDENCE TO DELINEATE DEMOGRAPHICALLY INDEPENDENT POPULATIONS OF MARINE MAMMALS

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1. Introduction

1.1 Purpose and scope

One of the primary directives of the Marine Mammal Protection Act (MMPA) is to use the best scientific information available to delineate population stocks (henceforth referred to as stocks) and prepare stock assessment reports (SARs) for all marine mammals in U.S. territorial waters. The statute states that

*The term... ‘stock’ means a group of marine mammals of the same species or smaller taxa in a common spatial arrangement that interbreed when mature.*

Many lines of evidence can be brought to bear when delineating stocks, including acoustic differences, dietary differences, morphology, movements, and genetics (NMFS 2005). The original SARs identified most stocks at very large geographic scales, commensurate with the limited information on population structure at that time (Barlow et al. 1995a). The National Marine Fisheries Service (NMFS), which is responsible for assessing all marine mammal species except sea otters, walruses, polar bears, and manatees, has further subdivided some stocks since that time, but these revisions have primarily occurred for species where intensive studies based on genetic or movement data (through tagging or photo-identification) have indicated that subdivision was warranted. There are other species for which available data suggest that finer delineation of stocks is likely warranted, but revision is hindered by uncertainty regarding how best to interpret and integrate other types of data in the context of stock delineation when genetic and movement data are unavailable or inadequate. Uncertainty over integrating multiple lines of evidence can also contribute to inconsistencies among stock revisions made in the absence of strong genetic or movement data. Thus, there is a need for guidance to improve consistency and transparency in identifying, using, and integrating the evidence used to identify marine mammal stocks for management purposes.

Based on the management objectives of the MMPA, NMFS has determined that stocks should represent demographically independent populations (DIPs; see section 1.2.1 for definition; NMFS 2005, Eagle et al. 2008). The identification and delineation1 of DIPs is important in many research and management contexts beyond the MMPA (Waples & Gaggiotti 2006, Palsboll et al. 2007). Consequently, in this handbook we primarily use the term DIP, as it is the more general term with broader applicability. We use the term stock when discussing issues that are specific

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1 DIP delineation is the use of the scientific data to assess whether groups of animals are demographically independent and determine the geographic range of the DIP (which may shift through time, especially for migratory species).
to management under the MMPA and when referring to individual stocks or groups of stocks that have been designated\(^2\) under the MMPA.

In this handbook, we discuss the use of multiple lines of evidence (LoEs) to delineate DIPs of marine mammals, which can subsequently be designated as stocks under the MMPA. We first review the stock concept under the MMPA and document the rationale for equating stocks to DIPs. We review the different types of data currently available for inferring population structure and provide an assessment of the utility of each data type for inferring demographic independence. The MMPA directs NMFS to use the ‘best scientific information available’ to assess stocks. Because the availability and utility of different LoEs varies among species, stock delineation can and will be based on different LoEs in order to meet the MMPA directives. We therefore summarize the data that are available for the currently designated stocks and document some of the factors that limit our ability to collect robust data sets for certain groups of species.

In some cases, the best scientific information available regarding the presence of DIPs may come from weak LoEs or limited data sets. In other cases, robust data sets from strong LoEs will reveal that two groups sit right on the borderline of being demographically independent. We discuss the use of structured expert decision-making (SEDM) in delineating DIPs in these cases, and provide example SEDM questions based on instances where SEDM has been used for making stock delineation decisions under the MMPA. We also discuss the importance of clearly documenting all data and analyses that are used in designating new or revising existing MMPA stocks. We suggest that all delineation decisions be accompanied by a Technical Memorandum or published paper (or both) and we provide suggestions regarding the types of information that should be included in the publication.

This handbook was created in response to a recommendation of the Meeting on the Use of Multiple Lines of Evidence to Delineate Demographically Independent Populations (Martien et al. 2015). The purpose of the handbook is two-fold. First and foremost, it is intended to provide guidance to those tasked with delineating DIPs for the purposes of management under the MMPA, thereby promoting consistency in future DIP delineation efforts. Secondarily, it strives to improve transparency in the stock delineation process by documenting the methods and rationales for stock delineation under the MMPA. Given that our focus is on DIP delineation, we have not attempted to provide thorough literature reviews of research on the various lines of evidence. Rather, we cite a few specific applications of each LoE and, where possible, summarize articles that provide more detailed overviews.

This handbook does not propose a new approach to DIP delineation under the MMPA. Rather, we strive to be faithful to the definitions laid out in the Guidelines for Assessing Marine Mammal

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\(^2\) Stock designation is the official naming of a stock as a management unit that will then be assessed in Stock Assessment Reports. A stock is generally defined to be a single DIP but designation may in some situations (anticipated to be relatively few) combine DIPs for practical management reasons.
and to be consistent with the approach used in the past to delineate DIPs based on the best available scientific information. Our goal is to assemble in one document the methods and approaches that have already been used and should be considered ‘best practices.’ This handbook therefore serves as a comprehensive reference for science-based marine mammal DIP delineation. It should be recognized, however, that as science progresses and new techniques and technologies are developed, some aspects of DIP delineation are also likely to evolve.

1.2 Definitions

1.2.1 Demographically Independent Population (DIP)

Groups of organisms are structured along a continuum from family and social groups through subspecies, species, and higher taxonomic levels. The exact point along that continuum at which a group of organisms should be considered a ‘population’ depends on the purpose for which populations are being identified. Waples and Gaggiotti (2006) review some of the population concepts that have been published. The concepts have in common that they refer to groups of individuals that are in some way cohesive. Some focus on groups of individuals that are united by demographic forces, while other concepts focus on evolutionary cohesion as uniting individuals within a population. Waples and Gaggiotti (2006) refer to the former as adhering to an ‘Ecological Paradigm’ and the latter as adhering to an ‘Evolutionary Paradigm.’ The population concept that is relevant to the Ecological Paradigm is the demographically independent population (DIP).

Based on the goals and objectives of the MMPA, a DIP is the operational definition of a stock under the MMPA. The GAMMS defines the term ‘demographic independence’ to mean that

...the population dynamics of the affected group is more a consequence of births and deaths within the group (internal dynamics) rather than immigration or emigration (external dynamics). Thus, the exchange of individuals between population stocks is not great enough to prevent the depletion of one of the populations as a result of increased mortality or lower birth rates (NMFS 2016).

If a DIP was extirpated, the abundance and growth rates of other DIPs would not be substantially altered when immigration from the extirpated DIP ceased. Similarly, if internal recruitment within a DIP was suddenly reduced (for example, due to introduction of a disease or predator, loss of a prey resource, or human-caused mortality), immigration from neighboring DIPs would not be sufficient to prevent the abundance of the affected DIP from declining (see Box 1, Fig. 1.1).
Box 1: Demographic Independence

Demographic independence occurs when the dynamics (e.g., growth rate) of a group are determined primarily by local birth and death rates rather than by immigration and emigration rates. When populations are demographically independent, failure to manage and monitor them separately can result in the depletion or extirpation of populations. For example, imagine five populations of equal carrying capacity, each of which has a maximum population growth rate of 4% and exchanges dispersers at a rate of 0.5%/year with its adjacent populations. Human-caused mortality occurs at a rate of 1% of the combined abundance of the five populations. If the human-caused mortality is spread evenly across the range (i.e., 1%/year from each population), all five populations will persist (Figure 1.1A). If the mortality is all taken from one population, however, the impacted population will be severely depleted because the rate of human-caused mortality exceeds that of internal (4%/year) plus external (0.5%/year) recruitment (Figure 1.1B). Taylor (1997) used simulations to show that, if human-caused mortality is geographically concentrated, populations must exchange dispersers at rates exceeding a few percent per year in order to be safely managed as a single stock under the MMPA.

![Figure 1.1](image_url)

*Figure 1.1* A schematic of five interconnected DIPs with maximum population growth rates of 4% and which exchange dispersers with their adjacent populations at a rate of 0.5%/year. Population impacts realized with (A) 1%/year human-caused mortality for each population or (B) 5%/year human-caused mortality from only population 5. Reproduced from Taylor and Dizon (1999).
The primary quantitative criterion for determining whether or not a group of individuals constitutes a DIP is dispersal rate, a demographic parameter. Taylor (1997) conducted simulations to determine the critical dispersal rate below which two groups would be demographically independent and must therefore be managed separately in order to meet the MMPA objective of maintaining species as functioning elements of their ecosystem. Taylor considered any fragmentation or contraction of the species range to violate that objective (Figure 1.2). All of Taylor’s simulations featured a single putative stock that contained two or more discrete groups of animals between which there is very little dispersal. The simulations assumed that the allowable human-caused mortality (termed Potential Biological Removal under the MMPA) was calculated based on the total abundance of the stock, but that the human-caused mortality disproportionately impacted certain groups. If immigration into the impacted groups was insufficient to compensate for the human-caused mortality, the groups could be extirpated, resulting in a range reduction or fragmentation. In all of the models examined, the abundance of the impacted group declined below the level sought by management objectives if dispersal between groups was less than several percent of the population per year, with the exact value depending on the details of the simulated populations (Taylor 1997). Similarly, Hastings (1993) suggested that annual dispersal rates below 10% of the population size per year result in demographic independence based on numerical calculations aimed at examining the spatial scale at which density dependence can be detected. Note that even relatively low rates of demographic exchange (e.g., 1%/year) can be sufficient to homogenize genetic frequencies between two DIPs, so the power to detect genetic differentiation may be low without large samples and large numbers of genetic markers (see Appendix 1). Such rates would also not be expected to generate heritable morphological differences unless there were strong selective forces.

Figure 1.2. Abundance and distribution of five pristine populations (a), versus potential distributions and abundance after 50% of the total abundance is removed (b-d). Width represents abundance; length represents distance. Reproduced with permission from Taylor (1997).
1.2.2 Distinct Population Segment

Some marine mammals are also managed under the U.S. Endangered Species Act (ESA). The ESA has a very different management objective from the MMPA, and therefore has a different unit to conserve, called a Distinct Population Segment (DPS). The ESA focuses on preventing the extinction of species by preserving the genetic diversity and evolutionary potential of species. This evolutionary focus requires conservation units that are largely reproductively isolated and therefore conform to the Evolutionary Paradigm described by Waples and Gaggiotti (2006). The critical rate of gene flow below which two groups can be considered independently evolving and therefore qualify as separate DPSs is much lower than the threshold for DIPs. Therefore, while it is common for a single DPS to encompass multiple DIPs, a single DIP should not contain individuals from more than one DPS. DPSs tend to be delineated at much larger spatial scales and to exhibit substantially greater genetic differentiation than DIPs. Eagle et al. (2008) provide a detailed comparison of stocks (DIPs) and DPSs.

Since several marine mammal species are listed under the ESA as well as being managed under the MMPA, we consider some special cases that arise where the correspondence between management units under the two acts is simple. The main Hawaiian Islands (MHI) insular false killer whale population is a small population (about 150 individuals) that is restricted to the nearshore waters around the main Hawaiian Islands. Based on photo-identification and genetic data indicating little-to-no dispersal between it and neighboring populations (Chivers et al. 2007a, Baird et al. 2008), the MHI insular population was designated as a stock in 2008. Following a Status Review (Oleson et al. 2010) it was determined that the population was sufficiently discrete to also qualify as a DPS under the ESA. Although there are multiple social groups within the population, genetic and photographic evidence indicates these groups are not demographically independent (Baird et al. 2012, Martien et al. 2014). Therefore, the MHI insular population of false killer whales is designated as both a stock under the MMPA and a DPS under the ESA. A similar situation exists for southern resident killer whales (Krahn et al. 2002). However, the one-to-one correspondence between DIPs and DPSs demonstrated by MHI insular false killer whales and southern resident killer whales is atypical. In most cases, the rate of gene flow between DIPs is high enough to prevent them from being independently evolving groups that would qualify as DPSs. Rather, most DPSs will be composed of multiple DIPs. Since DPS delineation is not the focus of this document, DPSs will not be discussed in further detail.

2. History of the stock concept under the MMPA

2.1 The language of the Act and its original implementation

The 1994 Amendments to the MMPA name the population stock (henceforth referred to as ‘stock’) as the fundamental unit of management. The MMPA defines a stock as ‘a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature’ (Sec. 3). The rationale for this definition is given in Sec. 2(2) and Sec. 2(6) of the MMPA:
1. ... species and population stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element of the ecosystem of which they are a part, and, consistent with this major objective, they should not be permitted to diminish below their optimum sustainable population.

2. ... the primary objective of their management should be to maintain the health and stability of the marine ecosystem.

Based on the language in the MMPA, the original guidelines for delineating stocks (Barlow et al. 1995b) stated that:

...a risk-averse strategy of defining the stocks should be used to be consistent with these goals. A risk-averse strategy requires starting with a definition of stocks based on small groupings that are only "lumped" when there is compelling evidence to do so. Such evidence comes from biological studies. However, in the event of virtually no biological stock data, a stock should be defined simply as the area from which marine mammals are taken (i.e., the area in which the fishery is operating).

Despite setting forth this risk-averse definition and in the absence of data to define stocks for most species, nearly all stocks defined in the original SARs covered very large geographic regions. The tactic of starting with small stocks and requiring scientific evidence to amalgamate stocks (reversing the burden of proof in an explicitly risk-averse manner) was never implemented, perhaps with the sole exception of estuarine populations of common bottlenose dolphins in the Gulf of Mexico (Barlow et al. 1995a). Consequently, most stock delineation revisions that have occurred since stocks were originally designated have resulted in the splitting of single stocks into multiple stocks as our understanding of population structure has improved.

The year after the initial delineation of stocks under the MMPA, a workshop was held to develop official Guidelines for Assessing Marine Mammal Stocks (GAMMS) (Wade & Angliss 1997). The GAMMS defined a stock as ‘a management unit that identifies a demographically isolated biological population,’ commensurate with the goals and objectives of the MMPA. The GAMMS explicitly rejected the notion that stocks need be reproductively isolated. Two additional GAMMS workshops have since been held. Each of these workshops introduced relatively minor changes to clarify the definition of stocks, resulting in the current definition (see Section 1.2)(NMFS 2005, Moore & Merrick 2011, NMFS 2016).

2.2 Use of the term “interbreed when mature”

One source of confusion and concern regarding the differences in NMFS’s definitions of conservation units under the MMPA and the ESA stems from the fact that both Acts use the phrase ‘interbreed when mature’ in their definitions of conservation units, stocks and DPSs, respectively. This similarity in wording could be interpreted to suggest that the conservation units under the two Acts should also be similar. In 2006 NMFS convened a workshop of scientists, managers, and policy advisors to discuss the similarities and differences in the NMFS
definitions of conservation units under the MMPA, ESA, and the Magnuson-Stevens Act (Eagle et al. 2008). Specifically, participants were asked to address the questions, “Why are conservation units different under the three statutes?” and “Are differences between the three conservation units biologically justified?” The workshop participants concluded there are important differences between the three conservation units that stem from the differing objectives of the three Acts and that those differences are biologically justified (Eagle et al. 2008).

The draft second revision of the GAMMS (69 FR 67541, 18 November 2004; following the GAMMS II workshop) included language clarifying NMFS’s interpretation of ‘interbreed when mature’ with respect to the MMPA. The term was defined as cases in which either:

1. *mating occurs primarily among members of the same demographically isolated group*

or

2. *the group migrates seasonally to a breeding ground where its members breed with members of the same group as well as with members of other demographically distinct groups which have migrated to the same breeding ground from a different feeding ground*

The first case is fairly obvious and adheres to the first GAMMS definition asserting demographic independence as the basis for delimiting a stock under the MMPA. The second case is somewhat less intuitive. Although public comments on the draft GAMMS did not result in any objection to these interpretations, a request from the Marine Mammal Commission for additional clarification of the definition resulted in it being omitted from the final revision (70 FR 35397, 20 June 2005).

The explicit rejection in the GAMMS of the notion that stocks need be reproductively isolated reflects the fact that gene flow (the transfer of genetic material from one group to another through interbreeding) does not necessarily equate to dispersal (and vice versa). In the case of seasonally migrating animals with strong site fidelity to feeding grounds, gene flow can occur on shared breeding grounds without any animals ever dispersing between feeding grounds. In cases where gene flow occurs between two groups because they co-occur in one season but there is little or no dispersal of individuals between them, the two groups are demographically independent (due to minimal immigration or emigration) and should be managed separately to meet the objective of maintaining population stocks as functioning elements of their ecosystem. For instance, currently recognized beluga stocks and some currently recognized humpback whale stocks are based on feeding aggregations between which there is limited dispersal, but there is gene flow (on the breeding grounds). Thus, while reproductive isolation is an appropriate criterion to consider when delineating conservation units under the ESA, it is neither required nor expected between stocks under the MMPA (Eagle et al. 2008).
3 Review of Lines of Evidence

3.1 Types of Evidence Reviewed

The GAMMS recognize that many types of information, i.e. lines of evidence (LoEs), can be used to identify and evaluate demographic independence, including “distribution and movements, population trends, morphological differences, genetic differences, contaminants and natural isotope loads, parasite differences, and oceanographic habitat differences.” The GAMMS do not, however, provide further guidance on how to consider, weigh, or integrate these LoEs.

Participants at the GAMMS III workshop (Moore & Merrick 2011) recommended that the Agency conduct a review of these different LoEs and their utility in stock delineation. In response, the Stock Delineation Guidelines Initiative Working Group conducted a series of web-based discussion groups, each focused on a different LoE. Each of the discussion groups began with presentations on the strengths and weaknesses of that LoE for identifying DIPs and examples of cases where it had been applied to marine mammals. The presentations were typically given by scientists with expertise in the LoE under discussion (see Appendix 1). Additional experts in the LoE were also invited to attend and participate in the discussion. The summaries of the discussion groups provided detailed information about the use of each LoE for DIP delineation and the many factors that have to be considered when evaluating the strength of a particular data set or analysis that uses that LoE. The discussion group summaries formed the basis of much of the review of LoEs presented below and are available from the lead author upon request.

Discussion groups were held for each of the following LoEs: morphology, movement data, acoustics, stable isotopes and fatty acids, contaminants, life history, trends in abundance, physiographic and oceanographic differences in habitat, distributional hiatuses and low-density areas, and association data. Though it is not specifically mentioned in the GAMMS III, association data, particularly in the form of social networks and association indices, were included in the review because they have been central to DIP delineation in several cases in the past decade, primarily for island-associated populations in the Hawaiian Islands (Baird et al. 2008, Aschettino et al. 2012, Martien et al. 2014, Martien et al. 2017). The working group did not organize a discussion group to review genetic data because its utility in DIP delineation has been well documented and accepted (Waples & Gaggiotti 2006, Palsboll et al. 2007, Taylor et al. 2010). Nonetheless, genetic data are included in this handbook as an LoE.

3.2 Assessing strength of inference for LoEs

The utility of different LoEs for inferring demographic independence among groups of animals will vary among species due to their different life histories, mating strategies, and geographic ranges. Participants at the 2014 Meeting on the Use of Multiple Lines of Evidence to Delineate Demographically Independent Populations (Martien et al. 2015) conducted a species-by-species evaluation of the strength of each LoE in order to document this variation. They conducted this evaluation for every cetacean and pinniped species listed in the 2012 SARs. For species that
have separate coastal/insular and pelagic populations (e.g., bottlenose dolphins), the coastal and pelagic populations were evaluated separately, as both the utility of an LoE and the feasibility of collecting data could vary between them. Species managed by the U.S. Fish and Wildlife Service (sea otters, polar bears, manatees, and walruses) were not included in the evaluation because there were no meeting participants with expertise in those species. Nonetheless, though they are not explicitly considered in this guidebook, the principles discussed and some of the specifics would apply to evaluating the strengths of LoEs for these species.

The utility of each LoE for each species was evaluated by addressing the question ‘Assuming that you have robust data that show a difference among two or more groups of animals in the line of evidence concerned, then, based upon the current state of knowledge of that species, how useful would you rate this LoE as a means of delineating DIPs?’ The answers to this question were coded as follows:

**Unknown**: Utility of this LoE for this species is unknown, meaning that there are no data for this species or a similar species from which generalizations can be made

**Not informative**: This LoE is not informative or potentially misleading

**Weak**: This LoE must be combined with multiple additional LoEs in order to delineate at DIP

**Moderate**: This LoE must be combined with at least one other LoE in order to delineate at DIP

**Strong**: This LoE can be used alone to delineate DIPs

The ratings were predicated on the assumption that there are robust data (see below) showing a difference between two groups for a particular LoE. Ratings by participants did not address the likelihood of detecting a difference between DIPs using a particular LoE. Consequently, the ratings should not be used in isolation to decide which types of data to collect when planning a research program aimed at delineating DIPs. For instance, morphological differences are typically indicative of divergence well beyond the level of DIPs. Thus, if a robust data set shows morphological differences between two groups and phenotypic plasticity can be ruled out as a cause, then the groups are definitely demographically independent and may well be evolutionarily independent. However, it is unlikely that morphological differences will exist between most DIPs. Similarly, many species of beaked whales produce highly stereotyped calls that vary little within but much between species (though Blainville’s beaked whale is an exception; Baumann-Pickering et al. 2018). Thus, acoustic differences between two groups in most beaked whale species strongly suggests separation that may even represent unrecognized taxa. However, a lack of acoustic differences between beaked whale groups cannot be construed to indicate evidence that the groups are not DIPs. We return to this point in more detail in the acoustics section as it requires special treatment when assessing how data availability affects DIP delineation for beaked whales.

The ratings also assume that the data set showing differences is ‘robust’, meaning there has been appropriate evaluation of all of the relevant factors (e.g., age and sex differences, sample size, analytical methods, etc.) such that the observed difference is real, not a sampling or analytical artifact. The factors that should be taken into consideration when evaluating a data
set are discussed in detail in Section 3.3 of this Handbook. Many of these factors are common to all LoEs, while others are specific to only one or a few LoEs.

In addition to determining the number of DIPs, DIP delineation requires specifying boundaries between DIPs. Boundary placement can often be much more challenging than DIP identification. In rating the utility of LoEs, assessments were based only on the utility for identifying DIPs, not placing the boundaries. Thus, some LoEs that are rated as very useful for determining the number of DIPs may not be useful for placing boundaries, and vice versa.

The meeting participants who evaluated the utility of the different LoEs were all experts in DIP delineation in marine mammals and had expertise in one or more of the specific LoEs. In addition, they had access to an early draft of the Review of Lines of Evidence presented in Section 3 of this document. Thus, these ratings reflect the consensus of a group of well-informed subject matter experts.

A detailed discussion of the strength of each LoE for each species can be found in Appendix 2, while Table 3.1 (below) summarizes the strength of each LoE within each of three broad taxonomic groups – mysticetes, odontocetes, and pinnipeds. Condensing all of the information regarding the utility of a particular data type for a particular species down to a single categorical rating is challenging, and arguments could likely be made for altering some of the individual values in Appendix 2. Furthermore, as more data are collected and new technologies and analytical techniques become available, the ratings will likely need to be updated. Nonetheless, we believe that the overall patterns documented below and in Appendix 2 accurately reflect the current state of knowledge.

We found that the strength of most LoEs did not vary substantially among species or across taxonomic groups (Table 3.1). Robust data demonstrating genetic or morphological differences between two groups were uniformly judged to be strong evidence of demographic independence, regardless of the species. Movement data were also judged to constitute a strong line of evidence supporting demographic independence for nearly all species. The exceptions were a few species of migratory whales and odontocetes with strong social structure that could be mistaken for population structure. In those cases, movement data were considered to be moderate, meaning that additional data would have to be considered in order to determine whether the differences observed from movement data truly reflected demographically independent populations.

Distributional hiatuses or low-density areas were judged to be of moderate strength for nearly all species. Stable isotope and fatty acid differences were uniformly considered to be weak to misleading as evidence of demographic independence given that they generally reflect foraging behavior over short time scales (weeks to months) and that there are many possible causes for differences in stable isotope signatures, such as differences in individual diet preferences, prey switching, and within- and between-year changes in background isotope profiles. Contaminant data were judged to be somewhat stronger (i.e., moderate strength) indicators of demographic independence, largely because contaminant profiles are integrated over the lifetime of an
animal (with the notable exception of females offloading some contaminants to offspring) rather
than representing a short (one to six month) snapshot of an animal’s diet, as is the case with
stable isotopes and fatty acids. Differences in trends or life history parameters between two
groups were judged to represent weak evidence of demographic independence for most
species, primarily due to the large amount of other data needed in order to properly interpret
results from these LoEs.

Ratings for the utility of physiographic or oceanographic differences in habitat and association
data varied among the three broad taxonomic groups, but were relatively consistent within a
taxonomic group. Acoustic data were the only LoE for which the utility for delineating DIPs was
judged to be very species specific.

Table 3.1. Strength of different lines of evidence for evaluating demographic independence.
These evaluations are predicated on the assumption that a difference among two or more groups
of animals has been found for that line of evidence, and that there has been an appropriate
evaluation of all relevant factors to ensure that the observed difference is not a sampling or
analytical artifact. This table reflects the predominant rating for a given LoE within broad
taxonomic groups. Exceptions to these ratings are detailed in Appendix 2.

<table>
<thead>
<tr>
<th>Line of Evidence</th>
<th>Mysticetes</th>
<th>Odontocetes</th>
<th>Pinnipeds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morphology</td>
<td>Strong</td>
<td>Strong</td>
<td>Strong</td>
</tr>
<tr>
<td>Genetics</td>
<td>Strong</td>
<td>Strong</td>
<td>Strong</td>
</tr>
<tr>
<td>Movements</td>
<td>Strong</td>
<td>Strong</td>
<td>Strong</td>
</tr>
<tr>
<td>Distributional hiatuses or low density areas</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Moderate</td>
</tr>
<tr>
<td>Contaminants</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Moderate</td>
</tr>
<tr>
<td>Stable isotopes and fatty acids</td>
<td>Weak/Not Informative</td>
<td>Weak</td>
<td>Not Informative</td>
</tr>
<tr>
<td>Life history</td>
<td>Weak</td>
<td>Weak</td>
<td>Weak</td>
</tr>
<tr>
<td>Trends in abundance</td>
<td>Weak</td>
<td>Weak</td>
<td>Weak/Not Informative</td>
</tr>
<tr>
<td>Physiographic or oceanographic differences in habitat</td>
<td>Not informative</td>
<td>Moderate</td>
<td>Weak</td>
</tr>
<tr>
<td>Association data</td>
<td>Not Informative</td>
<td>Moderate/Weak</td>
<td>Unknown</td>
</tr>
<tr>
<td>Acoustics</td>
<td>Species Specific</td>
<td>Species Specific</td>
<td>Species Specific</td>
</tr>
</tbody>
</table>
3.3 General considerations when evaluating the strength of an LoE

The question that must be answered to delineate DIPs is whether the rate of immigration into a population is less than the rate of internal recruitment. If so, the population constitutes a DIP. When evaluating positive results (i.e., showing a difference between strata) and negative results (i.e., not showing a difference) for a particular LoE, the researcher must evaluate the implication of those results to rates of movement. Failing to find differences between two populations that are demographically independent (henceforth referred to as a false-negative) can result from inadequate statistical power, while positive results showing differences between strata that are not demographically independent (henceforth referred to as a false-positive) can reflect a result that is statistically significant, but not necessarily reflect movement rates low enough to result in demographic independence. Both false-positive and false-negative results can be caused by inadequate sample size, sampling bias, lack of statistical power (e.g., due to a small difference in what is being measured), or the characteristics of the specific traits being evaluated. Because these considerations are common to all LoEs, we review them here before discussing the LoEs separately.

3.3.1 Sample size

An adequate sample size is required to statistically evaluate the demographic independence of two strata, regardless of the LoE being brought to bear on the question. Inadequate sample size will result in low statistical power and failure to detect demographic independence when it is present (a false-negative result). The number of samples required to evaluate demographic independence depends on many factors, including the LoE being analyzed. For some LoEs, it is possible to calculate the amount by which two strata would be expected to differ (the effect size) if the strata are demographically independent. In those cases, researchers can estimate the statistical power given their sample size, or, conversely, estimate the number of samples needed in order to achieve a given level of statistical power.

When evaluating the adequacy of a set of samples, it helps to keep in mind that the underlying goal is to ensure that samples accurately reflect the diversity of the stratum they represent. For some LoEs, inadequate sampling can actually lead to overestimating the degree of demographic independence between two strata (a false-positive result). For instance, movement data from a small number of satellite-tagged animals or low photo-identification effort could suggest little to no movement between two strata, when in fact the sample size is simply too small to detect occasional movement or represents only one class of the population (i.e. only males, only juveniles, etc. see below).

In the case of some rare or elusive species of cetaceans (e.g., most beaked whales), obtaining enough samples to be truly representative and to have adequate statistical power to detect demographic independence with high confidence may not be feasible. In these cases, sample sizes should be evaluated not only with respect to representativeness and statistical power, but also how long it might take to substantially increase the sample size. Similarly, collecting adequate sample sizes from certain species may be impractical for some LoEs. For instance, building large morphological collections for species of large whales or a satellite tagging data set
that is representative for highly abundant species (e.g., many pelagic dolphins) may be logistically or financially impractical. In such cases, researchers should focus on the strongest LoEs for which adequate sample sizes can be collected.

3.3.2 Sample distribution with respect to age class, sex, and season

Attributes that are useful for assessing demographic independence can vary among individuals of different sexes or age classes. For instance, certain morphological characteristics differ between adults, sub-adults, and juveniles, or between males and females. Similarly, differences in diet or habitat use in different sexes or age classes can result in different stable isotope profiles. If the sample set from one putative DIP consists predominantly of juveniles while another is largely from adults, differences in an LoE may reflect age class effects rather than a lack of interchange between areas.

Even if the data from two putative DIPs are collected from the same sex/age class, the results can still be misleading if the wrong sex/age class is sampled. For many marine mammal species, dispersal only occurs at certain ages or is biased toward one sex (usually males). In species exhibiting high natal dispersal, a pattern that is common in many mammalian species but rare in marine mammals, data collected from adults may show strong differences in a particular LoE even though the two groups may not be demographically independent. In other species, individuals remain in their natal population until they reach maturity, at which point the adults disperse to other areas. In this case, collecting data only from immature animals could lead to a false conclusion of demographic independence. Some LoEs would be impacted more than others in these conditions and so it is important that life history information be considered when choosing data types and designing sampling schemes. For instance, LoEs based on heritable traits (e.g., genetics and morphology) are less susceptible to false inference as a result of high natal dispersal.

Many of the data types discussed below can vary seasonally. For example, the stable isotope profile of an individual can vary among seasons due to distributional shifts or seasonal changes in prey availability (e.g., Samuel & Worthy 2004, Young & Ferguson 2013). Many marine mammals exhibit site fidelity only during part of the year. This is true of many pinniped species, which return to the same haul-out sites year after year during their pupping and molting seasons, but range broadly otherwise. Some species of odontocetes also exhibit seasonal shifts in distribution (e.g., resident killer whales, belugas). These aspects of life history must also be considered when collecting data or samples for studies aimed at delineating DIPs and when interpreting the results of such studies. Errors can occur with nearly every other line of evidence discussed below if seasonal effects are not properly accounted for.

Many baleen whale species undertake seasonal migrations between summer feeding grounds and winter breeding/calving grounds. The nature and extent of population structure can vary during different parts of the migration, with animals from the same breeding ground utilizing different feeding grounds, or vice versa. Animals from different DIPs may also have overlapping migratory paths. Thus, attributing data collected from a migratory species to one population or
another may be difficult and will depend on knowledge of migratory behavior. This seasonal variation must be carefully considered and generally can be mitigated with careful sample design. Since the demographics of a population are driven by impacts and conditions across its migratory cycle, correct delineation of DIPs in migratory whales generally requires identifying groups of animals that share the same breeding, feeding, and migratory habitats.

Sampling must also be random with respect to relatedness, especially in highly social species. If closely-related individuals are sampled preferentially, overall diversity within groups will be underestimated, which in turn could result in an overestimate of the extent to which groups differ in a particular LoE. Oversampling of related individuals can occur when close relatives travel together and are sampled (e.g., via biopsy, photo-identification, or tagging) during the same encounter. Close relatives should not necessarily be excluded from a data set, as a sample set from a population with low abundance is likely to include close relatives. So long as the DIP is sampled randomly, the inclusion of close relatives will not introduce a bias. Nevertheless, consideration should be given to whether close relatives may result in bias.

### 3.3.3 Temporal stability of LoEs

When evaluating data suggesting that two strata represent different DIPs, it is important to consider the temporal stability of the LoEs being measured. While an animal’s genetic makeup will not change if it moves from one stratum to another, many other LoEs can. Stable isotope and fatty acid profiles generally only reflect the animal’s habitat and diet over the weeks or months prior to when it was sampled. Thus, an animal will only carry the signal of its previous stratum for a short period of time after dispersing. Similarly, certain life history attributes, such as reproductive seasonality, can change when an animal changes location as a result of environmental changes. Thus, strong differences in some LoEs can persist between geographic strata despite high rates of movement between them.

The signal from some LoEs can also change due to inter-annual changes in prey distribution or oceanographic conditions. For instance, inter-annual oceanographic changes result in changes in the relative abundance of schooling fish in the California Current, which is reflected in changes in the isotopic signatures of humpback whales as their diets shift between schooling fish and krill (Fleming et al. 2016). Thus, caution should be taken to ensure that differences driven by environmentally-induced variation are not mistakenly interpreted as evidence of demographic independence.

In some species, vocal characteristics are vertically transmitted and stable over an animal’s lifetime. However, in other species songs and calls change over time and can be learned from conspecifics. Even morphological differences between areas can be due to phenotypic plasticity rather than a lack of movement between them. Thus, when delineating DIPS, researchers must consider whether the differences observed between strata could reflect limited movement or instead result from environmental influences.
3.4 Caveats and Considerations for Specific LoEs

Detailed review of LoEs and their application to DIP delineation are provided in Appendix 1. The bullet points below are meant to serve as brief reminders of important considerations. However, researchers should not attempt to delineate DIPs or evaluate a DIP delineation study without reading the full text for the relevant LoEs in Appendix 1.

3.4.1 Morphology

- Comparisons of external morphology, osteology, and pigmentation typically require large numbers of carcasses, which may not be available for species without high bycatch or stranding rates.
- Caution should be taken to ensure that differences between groups are not due to variation in age and/or sex classes of the samples, phenotypic plasticity, or differences in data collection methods between investigators.
- If animals of different DIPs cannot be distinguished during field observations, the determination of DIP boundaries based on morphological differences alone may be difficult.

3.4.2 Genetics

- The mode of inheritance should be considered when interpreting results of a genetic study of population structure.
- Under some circumstances (e.g., maternally-driven fidelity to feeding grounds), DIPs may only exhibit genetic differentiation at mitochondrial loci, not nuclear loci.
- If different geographic regions are used for breeding and feeding, then the location of sample collection in the context of the migratory cycle needs to be considered when interpreting results.
- Genetic data represent an average over several to many generations. While some analyses can provide estimates that reflect the past couple of generations or individual dispersal, others reflect evolutionary time scales and therefore may not accurately represent current population structure.
- The critical level of dispersal below which two groups should be considered separate DIPs is high enough that genetic differentiation is expected to be low and therefore may be difficult to detect.
- Using genetic data to delineate DIPs in species with high abundance is especially difficult due to the inverse relationship between abundance and expected differentiation.

3.4.3 Movements

- Caution should be taken to ensure that differences in movement patterns between sexes, age classes, or reproductive classes are not mis-interpreted as indicating the presence of different DIPs.
- Photographic-identification studies can be limited by the nature of the markings used to identify individuals. Marks that differ between age or sex classes, only occur in a small
proportion of individuals, or can change or be lost over time can complicate the analysis and interpretation of movement data from photographic identification.

- Movement data are only representative of the time period over which they are collected and therefore may fail to capture infrequent but demographically important movements.
- Using movement data to delineate DIPs in species with high abundance is especially difficult due to the practical and financial constraints of photographing or tagging a sufficient percent of the population to estimate movement rates.
- If different geographic regions are used for breeding and feeding, then the location and timing of data collection in the context of the migratory cycle needs to be considered when interpreting results.
- Movement data is most useful for evaluating demographic independence when it allows for the estimation of the rate of dispersal into a population.

3.4.4 Distributional hiatuses or low-density areas

- The temporal scale of distributional hiatuses is important. The presence of stable gaps that are persistent over generations may provide stronger evidence of demographic independence, especially if there are corresponding habitat differences.
- Distributional gaps that are larger than the documented home range of animals provide stronger evidence of demographic independence than smaller gaps.
- Data on low-density areas can be particularly helpful in placing boundaries between DIPs that have been identified by other means.
- When evaluating distributional data, researchers must consider the possibility of seasonal differences in distribution and differences between age and sex classes.
- For some species, distributional data may be the only data that can be feasibly collected, and may therefore represent the “best scientific information available” for delineating DIPs.

3.4.5 Contaminants

- Differences in contaminant and/or trace element profiles in marine mammals will only be detected if variation in chemical signatures exists within the habitat at the appropriate spatial scale.
- Temporal variation in contaminant and trace element profiles can occur and needs to be considered when interpreting the results if samples were collected over multiple years/seasons.
- The turnover time of contaminants and/or trace elements varies between tissue types; tissues with longer turnover times are preferred to allow inferences about long-term foraging strategies.
- Extrinsic sources of variability can be introduced when protocols for sample collection, storage, and analysis differ between labs or over time.
- Intrinsic sources of variability (e.g., individual foraging specializations, tissue types and sources, age, sex, reproductive status, and nutritive condition) need to be considered when interpreting any differences in contaminant and/or trace element profiles that are found. For trace elements, intrinsic sources of variation may have impacts that vary
between species and/or between elements; as such, interpretation of any differences found between groups requires some understanding of specific bioaccumulation patterns.

- The collection of full-depth biopsy samples is preferred for contaminant analyses as concentrations can vary between the inner and outer layer of blubber.
- Biopsy samples may not be useful in the analysis of some trace elements due to very low concentrations in skin and/or blubber.
- A lack of correlation between contaminant concentrations in skin or blubber with those found in tissues collected from internal organs or blood precludes the combination or comparison of data across tissue types in many cases.
- Given that contaminants and trace elements are integrated over the lifespan of an individual in some tissues, immigrants may carry intermediate signatures. Thus, the magnitude of differences between regions needs to be substantial to avoid delineating DIPs between groups with relatively high connectivity.

### 3.4.6 Stable isotopes (SI) and fatty acids (FA)

- Differences in stable isotope (SI) ratios or fatty acid (FA) profiles reflective of DIPs in marine mammals will only be detected if stable gradients exist between the groups being compared as a result of differences in either prey selection/availability or geochemical process.
- Intrinsic sources of variability (e.g., age, sex, reproductive status, sampling depth, individual specialization) can result in differences in SI ratios or FA profiles that are not correlated to population structure.
- The turnover time of the stable isotopes or fatty acids in the tissue being sampled must be appropriate to evaluate demographic independence (e.g., tissues with longer turnover times will be more useful).
- Temporal variation in SI ratios and FA profiles can occur and needs to be considered when interpreting the results if samples were collected over multiple years/seasons.
- If different geographic regions are used for breeding and feeding, then the location of sample collection in the context of the migratory cycle needs to be considered when interpreting results.

### 3.4.7 Life History

- Life history traits may exhibit plasticity in response to environmental factors (e.g., timing of reproduction varying with photoperiod), thus allowing for differences in traits to develop within a DIP if the range of the DIP is large enough to encompass sufficient environmental variability.
- Life history traits that reflect different density-dependent responses may be informative for delineating DIPs, but without additional information it is not possible to rule out other explanations.
- Measures of reproductive seasonality may have the most utility in delineating DIPs due to the potential for reproductive isolation. Hormonal analyses for determining
reproductive state from biopsy samples should greatly increase the amount of data available on reproductive timing in marine mammal species.

3.4.8. Trends in abundance

• Given that surveying the entire range of a species is often not feasible, it is important to evaluate if apparent trends in abundance based on data collected in a portion of the range could instead reflect shifts in distribution over time.
• The detection of trends requires that long-term time series of abundance estimates are available. The power to detect trends is increased if surveys are frequent and conducted at regular intervals and if coefficients of variation are low.
• Other lines of evidence, in particular movement data, are needed to rule out alternate explanations for any observed trends in abundance.

3.4.9 Physiographic or oceanographic differences in habitat

• Habitat can be described using spatially static physiographic variables, such as bathymetry and distance to shore, or dynamic oceanographic variables, ranging from water temperature to prey distributions.
• Different DIPs often specialize on different habitats. Thus, habitat differences between groups can be an indication that they are different DIPs.
• Habitat characteristics known to be important in shaping demographic independence of a species in one area may have utility in guiding DIP delineation in the same species in other regions as well as for guiding DIP delineation for species with similar ecology, but little other information, in the same region.
• In cases where the habitat variables that distinguish different DIPs are spatially dynamic, the boundaries between those DIPs will also be dynamic.
• Habitat data cannot be used to directly estimate the degree of mixing between putative DIPs.
• When collecting the data necessary to parameterize a species-specific and/or region-specific habitat model is not possible, researchers should consider delineating DIPs that align with Spalding et al.’s (2007) Ecoregions or other well-defined regional ecoregions.

3.4.10 Association data

• By identifying groups of animals that rarely or never interact with each other, association data can be a valuable tool for helping to delineate DIPs.
• Association data are particularly useful for stratifying data from other LoEs and for identifying cryptic populations.
• Because it requires photo-identification of a large fraction of the relevant populations, including multiple re-sights, using association data to delineate DIPs is only practical for populations with abundances in the hundreds to low thousands that occur in areas that are reasonably accessible to researchers.
• Association data can be particularly useful for identifying island/coastal populations of otherwise pelagic species.
Inferences that can be made from association data are limited by the time span of the photo-identifications used in the analysis.

Other LoEs are required to determine whether groups identified by association data represent family groups, social groups, or DIPs.

### 3.4.11 Acoustics

- Interpreting the significance of differences in vocal characteristics between two groups requires an understanding of whether these characteristics are passed from mother to offspring (vertical transmission) or can be learned later in life from conspecifics (horizontal transmission). If horizontal transmission of vocalization patterns occurs, substantial connectivity between groups could exist but not be evident in comparisons of vocal characteristics between groups.
- Comparisons of vocalization characteristics between groups should utilize datasets collected from both groups during the same season and over multiple years.
- Behavioral and/or environmental factors (social and physical) can influence vocalization characteristics and could lead to over-splitting if not considered when making comparisons between groups.
- Some vocalizations are only produced by males and should not necessarily be considered representative of patterns of structure among females.

### 4 Data availability

#### 4.1 Defining ‘best scientific information available’

The MMPA directs NMFS to prepare stock assessment reports for each marine mammal stock using ‘the best scientific information available’. The purpose of Section 4 is to give a broad overview of the state of data availability for current stocks delimited under the MMPA. Initially, SARs identified most stocks at very large scales, commensurate with the limited information on population structure available at that time. For some species the agency has since delineated smaller stocks, but with 25 years of accrued data since the first SARs, the process of stock revision would benefit from further guidance regarding what constitutes “best scientific information available,” particularly for stocks for which data are limited and where human-caused mortality may be a concern.

Gathering the information given here required input from marine mammal experts with various levels of practical experience in actually delineating stocks. Therefore, the individual items for each LoE are not perfectly consistent, but the group attempted to assemble guidance that, overall, would be considered the best available scientific information on LOEs for delineating DIPs. An example of the inconsistency is the assessment of the strength of evidence for acoustic data for fin whales within the Pacific (see Table 4.1 below) where some judged the evidence to be weak and others moderate in different regions. Such inconsistencies would need to be addressed (perhaps
through an SEDM process described in section 5), but the objective here is to give a broad overview of data availability.

It is clear that availability and suitability of data for different LoEs will vary among species. Thus stock delineation must be based on different LoEs to meet the MMPA requirement to use the best available scientific information. We have undertaken to document what data are available for currently defined stocks, where ‘currently’ covers the period from 2015-2020 (see below).

4.2 Examples of factors affecting data availability

Over the past few decades, stock revisions have primarily occurred for species where collecting data on a strong lines of evidence (LoEs) was attainable, which often occurred when samples from bycatch were available. For example, tissues obtained from observer programs in California fisheries provided the genetic samples that revealed that DIPs of harbor porpoises existed on a finer scale than previously realized. Those genetic data, together with distributional data, were used to delineate new harbor porpoise stocks (Carretta et al. 2018). Areas of lower density guided placement of stock boundaries. Similarly, data from harbor seals in Alaska, including genetics, abundance, trends, and satellite tagging showing movement patterns, revealed the existence of finer-scale DIPs than had been previously recognized. Those data, along with traditional subsistence hunting boundaries, were used to delineate 12 stocks where there had only been three (Muto et al. 2018). Later, the new stock boundaries were noted to correspond well to fine-scale ecoregions described for Alaska (Piatt & Springer 2007). Finally, multiple lines of evidence for common bottlenose dolphins along the Atlantic coast (Hayes et al. 2018) and for Hawaiian insular false killer whales (Carretta et al. 2018) revealed previously unrecognized DIPs. All these cases had genetics and/or movement data available, which are each considered a strong LoE.

In contrast, there have been no stock revisions for species where genetic or movement data (through tagging or photo-identification) are particularly difficult to obtain. Many such species have largely inaccessible distributions, including some of the ice seals and many beaked whales. Other species are difficult to obtain biopsy samples from (e.g., harbor porpoises, minke whales, and most deep diving cetaceans). Photographic-identification to document movement is impractical for species of high abundance (e.g., common dolphins and pelagic dolphin species generally) or that have too few markings (e.g., harbor porpoises) or unstable markings (e.g., Risso’s dolphins). Satellite tagging is expensive and is thus not a practical method to gather sufficient movement data from which to draw inference for many species with moderate to high abundance. Consequently, there are many species that have few or no data for LoEs that are considered strong for stock delineation. There is also little prospect of attaining such data in the near future (5 years).

4.3 Details of how the Data Availability Table was completed

The Data Availability Table was completed for every stock of cetacean and pinniped managed by NMFS, using the stocks listed in the 2012 Stock Assessment Reports and expertise from identified
assessors and consulted scientists. The Data Availability Table asks the question, “Are results currently available from this LoE that are sufficient to determine whether there are multiple DIPs present within a currently defined stock? If not, are results likely to be available within the next five years?” Responses were coded as follows:

‘-’: Not applicable; this LoE is not useful for DIP delineation for this stock/species
0: Not feasible to collect or analyze sufficient data within five years
1: Feasible to collect sufficient data or analyze samples within five years, but no plans to do so
2: Sufficient results for reviewing DIP delineation expected within five years
3: Sufficient results for review of DIP delineation are currently available

‘Sufficient’ requires some judgment to determine not simply whether data are available but whether the sample size and distribution will allow a good chance that the question of whether multiple DIPs are present can be resolved at least as far as the strength of that LoE allows. This does not imply that data that are not ideal will not be used for DIP delineation if they are the best available, but rather indicates whether robust data are available (or could be soon). One way to think about ‘sufficient’ is to imagine whether these data would be acceptable in a publication as evidence for or against presence of population structure.

Another general issue is the geographic scale considered in the question. Many currently defined stocks have very large ranges. For the purposes of this exercise, the data availability should not require sufficient data to resolve DIP structure within the entire area, but rather should be relative to whether data are sufficient to resolve that there are ‘multiple’ DIPs (meaning more than one can be delineated). Thus, if the current stock was the entire west coast and there were data supporting a DIP in the southern portion but poor data in far northern regions (such that the remainder could still contain multiple DIPs), the evidence supporting the new delineation would rate a 2 or 3 based on the potential for adding a single new DIP.

Instructions provided to assessors on how to complete the Data Availability Table are given in Appendix 3. Appendix 4 has the full data availability table that lists all stocks alphabetically by common name and allows readers to find the relevant row for a stock of interest and see both the strength of evidence and data availability for that stock.

To facilitate discussion of the summary results of the data availability exercise, we present an excerpted selection for large whales (Table 4.1) The color key below the table indicates the strength of evidence for each stock where the darker colors represent data likely to be sufficient to resolve whether there are multiple DIPs within the next 5 years (Data Availability Codes of 2 or 3) and light colored shades indicate data could be available within that period but there are no plans/funding. A gray cell indicates that data were either deemed not suitable evidence for DIP delineation or are not available/will not be available in 5 years (i.e., by 2020) for that LoE regardless of strength.
### Table 4.1 Excerpt from data availability table.

Data availability codes are described in the text above. Dashes indicate that the LoE is not useful for stock delineation for this stock/species. See Appendix 4 for full table. Key below. Note that the color codes for the lines of evidence are retained from the full table (“Association data” is colored blue because for some species, like beluga whales, association data were considered moderate strength and were sometimes available).

<table>
<thead>
<tr>
<th>Species</th>
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</table>

Note: The color codes for the lines of evidence are retained from the full table. For some species, like beluga whales, association data were considered moderate strength and were sometimes available.
4.5 Summary of Results

Stocks were categorized into Pinnipeds, Large whales, Deep diving whales, and Other odontocetes. Data availability clearly differs across these categories (Figure 4.1). Available-strong is defined as LoEs listed as ‘strong’ for that stock, with an availability category of 2 or 3. Available-moderate is defined as a minimum of 2 LoEs listed as ‘moderate’ and an availability category of 2 or 3. If neither of the conditions for Available-strong or Available-moderate are met, the category is Weak. For deep divers, the Weak category has the highest frequency with over half of the stocks in the SARs qualifying as Weak. It is worth noting that even for pinnipeds, which typically have strong LoEs because they haul-out on land, the proportion of stocks that have Weak data availability is over 20%. Of 244 stocks evaluated, 124 or just over half had strong data available. Thus, if DIP delineation was restricted to ‘strong scientific data available’ rather than ‘best scientific data available’, delineation could not be further considered for roughly half of the stocks.

When new stocks should be designated or how research should be prioritized to improve DIP delineation must weigh what data are available now and whether sufficient data can be obtained with available resources in the near future against the potential consequences of continuing to manage with plausibly incorrect stocks in the face of known or likely threats. Such decisions and prioritization are beyond the scope of this handbook. However, describing the state of data availability for DIP delineation in the Stock Assessment Reports will improve readers’ ability to interpret the adequacy of those assessments.

Figure 4.1 Percentage of stocks (with actual number of stocks above the bars) in different data availability states: available-strong (code 2 or 3 in a strong LoE), available-moderate (code 2 or 3 in at least 2 LoEs with moderate strength), available-weak (all other cases).
5 Integrating multiple LoEs and handling uncertainty

5.1 Introduction
In many cases, sufficient data will be available to allow the delineation of DIPs with relatively little ambiguity. However, in some cases DIP delineation will be particularly difficult because 1) strong LoEs contain some degree of uncertainty, 2) strong LoEs are not available and multiple LoEs must be integrated, and/or 3) estimates of dispersal are at the threshold for demographic independence. This section describes and recommends Structured Expert Decision Making (SEDM) as a method to improve DIP delineation in such cases. Making sound management decisions in these cases will often require taking into account specific management objectives rather than relying entirely on biological data during the decision-making process. Consequently, this section discusses stock delineation, specific to the MMPA, rather than the more generic term of DIP delineation. Though the terminology of the MMPA is used in this section, the concepts apply to the delineation of management units under other national or international conservation regulations.

Each case will differ in the amount and strength of available evidence and as such, there can be no single method that will fit all cases. In addition, most lines of evidence cannot be quantitatively integrated in a single analysis because the data types are different or estimate different quantities. For example, genetic and morphological data (both strong LoEs for all taxa) can reflect direct measures of long-term gene flow. In contrast, except in unusual cases of long-term (decadal) studies, photographic-identification data can provide evidence that there is little movement between areas now, but it cannot provide information on populations that have mixed in the past (i.e., before the start of the study) and may in the future but are currently recovering from a depleted level. Nevertheless, all LoEs are useful, to varying degrees, in examining current population structure. The weaker LoEs often provide more qualitative data that need supporting data to draw good inferences. For example, finding positive differences in stable isotopes could result from a recent temporary dietary shift or even inadvertently sampling different age or sex classes in two different strata. Thus, additional evidence is needed to make an inference based on these data.

As was seen in the section on data availability, there are rather few cases where multiple lines of weak evidence are available. However, there may be cases where inferences from strong data, like movement data, are limited by uncertainties due to a limited amount of movement data or due to incomplete understanding of the implications of having samples predominantly from one age or sex class. In these cases, there may be sufficient auxiliary data, either from the same population, other populations or in some cases similar species, to deal with the uncertainty in a particular LoE from which a strong verbal argument may be made.

There is no easy way to combine multiple weak lines of evidence into an inference about population structure analytically. Instead, these cases will likely require integration through a structured expert opinion elicitation. We follow with a description of the process of such elicitation and call it by the common name Structured Expert Decision Making (SEDM) even though in this case, the result will be a recommendation concerning DIP delineation based on the best available scientific evidence.

5.2 Background on SEDM
Structured Expert Decision Making (SEDM) is a process that first went by the name of the Delphi method and is also called Expert Elicitation. It was developed by the RAND corporation in 1948 to overcome groupthink and the influence of dominant individuals. Burgman (2015) modified this method and called it IDEA (for Investigate, Discuss, Estimate, Aggregate). For the purposes of addressing DIP delineation questions, we modify this slightly and put it under the general SEDM rubric. The entire process involves the following steps: 1) identify the questions to be resolved, 2) identify experts, 3) train experts, 4) compose questions, 5) complete SEDM.

SEDM has been used in a review of stock structure for gray whales (Weller et al. 2013), as well as in numerous status reviews under the Endangered Species Act (ESA) (e.g., Krahn et al. 2002, Oleson et al. 2010). In SEDM, lines of evidence for demographic independence, as well as potential threats and other factors, are evaluated by experts using categorical or numerical scoring. Evaluations consider the inference quality of the data (e.g., how useful are stable isotope data for evaluating stock structure in a particular species or population?), as well as the data quality (e.g., how robust are the available data and analyses?). SEDM is particularly useful in identifying weaknesses in data and differences among experts in data interpretation for borderline cases for which many data are available but definitive conclusions are difficult (e.g., the gray whale Pacific Coast Feeding Group) and for identifying inconsistencies in approach across species or stocks.

The utility of judgements from single experts has been repeatedly shown to be inferior to using the judgement of groups of experts (see Burgman 2015 for many examples). Using a group can overcome universal biases, such as overconfidence (and hence under-estimating uncertainty and biasing towards rosy outcomes). However, groups can be subject to “group think” where the group adopts a single over-confident viewpoint often biased toward certain group members, thereby losing the benefit of gaining knowledge from the entire group. Methods have been developed to structure expert elicitation to avoid the “group think” phenomenon. The SEDM process we recommend for stock delineation is a slight modification of Burgman’s IDEA protocol (Investigate, Discuss, Estimate, Aggregate). The process has three steps: pre-elicitation, elicitation and post-elicitation. Details are given in Appendix 5.

**5.3 What type of questions need SEDM for DIP delineation**

The first step in SEDM is giving careful consideration to the type of questions that cannot be answered by standard statistical analyses. These questions will identify what the minimal needs are for choosing experts. Generally, the questions will be of two categories: 1) how many DIPs are in the area under consideration, and 2) where should boundaries be placed. Each category may need to be de-composed into several questions that lead up to the final question. For example, if there are several different LoEs, each may need to be addressed separately to help experts assemble the pieces of the puzzle before the elicitation of the main categorical questions. In this first step, the types of data should be listed to use as a guide to assembling a group of experts. Question refinement can be done after the group is assembled.

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³ A process in which arbitrary starting positions and hidden agendas of a few lead a group to a decision that does not reflect the individual participants’ private opinions.
5.4 What experts should be gathered to address these questions

Potential experts must be versed in the definition of a DIP and DIP delineation under the MMPA and GAMMS, be knowledgeable about the biology of population structure of the species under consideration and understand how the PBR management system works. In addition, any case of DIP delineation in need of the SEDM process will involve integrating knowledge about a diverse set of marine mammal distributional behaviors, consideration of how to treat uncertainty and awareness of the consequences of incorrect placement of a boundary for a particular group of animals. A core group of experts will promote consistency and efficiency. It may be useful to add a smaller number of members new to the process but with specific expertise for a particular case, for example in localized threats that can result in non-intuitive source/sink dynamics. All members will benefit from using a common training tool. Such a tool would need to be essentially a flight simulator to allow experts to learn the consequences of delineating DIPs for different plausible scenarios.

A basic minimal list of expertise needed would include experts in the taxon under consideration (or similar taxa), experts in interpretation of the types of available data for this taxon, and experts in general DIP delineation and assessment under the MMPA.

5.5 Composing questions for SEDM

There are several types of questions likely to arise in DIP delineation: 1) numeric questions (for example, the number of DIPs within an area), 2) questions of alternative hypotheses (DIP scenario A or B), and 3) questions of boundary placement.

5.5.1 Quantitative questions

The objective of composing quantitative questions is to draft questions that seek a precise unambiguous quantity. Burgman recommends a method to elicit such quantities called the 4-point format: 1) Realistically, what do you think is the lowest plausible value?, 2) Realistically, what do you think is the highest plausible value?, 3) Realistically, what is your best estimate?, and 4) How confident are you that the interval you created, from lowest to highest, captures the true value?

Here, we recommend that experts be instructed to answer questions 1 and 2 such that their answer to question 4 is 90%. A value other than 90% could be chosen but it is important that groups of experts use the same value so that DIP delineation follows a consistent approach. This approach would ensure that all experts are aiming at the same objective and that their responses can be easily integrated into a single group value. We refer to this modification as the 3-point format. This format can be used for both single integer-type questions (the number of plausible DIPs), or continuous values (abundance, trends in abundance, probabilities).

5.5.2 Alternate hypotheses

As much as possible, alternate hypotheses should be treated similarly with the quantitative questions above. However, when integrating multiple LoEs it may be best to simplify to a few hypotheses that can be fully explored across all evidence. For example, consider a case that has some distributional data including some areas of low abundance, a range that spans several eco-zones, and genetic data from the extremes of the range showing significant differences but a large gap in the distribution of
samples. Once the range in number of plausible DIPs is elicited, each alternative option could have the
group write arguments for and against that number of DIPs (in the style used in many voter
manuals for referendums where proponents for each option martial arguments for that option and
against the other option). Experts can then be asked to distribute plausibility points among the
hypotheses. This is often called the FEMAT-style structured decision-making process (from the
process developed by the Forest Ecosystem Management Team). Examples using this process for
gray and beluga whales are in Appendix 6.

5.5.3 Determining the number of DIPs

Whether using the quantitative or alternate hypotheses format, any DIP delineation exercise involves
some decision regarding the number of DIPs, be it one or some number greater than one.

To date, only the example of gray whales (Weller et al. 2013) uses SEDM to consider the number of
DIPs (see Appendix 6 for example questions). This case represents a good use of SEDM because one
of the DIPs in question was a borderline case where the level of external recruitment could have been
as high or higher than the internal recruitment. Other cases where new stocks have been delineated
involved proposals made to Scientific Review Groups (e.g., harbor seals O’Corry-Crowe et al. 2003,
harbor porpoise Chivers et al. 2007b) but the full decision process, which took many years, was not
recorded. However, in these latter examples, there were strong LoEs and the discussion often
revolved around the placement of boundaries (discussed below) more than the number of DIPs.

The use of SEDM considered here is to make progress for species with weaker LoEs, which has not
been done. Beaked whales are a good example of a group of species where there are some known
localized threats, poor data for strong LoEs (see Data Availability for Deep diving whales) and
consequently stocks often delineated at the ocean basin level. An SEDM consideration of beaked
whale DIPs may need to consider the LoEs for a particular case as well as whether new evidence is
likely to become available in the near future and whether evidence from similar cases can be
reasonably brought to bear.

5.5.4 Boundary placement

Boundary placement is conditional on the number of DIPs. The group of experts will first need to
address which hypotheses regarding the number of DIPs warrant actual boundary placement. In the
end, implementing the MMPA will be based on a single set of DIPs, so it does not make sense to
spend effort in placing boundaries for scenarios with low probability. Determining boundary
placement for the one or two most plausible hypotheses regarding the number of DIPs will likely
provide sufficient flexibility to managers. We recommend doing a similar exercise to the 3-point
format but using an actual map.

The population structure of marine mammals takes many forms including continuous distributions
where animals remain residents year-round (most harbor seals), highly migratory species (humpback
whales) and some cases where different age and sex classes occupy different habitats and have
different movement patterns (sperm whales). Some species’ distributions are linked to certain
temperatures or other oceanographic conditions and therefore their population structure may not be
tightly linked to geography (Dall’s porpoise, some eco-types of killer whales). Threats can be widely
distributed or very localized. These complex relationships are best communicated to the group by first creating a DIP archetype and then putting that archetype onto a map.

Resident (non-migratory) population structure is relatively common in species strongly associated with coastline features. Numerous examples are available where initial DIP delineation (both the number of DIPs and their boundary placement) has been revised based on multiple LoEs. Delineation of harbor seals within Alaska, for example, utilized genetics, movements, diet, trends in abundance, distributional hiatuses, traditional tribal hunting boundaries and major oceanographic regions (O’Corry-Crowe et al. 2003). Similarly, delineation of harbor porpoise along the coasts of California, Oregon and Washington used genetics when possible but where sampling gaps did not allow resolution of boundary placement, distributional gaps were used. Although there was extensive consultation on both these examples, SEDM was not used. In both of these cases, the ranges of the DIPs are non-overlapping.

False killer whales in the vicinity of Hawai’i provide an interesting example of resident DIPs that overlap and apparently are maintained as DIPs through their social structure. Bradford et al. (2015) record the decision process of a group formed to revise boundary placement of false killer whales. Although data remain sparse in many areas, especially in the western portion of the Northwest Hawaiian Islands and the pelagic areas, new data in the Main Hawaiian Islands, the range of the endangered DPS, suggested boundary revisions were needed. The group did not use SEDM and note there was a lack of guidance on the boundary placement process. They did assemble the best available data and examined various plausible options for each DIP. The narrative implies that the group strove for a consensus approach. This approach is subject to ‘groupthink’ and future boundary revisions might benefit from an SEDM approach to get the most out of assembling a group.

Migratory species present a different set of problems both for designating stocks but also for placing boundaries as the threats that may result in not meeting the ecosystem goals of the MMPA can occur on the calving/breeding grounds, on migration, on feeding grounds or any combination of these areas.

Humpback whales provide a good example of the complexity that needs to be considered for migratory species. Figure 5.1 shows a population structure archetype for North Pacific humpback whales where each arrow represents a connection between a group of whales that share both a breeding and feeding ground based on genetic and photo-id data. Each of the four breeding grounds corresponds to a recognized DPS. Although there are four different feeding areas, all are used by members of more than one DPS. In addition, not all whales that belong to the same DPS use the same feeding ground. In this complex scenario, there are multiple ways to delineate DIPs. For example, DIPs could be delineated based solely on feeding ground affiliations without regard to breeding structure, or they could be delineated to align directly with the DPS designations, in which case all the whales using a given breeding ground would be part of a single DIP. Another possibility is that whales that share both the same feeding and breeding area (e.g. migratory herds of whales) are considered separate DIPs, in which case some DPSs (here, Mexico and HI) would contain multiple DIPs. While the most appropriate way to delineate DIPs among North Pacific humpback whales remains to be resolved, in all three scenarios boundary placement will result in multiple DIPs within the same geographic area, which presents challenges for management. For example, consider the endangered Central American distinct population segment (DPS), which contains a single migratory herd and also...
comprises a single DIP. A known threat is entanglement in California. Thus, the boundary for this DIP would run from Central America, through its migratory corridor in Mexico and to California and Oregon. Meanwhile, the Mexican DPS will also have some of its feeding range in the same California/Oregon region, and hence some of the entanglements will be of Mexican whales. Similarly, DIP boundaries for some DIPs of common bottlenose dolphins in the western North Atlantic overlap spatially and temporally, and this overlap can vary seasonally as well.

Figure 5.1. A population structure archetype for humpback whales in the North Pacific. Calving/breeding grounds are symbolized with circles and feeding grounds with rectangles. Numbers indicate approximate numbers in each geographic feeding and breeding area. The top number along the arrow is the proportion of the breeding group (DPS) that migrates to a particular feeding ground with the number of animals below that proportion.

6 Documenting a DIP delineation review

6.1 The importance of lasting documentation

The overall strength of data in DIP delineation reviews will always have to be evaluated on a case-by-case basis. Such evaluations need to be documented in order to ensure transparency in the DIP delineation process and to promote consistency across delineations. A thorough explanation of the data and methodology behind a delineation can also be used to inform future management, including future DIP delineation revisions. This includes studies or reviews concluding that a currently designated stock is comprised of a single DIP and therefore should not be further subdivided. SARs
are not the appropriate place to document the complete rationale for a DIP delineation, as the SARs need to be concise, and therefore cannot include the level of detail necessary. A DIP delineation revision should therefore be accompanied by a publication that can serve as a permanent record of the basis for the delineation of a DIP or DIPs. The publication should become part of the permanent scientific record and therefore should be a peer-reviewed journal paper, a NOAA Technical Memorandum (or other internal agency publication with review) or both if additional rationale or evidence is needed beyond the peer-reviewed publication.

6.2 Recommended components of a DIP delineation document

The publication documenting a DIP delineation revision must contain enough information to enable the reader to understand the basis for the DIP delineation and evaluate the degree of support for the new DIP(s) or for combining previously delineated DIPs. It should provide a clear and concise explanation of all data and analyses that were used to determine the number of DIPs and to identify the boundaries between them. Published work can be summarized and cited, while unpublished data and analyses should be more fully described. Documenting unpublished work could be accomplished by appending an unpublished report (e.g., a paper presented to an SRG meeting) to the publication. The publication should also explicitly discuss the extent to which each LoE indicates demographic independence, the limitations of the data sets and analyses used (e.g., sample size, seasonality or distribution of samples, violated assumptions, etc.), and how those limitations might impact the results. If SEDM is used in the decision-making process, a summary of the SEDM report should also be included in the document.

The existence of DIPs is often clearer than the location of the boundaries between them. An important function of the Technical Memorandum will be to explain the rationale behind boundary placement. Though this handbook has focused primarily on identifying DIPs rather than placing boundaries, many of the data used for DIP delineation are also useful for boundary placement. For example, bathymetric isoclines, maximum extent of tag data, and areas of reduced density have all been used in the past. The publication documenting a proposed DIP delineation should present all data and information that influenced boundary placement. The proposed boundaries should be clearly described and shown on a map. The authors should also describe alternative boundaries that were considered and why they were rejected. Bradford et al. (2015) provide an excellent example of how to clearly and thoroughly document boundary placement.

Because there are often limited data upon which to base precise boundary placement, it should be expected that boundary locations could be revised frequently as new data become available. For instance, boundaries that are chosen so as to encompass the maximum range documented by a small number of satellite tags may need to be expanded as additional tag data are collected. When documenting a proposed boundary revision, the authors should clearly state the likelihood that the boundary will be revised in the near future, and provide suggestions for additional data and analyses that could help to refine and ultimately stabilize boundary placement.
7 Acknowledgments
We would like to thank Shannon Bettridge for her tireless support of all of the efforts that have culminated in this handbook, from her participation on the Stock Delineation Guidelines Initiative (SDGI) Steering group through to her thoughtful review of this document. We would also like to thank the many people who contributed to this effort. Robin Baird, Shannon Bettridge, Amanda Bradford, Jim Carretta, Phil Clapham, Donna Darm, Karin Forney, Lloyd Lowry, Erin Oleson, Michael Scott, Paul Wade, Randall Wells, and Chris Yates in the SDGI workshop. Robin Baird, Christiane Elfes, Jim Estes, Brian Fadely, Patricia Fair, Alyson Fleming, Karin Forney, David Herman, Aleta Hohn, Sarah Mesnick, Jeff Moore, William Perrin, Shannon Rankin, Denise Risch, Melissa Soldevilla, Sofie Van Parijs, and Paul Wade provided expert presentations at SDGI discussion group meetings. Eric Archer, Jim Carretta, Brittany Hancock-Hanser, and Chris Yates reviewed earlier versions of this document.

8 References Cited


NMFS (2016) Guidelines for preparing stock assessment reports pursuant to the 1994 amendments to the MMPA. National Marine Fisheries Service Instruction 02-204-01, 25 pp


Taylor BL, Dizon AE (1999) First policy then science: why a management unit based solely on genetic criteria cannot work. Molecular Ecology 8:S11-S16


Young BG, Ferguson SH (2013) Seasons of the ringed seal: pelagic open-water hyperphagy, benthic feeding over winter and spring fasting during molt. Wildlife Research 40:52-60
Appendix 1: Review of Line of Evidence

The summaries below were generated through a series of journal club-style discussion groups and a three-day meeting, all organized as part of the Stock Delineation Guidelines Initiative (SDGI; Martien et al. 2015). Each discussion group focused on one LoE and featured presenters who were experts on that LoE (Table A1.1). The discussion groups were conducted via Webex to allow maximum participation.

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In these summaries we have not attempted to provide thorough literature reviews of research on the various lines of evidence. Rather, we cite a few specific applications of each LoE and, where possible, summarize articles that provide more detailed overviews.

Many issues related to sample size, sample distribution, and temporal stability are common to all LoEs and are reviewed in Section 3.2 of this document. The reader is strongly encouraged read Section 3.2 in addition to the LoE summaries relevant to a particular study.

A1.1 Morphology

A1.1.1 General Considerations – Morphological differentiation implies differential adaptation that has evolved over substantial time periods. As such, a finding of morphological differences between groups represents strong evidence that the groups being compared are demographically independent. However, morphological differences could also suggest that higher-level structure (e.g., subspecies, species) is present, and it is not always clear what the magnitude of such differences is at the upper boundaries of demographic independence. While certainly there are cases where stocks with morphological differences have subsequently been elevated to subspecies or species (e.g., Maui’s dolphin, Baker et al. 2002), there are other cases, such as common bottlenose dolphins in the...
eastern North Pacific, where morphological differences have been identified among what are considered “good” stocks. For the coastal and offshore stocks of ENP common bottlenose dolphins, significant differences in tooth counts were identified but the differences were modal rather than diagnostic. However, this case also highlights the strength of using a suite of characters for such analyses, as 23 of the 28 measures, as well as the tooth counts, were significantly different between the coastal and offshore dolphins (Perrin et al. 2011).

The characters typically utilized in morphological comparisons include body size and shape (proportions), skull dimensions, vertebral counts, and pigmentation patterns. Such comparisons usually require large samples of dead animals, which are often only available for species exposed to substantial bycatch (e.g., ETP spotted dolphins, Douglas et al. 1984, ETP spinner dolphins, Perrin et al. 1991) However, while cranial and osteological measurements will continue to rely on collection of dead animals, photogrammetric methods are making it more feasible to collect data on a range of external morphological characters (e.g., body lengths in common dolphins, Perryman & Lynn 1993, dorsal fin size in odontocetes, Durban & Parsons 2006, Rowe, 2009 #173, mean lengths in pinnipeds, Waite et al. 2007, Meise, 2014 #153, Sweeney, 2014 #180).

As with the other lines of evidence, it is important to consider alternative explanations for any differences found between groups. Both cetaceans and pinnipeds exhibit variation in size, shape, and pigmentation associated with ontogenetic developmental changes and sexual dimorphism (see taxon-specific references below); thus, it is important to ensure that differences detected between groups are not due to differences in the age and/or sex classes sampled. Determining if a specimen was collected from an adult animal, however, can be difficult if no additional data are available. While the identification of specific features associated with physical maturity (e.g., rostral distal fusion in Stenella spp., Dailey & Perrin 1973) is straightforward and commonly used in some species, it is more challenging in others (Pacific white-sided dolphins, Walker et al. 1986) and requires large sample sizes.

In addition, phenotypic plasticity can occur in some morphological characters. Although such plasticity could be indicative of demographic independence, it could develop between groups with high connectivity due to extrinsic factors. For example, adult size has been linked to nutritional status in several species of pinnipeds (e.g., Calkins et al. 1998, Dragon et al. 2010), and such a link has been suggested for southern resident killer whales (Fearnbach et al. 2011). In such cases, a juvenile animal that migrates from a low-quality natal area into a region with increased resources would likely not demonstrate growth patterns associated with nutritional stress but rather those of its current environment. In cases where phenotypic plasticity due to extrinsic factors cannot be ruled out, additional lines of evidence would be needed to delineate DIPs.

A third alternate explanation is that the differences detected could be due to clinal variation. If morphological comparisons rely only on specimens collected at the extremes of the range, such clinal variation could result in underestimation of the degree of connectivity throughout the range. As such, in cases where animals are known to inhabit areas in between the two regions being compared, care should be taken to ensure that specimens from that area are included in the analysis. Nonetheless, clinal morphological differences are strong indicators that movement across the range is sufficiently limited that it should be divided into multiple units for management purposes.
Finally, it is important to ensure that data collection and analytical methods are comparable across regions or studies included in the comparison, as inter- and intra-researcher variation in the measurement of morphometric characters can occur (e.g., Waite & Mellish 2009). Specifying how measurements are taken can be difficult, resulting in variation between investigators. This concern particularly applies to measures of external morphology (e.g. body length, dorsal fin heights, etc.); given that such carcasses are not maintained intact, no calibration between investigators can be conducted. In the case of skulls maintained in museum collections, it may be possible for the investigators to take measurements on some of the same specimens and thus identify any issues.

Although morphological differences are considered strong evidence that multiple stocks exist, in some cases determining where the boundary between those stocks lies is difficult in the absence of other information. For example, genetic and morphological differences have been identified between Pacific white-sided dolphins in Baja California and those north of Point Conception (Walker et al. 1986, Lux et al. 1997). However, samples of both forms have been collected within the Southern California Bight, which may represent a region of sympatry or could indicate seasonal and/or interannual differences in occurrence patterns of the two forms (Carretta et al. 2017). It is not possible to distinguish the two forms in the field, and the geographic stock boundary is not well understood and is likely dynamic. Consequently, despite their differences, the two forms have continued to be managed as a single unit.

Summary of Caveats and Considerations –
- Comparisons of external morphology, osteology, and pigmentation typically require large numbers of carcasses, which may not be available for species without high bycatch or stranding rates.
- Caution should be taken to ensure that differences between groups are not due to variation in age and/or sex classes of the samples, phenotypic plasticity, or differences in data collection methods between investigators.
- If animals of different DIPs cannot be distinguished during field observations, the determination of DIP boundaries based on morphological differences alone may be difficult.

A1.1.2 Taxon-specific considerations

A1.1.2.1 Baleen whales – In the past, data collected during commercial whaling operations has allowed analyses of geographic patterns of variation in morphology in baleen whales (e.g., Kato et al. 1995, Branch et al. 2007). With the cessation of commercial whaling, however, additional data on cranial and osteological differences will be limited to strandings, which are infrequent for most species. Photogrammetry will be a valuable tool allowing comparisons of external morphology to be made (e.g., Gilpatrick & Perryman 2008). Ideally, these measurements would be calibrated with measurements from whaling data to expand the range and number of samples.

A1.1.2.2 Odontocetes – For several odontocetes, stock structure was initially described primarily on the basis of morphological differences and later confirmed using genetic analysis (e.g., ENP common bottlenose dolphins, Walker 1981, Lowther-Thieleking et al. 2015). Morphological comparisons of cranial and osteological measurements have typically been limited to species for which large numbers of specimens are available, due to hunting (e.g., narwhals, Wiig et al. 2012), bycatch (e.g., ETP spinner dolphins, Perrin et al. 1991), and/or high stranding rates (typically coastal species, e.g. short-beaked
common dolphins, Westgate 2007). As with baleen whales, however, the utility of photogrammetry will expand the opportunities to collect measures of external morphology in a wider range of odontocetes (e.g., Perryman & Westlake 1998).

If sufficient numbers of specimens are available, however, morphological comparisons may be of particular value in species where opportunities to collect biopsies and/or movement data are limited. For example, many of the beaked whales inhabit deep waters, have low detection probabilities, and exhibit evasive behavior when approached, making the collection of sufficient data from free-ranging animals difficult if not impossible. However, the collection of measurements from stranded animals over a ten-year period allowed morphological variation between Gray’s beaked whales on the eastern and western coasts of New Zealand to be detected (Thompson et al. 2014).


A1.1.2.3 Pinnipeds – Many pinnipeds, including all species of Otariids, exhibit extensive sexual dimorphism (Weckerly 1998), highlighting the importance of subdividing specimens by age and sex for cranial and other morphometric analyses. Geographic differences in cranial measurements have been identified in both phocids (e.g., gray seal, Berry 1969) and otariids (Galapagos sea lions, Wolf et al. 2008). Although geographic differences in pelage coloration or patterns have been identified in some pinnipeds (e.g., harbor seals, Stutz 1967), extensive age and sex-related variation in pelage coloration occurs in some species (e.g., Mediterranean monk seals, Samaranch & Gonzalez 2000) and needs to be accounted for in any comparisons. As well, pelage coloration can change with molting patterns (e.g., Samaranch & Gonzalez 2000), and in some cases discolorations due to habitat and/or feeding strategies have been identified (Neumann & Schmahl 1999, Lydersen et al. 2001).

A1.2 Genetics

A1.2.1 General Considerations – Genetic data have become a powerful tool for delineating units to conserve (Moritz 1994, Taylor et al. 2010). When gene flow between two groups is restricted, those groups will become genetically differentiated due to the forces of drift and mutation. Thus, measuring the magnitude of differentiation can help to determine whether the two groups should be managed as separate units under a particular management scheme (Waples & Gaggiotti 2006, Palsbøl et al. 2007). Genetic data have played a key role in the delineation of many MMPA stocks (e.g., Chivers et al. 2002, Rosel et al. 2009, Andrews et al. 2010, Martien et al. 2012), as well as the delineation of management units for marine mammals around the world (e.g., Parsons et al. 2002, Mendez et al. 2008, Gravena et al. 2015). Early applications of genetic data focused on rejection of the null hypothesis of panmixia (random mating among groups) as the basis for determining whether two groups should be managed separately (Moritz 1994), but efforts now focus on determining the critical level of dispersal below which groups should be managed separately and comparing the observed genetic differentiation to the degree of differentiation expected at the critical dispersal rate (Waples & Gaggiotti 2006, Palsbøl et al. 2007, Taylor et al. 2010). This focus on the magnitude of differentiation rather than statistical significance is increasingly important as the size of genetic data
sets grows, both in terms of the number of loci and the number of samples, as larger data sets result in greater statistical power to detect differentiation even within populations (e.g., between family groups or social groups).

The inheritance mode of a particular genetic marker affects its utility and interpretation in studies aimed at delineating stocks. Both nuclear and mitochondrial (mtDNA) genetic markers can be used to assess population structure. Because of its strict maternal inheritance, mtDNA only reflects the structure of the female component of the population. Though this characteristic prevents mtDNA data from providing a complete picture of all movements between and relationships among populations, it makes mtDNA particularly useful for assessing demographic independence. Because the reproductive capacity of a population is determined by the number of females, movement of males into an area will not prevent local depletion or extirpation of an area. For instance, if a population of dolphins around an island were being heavily impacted by bycatch, the birth rate within the population (internal recruitment) would decline regardless of the number of male emigrants the population received. Thus, a finding of differentiation in the mtDNA genome would provide evidence of demographic independence regardless of the degree of differentiation in nuclear markers.

Patterns of differentiation can also differ between mtDNA and nuclear DNA in migratory species in which individuals from multiple feeding grounds share a single breeding ground. For instance, humpback whales in the western Atlantic Ocean all use the same low-latitude breeding grounds, but show strong fidelity to one of six different feeding grounds (Clapham et al. 1993). Gene flow on the breeding ground precludes the development of nuclear differentiation among the feeding grounds. However, because calves learn their migratory routes from their mothers, there is strong genetic differentiation among feeding grounds in mtDNA (Larsen et al. 1996).

Regardless of the type of genetic marker used, care must be taken when collecting samples or interpreting results from species that exhibit seasonal movements. Whether the focal species exhibits site fidelity only seasonally or undertakes regular seasonal migrations, samples collected at times when populations are mixed are likely to result failure to detect population structure.

Management schemes can be categorized as falling under an “Evolutionary paradigm” (focused maintaining evolutionary potential and preventing extinction) or an “Ecological paradigm” (focused on demographic cohesion and ecosystem function) (Waples & Gaggiotti 2006). The MMPA, with its focus on maintaining stocks as functioning elements of the ecosystem, falls under the latter. Using genetic data to delineate management units under the Ecological paradigm can be difficult because the MMPA and similar management schemes focus decadal time scales, whereas genetic data generally reflect evolutionary time scales. The magnitude of genetic differentiation between two groups represents an average over multiple generations. Given the long generation times of most marine mammals (Taylor et al. 2007a), that can mean many centuries. If population structure has changed recently as a result of human exploitation, habitat degradation, or changing environmental conditions, estimates of genetic differentiation may not reflect the current status of the groups. However, many genetic analytical methods based on assignment tests and identification of close kin within a sample can produce results that reflect contemporary conditions.

The critical dispersal rate below which two groups must be managed as separate stocks in order to meet the management objectives of the MMPA depends on many factors, including the relative sizes
of the groups and the spatial distribution of human impacts (see section 1.2.1, Figures 1.1 and 1.2). However, simulations have shown that the critical dispersal rate below which populations remain demographically uncorrelated can often be between 1% and 10% of the population per year (Hastings 1993, Taylor 1997). Such dispersal rates are often high enough to render two populations genetically indistinguishable. Thus, while a finding of genetic differentiation between two groups is strong evidence that they are demographically independent, the converse is not true.

The degree of genetic differentiation between two populations is inversely proportional to both their abundance and the rate of dispersal between them (see eq. 1 and Figure 1 in Taylor et al. 2000). Consequently, using genetic data to evaluate groups with very large abundances is also difficult. Spinner dolphins and pantropical spotted dolphins in the eastern tropical Pacific have long been divided into multiple management units on the basis of strong morphological differences (Perrin et al. 1991). However, the high abundances of these groups (likely in the low millions historically) has resulted in such low levels of genetic differentiation that it is only recently, through the use of very large genetic data sets and examination of non-neutral variation, that they have been shown to be genetically distinct (Andrews et al. 2013, Leslie & Morin 2016).

As with morphological data, the possibility of clinal variation should be considered when evaluating genetic data from continuously distributed species, especially if samples are only available from geographically distant locations. In the absence of proportionally sampling across a continuous range it can be very difficult to distinguish between a stepping-stone structure with discrete DIPs and continuous clinal variation. Nonetheless, clinal genetic variation is a strong indicator that movement across the range is sufficiently limited that it should be divided into multiple units for management purposes.

Though genetic data has been of great utility in elucidating the population and stock structure of many marine mammal species over recent decades, collecting sufficient sample sizes continues to be a challenge for many species. Many species (e.g., beaked whales and harbor porpoises) exhibit evasive behavior when approached, making the collection of sufficient data from free-ranging animals difficult if not impossible. However, technological advances in DNA collection and sequencing may soon help to mitigate this issue through the use of “environmental DNA” (eDNA) sampling. Water collected from the ‘footprint’ of whales and dolphins has yielded sufficient DNA to identify individuals to species (Foote et al. 2012, Ma et al. 2016, Baker et al. 2018), and to generate full mitochondrial control region haplotypes for one difficult-to-biopsy species, the harbor porpoise (Parsons et al. 2018). eDNA applications hold the promise to substantially improve scientists’ ability to evaluate population structure of elusive species in the near future.

Summary of Caveats and Considerations –

- The mode of inheritance should be considered when interpreting results of a genetic study of population structure.
- Under some circumstances (e.g., maternally-driven fidelity to feeding grounds), DIPs will only exhibit genetic differentiation at mtDNA loci, not nuclear loci.
- If different geographic regions are used for breeding and feeding, then the location of sample collection in the context of the migratory cycle needs to be considered when interpreting results.
• Genetic data represent an average over several to many generations. While some analyses can provide estimates that reflect the past couple of generations or individual dispersal, others reflect evolutionary time scales and therefore may not accurately represent current population structure.
• The critical level of dispersal below which two groups should be considered separate stocks under the MMPA is high enough that genetic differentiation is expected to be low and therefore can be difficult to detect.
• Using genetic data to delineate DIPs in species with high abundance is especially difficult due to the inverse relationship between abundance and expected differentiation.

A1.2.2 Taxon-specific considerations

A1.2.2.1 Baleen whales – Many baleen whales undertake regular seasonal movements that complicate the interpretation of results from most LoEs, including genetic data. Interpreting results from genetic studies of stock structure must include consideration of the patterns of genetic differentiation expected at nuclear versus mitochondrial loci from samples collected at different parts of the migratory cycle.

A1.2.2.2 Odontocetes – Some species of odontocetes, particularly members of the Delphinidae, exhibit social structure that could be mis-identified for DIPs if genetic analyses are limited to only an assessment of statistically significant differentiation between groups (Parsons et al. 2013, Martien et al. 2014, Van Cise et al. 2017). In cases where social structure is known or suspected to be present, particular care is necessary in ensuring that sample collection and data analyses account for the possibility of social structure and that the magnitude of genetic differentiation is assessed relative to expectations under critical values of dispersal (e.g., Martien et al. 2012) or that additional LoEs corroborate demographic independence of groups (e.g., Martien et al. 2014, Martien et al. 2017).

Like many baleen whales, some odontocetes undertake regular seasonal movements that complicate the interpretation of results from most LoEs, including genetic data. Notable examples include beluga whales, which exhibit seasonal fidelity to breeding grounds (ref.), and some fish-eating (aka resident) killer whales, which inhabit inland waterways in the summer but roam widely along the US west coast in winter (ref.). As with migratory baleen whales, the season in which samples are collected must be carefully considered when evaluating results of genetic studies of population structure for these species. Similarly, for stocks that may overlap in space or time, care must be taken during sample collection to minimize the possibility of creating mixed data sets.

A1.2.2.3 Pinnipeds – Age and sex-related differences in movement patterns exist in many pinnipeds. For instance, juvenile harbor seals tend to range widely before settling into smaller home ranges as adults, typically near their natal site (Small et al. 2005). Including a large number of samples from juveniles in a genetic analysis of stock structure could therefore result in under-estimating the degree of genetic differentiation between two areas. In cases such as these, it is important that genetic samples are collected from the age/sex classes most relevant to assessing demographic independence.

As in baleen whales, the use of different areas for feeding and breeding makes it particularly important to take seasonal in which samples were collected into account for pinnipeds.
A1.3. Movements

A1.3.1 General Considerations – Data on movements typically come from photographic-identification and satellite telemetry studies, as well as from tagging/marking studies for pinnipeds. For small populations, genetic identification may be used in the same manner as photographic identification but with the advantage that the identification remains constant with age, whereas features used in photographic-identification may change. When evaluating the utility of movement data to delineate DIPs in marine mammals, the primary concern is to ensure that the movement data collected are representative of the groups being compared. In most cases, evaluating whether movement data are representative requires some auxiliary information on the life history of the species. Differences in affiliation and habitat use patterns between age, sex, and reproductive class have been documented in numerous marine mammal species (Wells et al. 1987, Van Parijs et al. 2003, Breed et al. 2006, Hartman et al. 2008).

There may also be differences between age/sex classes in the presence of markings that are useful for photographically identifying individuals. Though dependent on the identifying character, it is typical for young animals to be less distinctive than older animals, particularly in cases where the identifying features are permanent scars that individuals obtain throughout their lives (e.g., Tolley et al. 1995, Blackmer et al. 2000, Rowe & Dawson 2009).

In mammals, females are generally considered to demonstrate higher levels of philopatry than males (Greenwood 1980). While baleen whales have generally been considered to follow this pattern, little unequivocal evidence supporting male-biased dispersal in baleen whales exists. However, there is evidence of sex-biased dispersal in a wide range of odontocete and pinniped species (e.g., Escorza-Treviño & Dizon 2000, Möller & Beheeregay 2004, Cassens et al. 2005, Breed et al. 2006, Chilvers & Wilkinson 2008, Engelhaupt et al. 2009). Though the gene flow associated with male-biased dispersal can prevent evolutionary divergence between populations, demographic independence can persist if females exhibit strong site fidelity (Rosel et al. 1999). This is because male immigrants have little to no impact on birth rates within a population, and therefore cannot compensate for the reduced rate of internal recruitment that would result from an increased mortality rate, due to either natural or anthropogenic impacts.

Many species of marine mammals, particularly baleen whales and pinnipeds, exhibit strong seasonal movements between habitats used for foraging and habitats used for breeding and calving/pupping. Thus, structure that is apparent at one time of the year (e.g., breeding season) may not be detectable during other parts of the year.

Sperm whales represent a particularly good example of the potential for movement data to be misleading when delineating DIPs of animals for which little information on the life history and behavior is known. In North Pacific sperm whales, movement data suggest that both sexes may be nomadic in response to temporal and geographic changes in prey distribution and abundance (Whitehead 2003, Mizroch & Rice 2013). If interpreted in the absence of other data, these movement data would suggest that no population structure is present in the North Pacific. However, association and genetic data indicate that females of all ages, their dependent offspring, and immature males form partially matrilineal stable social units (Mesnick 2001, Mesnick et al. 2003, Mesnick et al. 2003, 46).
Whitehead 2003) that are organized into culturally-defined ‘vocal clans’ (Rendell et al. 2012). Recent genetic work suggests that California Current sperm whales are demographically independent from those off Hawai‘i and the eastern Tropical Pacific (Mesnick et al. 2011), demonstrating that, in cases like sperm whales where individuals demonstrate social rather than geographic fidelity, movement data alone are not sufficient to evaluate demographic independence.

Movement data collected via photographic-identification and telemetry represent contemporary connectivity between groups, which is consistent with the goal of the MMPA to maintain stocks as functioning elements of their ecosystem. However, both methodologies have limitations with respect to the temporal scale they represent. Unlike genetic data, which is integrated over contemporary and historic time scales, movement data are only representative of the temporal scale at which they are collected. For photographic-identification, each sighting represents only a “snapshot” of the animal’s location on a given day, but does not provide much information about movements of an individual between sightings (Falcone et al. 2011). In contrast, telemetry data provide detailed, fine-scale movement data, sometimes for periods long enough to capture the full migratory cycle in a given year (Mate et al. 2015). However, the relatively high cost of instruments often constrains sample size in telemetry studies, raising questions about whether observed patterns are representative of the group as a whole.

One significant problem with utilizing movement data exclusively is that it is not possible to provide direct evidence of interbreeding based on photographic-identification or telemetry data. Just because an animal moves from one group to another does not necessarily mean it is breeding in the population it has moved to.

Natal fidelity can be evaluated if calves/pups can be marked or otherwise individually identified and the study is long enough to assess whether the young disperse or stay with the group into which they were born.

Additional methodological constraints exist for both photographic-identification and satellite telemetry studies. In some species, only a very small proportion of a group is individually identifiable, which limits the utility of photographic-identification methods to identify movements. In addition, loss of marks or changes to marks over time is known to occur in some species, complicating longer-term studies. For highly abundant species even if most individuals are identifiable, the practical and financial constraints of photographing or tagging a sufficient percent of the population to estimate movement rates limit the feasibility of these types of studies. In addition, the size and behavior of some species can constrain the feasibility of telemetry studies. This constraint can include those species that are too small for remote deployment or which cannot be safely captured (e.g. Dall’s porpoise), or cases where tagging opportunities may be limited due to the behavior or remote distribution of the group (e.g., many beaked whale species with very low encounter rates).

A final consideration regarding the use of movement data is that demographic independence is evaluated based on the balance of internal versus external recruitment. Thus, to be useful in delineating DIPs, it is not usually sufficient to demonstrate only that movements occur; ideally, movement data should allow inferences to be drawn about the proportion of immigrants in a group.

**Summary of Caveats and Considerations**
• Caution should be taken to ensure that differences in movement patterns between sexes, age classes, or reproductive classes are not mis-interpreted as indicating the presence of different DIPs.

• Photographic-identification studies can be limited by the nature of the markings used to identify individuals. Marks that differ between age or sex classes, only occur in a small proportion of individuals, or can change or be lost over time can complicate the analysis and interpretation of movement data from photographic identification.

• Movement data are only representative of the time period over which they are collected and therefore may fail to capture infrequent but demographically important movements.

• Using movement data to delineate DIPs in species with high abundance is especially difficult due to the practical and financial constraints of photographing or tagging a sufficient percent of the population to estimate movement rates.

• If different geographic regions are used for breeding and feeding, then the location and timing of data collection in the context of the migratory cycle needs to be considered when interpreting results.

• Movement data is most useful for evaluating demographic independence when it allows for the estimation of the rate of dispersal into a population.

A1.3.2 Taxon-specific considerations

A1.3.2.1 Baleen whales – For baleen whales, it is particularly important to interpret movement data in the context of what is known about the spatial and temporal structure of the migration and the location and timing of breeding. Although the contemporary migration patterns of some species and populations are well understood, limited information exists about others. In the context of delineating DIPs, it is important to know whether documented movements are between feeding areas or between breeding areas, as these types of movements have different implications with respect to demographic independence.

In several species of whales, calves learn their migratory route to feeding grounds from their mothers (called matrilineal fidelity). Both male and female calves show life-long fidelity to those feeding grounds. Understanding these patterns of fidelity can be important in evaluating demographic independence. Detecting these patterns using photographic-identification alone requires multiple field seasons to allow for calves first brought to the area by their mothers to return as juveniles and/or adults. Given that the tag durations are generally less than a year, most telemetry studies have at best been able to capture one full migratory cycle for an individual, as opposed to return over multiple seasons as can be done with long-term photographic-identification studies. As well, unless calves are tagged (which is generally prohibited), telemetry data on its own does not provide information on matrilineal fidelity, which is important in evaluating the balance between internal and external recruitment.

A1.3.2.2 Odontocetes – Interpretation of movement data in many odontocetes is hampered by a lack of life history information. In particular, information about the life history of pelagic dolphins (versus coastal or insular odontocetes) is often limited, due in part to the difficulty of studying these species. As such, little information is available on whether age or sex-based structure exists. Given the lack of
available life history data, it may be difficult to interpret the significance of movement data, limiting its utility in DIP delineation. In addition, the broad ranges and often inaccessible habitat of many pelagic species constrain the amount of effort that can be invested in such studies, and their generally high abundance means that re-sightings based on photographic-identification are likely to be low. Taken together, these limitations suggest that the utility of movement data in pelagic odontocetes may be limited.

Strong social structure is present among some odontocetes, in particular the blackfish (killer whales, false and pygmy killer whales, pilot whales and melon-headed whales). This social structure is typically easy to detect using photographic-identification, although relatively long-term studies may be required. The use of telemetry data alone, however, may not detect such structure, given limits on tag durations and the number of tags that can be deployed. However, for odontocetes in which photographic-identification studies have validated long-term social cohesion, such as resident killer whales in the eastern North Pacific, the value of tagging data is markedly increased, as movements of the social unit can be inferred from the tagging of a single individual.

**A1.3.2.3 Pinnipeds** – The use of natural marks to document movements in pinnipeds is much less widespread than it is for cetaceans. Some studies have relied on branding or on placing artificial tags on the fore or hind flippers to track movements; while this avoids biases associated with greater distinctiveness of different age or sex classes, the rate of tag loss can be high and difficult to quantify. Studies utilizing natural marks in pinnipeds have relied on pelage patterns in phocids (e.g., Karlsson et al. 2005, Forcada & Robinson 2006, Thompson & Wheeler 2008) and body scars and flipper abnormalities on otariids (e.g., McConkey 1999). In at least some phocid species, the distinctiveness of patterns varies among age and sex classes (e.g., Vincent et al. 2001), while body scars on otariids become more prevalent with age.

Branding or marking pups with flipper tags has allowed natal philopatry to be detected in both phocids and otariids, for which it can be exceptionally strong. This philopatry exists in both sexes, but in many, but not all cases (Cameron et al. 2007), philopatry is stronger in females (e.g., Pomeroy et al. 2000, Raum-Suryan et al. 2002, Chilvers & Wilkinson 2008).

With the exception of Galapagos (Villegas-Amtmann et al. 2009) and Australian sea lions (Gales et al. 1994), the timing of reproduction in pinnipeds is highly synchronous, and in most cases the breeding season is relatively well-defined (Atkinson 1997). Thus, lack of knowledge about when breeding occurs is less of a limitation in interpreting movement patterns than in some of the other taxa.

**A1.4 Distributional hiatuses or low-density areas**

**A1.4.1 General Considerations** – Distributional hiatuses and areas of low density within a species suggest the presence of unsuitable or non-preferred habitat, which can serve as a barrier to movement. Thus, demographic independence can develop between groups separated by hiatuses or low-density areas. Distributional hiatuses have been important factors in the delineation of many DIPs, including the California and Eastern Pacific stocks of Northern fur seals (Carretta et al. 2018) and coastal and offshore stocks of common bottlenose dolphins off of California (Defran & Weller 1999, Weller et al. 2013). Distributional differences also provide insight into potential demographic independence in the California Current stock of Risso’s dolphins (Becker et al. 2016). Although
currently only a single stock is recognized, it has been suggested that three stocks may exist on the basis of gaps in distribution that correspond with boundaries between different water masses (see Habitat section), along with differences in group size and inter-species associations.

Low density areas are more useful in placing boundaries than in inferring demographic independence. For instance, distribution data were key to delineating harbor porpoise stocks along the west coast. Harbor porpoises have an essentially continuous distribution from Point Conception, California, through Alaska, and on to Japan. Nonetheless, genetic analyses identified genetic differentiation, and therefore likely demographic independence, between five strata within the U.S. portion of the range (Chivers et al. 2002). However, the majority of samples used in the genetic study were derived from incidental fishery takes, resulting in sampling gaps and uncertainty regarding where boundaries between stocks should be drawn. To address this issue, data from aerial surveys were used to define stock boundaries in areas with low densities of harbor porpoises, resulting in the recognition of six different stocks within this region, including some stocks from which no genetic data were available at the time of delineation (Carretta et al. 2004). However, the location of these density discontinuities varied over time, resulting in dynamic boundaries that shift from year to year. The challenge in delineating stocks in these cases is that, for management purposes, it may be necessary to draw lines on a map, and these lines may not always reflect biological reality at any point in time.

It is important to consider the geographic scale and persistence of hiatuses and low-density areas when utilizing them in delineating DIPs. Distributional gaps that are persistent over many years and are equal to or greater than the typical scale at which individuals of a particular species move are more likely to be indicative of demographic independence than are ephemeral gaps or ones that individuals can easily cross. Nonetheless, even distributional breaks that are small or shift over time can indicate the presence of multiple DIPs when they are correlated with habitat features. For instance, a deep-water channel may present a stable movement barrier between two DIPs that both specialize on shallow-water habitat (e.g., Hawaiian common bottlenose dolphins, Martien et al. 2012). Similarly, the fact that distributional gaps in Risso’s dolphins along the west coast of the U.S. correlated to habitat differences provides added support for the idea that they represent gaps between DIPs (Becker et al. 2016).

For some species, particularly those with large offshore ranges, high abundances, or elusive behavior, collecting robust data sets from most LoEs for use in delineating DIPs is not possible given current technologies and resources. In these cases, data on distribution, combined with broad-scale habitat information (see Habitat section) may constitute the “best scientific information available” for delineating DIPs.

Summary of Caveats and Considerations –

- The temporal scale of distributional hiatuses is important. The presence of persistent, stable gaps may provide relatively stronger evidence of demographic independence, especially if there are corresponding habitat differences.
- Distributional gaps that are larger than the documented home range of animals provide stronger evidence of demographic independence than smaller gaps.
- Data on low-density areas can be particularly helpful in placing boundaries between DIPs that have been identified by other means.
When evaluating distributional data, researchers must consider the possibility of seasonal differences in distribution and differences between age and sex classes.

For some species, distributional data may be the only data that can be feasibly collected, and may therefore represent the “best scientific information available” for delineating DIPs.

A1.4.2 Taxon-specific considerations

A1.4.2.1 Baleen whales – The migratory nature of many baleen whales means that distributional gaps may be present in some seasons but not others. Researchers must consider whether apparent gaps or low-density areas occur on the breeding grounds, the feeding grounds, or both. In the Pacific, northern and southern hemisphere blue whales utilize the same breeding areas, but approximately 6 month apart (austral and boreal winter season). Thus, evaluation of distributional data in this and other migratory species must include a temporal/seasonal component.

In some species of baleen whales, different age and sex classes exhibit differences in migratory timing, routes, or destinations. Such is the case for minke whales in the western north Pacific, where the location of feeding grounds seems to vary by both sex and age (Perrin et al. 2018). Thus, researchers must consider whether baleen whale groups on either side of a distributional hiatus may represent different age/sex classes rather than DIPs.

The distribution of sei whales has been observed to shift dramatically over the course of a few years (Hayes et al. 2017), possibly in response to changing oceanographic conditions (Gregr & Trites 2001, Murase et al. 2014). Until these distributional shifts are better understood, distributional data are unlikely to be useful in delineating sei whale DIPs.

A1.4.2.2 Odontocetes – The utility of distribution data may be limited in odontocetes in which different age/sex classes or social groups differ in their habitat use patterns. As noted above, sperm whales in the north Pacific are a good example of how age/sex segregation can lead to mis-identification of DIPs if it is not taken into account.

A1.4.2.3 Pinnipeds – Age and sex-related differences in habitat use and movement patterns exist in many pinnipeds, complicating interpretation of distributional data. As in baleen whales, the use of different areas for feeding and breeding makes it particularly important to take seasonality of distributional data into account for pinnipeds.

A1.5 Contaminants

A1.5.1 General Considerations – Chemical signatures in the tissues of marine mammals can be used to infer movement patterns. The most commonly used chemical signatures are contaminants and trace elements, both of which are dependent upon the type of prey consumed and the region from which the prey were taken. Although accumulation patterns differ by tissue type, contaminants and trace elements typically reflect long-term foraging patterns. Consequently, if two groups demonstrate fidelity to different foraging areas, the concentration (or ratio of concentrations) of these chemicals may vary between groups, allowing inference on the degree of demographic independence.
Geographic variation in chemical signatures will only be useful for delineating DIPs if the variation exists at the appropriate spatial scale. Although some trace elements have natural sources (Law 1996), geographic gradients in anthropogenic compounds or elements are generally driven by distance from shore or by patterns of atmospheric transport, making them potentially useful for distinguishing between coastal and offshore populations. However, their utility in delineating DIPs within species inhabiting pelagic regions, where gradients in chemical signatures may be less pronounced, is likely limited. Similarly, in coastal and estuarine areas geographic variation in contaminant concentrations may exist at such small spatial scales that differential habitat use by individuals can result in differences in chemical signatures among individuals that are part of the same DIP (Litz et al. 2007, Elfes et al. 2010).

Temporal trends in the concentration of contaminants and heavy metals have also been identified and may confound comparisons between groups if samples were collected over long time frames (e.g., Wagemann et al. 1996, Addison & Stobo 2001, Aubail et al. 2010). In particular, concentrations of legacy contaminants (e.g., DDT, PCBs) are generally decreasing while those of emerging contaminants (e.g., PBDEs) are increasing in many areas (Lebeuf et al. 2014). In addition to changes in the baseline levels of chemicals, temporal changes in the concentration of heavy metals in some species have been linked to shifts in prey availability due to environmental changes (Gaden et al. 2009).

The concentrations of both contaminants and trace elements can vary between individuals of different age, sex, or reproductive classes [see taxon-specific examples below]. Diet and habitat use differ markedly among age, sex, and reproductive state classes in some species (Bernard & Hohn 1989, Loseto et al. 2006), resulting in differences in chemical signatures (Aguilar et al. 1999, Evans et al. 2004). Reproductive transfer of some contaminants from a mother to her offspring, primarily through lactation, can result in differences in accumulation patterns between adult males and adult females (Aguilar & Borrell 1994, Westgate et al. 1997, Beckman et al. 1999, Krahn et al. 2009), as well as between first-born versus subsequent offspring of a female (e.g., Beckman et al. 1999, Ylitalo et al. 2001, Wells et al. 2005, Yordy et al. 2010). Thus, from a comparative standpoint, contaminants are most easily interpreted between adult males. However, as noted above, finding a difference in contaminants between males is sufficient, but not necessary, evidence for demographic independence. A lack of differences between males could be consistent with either male-mediated dispersal between DIPs or no population structure. Thus, negative findings are not definitive for demographic independence.

In many species of marine mammals, particularly baleen whales and pinnipeds, individuals that demonstrate fidelity to different breeding areas may utilize the same foraging areas during part of the non-breeding season and thus may share similar chemical profiles despite being part of separate DIPs. Conversely, in some species individual specialization in foraging strategies results in differences among individuals within the same DIP (e.g. Elfes et al. 2010, Baylis et al. 2012, Hückstädt et al. 2012, Lowther et al. 2012).

Nutritive condition can also affect contaminant concentrations (Willcox et al. 2004, Hall et al. 2008), such that comparison of samples collected from stranded animals, which are often in poor condition and/or diseased, with those collected from healthy living animals could introduce variation that could confound detection of differences between DIPs (Aguilar et al. 2002, Krahn et al. 2003). Decomposition may also affect concentrations of both contaminants (Borrell & Aguilar 1990) and trace elements (Lahaye et al. 2006), further limiting the utility of samples from stranded individuals.
It is not well understood how quickly chemical signatures change following an animal changing affiliation from one feeding area to another. If the chemical signature of an immigrant becomes intermediate between the two areas over time, then small differences in chemical signatures might develop despite substantial dispersal between groups. Thus, the magnitude of differences in chemical signatures between groups needs to be considered when interpreting the results of these comparisons. Chemical signatures may be particularly informative in cases where genetic data suggest that a “borderline” case exists, as individuals with outlier signatures may represent immigrants, although whether the immigrant interbreeds with the new population cannot be determined from the contaminants data.

Contaminant analyses are typically performed on the blubber taken from biopsy samples, though blood samples have been used for some pinnipeds. Contaminant signatures in blubber are typically integrated over the lifespan of the individual (except for cases of reproductive transfer – see below), making this tissue type informative in comparisons of long-term foraging patterns between groups. Collection of a full-depth biopsy is preferred where possible, as contaminant concentrations have been found to differ between the inner and outer layer of blubber in some species (Aguilar & Borrell 1991, Krahn et al. 2004, Peterson et al. 2014), which could confound comparisons if blubber depth is not standardized among samples. Concentrations also differ between blood and blubber taken from the same individual, rendering comparisons made between different tissue types invalid (Lyderson et al. 2002, Ylitalo et al. 2008).

For trace elements, patterns of bioaccumulation are complex and less well understood than for contaminants. Patterns vary between elements, tissue types, and potentially between species (Kunito et al. 2002, Aubail et al. 2013, Borrell et al. 2015; see taxon-specific discussion below). Many trace elements accumulate primarily in internal organs, while others also accumulate in skin, blubber, or even keratinous tissue (e.g., claws, whiskers, baleen) and bone (Hobson et al. 2004, Aubail et al. 2010, Ferreira et al. 2011, Castellini et al. 2012). However, concentrations do not always correlate well with age; while significant positive correlations have been found in some studies (e.g., Stavros et al. 2011, Yang et al. 2002, Ikemoto et al. 2004), others have found that concentration of an element increases early in life but then declines or plateaus (Honda et al. 1983, Watanabe et al. 1998, Watanabe et al. 2002, Dietz et al. 2004, Dehn et al. 2005, Brookens et al. 2007). The strength of correlations can vary among tissue types and sexes (Caurant et al. 1994, Kunito et al. 2002, Bustamante et al. 2004, Gray et al. 2008, McHuron et al. 2014, Braune et al. 2015, Vighi et al. 2015). Accumulation rates often do not correlate well across tissue types. Given the many sources of variation in concentrations of trace elements, the utility of these chemicals may be more limited than that of contaminants, where bioaccumulation patterns and life history-related variation is better understood.

The use of different protocols for sample collection, storage, and/or analysis can create artifactual differences between sample sets collected at different times or by different laboratories (reviewed in Aguilar 1987, Krahn et al. 2003).

Both contaminants and trace elements may have increased utility in delineating DIPs when compared to dietary measures reflecting only recent feeding (e.g., stable isotopes in skin, fatty acids). However, given the multiple sources of both intrinsic and extrinsic variation that can affect chemical signatures
in marine mammals, the use of contaminants and/or trace elements is insufficient to identify DIPs with confidence when no additional lines of evidence are available.

Summary of caveats and considerations:

- Differences in contaminant and/or trace element profiles in marine mammals will only be detected if variation in chemical signatures exists within the habitat at the appropriate spatial scale.
- Temporal variation in contaminant and trace element profiles can occur and need to be considered when interpreting the results if samples were collected over multiple years/seasons.
- The turnover time of contaminants and/or trace elements varies between tissue types; tissues with longer turnover times are preferred to allow inferences about long-term foraging strategies.
- Extrinsic sources of variability can be introduced when protocols for sample collection, storage, and analysis differ between labs or over time.
- Intrinsic sources of variability (e.g., individual foraging specializations, tissue types and sources, age, sex, reproductive status, and nutritive condition) need to be considered when interpreting any differences in contaminant and/or trace element profiles that are found. For trace elements, intrinsic sources of variation may have impacts that vary between species and/or between elements; as such, interpretation of any differences found between groups requires some understanding of specific bioaccumulation patterns.
- The collection of full-depth biopsy samples is preferred for contaminant analyses as concentrations can vary between the inner and outer layer of blubber.
- Biopsy samples may not be useful in the analysis of some trace elements due to very low concentrations in skin and blubber.
- A lack of correlation between contaminant concentrations in skin with those found in tissues collected from internal organs or blood precludes the combination or comparison of data across tissue types in many cases.
- Given that contaminants and trace elements are integrated over the lifespan of an individual in some tissues, immigrants may carry intermediate signatures. Thus, the magnitude of differences between regions needs to be substantial to avoid delineating DIPs between groups with relatively high connectivity.

A1.5.2 Taxon-specific concerns

A1.5.2.1 Baleen whales – In those baleen whales that exhibit prolonged fasting during migration and on wintering grounds, seasonal changes in nutritive state are pronounced and can introduce artefactual differences if samples are collected year-round (Aguilar 1987).

The thickness of the blubber in some baleen whale species (particularly Balaenids) may make it difficult to obtain full-depth biopsy samples, which are preferred to avoid introducing variation associated with blubber depth. Although biopsy techniques designed to collect full depth samples from baleen whales have been designed (e.g., Lambertson et al. 1994, Reeb & Best 2006), these methods are more invasive and, in the case of the Reeb and Best (2006) method, may not be feasible in all species given the requirement for a close approach to the whales.
The pattern of bioaccumulation of contaminants in Antarctic minke whales varies from the typical pattern seen in baleen whales. Although adult females had lower concentrations of contaminants than did adult males, the highest concentrations were observed in immature animals (Tanabe et al. 1986). This difference was thought to reflect shifts in foraging strategies with age, such that immature whales feed at lower latitudes during summer while adults feed on krill at higher latitudes.

A1.5.2 Odontocetes – Given that odontocetes typically feed year-round, seasonal variation in contaminant and trace element concentrations is less of a concern in this group than in baleen whales and pinnipeds. The magnitude of differences in contaminant loads between adult males and adult females is directly related to the duration of lactation; thus, some odontocete species show greater differences between the sexes than do baleen whales (reviewed in Aguilar et al. 1999). Analysis using samples from males is preferred for interpreting stock structure.

A1.5.2.3 Pinnipeds – Marked sexual dimorphism is characteristic of terrestrially mating pinnipeds, as are sex-specific foraging strategies (Le Boeuf et al. 1993, Breed et al. 2006, Sterling et al. 2014). As such, sex-based differences in chemical signatures may be more extreme in these species. Some pinnipeds fast during the breeding-lactation period as well as during the molting period. In these species, care should be taken to avoid introducing artefactual variation related to seasonal variations in body condition when comparing chemical signatures between groups.

Hair is an additional tissue type that can be used in comparisons of trace element concentrations among groups of pinnipeds. Trace elements are delivered to hair primarily through the blood supply (Ikemoto et al. 2004) and incorporation takes place during the period of hair growth (Brookens et al. 2007). Though some studies have shown a correlation between the concentration of TE found in hair and those in internal organs (Watanabe et al. 1998, Ikemoto et al. 2004), most hair growth occurs during only a portion of the year, with hair grown over the previous year lost during the annual molt. Consequently, trace element concentrations in hair represent relatively short-term foraging patterns and may have limited utility in DIP delineation. In addition, concentrations can vary with hair type (molted vs. new hair Wenzel et al. 1993, Gray et al. 2008) and the body location sampled (McHuron et al. 2014).

A1.6 Stable isotopes and fatty acids

A1.6.1 General Considerations – Stable isotope ratios and fatty acids found in an animal’s tissue reflect those of its regional food web; thus, differences in these biomarkers can be generated between demographically independent groups that feed in different areas and/or on different prey. However, such differences can only develop if geographic variation in the isotopic signatures and/or fatty acid profiles of prey species exists and are constant over time. For stable isotopes, gradients typically exist on broad scales within pelagic waters and at much finer scales in coastal and estuarine waters (Bowen 2010, Kurle & McWhorter 2017). Thus, fine-scale differences are more likely to be generated in coastal versus offshore species, though care must be taken in evaluating the demographic significance of such differences.
The utility of SI and/or FA signatures in DIP delineation relies on the turnover time of the tissue that is being sampled. Stable isotope ratios in skin and blood reflect recent foraging (on the order of weeks to months, Hicks et al. 1985, St. Aubin et al. 1990, Hobson et al. 1996, Vander Zanden et al. 2015, Giménez et al. 2016, Wild et al. 2018), limiting their value when evaluating whether longer-term fidelity to a particular area is occurring. Although tissues like teeth, bone, and baleen provide a record of isotopic incorporation over time, such tissues can typically only be obtained from dead animals, which limits the possibility of obtaining sufficient numbers of samples in most species. Within marine mammals, fatty acid signatures are typically obtained from blubber or adipose tissue. Although less is known about the turnover times of fatty acids, they are generally considered to represent relatively recent foraging (on the order of weeks to months; Iverson et al. 2004, Budge et al. 2006).

Several intrinsic sources of variability in SI ratios or FA profiles can exist within a DIP and should be considered when interpreting the results of comparisons. For both biomarkers, the use of different foraging strategies by animals of different age, sex, or reproductive status can create within DIP variability (e.g., Iverson et al. 1997, Kurle & Worthy 2001, Ruiz-Cooley et al. 2004, Samuel & Worthy 2004, Beck et al. 2005, Tucker et al. 2008, Newsome et al. 2009). Fatty acid profiles also show variation with the depth of blubber sampled (e.g., Koopman et al. 1996, Best et al. 2003, Olsen & Graith-Nielsen 2003, Budge et al. 2006, Ellisor et al. 2013) and potentially with the region of the body sampled (e.g., Arnould et al. 2005). Intrinsic variation in both SI ratios and FA profiles can also be generated if individual specialization in foraging strategies exist, as has been documented in some species of otariids (e.g., Arnould et al. 2011, Lowther et al. 2012) and may also occur among cetaceans (e.g., Rossman et al. 2015).

In addition, seasonal and annual variation can also exist in SI ratios and FA profiles (Samuel & Worthy 2004, Budge et al. 2006, Tucker et al. 2008, Young & Ferguson 2013). This variation is often a result of shifts in prey availability or composition that occur in response to environmental changes (Hirons et al. 2001, Hindell et al. 2012, Watt & Ferguson 2015, Fleming et al. 2016), but can also result from changes in temperature, water flow, and other geochemical changes. Proper accounting for this variation is critical, as differences could be identified that are not representative of stock structure.

Of note, differences in SI ratios and/or FA profiles between groups are driven by differences in foraging location and prey composition. Particularly for those species which feed in one area and breed in another (e.g., many baleen whales, some otariids and phocids), differences in foraging locations or diet do not necessarily provide any information on whether such groups interbreed. As such, it is necessary to understand the life history of the species so that differences in these biomarkers can be put in the appropriate context.

In light of the considerations listed above, the use of SI ratios and/or FA profiles to delineate DIPs should be considered, at best, a weak line of evidence and, at worst, a potential source of misleading information. Without additional information, it is not possible to evaluate whether intrinsic sources of variability could be creating differences within rather than between DIPs. More importantly, unless tissues with longer turnover times are utilized, any patterns identified by these biomarkers are uninformative at the temporal scale (decades) relevant to DIP delineation. Determining whether such patterns persist over time would require collection of samples over multiple years, which has the potential to confound the detection of demographic independence given that isotopic baselines and
fatty acid signatures in prey may shift over time. Stable isotope results could, however, be used to posit new hypotheses of stock structure to be tested with stronger lines of evidence.

**Summary of considerations and caveats:**
- Differences in SI ratios or FA profiles in marine mammals will only be detected if stable gradients exist between the groups being compared as a result of differences in either prey selection/availability or geochemical process.
- Intrinsic sources of variability (e.g., age, sex, reproductive status, sampling depth, individual specialization) can result in differences in SI ratios or FA profiles that are not correlated to population structure.
- The turnover time of the stable isotopes or fatty acids in the tissue being sampled must be appropriate to evaluate demographic independence (e.g., tissues with longer turnover times will be more useful).
- Temporal variation in SI ratios and FA profiles can occur and needs to be considered when interpreting the results if samples were collected over multiple years/seasons.
- If different geographic regions are used for breeding and feeding, then the location of sample collection in the context of the migratory cycle need to be considered when interpreting results.

**A1.6.2 Taxon-specific concerns**
*See Budge et al 2006 for a review of taxon-specific considerations for FAs*

**A1.6.2.1 Baleen whales** – In baleen whales, studies of a few species have utilized stable isotope ratios to assess population structure (e.g., North Atlantic minkes, Born et al. 2003, North Pacific humpback whales, Witteveen et al. 2009, North Atlantic fin whales, Giménez et al. 2013, Ryan et al. 2013, South Atlantic right whales, Vighi et al. 2014). In some cases, it was possible to compare the groupings that could be discriminated by stable isotope signatures with those identified genetically; in such cases, the patterns identified by each method were largely consistent (e.g., Witteveen et al. 2009, Giménez et al. 2013).

Some migratory whales fast during migration and on their breeding grounds. In these species, SI ratios and FA profiles are only useful for elucidating feeding ground structure. Although isotopes have a relatively short turnover time in skin, the isotopic signatures remain detectable for up to a month after feeding ceases and the migration begins, allowing recent movements between feeding and breeding/wintering grounds to be inferred. Thus, individuals sampled on breeding grounds may be assigned to particular feeding areas using a classification analysis (Witteveen et al. 2009), and the presence of multiple DIPs from different feeding grounds on a single breeding ground can potentially be detected even when the location of the feeding grounds is unknown (Valenzuela et al. 2009).

**A1.6.2.2 Odontocetes** – SI/FA differences between social units have been identified in studies of both sperm whales and pilot whales, suggesting that some level of specialization in habitat or prey choice among social units exist (Marcoux et al. 2007, Mendes et al. 2007, De Stephanis et al. 2008, Zupcic-Moore et al. 2017). Differences in habitat preference have also been identified between social units of other odontocetes (e.g., Baird et al. 2012, Browning et al. 2014), though it is unknown whether
these differences are reflected in SI ratios or FA profiles. Nonetheless, habitat specialization among social units could result in within-DIP differences in SI/FA in other social odontocetes.

As with other lines of evidence, the utility of stable isotope analysis is more limited among offshore odontocetes, not only because of the difficulty of obtaining samples from these areas but also because isotopic gradients in pelagic waters vary at broader scales than do coastal and estuarine waters.

A1.6.2.3 Pinnipeds – Regional differences in SIRs of pinnipeds have been identified (Aurioles et al. 2006, Kurle & Gudmundson 2007). However, multiple factors have been shown to create variation in SIRs among animals that are considered part of the same DIP, including variation in SIRs with age, sex, and reproductive state (e.g., Kurle & Worthy 2001, Young et al. 2010, Orr et al. 2011, Lowther et al. 2012, Chaigne et al. 2013).

Marked sexual dimorphism is characteristic of terrestrially mating pinnipeds, as are sex-specific foraging strategies (Le Boeuf et al. 1993, Breed et al. 2006, Sterling et al. 2014). As such, sex-based differences in SI and FA profiles may be more extreme in these species.

A1.7 Life History

A1.7.1 General Considerations – Demographically independent populations may exhibit differences in life history traits. A number of different life history traits may vary with the degree of density dependence and thus could be indicative of demographic independence. These traits include body length, mean age of sexual maturity or first reproduction, survival rates, ovulation rates, proportion of pregnant females, proportion of mature females/males, pupping/calving interval, and breeding/birthing seasonality (Barlow 1985, Chivers & Myrick 1993). Differences in breeding seasonality, in particular, may be informative given that such differences could result in a lack of opportunity for interbreeding.

An important consideration when evaluating the utility of differences in life history traits in informing DIP delineation is that such traits can exhibit plasticity as a response to changes in environmental conditions, such as prey availability (Barros & Odell 1990, Urian et al. 1996), water temperature (Wells et al. 1987), and/or predation (e.g., Fearnbach et al. 2012). While changes in environmental conditions could, over time, lead to the evolution of adaptive behaviors representative of demographically independent groups, they can also result from spatially or temporally variable conditions within the range of a DIP. For example, if the timing of reproduction is linked to photoperiod, then animals at the northern end of the range may reproduce earlier than those at the southern end of the range. However, an individual moving between these areas would demonstrate the response appropriate to that portion of the range, and thus could have different reproductive timing from one year to the next.

Although assessment of stranded animals collected over all seasons has provided information on reproductive patterns, the determination of reproductive timing in live animals typically relies on observations of neonates. In many cases this results in large uncertainties associated with estimates of reproductive timing due to small sample sizes. The recent use of hormonal analyses to estimate reproductive timing by evaluating seasonal patterns in testosterone and progesterone concentrations
(Kellar et al. 2009, Kellar et al. 2013, Vu et al. 2015) provides a means by which to start to address this limitation.

If variation in life history traits between groups is driven by density dependence, then it is likely to be informative with respect to DIP delineation given the need for separate management. However, without additional lines of evidence, it is not possible to distinguish between different density-dependent responses exhibited between two DIPs and shifts in distribution within the range of a DIP in response to environmental variability [see also Trends discussion].

Given these considerations, differences in life history traits are considered to represent a weak line of evidence in almost all taxa, indicating that additional lines of evidence must be considered to aid in interpreting data. Importantly, the additional line(s) of evidence must provide information on movements of animals between areas. For example, a distributional hiatus could exist between two regions, with the animals in each region demonstrating differences in life history traits. However, if immigrants between areas adopt the trait associated with its current habitat, then substantial immigration (i.e., greater than internal recruitment levels) between areas could be occurring despite differences in multiple lines of evidences.

Summary of considerations and caveats

- Life history traits may exhibit plasticity in response to environmental factors, thus allowing for differences in traits within a DIP to develop.
- Life history traits that reflect different density-dependent responses may be informative in delineating DIPs, but without additional information it is not possible to rule out other explanations.
- Measures of reproductive seasonality may have the most utility in delineating DIPs due the potential for reproductive isolation. Hormonal analyses for determining reproductive state from biopsy samples should greatly increase the amount of data available on reproductive timing in marine mammal species.

A1.7.2 Taxon-specific considerations

A1.7.2.1 Baleen whales – The reproductive cycles of most baleen whales are tightly synchronized with their migration patterns and may be triggered by environmental cues such as photoperiod, as hypothesized for humpback and gray whales (Dawbin 1966, Rugh et al. 2001). As such, variation in this parameter may occur within DIPs as well as between them.

In addition, for several of the migratory baleen whales, animals from multiple feeding grounds may utilize the same wintering area or breeding ground, or animals from a single feeding ground may migrate to different breeding grounds (Palsbøll et al. 1997, Weller et al. 2012, Baker et al. 2013). Given that body condition is thought to be linked to reproduction (Lockyer 1986, Perryman et al. 2002, Miller et al. 2011), recovery rates, and thus density dependent responses, may vary among feeding grounds in response to differences in resource availability. As such, demographic independence may occur between feeding grounds rather than (or in addition to) on the common breeding/wintering area.
A1.7.2.2 Odontocetes – Within odontocetes, there is a general trend toward increased reproductive synchrony in species inhabiting higher latitudes (Perrin & Reilly 1984, Borjesson & Read 2003), likely as a result of the more extreme seasonal fluctuations in photoperiod, water temperature, and prey availability. Species in the tropics tend to breed throughout the year and/or have less distinct peaks in calving (Perrin et al. 1976, Barlow 1985), suggesting that comparisons of reproductive timing may be less useful when examining stock structure in these species. As well, several studies have suggested that reproductive seasonality in odontocetes may be associated with local environmental conditions and prey availability (e.g., Urian et al. 1996, Börjesson & Read 2003, McGuire & Aliaga-Rossel 2007), indicating that extrinsic factors can influence reproductive timing both within and between DIPs.

Determining reproductive seasonality in odontocetes may be more complicated than in many baleen whales, which have specific calving areas, or in pinnipeds that haul out on land. Estimates of reproductive timing based on observational sighting data can be confounded by the difficulty of identifying neonates in the field (Caughley & Caughley 1974, Fernandez & Hohn 1998, Thayer et al. 2003). Estimates of reproductive seasonality that are based on neonate stranding data may also be subject to bias, as neonates born earlier in the season may be less likely to survive (Urian et al. 1996).

A1.7.2.3 Pinnipeds -- With a few exceptions (e.g., Gales et al. 1994, Galapagos sea lions, Villegas-Amtmann et al. 2009), pinnipeds have synchronous and seasonal reproductive patterns, facilitating studies of differences in reproductive timing among areas. However, photoperiod is considered to play a role in the timing of delayed implantation in pinnipeds (Boyd 1991, Tempte & Tempte 1993), and in some species the timing of birth has been linked to changes in prey availability (e.g., South American sea lions, Soto et al. 2004) and increased intra-specific competition (e.g., harbor seals, Bowen et al. 2003). These studies suggest that extrinsic factors may influence reproductive timing in pinnipeds as well.

A1.8 Trends in abundance

A1.8.1 General considerations – For most marine mammals, the power to detect trends in abundance indices is low due to the difficulties of collecting data over the appropriate spatial and temporal scales (Taylor et al. 2007b). Given the broad and/or pelagic ranges inhabited by many species, surveying the entire range is challenging and often infeasible, limiting most surveys to only a portion of the species’ range. Interpreting the results of such surveys is problematic, as apparent fluctuations in local abundance may instead be a result of shifts in distribution due to environmental variability (Barlow & Forney 2007, Gerrodette et al. 2008, Calambokidis et al. 2009, Boyd et al. 2018). Incorporating models of species-environment relationships may be one alternative to address this concern (Forney 2000, de Segura et al. 2007), although such an approach requires that additional data linking habitat variables and species distribution exist. For species that are naturally marked or can be artificially tagged, mark recapture methods can be used to estimate abundance. Although these methods do not assume that the full range is sampled, they are based on a number of assumptions and can produce biased estimates if geographic coverage is not randomly distributed (Barlow et al. 2011). In terms of detecting trends, this approach is most useful in species with relatively limited and easily accessed ranges (e.g., feeding grounds of the CA/OR/WA stock of humpback whales, Calambokidis & Barlow 2004, estuarine populations of common bottlenose dolphins, McDonald et al. 2017) as more precise estimates, and thus higher probabilities of detecting trends, can be produced when capture probabilities are high.
In addition, the detection of trends in abundance requires long-term time series, and power is increased if surveys can be conducted both frequently and at regular intervals (Taylor et al. 2007b). Given the expense and other challenges associated with conducting surveys by ships or in ice, such datasets are largely limited to species that can be surveyed from land (Small et al. 2003, e.g., sea otters, Burn & Doroff 2005, harbor seals, Jemison et al. 2006, Small et al. 2008, gray whales, Laake et al. 2009, Hoover-Miller et al. 2011, Durban et al. 2015), or those with smaller or confined ranges, such as common bottlenose dolphins.

Even if datasets at the appropriate spatial and temporal scales can be obtained, the utility of using trend data to delineate DIPs is limited in data-poor species. Trend data rely on demonstrating the statistical independence of two time series, which could result from demographic independence but could also have alternate explanations. For example, spatial variation in survival rates has been observed among Hawaiian monk seals (Baker & Thompson 2007, Baker et al. 2011). However, both movement (Johanos et al. 2014) and genetic (Schultz et al. 2011) data support range-wide connectivity, indicating that habitat heterogeneity, rather than demographic independence, is likely driving the observed differences in survival (Baker & Thompson 2007, Baker et al. 2011). Conversely, two DIPs could demonstrate the same trend if they have similar environmental drivers or, in the case of recovering populations, are growing at the same maximum rate given the lack of resource depletion. Differentiating between these scenarios requires additional sources of information; in particular, movement data and/or data on whether known human-caused mortality was occurring would allow discrimination between alternate explanations.

**Summary of considerations and caveats:**

- Given that surveying the entire range of a species is often not feasible, it is important to evaluate if apparent trends in abundance based on data collected in a portion of the range could instead reflect shifts in distribution over time.
- The detection of trends requires that long-term time series of abundance estimates are available. The power to detect trends is increased if surveys are frequent and conducted at regular intervals and if coefficients of variation are low.
- Other lines of evidence, in particular movement data, are needed to rule out alternate explanations for any observed trends in abundance.

### A1.8.2 Taxon-specific considerations

#### A1.8.2.1 Baleen whales

Many baleen whales species exhibit complex population structure, where whales that utilize the same feeding ground may migrate to different breeding grounds (e.g., North Pacific humpback whales, Palsbøll et al. 1997, Baker et al. 2013) or whales utilizing different feeding grounds may migrate to the same wintering area (e.g., gray whales, Weller et al. 2012). In such species, localized depletion on one feeding ground may impact multiple breeding grounds (or vice versa), complicating the interpretation of differences in trends between regions. As well, many baleen whales have large ranges that span international boundaries and are thus subject to the issues associated with estimating trends based on partial surveys of their range. Using mark-recapture approaches may provide a viable alternative for estimating abundance in some baleen whales, but this approach requires that some prior knowledge of the behavior (e.g., site fidelity) and migratory patterns is available.
A1.8.2.2 Odontocetes -- Utilizing trend data to delineate DIPs in odontocetes is particularly challenging in 1) pelagic species, which inhabit areas that are difficult to access and to completely survey, and 2) species with low detection probabilities, such as beaked whales that typically inhabit deep water and have inconspicuous surfacing patterns. The latter challenge may be addressed by the use of a Bayesian approach, which has been shown to provide increased precision and power (when compared to line transect estimates of cetacean abundance), allowing the detection of declines in beaked whale abundance in the eastern North Pacific (Moore & Barlow 2013).

A1.8.2.3 Pinnipeds -- Trend analysis is facilitated in species that demonstrate inter-annual site fidelity to land-based breeding colonies or haul-outs, where direct counts can be made while animals are clustered and easily detected. In contrast, the power to detect trends in abundance among ice seals is low (Taylor et al. 2007b), given their broad distribution across difficult-to-access habitats and the challenges associated with estimating proportion of missed animals that are underwater or, in the case of species such as the ringed seal, under the snow. More recently, the use of airborne thermal imagery, which allows for expanded survey coverage due to increased flight speed and height, has made it more feasible to survey ice-associated pinnipeds (e.g., Pacific walrus, Burn et al. 2006, Udevitz et al. 2008, Arctic ice seals, Conn et al. 2014).

A1.9 Physiographic or oceanographic differences in habitat

A1.9.1 General Considerations – Habitat specialization is often a driver of divergence among groups of animals at many levels, including between populations. A physiographic or oceanographic difference in habitat means that two groups of animals tend to be associated with different habitat features. These features can be static (e.g. bathymetry) or dynamic (e.g. water temperature). For example, re-sighting or satellite tag data could consistently show that one group of animals inhabits coastal or insular waters while another group is found in offshore waters. Differences may also be identified from survey data or habitat-based models of species distribution that document the presence of a species in multiple distinct habitat types or marked gaps in distribution associated with specific habitat features, suggesting the presence of two or more groups specializing on different habitats (e.g. Risso’s dolphins within the California Current Ecosystem; Becker et al. 2016). If these habitats are characterized by dynamic ocean processes, the distributions of these groups may vary considerably between years while maintaining a consistent association with specific oceanic conditions.

Habitat data have been useful in numerous DIP delineations in the recent past. Within the Gulf of Mexico, the distribution and habitat use patterns observed in common bottlenose dolphins inhabiting Sarasota Bay and estuarine waters in Texas (Shane 1977, Gruber 1981, Wells 1986, Scott et al. 1990) were used to identify additional (n=32) stocks in areas of similar habitat defined by contiguous, enclosed, or semi-enclosed waters adjacent to the northern Gulf of Mexico (Hayes et al. 2018). The subsequent analysis of additional genetic, photographic-identification, and tagging data has continued to support the original stock designations where available. In other cases, such as for island-associated cetaceans around Palmyra, similarities in habitat (e.g., structural features) between this region and the Hawaiian Islands were used to propose the existence of structure at similar scales for island-associated odontocetes in nearshore waters of Palmyra, although formal stock designations for Palmyra were not made until data from additional lines of evidence confirmed the similarities.
The above examples suggest that information on habitat characteristics known to be important in shaping demographic independence of a species in one area may have utility in guiding DIP delineation in the same species in other regions, as well as for guiding stock delineation for species with similar ecology, but little other information, in the same region. However, such an approach may only be appropriate for a very specific system and could lead to drawing boundaries at inappropriate scales if generalized too broadly. For example, delineating DIPs of spinner dolphins in the Marianas Islands based on the same spatial scale as that identified among spinner dolphins in the Hawaiian Islands would not have provided an accurate reflection of the scale of spinner dolphin stock structure in the Marianas.

Many habitat variables are dynamic and thus shift over time. For example, during periods (seasons, years) with cool water conditions in the North Pacific, the distribution of Dall’s porpoise will shift south, while during periods with warm water conditions, the distribution of short-beaked common dolphins will shift north (Forney & Barlow 1998, Becker et al. 2014, Barlow 2016). While in some cases these habitat boundaries may continue to shift back and forth over time, in other cases, the shift in habitat boundary may be more more permanent, such as the northward range extension demonstrated by common bottlenose dolphins along the Pacific coast, which formerly were only found off southern California and Mexico, but expanded their range northward into waters off central California following the 1982-83 El Nino (Wells et al. 1990, Feinholz 1996).

The boundaries of some stocks may be driven by habitat variables that allow for niche partitioning but result in overlapping distributions at times. For example, along the east coast, common bottlenose dolphins that are part of a coastal stock may on occasion move into estuarine areas, while animals that are part of the estuarine stocks may move into coastal waters at times. In such a case, structure may be missed due to the physical overlap of animals and a lack of understanding of how the animals from different stocks are partitioning the habitat. This points to the need to look at “environmental isolation by distance”, which has been correlated to genetic differences in some species (e.g., franciscana, Mendez et al. 2010).

In some cases, underlying habitat differences can be used to corroborate DIPs that are detected using other data types. For example, the western Steller sea lion DPS appears to have a continuous distribution across the Aleutians. However, genetic studies identified differentiation between sea lions on either side of Somalga Pass, where a region of oceanographic divergence between the continental shelf and ocean basin waters exists (O’Corry-Crowe et al. 2006). Without genetic data to suggest that more than one DIP was present within this range, this boundary may not have been detected based on habitat data alone.

In other cases, habitat differences between regions may be apparent but not result in demographic independence. For example, variation in habitat quality has been identified between sites within the range of the Hawaiian monk seal, and spatial variation in age-specific survival rates exists (Baker & Thompson 2007). However, movements of individuals between sites are known to occur, indicating that seals using these sites are not demographically independent. As is the case with distributional data, care must be taken when interpreting habitat differences between groups to ensure that the differences do not simply reflect differences between age or sex classes.
One caveat to the use of distribution data to delineate DIPs is that some mixing could be occurring at levels that are not detectable in survey data but may be demographically important. As such, data on distribution and habitat cannot be used to estimate what proportion of animals in the group are immigrants.

Most cases where habitat data have been utilized in DIP delineation have involved the use of detailed habitat modeling efforts that are specific to the species and region being studied. However, a number of global modeling efforts have resulted in the development of habitat classification systems that can be used in evaluating habitat differences between areas. The most useful of these systems with respect to DIP delineation is the Ecoregions developed by Spalding et al. (2007), which are areas that “reflect unique ecological patterns”. In species for which gathering the data necessary to evaluate DIPs based on a detailed habitat model or other lines of evidence is impractical, delineating DIPs that align with Spalding et al.’s Ecoregions, or more fine-scale ecoregions defined for some areas (e.g., Piatt & Springer 2007), may be the most scientifically sound option.

Summary of considerations and caveats:

- Habitat can be described using spatially static physiographic variables, such as bathymetry and distance to shore, or dynamic oceanographic variables, ranging from water temperature to prey distributions.
- Different DIPs often specialize on different habitats. Thus, habitat differences between groups can be an indication that they are different DIPs.
- Habitat characteristics known to be important in shaping demographic independence of a species in one area may have utility in guiding DIP delineation in the same species in other regions as well as for guiding DIP delineation for species with similar ecology, but little other information, in the same region.
- In cases where the habitat variables that distinguish different DIPs are spatially dynamic, the boundaries between those DIPs will also be dynamic.
- Habitat data cannot be used to directly estimate the degree of mixing between putative DIPs.
- When collecting the data necessary to parameterize a species-specific and/or region-specific habitat model is not possible, researchers should consider delineating DIPs that align with Spalding et al.’s (2007) Ecoregions or other well-defined regional ecoregions.

A1.9.2 Taxon-specific considerations

A1.9.2.1 Baleen whales – The use of habitat data for baleen whales is complicated by the migratory patterns of many species, which can entail movements across large oceanographic regimes. In these cases, habitat is best evaluated on feeding grounds, as whales interact relatively little with the ecosystem on their breeding grounds.

A1.9.2.2 Odontocetes – The scale at which both population structure and habitat partitioning occur varies dramatically between species of odontocetes. Information from the same or closely-related species in data-rich regions can therefore be particularly helpful in interpreting habitat data from odontocetes in less well-studied regions.
Particular care should be taken interpreting habitat data for odontocetes that demonstrate differences in habitat use patterns according to age, sex and/or with social structure, such as sperm whales and some blackfish.

A1.9.2.3 Pinnipeds -- Age and sex-related differences in habitat use and movement patterns exist in some pinnipeds, complicating interpretation of distribution and habitat data. As in baleen whales, the use of different areas for feeding and breeding further clouds interpretation of habitat data.

The distribution of many pinnipeds appears continuous. However, in many cases research using multiple lines of evidence has revealed considerable population structure, which often correlates with fine-scale habitat features. Thus, habitat variables such as haul-out substrate, distance to open ocean waters (e.g., inland waterways versus outer coast of southeast Alaska), and ocean currents maybe particularly helpful in either stratifying data from other lines of evidence or placing boundaries between DIPs of pinnipeds.

A1.10 Association data

A1.10.1 General Considerations – Understanding the frequency and extent to which individuals interact can be useful in inferring demographic independence between groups. Such ‘association’ data are generally gleaned from social network analysis of photographic-identification data (Newman 2004, 2006, Whitehead 2008) and have been used in a wide variety of marine mammals to identify groups ranging from bonded pairs and family units to demographically independent populations (e.g., Connor et al. 1992, Aschettino et al. 2012, Mahaffy et al. 2015). Association data can be used to infer DIPs when it reveals the existence of groups with non-overlapping or minimally overlapping distributions that are rarely or never observed ‘in association,’ i.e., in the same encounter (Baird et al. 2008, Aschettino et al. 2012, Baird et al. 2012).

Association data can be used to corroborate population structure hypotheses that are based on other lines of evidence, such as habitat or movements. However, it more commonly serves as a guide to stratifying data sets from other lines of evidence or identifying boundaries. For instance, in the Hawaiian archipelago there are three populations of false killer whales (Pseudorca crassidens) with partially overlapping ranges. Association data have been critical in both identifying the areas of overlap and stratifying data collected in those areas for subsequent genetic and movement analyses (Baird et al. 2008, Baird et al. 2010, Martien et al. 2014).

Association data can be particularly powerful in identifying ‘cryptic’ populations, as illustrated by studies of melon-headed whales (MHWs) in the main Hawaiian Islands. Satellite tagging and photographic-identification resighting data indicated that, like many other delphinid species, MHWs form a resident population around the main Hawaiian Islands, although their range extends into offshore waters. However, network analysis revealed that, in addition to the large (N = ~6,000) population that ranges through the MHI and in offshore waters, there is a much smaller (N = ~450) group of animals that is restricted to a small, shallow-water shelf off the Kohala coast of Hawai’i Island. This finding was then used as a basis for stratification in subsequent tagging, photographic-identification, and genetic analyses, all of which confirmed that the groups represent DIPs rather than social groups within the same population (Aschettino et al. 2012, Baird 2016, Martien et al. 2017).
Because association data can be used to identify structure within populations as well as between them, care must be taken to ensure that the groups identified with association data represent DIPs rather than social groups or family groups within a DIP. Additional LoEs can be used to evaluate the degree of independence between groups identified by association data. The extent of interactions between groups can also be informative, as illustrated by false killer whales in the Hawaiian Archipelago. Association data were used to identify multiple social clusters with the main Hawaiian Islands (MHI) insular population of false killer whales (Baird et al. 2008, Baird et al. 2012). Though individuals interact primarily within their social cluster, there are numerous instances of interaction between social clusters. Furthermore, the ranges of the social clusters are almost entirely overlapping, though different social clusters have different preferred habitats (Baird et al. 2012). In contrast, the MHI insular population has never been documented interacting with the neighboring Northwestern Hawaiian Islands insular population, and the ranges of two populations only overlap at the islands of Kaua‘i, Ni‘ihau, and off western O‘ahu (Baird et al. 2013, Baird 2016).

Robust assessment of association requires a relatively large number of identifications and multiple re-sightings of many individuals. Consequently, the use of association data to identify DIPs is only practical for populations with abundances of a few thousand individuals or fewer that are located in regions where long-term photographic-identification studies are practical. Furthermore, like movement data based on satellite telemetry or photographic-identification, association data are only representative of the temporal scale at which they are collected.

In addition to their utility in studies aimed at identifying DIPs, association data can also provide insight into the social structure, sociality, and culture of groups or species. The use of culture and social structure in the delineation of manage units is not addressed in this handbook. However, we refer readers to the report of a recent meeting focused on the use of culture in delineating management units (United Nations Environment Programme 2018) for further discussion of the issue.

Summary of caveats and considerations:

- By identifying groups of animals that rarely or never interact with each other, association data can be a valuable tool for helping to delineate DIPs.
- Association data are particularly useful for stratifying data from other LoEs and for identifying cryptic populations.
- Because it requires photographic-identification of a large fraction of the relevant populations, including multiple re-sights, using association data to delineate DIPs is only practical for populations with abundances in the hundreds to low thousands that occur in areas that are reasonably accessible to researchers.
- Association data can be particularly useful for identifying island/coastal populations of otherwise pelagic species.
- Inferences that can be made from association data are limited by the time span of the photographic-identifications used in the analysis.
- Other LoEs are required to determine whether groups identified by association data represent family groups, social groups, or DIPs.

A1.10.2 Taxon-specific considerations
A1.10.2.1 Baleen whales — Baleen whales are generally not known to form the types of long-term stable social bonds that are identified by association data. Therefore, this LoE is generally not used when evaluating DIPs in this taxonomic group.

A1.10.2.2 Odontocetes — The utility of association data for delineating DIPs is greatest in social species with low to moderate abundance. Odontocetes vary in the degree to which they display these characters. Most of the globicephalids (aka ‘blackfish’) are highly social, with many exhibiting complex social structures (e.g., Bigg et al. 1990, Baird & Whitehead 2000, Baird et al. 2012, Mahaffy et al. 2015). Coastal and island-associated bottlenose and spinner dolphins tend to have more fluid social structure, often described as a fission-fusion system, but nonetheless exhibit a high degree of sociality. Thus, association data has proven useful in these groups.

A1.10.2.3 Pinnipeds — The utility of association data in delineating DIPs has not been studied in pinnipeds.

A1.11 Acoustics

The discussion below reflects discussions held under the auspices of the Stock Delineation Guidelines Initiative (Martien et al. 2015). In addition to, there was considerable discussion on the use of acoustic data for stock delineation as part of a recent NMFS and Marine Mammal Commission workshop on use of passive acoustic data for stock assessment. The resulting report (Heinemann et al. 2016) provides additional detail and examples that may be a valuable reference for researchers considering using acoustics as an LoE for DIP delineation.

A1.11.1 General Considerations — Many species of marine mammals use vocalizations that exhibit stereotypical spectral or temporal characteristics, or may exhibit a stereotyped repetition rate of certain sounds. The degree to which variation in acoustic characteristics corresponds to reproductive isolation varies considerably among marine mammal species. In beaked whales, acoustic differences are typically indicative of species-level differentiation. In other species, geographic variation in acoustic characteristics have been found to correspond with population structure within the species (e.g., blue whales, McDonald et al. 2006). However, there are cases where acoustic differences are not indicative of demographic independence (e.g., Johnson et al. 2007, May-Collado & Wartzok 2008, Simard et al. 2010, May-Collado & Quiñones-Lebrón 2014). In addition, the utility of this line of evidence in delineating DIPs varied even among closely related species (e.g., Noad et al. 2000, McDonald et al. 2006). Thus, the utility of acoustic data in delineating DIPs is considered to be species-specific across all of the taxa considered.

One of the limitations of using differences in vocalization characteristics to delineate DIPs is that the mechanism by which vocal learning occurs is not well understood for most marine mammal species. If offspring learn vocalization patterns from their mothers (e.g., vertical transfer), then acoustic differences are driven by internal recruitment and thus are useful in delineating demographic independence. If transmission is horizontal, however, such that post-dispersal learning of vocalization patterns is possible, then immigrants could adopt the vocalization patterns of their surrounding conspecifics and abandon their natal vocalization patterns. In this case, substantial immigration between groups could occur even if acoustic differences are present.
One of the strengths of using acoustic data to delineate DIPs is that acoustic differences can develop more rapidly than differences in some of the other lines of evidence, such as morphology and genetics. As such, they are likely to represent contemporary movement patterns and can be a good tool for detecting cryptic structure that has evolved relatively recently. However, shifts in song characteristics over very short time scales have also been documented (e.g., shifts within a breeding season, fin whales, Oleson et al. 2014) and could lead to falsely concluding that multiple stocks are present. Thus, to ensure that differences in acoustic characteristics are not an artifact of temporal shifts within a DIP, the data representing each of the groups that are being compared should be collected within the same season and across multiple years.

The behavioral context and variation in the physical and/or social environment in which the vocalizations are being made should also be considered when comparing vocalization patterns between groups. Vocalizations that are associated with mate choice are likely good candidates for evaluating demographic independence, as they are involved in the maintenance of reproductive autonomy. However, while differences in the acoustic properties of vocalizations used for foraging could be indicative of local adaptation, these vocalizations have also been shown to vary in response to prey type and/or dive depth (e.g., bottlenose dolphins and water depth, Simard et al. 2010) (beaked whales and prey type, Johnson et al. 2008). Such plasticity could lead to incorrectly identifying multiple stocks in an area if animals that are part of the same stock use vocalizations with different characteristics when foraging in different regions within their range. Vocal characteristics have also been shown to change in response to the presence of boat traffic, differences in ambient noise, and/or interactions with other species (May-Collado & Wartzok 2008, May-Collado 2010, Tripovich et al. 2012, May-Collado & Quiñones-Lebrón 2014, Papale et al. 2015). These changes suggest that variation in the social or physical environment can create differences in acoustic characteristics that are unrelated to stock structure. The use of acoustic characteristics that demonstrate plasticity in response to environmental variation or behavioral context should therefore be avoided when drawing inferences about demographic independence.

A final consideration is that in some species the vocalizations of interest are produced only by males (e.g., humpback whale songs, bearded seal trills). While male-specific calls would generally be expected to play a role in mate choice or territoriality and thus to reflect population-wide patterns, in such cases another line or lines of evidence will be needed to ensure that the patterns evident among males are also representative of females.

Summary of Caveats and Considerations –

- Interpreting the significance of differences in vocal characteristics between two groups requires an understanding of how these characteristics are passed between animals (horizontal v. vertical transmission).
- If horizontal transmission of vocalization patterns occurs, substantial connectivity between groups could exist but not be evident in comparisons of vocal characteristics between groups.
- Comparisons of vocalization characteristics between groups should utilize datasets collected from both groups during the same season and over multiple years.
- Behavioral and/or environmental factors (social and physical) can influence vocalization characteristics and could lead to oversplitting if not considered when making comparisons between groups.
Some vocalizations are only produced by males and should not necessarily be considered representative of patterns of structure among females.

**A1.11.2 Taxon-specific considerations**

**A1.11.2.1 Baleen whales** – The utility of acoustics in DIP delineation varies considerably across species of baleen whales. For blue whales and north Pacific minke whales, it appears to be a highly valuable LoE (Rankin & Barlow 2005, McDonald et al. 2006). Acoustics may also prove useful for delineating DIPs of fin whales, though variation within seasons and across years could be misleading in this species if not properly accounted for (Hatch & Clark 2004, Oleson et al. 2009). In all of these cases, acoustics, like association data, may provide a useful means of stratifying other datasets for use in delineating DIPs.

In contrast to the above examples, humpback whale songs demonstrate annual variation as well as continual cultural evolution (Payne 1983), limiting their usefulness in delineation of DIPs. Furthermore, evidence for rapid horizontal transmission of song characteristics across ocean basins has been documented (Noad et al. 2000, Garland et al. 2011, Garland et al. 2013). These studies suggest that humpback whales are able to adopt songs of whales from other areas, raising the possibility that acoustic differences between groups could be maintained even if substantial immigration between groups was occurring.

The mode of transmission and sources of variation in acoustic characteristics in other species of baleen whales is not well understood. However, given the variation in utility of this LoE among different species of baleen whales, including between closely related species (e.g., blue and fin whales), acoustics differences between groups cannot be assumed to be a reliable indicator of demographic independence in baleen whales for which acoustic behavior is not well understood.

In several species of baleen whales, only males have been documented to sing (Darling & Berube 2001) (Watkins 1981, McDonald et al. 2001, Croll et al. 2002), and the production of song is thought by some to be a male reproductive display (Payne & McVay 1971, Tyack 2000, Darling & Berube 2001, Croll et al. 2002). If females choose mates based on song preferences, then assortative mating could provide a mechanism for pre-mating isolation and thus be important in the development of DIPs. However, additional LoEs would be needed to verify that differences in male song reflect patterns of population structure in females as well.

**A1.11.2.2 Odontocetes** – Odontocete vocalizations include impulsive clicks, pulsed calls, and whistles. Impulsive clicks are made by all odontocetes and are typically used for echolocation. However, the spectral structure of these clicks may be tied to morphology and have shown spectral plasticity in captive dolphins, indicating that their use in delineating DIPs is limited. Whistles are also used by some odontocetes for communication and may be stereotyped. However, odontocetes are able to modulate the frequencies used in whistles, suggesting that some plasticity may exist, again limiting their utility in delineating DIPs. Not all odontocetes make whistles.

In odontocetes, pulsed calls are likely to have the most utility in DIP delineation. They consist of a series of impulsive clicks produced very rapidly. These types of sounds are thought to be used for
communication and can have highly stereotyped rates of production (Ford & Fisher 1983, Rankin et al. 2007). However, it can be quite difficult to evaluate differences related to time when recordings are from large groups with many animas vocalizing simultaneously, as is often the case.

Like baleen whales, odontocetes exhibit variation both within and between species with respect to the utility of acoustic characteristics for delineating DIPs. For instance, research suggests that acoustic clans in sperm whales from the North Atlantic may correlate with DIPs (Rendell & Whitehead 2005), but in the North Pacific they do not (Rendell et al. 2012). In the absence of additional lines of evidence, it will be difficult to know whether acoustic differences correlate with demographic independence in most species of odontocetes.

Many species of beaked whales produce highly stereotyped clicks where variation within species is much less than variation between species (Baumann-Pickering et al. 2014). As the sounds of many beaked whale species have now been well-described, finer evaluation of within species variability may yield differences that could be indicative of DIPs. However, like other odontocete species, differences in prey preferences, habitat, and other factors must also be considered before acoustic differences in acoustic characters would provide strong evidence of DIPs.

A1.11.2.3 Pinnipeds – Geographic variation in vocalizations has been reported for several phocid species (harp seals, Terhune 1994, leopard seals, Thomas & Golladay 1995, harbor seals, Van Parijs et al. 2000, see review in Van Parijs & Schusterman 2003, Bjørgesæter et al. 2004, ribbon seals, Mizuguchi et al. 2016, Sabinsky et al. 2017). The function of these vocalizations, and their stability over time, has not been well-studied in all species. Two of the most well-studied species are the bearded (e.g., Risch et al. 2007, Charrier et al. 2013) and Weddell seals (e.g., Abgrall et al. 2003, Terhune et al. 2008). Male bearded and Weddell seals appear to use vocal trills in territory defense, suggesting that they may be important in maintaining some degree of reproductive isolation between populations.

Geographic variation in vocalization patterns of otariids has been described in only two species. One of these, the Australian sea lion, shows geographic variation between colonies that are relatively close together (~180 km), and males react differently to sounds made by foreign versus local males (Attard et al. 2010, Ahonen et al. 2014). As noted above, acoustic discrimination of this type may facilitate reproductive isolation.

Similar to cetacean studies, environmental drivers can also influence signal properties of pinniped vocalizations (e.g., Van Parijs et al. 1999), resulting in convergence or divergence of calls in the absence of demographic independence. As well, evidence that supports vocal learning in at least some pinniped species exists (reviewed in Reichmuth & Casey 2014) and could lead to acoustic divergence in the absence of reproductive isolation.

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Appendix 2: Species-specific evaluation of the utility of different lines of evidence for inferring demographic independence

The utility of different lines of evidence (LoEs) for inferring demographic independence between groups of animals will vary between species due to the different life histories, mating strategies, and geographic ranges of the species. Participants at the 2014 Meeting on the Use of Multiple Lines of Evidence to Delineate Demographically Independent Populations (Martien et al. 2015) conducted a species-by-species evaluation of the strength of different LoEs in order to document this variation (Table A2.1).

For each species/LoE combination, participants addressed the question ‘Assuming that you have robust data that show a difference among two or more groups of animals in the line of evidence concerned, then, based upon the current state of knowledge of that species, how useful would you rate this line of evidence as a means of delineating demographically independent populations?’ The answers to this question were coded as follows:

**Unknown**: Utility of this LoE for this species is unknown, meaning that there are no data for this species or a similar species from which generalizations can be made

**Not informative**: This LoE is not informative or potentially misleading

**Weak**: This LoE must be combined with multiple additional LoEs

**Moderate**: This LoE must be combined with at least one other LoE

**Strong**: This LoE can be used alone to delineate DIPs

The ratings were predicated on the assumption that there are robust data showing a difference between two groups for a particular LoE. Thus, they do not address the likelihood of detecting a difference between DIPs. Consequently, the ratings should not be used to decide which types of data to collect when planning a research program aimed at delineating DIPs. For instance, morphological differences are typically indicative of divergence well beyond the level of DIPs. Thus, if morphological differences are found between two groups, they are definitely demographically independent and may well be evolutionarily independent. However, it is unlikely that morphological differences will exist between most DIPs. Similarly, many species of beaked whales produce highly stereotyped clicks where variation within species is much less than variation between species (Baumann-Pickering et al. 2014). Thus, acoustic differences between DIPs should not be expected within beaked whale species unless cryptic species are present, though finer evaluation of within species variability may yield differences that could be indicative of DIPs.

The ratings also assume that the data set showing differences is ‘robust’, meaning that there has been appropriate evaluation of all of the relevant factors (e.g., age and sex differences, sample size, analytical methods, etc.) such that the observed difference is real, not a sampling or analytical artifact. The factors that should be taken into consideration when evaluating a data set are discussed in detail in section 3 of this Handbook. Many of these factors are common to all LoEs, while others are specific to only one or a few LoEs.
Table A2.1. Strength of a given LoE for delineating DIPs, assuming that robust data show a difference between two groups in that LoE. 3=Strong, 2=Moderate, 1=Weak, 0=Not informative, ‘-’=Unknown.

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<th>Morphology</th>
<th>Genetics</th>
<th>Movement</th>
<th>Distributional hiatus or low-density areas</th>
<th>Contaminants</th>
<th>Stable isotopes and fatty acids</th>
<th>Life History</th>
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Section 4.2 of this handbook summarizes the strength of each LoE within each of three broad taxonomic groups – large whales, odontocetes, and pinnipeds. Below, we briefly summarize species that received a strength rating that differed from that of their broad taxonomic group for each LoE.

A2.1 Morphology

Robust data demonstrating morphological differences between two groups were uniformly judged to be Strong evidence of demographic independence, though it was noted that we are very unlikely to obtain robust morphological data sets for most species.

A2.2 Genetics

Robust data demonstrating genetic differences between two groups were uniformly judged to be Strong evidence of demographic independence.

A2.3 Movements

Movement data were also judged to constitute a strong line of evidence supporting demographic independence for nearly all species, though for this LoE there were a few exceptions based on the behavior of certain species. Killer whales and pilot whales form stable pods or social clusters that tend to travel as a unit (Baird and Whitehead 2000; Mahaffy et al. 2015). Different pods/social clusters have different movement patterns that could result in them being mistaken for DIPs. Therefore, at least one additional LoE, such as genetic or association data, would be needed to confirm that differences in movement patterns are reflective of population structure rather than social structure. Similarly, false killer whales, pygmy killer whales, and melon-headed whales are known or suspected to form cohesive social clusters within populations (Aschettino et al. 2012; Baird et al. 2012), and differences in movement patterns these clusters could be mistaken for evidence of DIPs. Because there tends to be more interaction between social clusters in these species than there is between pods of killer whales, movement data were judged to be Moderate-Strong for them. In other words, a very large and robust movement data set should be sufficient to delineate DIPs for these species, though a second, corroborative LoE will often be necessary.

Movement data were also rated as a Moderate LoE for Baird’s beaked whales and Longman’s beaked whales. There is evidence to suggest that these two species may organize themselves into social units that are stable over long periods of time, similar to pilot whales or false killer whales (Baird et al. 2012; Fedutin et al. 2015; Mahaffy et al. 2015). Until more is known about social organization in Baird’s and Longman’s beaked whale, movement data should also be corroborated by at least one other LoE when delineating DIPs for these species.

Movement data was judged to be a Moderate LoE for island-associated spinner dolphins, as a long-term photo-identification study of spinner dolphins in the Northwest Hawaiian Islands has documented episodic dispersal between islands that could easily be missed, even in a robust Movement data set (Karczmarski et al. 2005).

Both minke whales and sperm whales tend to segregate by age and sex, with different age/sex classes exhibiting different movement patterns (Whitehead 2003; Perrin et al. 2018). Movement
data were therefore considered a Moderate LoE for these two species, as additional data would be needed to determine whether differences in movement patterns were reflective of DIPs or simply different age/sex classes.

Sei whales exhibit considerable interannual variability in movements that are not well understood (Hayes et al. 2017). Thus, data showing differences in movements between two groups would need to be corroborated with other data in order to determine whether the differences were indicative of different DIPs. Movement data were therefore considered a Moderate LoE for Sei whales.

In some areas of their range, individual fin whales have been observed to habitually return to specific locations repeatedly, such that they are photographed within a few tens of miles of the same location over multiple years (Falcone et al. 2011). These data could be interpreted to indicate very restricted movements in these animals. However, data from satellite tags show that, between sightings, the animals travel quite broadly. If considered alone, movement data from photo-identification could lead to the erroneous delineation of DIPs, whereas movement data from tags provide a much more reliable picture of these animals’ movements. Thus, movement data based on satellite tags was considered a Strong LoE for fin whales, movement inferred from photo-identification is a Moderate LoE that should be corroborated with at least one other LoE.

A2.4 Distributional hiatuses or low-density areas

Distributional hiatuses or low-density areas were generally judged to constitute a moderate LoE that would need to be combined with at least one other LoE when delineating DIPs. There are a few species that were exceptions to this evaluation. Killer whales have patchy habitat that results in large gaps in distribution that are not DIP boundaries. Thus, distributional hiatuses or low-density areas were considered a weak LoE for killer whales. Sperm whales and minke whales tend to segregate by age and sex, with different age/sex classes occupying different areas (Whitehead 2003; Perrin et al. 2018). Consequently, the groups on either side of a distributional hiatus may represent different age/sex classes rather than DIPs. This LoE was therefore also rated weak for sperm and minke whales.

The distribution of sei whales has been observed to shift dramatically over the course of a few years, making it difficult to even define their distribution (Hayes et al. 2017). Until these distributional shifts are better understood, this utility of this LoE is considered unknown.

On their feeding grounds, gray whale habitat is patchy, with areas of high density separated by areas of low density. However, animals that feed in the far northern areas migrate through more southerly feeding areas, and have been observed to sometimes spend a feeding season at a more southerly feeding aggregation before returning to the far northern feeding areas the next year (Weller et al. 2013). Due to this evidence of animals switching back and forth across low-density areas, this LoE was considered Weak evidence of demographic independence for gray whales.

A2.5 Contaminants

Contaminants were judged to be Moderate indicators of demographic independence. Contaminant profiles are not heritable and are therefore cannot be used to detect individuals that dispersed from
their natal populations at a very young age or were born to immigrant parents. However, the fact that contaminant loads are integrated over the lifetime of an animal rather than representing a one to six-month snapshot of an animal’s diet does create the potential for detecting immigrants into a population based on contaminant data. While large differences in contaminant loads indicate demographic independence, small differences can be maintained even in the face of relatively high dispersal rates. Thus, the strength of contaminant data for inferring demographic independence depends on the magnitude of the observed differences. We judged contaminants to be a Moderate LoE, assuming that large differences are detected. If differences are small, they would constitute Weak evidence of demographic independence and would need to be corroborated by several other LoEs.

Contaminants were considered to be a stronger LoE (Moderate to Strong) for bay, sound, and estuarine bottlenose dolphins, as the nature of the habitat occupied by these dolphins sometimes results in strong variation in environmental contaminant profiles across small spatial scales that are consistent with population structure (Balmer et al. 2011; Kucklick et al. 2011). Thus, contaminant profiles in BSE bottlenose dolphin has been shown to correlate well with DIPs in some areas of the east coast and Gulf of Mexico.

Guadalupe fur seals breed almost exclusively at one island (Aurioles-Gamboa and Trillmich 2018). However, it is not known whether there are demographically independent feeding populations that all utilize the same breeding ground. Therefore, the utility of contaminants for identifying DIPs in Guadalupe fur seals is currently unknown.

A2.6 Life history

Life history was judged to be a Weak LoE because most life history parameters are somewhat plastic, allowing animal’s life history characteristics to change in response to their environment (e.g., photoperiod) and changes in population density. Life history parameters therefore cannot be used to estimate dispersal rates, though they can corroborate data from other LoEs. The only exceptions to this rating were for three species of baleen whales. For Bryde’s and minke whales, large differences in breeding seasonality have provided compelling evidence of demographic independence and been used to delineate stocks (Horwood 1990; Donovan 1991; Best 2001). Life history was therefore deemed a Strong LoE for these species, though it should be noted that this rating is based on a specific life history parameter. Very little is known about life history of Sei whales, so the utility of this LoE is considered Unknown for this species.

A2.7 Trends in abundance

Differences in trends in abundance can be extremely informative when used in concert with other LoEs, but can be quite misleading in isolation. Thus, trends in abundance were considered a weak LoE. Information on movements (e.g., between locations or in and out of the study area) is particularly important for interpreting trend data. For ice-hauling pinniped species, it is unlikely that trend data could ever be informative due to the broad distributions of these species in inaccessible habitats and the difficulty in estimating the proportion of animals available to be counted. Thus, trends were deemed Uninformative for ice-hauling pinnipeds.
The distribution of Sei whales has been observed to shift dramatically over the course of a few years, with populations sometimes completely disappearing from a large area for a decade before returning (Barlow and Forney 2007; Hayes et al. 2017). These distributional shifts make it impossible to confidently interpret trend data. Thus, the utility of trends in abundance for delineating DIPs is considered Unknown for Sei whales.

### A2.8 Stable isotopes and fatty acids

For cetaceans, stable isotope (SI) and fatty acid (FA) differences were uniformly considered to be Weak to Non-informative as evidence of demographic independence due to the fact that there are many possible causes for differences in SI signatures, such as differences in individual diet preferences, prey switching, and within and between year changes in background isotope profiles. A score of Non-informative was given to species that are known or believed to exhibit a high degree of prey switching or individual variation in diet specialization (e.g., humpback whales, all pinnipeds), while all others were judged Weak. The distribution of Sei whales has been observed to shift dramatically over time (Hayes et al. 2017). While it is not known whether these distributional shifts coincide with shifts in prey, they will nonetheless result in changes in SI profiles due to differences in environmental isotope ratios in different oceanic regions. Differences in SI ratios due to distributional shifts could easily be mistaken for differences between DIPs. Therefore, SI and FA differences were considered Uninformative for identifying DIPs of Sei whales.

Not enough is known about the feeding habits of Gervais or True’s beaked whales to evaluate whether SI or FA differences would be a Weak or Non-informative LoE for these species, so it was rated as Unknown.

### A2.9 Physiographic or oceanographic habitat differences

The utility of physiographic or oceanographic habitat differences (hereafter habitat differences) varied across three broad groups – large whales, small whales and dolphins, and pinnipeds. Habitat differences were judge to be Not informative for most large whales due to their broad geographic distributions that span multiple habitat types. The exceptions were Bryde’s whales and gray whales. Bryde’s whales are known to form many resident populations (e.g., Best 1977). Consequently, if habitat differences could be combined with one other line of evidence to rule out migratory behavior, that would be sufficient to delineate DIPs. Therefore, habitat differences were judge to provide Moderate evidence of demographic independence in Bryde’s whales.

In gray whales, there is small group of animals called the Pacific Coast Feeding Group (PCFG) that exhibits site fidelity to a feeding area along the northwest coast of the United States and the southern British Columbia off the Canadian coast. A task force charged with determining whether or not the PCFG constitutes a DIP considered the fact that the PCFG feeds in a distinct ecosystem relative to the rest of the eastern Pacific population as supportive of it being a DIP (Weller et al. 2013). Habitat differences were therefore judged to provide Weak evidence of demographic independence for gray whales.

Habitat differences were considered to be more useful for inferring demographic independence in small whales and dolphins due to their generally smaller geographic ranges and non-migratory
behavior. Exceptions were offshore killer whales, narwhals, and beluga, for which habitat differences were considered Weak evidence of demographic independence. In each of these cases, populations are known to have ranges that span multiple Ecoregions (Spalding et al. 2007).

Habitat was also rated as a weak line of evidence for several species of beaked whales and for pygmy sperm whales. We do not know enough about how population boundaries in these species compare to habitat difference to consider this LoE Moderate for these species, but based on what is known about marine mammals in general, habitat differences should be considered at least Weak evidence of demographic independence.

For pinnipeds, habitat differences were considered Weak indicators of demographic independence. Ecoregion boundaries have been shown to correspond to boundaries between DIPs delineated based on other types of data for several pinniped species. However, the need to distinguish between breeding and feeding habitats and the differences in behavior and habitat use between juveniles and adults of many pinniped species results in a greater requirement for habitat differences to be corroborated by other LoEs when delineating DIPs for pinnipeds as compared to odontocetes.

A2.10 Association data

Baleen whales are generally not known to form the types of long-term stable social bonds that are identified by association data. Therefore, this association data was rated as Not Informative for this taxonomic group.

The utility of association data in delineating DIPs has not been studied in pinnipeds, and so was rated as Unknown for all pinniped species.

Association data were considered to be a Weak to Moderate indicator of demographic independence for most odontocetes, but was judged as Moderate for a large minority. These were species that exhibit strong social bonds that are stable through time: beluga, narwhal, Dall’s porpoise, Pacific white-sided dolphins, northern right whale dolphins, island-associated spinner dolphins, all bottlenose dolphins except for pelagic populations, and most of the Globicephalids (aka ‘blackfish’). Association data have already been used, in combination with other LoEs, to delineate stocks for many of these species (Baird et al. 2008; Aschettino et al. 2012; Baird et al. 2012).

The utility of association data for delineating stocks of harbor porpoise was rated as Unknown due to the fact that the degree of sociality in this species has not been evaluated.

A2.11 Acoustics

Unlike all other LoEs, whose utility was largely consistent across large taxonomic groups, the utility of acoustic data for inferring demographic independence was very species-specific. There are many species for which no studies have been conducted that would allow us to evaluate the utility of acoustic data for examining population structure. Consequently, the utility of acoustic data was rated as Unknown for many species, particularly of small whales and dolphins.
There is evidence that bottlenose dolphins change their acoustic characteristics in response to behavioral state, the specific prey they are pursuing, and ambient noise (Simard et al. 2010). Thus, acoustic differences between two different areas could simply reflect differences in, for example, the types of prey that are available in the two areas rather than being indicative of demographically independent populations. Acoustic data were therefore considered Not informative for bottlenose dolphins. In contrast, two genetically and morphologically distinct groups of Pacific white-sided dolphins exhibit acoustic differences that are stable across years (Soldevilla et al. 2008). Both call types occur in an area where the two groups overlap, indicating that the acoustic differences between the groups is not related to ambient noise and that, if it is due to differences in prey or foraging strategies, the two groups utilize prey differently in sympatry. A similar situation exists between the coastal and continental shelf populations of Atlantic spotted dolphins, which are acoustically distinct (Baron et al. 2008). Thus, acoustic data are useful in identifying DIPs of Pacific white-sided and Atlantic spotted dolphins, though multiple additional LoEs are necessary, making acoustics a Weak LoE for these species.

Relatively little is known about the acoustic characteristics of other small dolphins, largely due to the difficulty in amassing large data sets of calls that can be positively assigned to species. Consequently, we do not know whether most other species whistles are highly labile and context specific, like bottlenose dolphins, which would render them Uninformative for DIP delineation, or if they are likely to exhibit population-specific difference like Pacific white-sided dolphins. Thus, until more information is available from these species, the utility of acoustic data for delineating DIPs is Unknown.

Bigg’s killer whales are organized into distinct vocal clans that have proven useful in identifying population structure (Ford 1991). Consequently, acoustics was considered a Moderate LoE for this species. Other species of Globicephalids (‘blackfish’) also show acoustic variation between groups that may be useful in delineating stocks; thus, acoustic data were considered a Weak LoE for all other Globicephalids except offshore killer whales, for which the utility of acoustic data for stock delineation is unknown.

Many species of beaked whales produce highly stereotyped clicks where variation within species is much less than variation between species (Baumann-Pickering et al. 2014). Thus, the presence of two call types within a stock could suggest that the stock may actually be comprised of two cryptic species. Thus, a finding of acoustic differences between groups was judged to represent Strong evidence of demographic independence for most beaked whale species. As the sounds of many beaked whale species have now been well-described, finer evaluation of within species variability may yield differences that could be indicative of DIPs. However, like other odontocete species, differences in prey preferences, habitat, and other factors must also be considered before acoustic differences in acoustic characters would provide strong evidence of DIPs.

For blue whales and north Pacific minke whales, acoustic difference appear to be a Strong LoE for delimiting DIPs (Rankin and Barlow 2005; McDonald et al. 2006). Acoustics has also proven useful for delineating DIPs of fin whales, though variation within seasons and across years could be misleading in this species if not properly accounted for (Hatch and Clark 2004; Oleson et al. 2009). Thus, acoustic data are considered a moderate LoE for fin whales. Acoustic data were judged to be Not Informative for humpback whales due to annual variation and rapid horizontal transmission of song
characteristics across ocean basins (Noad et al. 2000; Garland et al. 2011; Garland et al. 2013), as well as for gray whales due to their limited vocal repertoire (Edds-Walton 1997).

Though geographic variation in vocalizations has been reported for several phocid species (harp seals, Terhune 1994; leopard seals, Thomas and Golladay 1995; harbor seals, Van Parijs et al. 2000; see review in Van Parijs and Schusterman 2003; Bjørgesæter et al. 2004; ribbon seals, Mizuguchi et al. 2016; Sabinsky et al. 2017), the function of these vocalizations, and their stability over time, has not been well-studied in all species. Similar to cetacean studies, environmental drivers can also influence signal properties of pinniped vocalizations (e.g., Van Parijs et al. 1999), resulting in convergence or divergence of calls in the absence of demographic independence. As well, evidence that supports vocal learning in at least some pinniped species exists (reviewed in Reichmuth and Casey 2014) and could lead to acoustic divergence in the absence of reproductive isolation. Consequently, acoustic data were considered Not informative for most pinniped species, with a few exceptions.

Bearded seals (Risch et al. 2007; Charrier et al. 2013) and Weddell seals (Abgrall et al. 2003; Terhune et al. 2008) exhibit geographic variation in the vocal trills they use in territory defense. This variation may be important in maintaining some degree of reproductive isolation between populations, resulting in acoustic data being considered a Moderate LoE for bearded seals (Weddell seals do not occur in the U.S. EEZ and are therefore not considered in Table A2.1). Similarly, downsweep vocalizations produced by male ribbon seals are believed to associated with mating behavior and exhibit geographic variation thought to be reflective of population structure (Miksis-Olds and Parks 2011; Mizuguchi et al. 2016), resulting in a Moderate rating for the species. There is also limited data suggesting temporally stable acoustic differences between two populations of harp seal (Terhune 1994; Perry and Terhune 1999). Thus, acoustic data were deemed a Weak LoE for this species.

A2.12 References


Appendix 3: Instructions to Data Availability Assessors

The objective of the Data Availability Table is to serve as a starting point for documenting the ‘best scientific information available’ (BSIA). When complete, this table should provide the basis for evaluating the BSIA from 2015-2020. It is envisioned that this be an evolving document with regular updates as new data and means of obtaining data on stock delineation change.

If you find that there are new stocks not listed in the table, please add them to the end of the appropriate SRG worksheet.

For each stock, the question is

Are results currently available from this LoE that are sufficiently robust to determine whether there are multiple stocks present within a currently defined stock? If not, are results likely to be available within the next five years?” Do not address availability of data for boundary determination.

For each stock, each Line of Evidence (LoE) will be coded as follows:

- ‘-’: Not applicable; this LoE is not useful for stock delineation for this stock/species; this code should be used for any LoE/species combination that received a 0 in the Strength of Evidence (SoE) table that we completed at the workshop; these cells have already been completed for you by reference to the SoE table and have a dark grey shaded cell with a ‘-’. There are a few cases where you may assess that for a particular stock this line of evidence is not applicable and should receive a ‘-’. For example, gray seals have recently re-occupied the U.S. Atlantic coast and would not be expected to have developed morphological differences, so that stock received a ‘-’ for morphology even though morphology is still considered a strong LoE for the species.

0: Not feasible to collect or analyze sufficient data within five years
1: Feasible to collect sufficient data or analyze samples within five years, but no plans to do so
2: Sufficient results for review of stock delineation expected within five years
3: Sufficient results for review of stock delineation are currently available

‘Sufficient’ requires some judgment to determine not simply whether data are available but whether the sample size and distribution will allow a good chance of determining if multiple stocks are present, at least as far as the strength of that LoE allows. This does not imply that data that are not ideal will not be used for stock delineation if they are the best available, but rather indicates whether good data are available (or could be soon). One way to think about ‘sufficient’ is to imagine whether these data would be acceptable in a publication as evidence for or against presence of population structure.

Another general issue is the scale considered in the question. Many currently defined stocks are very large. For the purposes of this exercise, the data availability code assigned does not need to reflect whether sufficient data to resolve stock structure within the entire area are available, but rather should be relative to whether data are sufficient to determine if ‘multiple’ stocks (meaning more than one can be delineated) exist within the currently defined stock. Thus, if the current stock was the entire west coast and there were data supporting a stock in the southern portion but poor data in far northern regions (such that the remainder could still contain multiple stocks), the evidence
supporting the new delineation would rate a 2 or 3 above based on the potential for adding a single new stock.

The column named “physiographic or oceanographic differences in habitat” is intended to indicate cases where empirical data for the stock in question are available. By empirical data in this case we mean that there are data that link population structure with something like depth (from tagging results) or sea surface temperature (from modeling results). We have added a column for whether the stock spans multiple Spalding ecoregions that you do not need to complete.

Filling out the table

Please enter values only into the SAR-level worksheet (AKSRG, ASRG or PSRG). These will automatically go into the ‘taxa’ worksheets (Large whales, etc.).

Assessors should give themselves an assessor number (Taylor is already ‘1’, Wade is ‘2’). Group Assessors are also fine (like, 3: Rosel, Wells). If you consult with someone and that should be recorded, please note their name in the Other considerations column unless they did the entire assessment for that stock, in which case they should get an assessor number and that number be entered into the Assessor box.

Following the Line of Evidence columns are footnote columns. In the Word document, these may be inserted as footnotes (not possible within Excel). In many cases, the same footnote will apply to multiple stocks. For example, for many beaked whales there are some data available for some LoEs and ongoing efforts to collect more, but little hope of amassing a ‘sufficient’ data set within five years. The footnote for these cases states ‘some samples available but slow accrual combined with small current sample sizes make within stock comparisons unlikely in five years.’ As such, before adding a new footnote, please review those already listed in the Word document to determine if an existing footnote is applicable. This footnoting process will be used to provide any species-specific rationales for the data availability ranking that was given. Starting your own footnote sheet is fine. If a caveat is uniform throughout a grouping (where Large Whales are a ‘grouping’) then there is no need to add a footnote, as that will be covered in the caveat section. If you struggled with ‘feasibility’ between 2 categories, the footnote option allows for explanation of your decision. However, I still expect most footnote cells will be blank and that is fine.

One other task we would like you to complete is to highlight stocks that we have high confidence, based on available data, do NOT contain multiple DIPs. You can see examples on the PSRG page within the rows I’ve already completed (CAORWA stocks). An example of how I chose to highlight and not highlight stocks can be seen in the harbor porpoise stocks (rows 60-65). The two southernmost stocks (Morro and Monterey) are small and have genetics and/or distribution and trends data supporting their independence. I have therefore highlighted them, indicating they do NOT contain multiple DIPs. The San Francisco – Russian River stock probably does not contain multiple DIPs, but sample size in previous studies was low in some areas and boundary placement based mostly on distribution. Thus, it is not highlighted because there are not sufficient data to be confident that it does not contain multiple DIPs. Even further north there are stocks that available data suggests may contain multiple DIPs, but the evidence was not considered sufficient over a decade ago to delineate multiple stocks. In Washington inland waters, there has been expansion/recovery within southern Puget Sound since harbor porpoise stock delineation was last considered that warrants re-
examination. These stocks are also not highlighted to reflect that we are not confident that they do not contain multiple DIPs. In short, the decision to highlight stocks, indicating that multiple DIPs can be ruled out, needs to be data-driven for this Data Availability exercise.

Feel free to look at and comment on the other worksheets, but please don’t do entries there.
Appendix 4

Data Availability for all stocks in 2013 Stock Assessment Reports

The table is sorted by species name, geographical region, and then by stock area. Data available to address the question: “Are results currently available from this LoE that are sufficiently robust to determine whether there are multiple stocks present within a currently defined stock? If not, are results likely to be available within the next five years?” The question of whether there is availability of data for boundary determination is not addressed.

Codes used in the table are:
- Not applicable; this LoE is not useful for stock delineation for this stock/species
0 Not feasible to collect or analyze sufficient data within five years
1 Feasible to collect sufficient data or analyze samples within five years, but no plans to do so
2 Sufficient results for reviewing stock delineation expected within five years
3 Sufficient results for review of stock delineation are currently available

Color codes for the table are:

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In tables and figures in the data availability chapter, “available-strong” would be 2-3 Strong (darker green), “available-moderate” would be 2-3 Moderate (darker yellow), and “weak or not available” would be all other cases.
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### Table: Summary

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Appendix 5: Structured Expert Decision Making process details

The Structured Expert Decision Making (SEDM) process we recommend has three steps: pre-elicitation, elicitation and post-elicitation.

**Pre-elicitation**
Pre-elicitation involves assembling the background information that will be provided to the experts. Experts are contacted and briefed on the elicitation process. In addition, we recommend that as part of pre-elicitation all experts, regardless of previous experience in serving on a DIP delineation expert group, go through training exercises to get feedback on the consequences of making DIP delineation decisions.

**Elicitation**
Elicitation is the part of the process where experts answer SEDM questions. During elicitation, each expert responds to the SEDM questions privately (first estimate). The group then discusses the first estimates and refines questions as necessary (feedback). Finally, the experts privately answer the refined SEDM questions (second estimate).

Best results come from composing unambiguous questions. Because lack of clarity in questions is often communicated through body language (raised eyebrows, furrowed brow) that cannot be easily seen when participants are remote, elicitation is best done in face-to-face meetings lasting at least 2 days. After an initial meeting at which a core of experts is trained, it may be possible to have some of those members participate remotely. In cases where a face-to-face meeting is not possible, facilitators must be more involved in engaging participants and ensuring that questions are unambiguous.

The elicitation process is most successful if it is led by a facilitator trained in SEDM who can strive to involve all experts in the process and steer the group away from hearing too much from influential members. Possible gains from using a group can be reduced if influential members sway the group towards ‘groupthink’.

**First estimate**
All panelists individually answer questions and make notes about reasons for their judgements. As much as possible, this first estimate should be done when panelists can contemplate the questions in a quiet and non-rushed fashion. It may be reasonable to set aside a few hours at the end of the first day for panelists to make these first estimates and even reconsider them when fresh in the morning prior to the group assembling.

**Feedback**
The traditional SEDM format maintains anonymity in this stage. However, it often becomes obvious who gave certain responses and can make the discussion onerous and artificial when discussing highly disparate responses that often result from lack of clarity in the question. We recommend discussing with panelists whether they are comfortable making the feedback phase non-anonymous. Thus, the initial responses would be associated with names with the understanding that the second estimate will be anonymous and the final write-up of the elicitation will also be anonymous.
The feedback stage is useful in identifying and reducing ambiguities in the language of the question and in revealing any evidence that was not presented to the entire group. Most frequently, the feedback session will result in clarifying the questions and revealing different ways of thinking about the problem that were not voiced in initial discussions. It is more likely than not that a second round of elicitation will be needed. Typically, this second round will take experts less time and can be done during a meeting break. It should be re-emphasized to the experts that from this point on, the results will be anonymous.

If there are large numbers of questions that have been addressed, the facilitator may identify questions where there is near group consensus and suggest that these questions need not be discussed unless some panelist would like to discuss them. The order of discussion of the remaining questions is often best done by identifying questions where there is likely linguistic uncertainty (one or a few experts have very different results from the main group) and then by questions where there are likely true differences of opinion (sometime characterized by bimodal outcomes). The former questions are usually easily resolved and allow the group to take some easy bites before tackling the meatier discussions.

**Second estimate**
The second estimate is done privately. Even if experts know that the final write-up will be anonymous, knowing that the group will see their final opinion has the result of experts consciously or unconsciously making their opinions more like the opinions voiced by influential experts.

**Post-elicitation**
Elicitation results are summarized (often the mean or median presented as the over-all outcome). Experts may review and discuss these outcomes, add commentary, and correct residual misunderstandings. Because the DIP delineation exercise will be read by managers and other interested lay parties, it is important to explain the results in common language. Group results can be summarized in tables, with individual results in an Appendix.
Appendix 6 Examples using SEDM for stock delineation

This Appendix provides two examples from Technical Memorandums that explicitly considered stock delineation under the MMPA: Pacific Coast Feeding Group (PCFG) of gray whales (Weller et al. 2013) and Sakhalin beluga whales (Bettridge et al. 2016). Because the text was excerpted from the full documents, we have spelled out abbreviations not used in this Handbook in square brackets. The text was left intact so that the full range of questions considered, the process used to develop and conduct the SEDM, and the text explaining the results verbally are presented in full.


In keeping with the objectives stated above for developing questions, the TF [task force] dedicated significant time during day 2 of the workshop agreeing on questions to be considered during the decision-making process. A key objective of this exercise was to focus on existing lines of evidence to help create the questions while at the same time being mindful of the existing definitions of the terms (e.g., demographic independence, interbreed when mature, functioning element of the ecosystem) contained in the MMPA and GAMMS guidelines. For instance, a simple example of this might be; “evidence of demographic independence is when the number of internal recruits is greater than the number of external recruits”. In general, this philosophy of creating questions was adopted by the TF and maintained during its deliberations.

After considerable work, the TF agreed to 11 questions. Overnight, TF members privately completed their point allocations for each of the questions. Point allocations were tallied and ready for discussion on the final day of the workshop. Allocating points in this manner allowed individual TF members to express their level of certainty on each of the questions, such that placement of all points in a single category indicated relative certainty in the lines of evidence discussed during the workshop. The TF agreed to view resulting scores with names associated to facilitate discussion and assure that linguistic uncertainty was not responsible for any disparate votes. The TF discussed the scores and, in some cases, members adjusted them when prior articulation of the lines of evidence had been unclear. The final 11 questions and likelihood point allocations for each of the TF members (anonymous, labeled A – G), as well as the proportional distribution of points overall, are provided below.

<table>
<thead>
<tr>
<th>Question 1.</th>
<th>Overall</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td>Does the ecosystem occupied by the PCFG when they are feeding differ from the ecosystems occupied by other ENP [Eastern North Pacific] gray whales?</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strongly Agree</td>
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<td>0</td>
<td>80</td>
<td>100</td>
<td>90</td>
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<tr>
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<td>10</td>
<td>100</td>
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<td>0</td>
</tr>
<tr>
<td>Somewhat Disagree</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Strongly Disagree</td>
<td>0</td>
<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
### Question 2.
If gray whales in the ENP continued to be managed as a single stock, would the future abundance of PCFG gray whales be maintained above 60% of their current abundance if annual HCM in the PCFG was 5?

<table>
<thead>
<tr>
<th>Strongly Agree</th>
<th>Somewhat Agree</th>
<th>Neutral</th>
<th>Somewhat Disagree</th>
<th>Strongly Disagree</th>
</tr>
</thead>
<tbody>
<tr>
<td>38</td>
<td>23</td>
<td>25</td>
<td>14</td>
<td>0</td>
</tr>
<tr>
<td>0</td>
<td>20</td>
<td>50</td>
<td>30</td>
<td>0</td>
</tr>
<tr>
<td>95</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

### Question 3.
If gray whales in the ENP continued to be managed as a single stock, would the future abundance of PCFG gray whales be maintained above 60% of their current abundance if annual HCM [human caused mortality] in the PCFG was 10?

<table>
<thead>
<tr>
<th>Strongly Agree</th>
<th>Somewhat Agree</th>
<th>Neutral</th>
<th>Somewhat Disagree</th>
<th>Strongly Disagree</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>24</td>
<td>21</td>
<td>17</td>
<td>29</td>
</tr>
<tr>
<td>0</td>
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<td>40</td>
<td>10</td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

### Question 4.
If gray whales in the ENP continued to be managed as a single stock, would the future abundance of PCFG gray whales be maintained above 60% of their current abundance if annual HCM in the PCFG was 20?

<table>
<thead>
<tr>
<th>Strongly Agree</th>
<th>Somewhat Agree</th>
<th>Neutral</th>
<th>Somewhat Disagree</th>
<th>Strongly Disagree</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>4</td>
<td>7</td>
<td>22</td>
<td>67</td>
</tr>
<tr>
<td>0</td>
<td>25</td>
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<td>10</td>
<td>90</td>
</tr>
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<td>0</td>
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<td>0</td>
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</tr>
</tbody>
</table>

### Question 5.
Given the lack of significant differences found in nuclear markers between PCFG whales and other eastern Pacific whales, how would you allot points to:

<table>
<thead>
<tr>
<th>There is complete random mating within the eastern NP</th>
<th>There could be some non-random mating within PCFG whales that is either too recent or at too low a level to be detected given current sample sizes and marker numbers</th>
<th>PCFG whales breed primarily with each other</th>
</tr>
</thead>
<tbody>
<tr>
<td>63 70 70 50 80 60 40</td>
<td>37 30 30 30 50 20 40 60</td>
<td>0 0 0 0 0 0 0 0</td>
</tr>
</tbody>
</table>
### Question 6.

<table>
<thead>
<tr>
<th>Overall</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nearly all recruitment into the PCFG area results from external recruitment (immigration)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>NA</td>
</tr>
<tr>
<td>Most recruitment into the PCFG area results from external recruitment</td>
<td>21</td>
<td>20</td>
<td>30</td>
<td>20</td>
<td>0</td>
<td>20</td>
<td>33</td>
</tr>
<tr>
<td>Recruitment is about equal between internal (births) and external (immigration) recruitment</td>
<td>56</td>
<td>60</td>
<td>50</td>
<td>60</td>
<td>100</td>
<td>30</td>
<td>34</td>
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<tr>
<td>Most recruitment into the PCFG area results from internal recruitment</td>
<td>24</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>0</td>
<td>50</td>
<td>33</td>
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### Question 7.

<table>
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<tr>
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<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nearly all recruitment into the PCFG area results from external recruitment (immigration)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>Most recruitment into the PCFG area results from external recruitment</td>
<td>38</td>
<td>30</td>
<td>55</td>
<td>50</td>
<td>0</td>
<td>30</td>
<td>50</td>
</tr>
<tr>
<td>Recruitment is about equal between internal (births) and external (immigration) recruitment</td>
<td>48</td>
<td>40</td>
<td>35</td>
<td>35</td>
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<td>35</td>
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<tr>
<td>Most recruitment into the PCFG area results from internal recruitment</td>
<td>14</td>
<td>30</td>
<td>10</td>
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<td>20</td>
<td>15</td>
</tr>
<tr>
<td>Nearly all recruitment into the PCFG area results from internal recruitment</td>
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<td>0</td>
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<td>0</td>
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</tr>
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</table>

### Question 8.

<table>
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<tr>
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<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td>Do the genetic and photo-identification data indicate that the PCFG is a demographically independent population?</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strongly Agree</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Somewhat Agree</td>
<td>35</td>
<td>25</td>
<td>10</td>
<td>80</td>
<td>100</td>
<td>30</td>
<td>0</td>
</tr>
<tr>
<td>Neutral</td>
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<td>30</td>
<td>10</td>
<td>0</td>
<td>40</td>
<td>20</td>
</tr>
<tr>
<td>Somewhat Disagree</td>
<td>25</td>
<td>25</td>
<td>50</td>
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<td>30</td>
<td>40</td>
</tr>
<tr>
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<td>10</td>
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<td>0</td>
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<td>40</td>
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</table>
Question 9.

<table>
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<th></th>
<th>Overall</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Given all lines of evidence, is the PCFG a “population stock” under the agency’s interpretation of the MMPA?</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Somewhat Agree</td>
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<td>25</td>
<td>10</td>
<td>80</td>
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<td>30</td>
<td>10</td>
<td>0</td>
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<tr>
<td>Neutral</td>
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<td>50</td>
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<td>10</td>
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<td>40</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>Somewhat Disagree</td>
<td>24</td>
<td>25</td>
<td>50</td>
<td>10</td>
<td>0</td>
<td>30</td>
<td>35</td>
<td>20</td>
</tr>
<tr>
<td>Strongly Disagree</td>
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<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>35</td>
<td>80</td>
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</table>

Question 10.

<table>
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<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Given that some whales identified in the WNP [western North Pacific] migrate through U.S. waters to Mexico, should a separate SAR be developed for the WNP?</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Yes</td>
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<td>50</td>
<td>80</td>
<td>50</td>
</tr>
<tr>
<td>No</td>
<td>21</td>
<td>0</td>
<td>30</td>
<td>0</td>
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<td>50</td>
<td>20</td>
<td>50</td>
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</table>

Question 11.

<table>
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<tr>
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<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Given the differences found in mtDNA and nDNA between Sakhalin Island (WNP) and ENP gray whales, is there a “population stock” within the WNP under the agency’s interpretation of the MMPA?</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>100</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Somewhat Disagree</td>
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<td>0</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Strongly Disagree</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

**Question outcomes and discussion**

The outcomes of each question above are discussed below and follow the convention of using “percentage of total points” to describe the results. For example, in Question 1 the “strongly agree” category was allotted 53% of the total available TF points (370 points allotted/700 total points = 53%).

**Question 1**

The TF expressed general agreement, by allocating 100% of their combined points to the categories “somewhat agree” (47%) and “strongly agree” (53%) that PCFG whales seasonally feed in a unique ecosystem that differs from other gray whale feeding areas in the Pacific. Therefore, the TF concurred that it is reasonable to consider that if the PCFG no longer existed and the region was not reoccupied via immigration, summer feeding gray whales would no longer be a functioning element of the coastal Pacific Northwest ecosystem. Although such a circumstance is plausible, keeping all other things equal (e.g., habitat, prey availability), the current lines of evidence from photo-identification studies suggest it is unlikely that the level of annual immigration into the PCFG in the past decade would cease. Thus, the likelihood of gray whales not being found in the PCFG area seems low. However, the time it might take for “recolonization” of the PCFG via immigration is undetermined and thereby puts into question whether this scenario would meet the MMPA objectives of maintaining stocks not only for ecological purposes but also for aesthetic, recreational and economic reasons.
Questions 2, 3 and 4
These three questions were meant to address the MMPA objective of maintaining population stocks as significant functioning elements in the ecosystem of which they are part, and that population stocks should not be permitted to decline below OSP. GAMMS II state that where mortality is greater than a PBR level calculated from the abundance for the region where human caused mortality (HCM) occurs, serious consideration should be given to identifying an appropriate management unit in the region. While estimates of PBR and HCM for a putative PCFG stock have been generated (Carretta et al. 2013), there is uncertainty about both estimates, especially with respect to: (1) whether HCM (e.g., ship strikes and fisheries bycatch) for whales in the PCFG area is indeed higher than for whales that migrate through the area, and (2) where HCM actually occurs. In response to these questions, the TF expressed increasing concern about the ability of the PCFG to be maintained above 60%\(^7\) of its current abundance once HCM exceeded 5 whales per year.

The point allocation in Question 2 indicates that the TF overall tended to agree that the future abundance of PCFG gray whales would be maintained above 60% of their current abundance if annual HCM in the PCFG was 5. However, the relatively equal distribution of likelihood points in all categories except “strongly agree” indicates a high level of uncertainty among the TF.

For Question 3, points were allocated more broadly across categories, indicating a higher level of uncertainty among TF members as to whether the PCFG could sustain levels of HCM at 10 whales per year.

There was increased consensus among the TF for Question 4 in that none of them responded “strongly agree”. Overall, the TF concurred that it somewhat (22%) or strongly disagreed (67%) that the future abundance of PCFG gray whales would be maintained above 60% of their current abundance if annual HCM in the PCFG was 20.

Question 5
The TF found no evidence to suggest that PCFG whales breed primarily with each other. While there was general agreement (63%) that the lack of significant differences found in nuclear DNA markers between PCFG whales and other ENP whales suggests random interbreeding among all ENP whales, the allotment of 37% of the total points to the intermediate category suggests TF members thought it was possible that some breeding segregation may exist based on migratory timing (see Lang et al. 2011) but there is no direct evidence presently available to support or further test this theory.

Question 6
The TF found no evidence in the results from genetics studies to suggest that nearly all recruitment into the PCFG area results from external recruitment (immigration). Based

\(^7\) The management goal of the MMPA is to prevent populations from “depletion”. NMFS considers a population depleted if it fall below its Maximum Net Productivity Level (MNPL). For marine mammals, this level is thought to be between 50% and 85% of carrying capacity and is more likely to be in the lower portion of that range (Taylor and DeMaster 1993). Therefore, populations are considered depleted by the U.S. government if they are directly estimated to be below their MNPL, or if they are estimated to be below 50%-70% of a historic population size which it thought to represent carrying capacity (Gerrodette and DeMaster 1990).
on the genetic data and simulations discussed during the workshop, the highest average TF response (56%) indicates that TF members believe recruitment is most likely about equal between internal (births) and external (immigration) recruitment. That being said, the remaining 45% of the total points were split between most recruitment into the PCFG area resulting from either internal or external recruitment, indicating some overall uncertainty among members regarding the presently available lines of evidence about recruitment in the PCFG. It should be noted that one member of the TF refrained from assigning any points to this question, so these results represent 6 of 7 TF members actively involved in the point assignment process.

**Question 7**

Based on the photo-identification data, the TF found no evidence to suggest that nearly all recruitment was either external or internal, but rather some combination of the two. As with the genetics evidence, the highest average TF response (48%) indicates that the TF felt recruitment from internal (births) and external (immigration) sources are comparable. That being said, 38% of the total points were allocated to most recruitment into the PCFG area resulting from external recruitment. Therefore, a majority of the total points were allocated to either recruitment being about equal between internal (births) and external (immigration) recruitment (48%) or most recruitment into the PCFG area results from external recruitment (38%). As was also true with the genetic lines of evidence, these results from the TF suggest a fairly high level of uncertainty regarding recruitment into the PCFG.

**Question 8**

Based on the genetic and photo-identification data, the TF did not strongly agree that the PCFG is a demographically independent population. Although the highest average TF response (35%) was “somewhat agree” that the PCFG is a demographically independent population, the combined categories of “somewhat disagree” and “strongly disagree” elicited 44% of the total points allocated. Overall, these results from the TF suggest a high level of uncertainty regarding recruitment in the PCFG.

**Question 9**

Given all lines of evidence, the point allocation of the TF reflects broad uncertainty as to whether the PCFG should be regarded as a population stock under the MMPA and GAMMS guidelines. Perhaps more than all of the other questions considered, Question 9 reflects the highest degree of uncertainty. For instance, the “strongly agree” (14%) and somewhat agree (22%) categories are almost perfectly counter-balanced by the “somewhat disagree” (24%) and “strongly disagree” (18%) categories. An additional level of uncertainty is indicated by the “neutral” category (21%). Given these results, it seems clear that TF was unable to reach a definitive response with respect to the PCFG being a population stock. That is, members of the TF ranged in their opinions from strongly agree to strongly disagree as to whether the PCFG should be considered a separate stock.

Given that this question represents the primary purpose of the workshop, the following two sections provide insight into the deliberations of the TF with regard to arguments.
for and against the PCFG being a demographically independent unit.

The return of individual whales to specific feeding areas for as long as the PCFG has been studied (30+ years) strongly suggests that site fidelity is key to maintaining gray whales as a functioning element of this ecosystem. There was agreement that this ecosystem differs from other feeding ecosystems occupied by gray whales. Gray whales are unique among the great whales in being found in only a single ocean basin. Within this ocean basin the PCFG is the only feeding group that does not rely on the dynamics of a sub-arctic ecosystem. As such, the PCFG deserves the protections afforded by being an MMPA stock because the ecosystem role of these animals is unique and also because it provides gray whales, as a species, the flexibility they may need given potential challenges in a changing sub-arctic ecosystem.

Although there is evidence of recruitment from other feeding aggregations, there is also evidence of direct internal recruitment because calves have been shown to return to the PCFG area and reside there. Furthermore, because photographic efforts take place after most calves would be weaned, the recruits into the population not first seen as calves are actually of unknown origin and cannot be definitively assigned as external recruits.

PCFG whales show a low but significant level of genetic differentiation at the mtDNA control region when compared to samples collected in Chukotka [representative of the ENP population and sampled at a single feeding location in the Bering Sea], and when compared to a set of samples collected primarily from animals that stranded along the west coast of the U.S. [representative of a broader sampling of the ENP population]. The significant differences found when the mtDNA haplotype data from the PCFG is compared with that of groups representing the larger ENP population provide indirect evidence of internal recruitment and matrilineally-directed site fidelity to feeding grounds. The level of differentiation is on par with levels identified among humpback whales feeding in different areas of the western North Atlantic (Palsbøll et al. 2001) as well as humpback whales using different breeding grounds in the Southern Hemisphere (Rosenbaum et al. 2009), suggesting that the PCFG exhibits demographic independence similar to what has been inferred for other large whales. Within the western North Atlantic, humpback whales feeding in the Gulf of Maine are managed as a separate stock despite the fact that they share a common breeding ground with humpbacks feeding in other areas.

Although evidence for nuclear DNA differentiation between PCFG whales and other areas has not been found, nuclear genetic differentiation has not always been required for stock delimitation. Pacific harbor seal stocks were delimited on mtDNA differentiation alone (nuclear data were not available at the time), while the Gulf of Maine/Bay of Fundy stock of harbor porpoises was delimited based on significant differentiation at mtDNA, contaminant loads, and life history differences, and despite a lack of differentiation at nuclear markers.

Arguments against the PCFG being a demographically independent unit

The evidence that external recruitment is not a rare event is quite strong. The genetic
data have numerous rare haplotypes that are not consistent with a small, closed population. Indeed, simulations are not consistent with a closed population. A sizable number of individuals seen in the main feeding season are identified as transients, which is consistent with an on-going level of the main ENP population investigating this new habitat but then moving on. Further, when all samples collected in summer in the PCFG area are used there is not a significant difference found in mtDNA frequencies compared to all samples collected north of the Aleutian Islands.

The number of recruits into the PCFG has been estimated, through genetic data, to be 4 to as high as 8 individuals per year. Photo-identification data suggest similarly high numbers of non-calf recruits per year (8-11). These numbers exceed the estimated number of internal recruits and, given that PCFG numbers appear to be relatively stable, an addition of 4 or more external recruits per year cannot be considered trivial. These external recruitment rates suggest the PCFG is not demographically independent from the larger ENP population.

Furthermore, unlike other large whale populations, the annual coastal migration of the vast majority of ENP gray whales brings most individuals into contact with the habitat used by the PCFG. Should there be increased removals from this area, the continual visitation to this area by a large number of gray whales would make it likely that external recruitment would increase to fill any voids. The apparent pulse recruitment in 1999-2000 when conditions in the sub-arctic feeding areas resulted in a large mortality event shows that gray whales can adapt to a new habitat when conditions dictate. Using data collected since 2002 (post-pulse recruitment event), an average of 29.3 new whales have been identified in summer in the area used by the PCFG, with 18.5 animals that are not seen in later years and 10.8 whales that are seen in later years.

Given that an average of 18.5 new whales (at least, as this does not account for new whales not photographed) visit the PCFG area each summer but do not return, this suggests that something on the order of 10% of the whales that occur in the PCFG area each summer are transients that otherwise feed north of the Aleutians, and serve as a substantial and continuous source of potential recruitment into the PCFG.

To date, there is no evidence for nDNA differentiation between Chukotka and PCFG whales based on 8 microsatellite loci or between the PCFG and one Mexican calving lagoon based on 15 loci. These results may be interpreted as female directed site fidelity to the PCFG area coupled with random mating between PCFG and ENP whales on the breeding ground. Lack of nuclear differentiation diminishes support for demographic independence.

All lines of evidence (photo-identification and genetics) are consistent with ongoing external recruitment that could be at a magnitude that is not trivial to the persistence of the feeding aggregation (more than a percent or two per year). Uncertainty in the number of recruits per year and exactly who those recruits are (PCFG calves misidentified as recruits, true recruits of adults, temporary immigrants who do not stay more than a few years and may not even be contributing to the gene pool) creates significant uncertainty as to whether internal recruitment exceeds
external recruitment. Given the high level of mtDNA haplotypic diversity, the precision of $F_{ST}$ estimates is also uncertain. Taken together, the available evidence is weak for concluding the PCFG is demographically independent.

**Question 10**
Given that some whales identified in the WNP have been observed to migrate through U.S. waters to Mexico, in combination with the 1994 amendments to the MMPA requiring that SARs be published for all stocks of marine mammals in U.S. waters, the TF agreed to a high degree (79%) that a separate SAR should be developed in the future for the WNP stock of gray whales.

**Question 11**
Based on the differences found in mtDNA and nDNA between Sakhalin Island (WNP) and ENP gray whales, the TF unanimously (100%) agreed that it qualifies as a population stock under the MMPA and GAMMS guidelines.

### 13. Concluding Remarks

The implications of new data pertinent to stock structure, including considerable information related to the PCFG and WNP gray whales, were thoroughly reviewed during the workshop. Evaluating the new findings relevant to the status of the PCFG proved particularly complex. After review of results from photo-identification, genetics, tagging, and other studies within the context of the GAMMS guidelines there remains a substantial level of uncertainty in the strength of the lines of evidence supporting demographic independence of the PCFG. Consequently, the TF was unable to provide definitive advice as to whether the PCFG is a population stock under the MMPA and the GAMMS guidelines. Members of the TF ranged in their opinions from strongly agreeing to strongly disagreeing about whether the PCFG should be recognized as a separate stock.

In the case of WNP gray whales, the work of the TF was more straightforward. The mitochondrial DNA and nuclear DNA genetic differentiation found between the WNP and ENP stocks provided convincing evidence that resulted in the TF providing unambiguous advice that the WNP stock should be recognized as a population stock pursuant to the GAMMS guidelines and the MMPA.

Additional research may narrow the uncertainty associated with the question of whether the PCFG should be recognized as a population stock. To work towards this objective, the TF recommended further investigation of recruitment into the PCFG. Presently, both the photo-identification and genetics data indicate that the levels of internal versus external recruitment are comparable, but these are not quantified well enough to determine if the population dynamics of the PCFG are more a consequence of births and deaths within the group (internal dynamics) rather than related to immigration and/or emigration (external dynamics). The TF offered a number of research recommendations, using the existing photo-identification and genetics datasets, that could provide increased resolution on the issue of recruitment and, in turn, the question of stock identification.
While the need for additional data collection was apparent, especially with regard to recruitment into the PCFG, the purpose of the workshop was for the TF to determine whether the existing best available science was sufficient to advise that the PCFG be recognized as a population stock under the language of the MMPA and GAMMS guidelines. Therefore, the advice of the TF offered in this report should be viewed as a contemporary “snapshot” taken from an emerging and ever-changing body of knowledge regarding the PCFG.

The TF emphasizes that the PCFG is relatively small in number and utilizes a largely different ecosystem from that of the main ENP stock. While the status of the PCFG as a population stock has yet to be resolved, continued research on these whales should be undertaken with particular attention dedicated to collecting data relevant to the question of stock identification.


Because of the limited evidence available regarding the stock structure of the Sakhalin Bay-Amur River beluga whales relative to other western Sea of Okhotsk beluga whales, the Team used SEDM procedures to evaluate the available genetic and telemetry data for beluga whales in the western Sea of Okhotsk as they relate to delineating stocks. Learning from the gray whale lesson, this beluga status review team decided on a different formulation of questions for the stock delineation exercise. For each question, each of the ten Team members assigned 100 plausibility points across multiple statements that spanned what was felt to be plausible for the question. The Team agreed that members should allocate points evenly across all possible statements for a given question if they felt the available data were insufficient to address the statement. Scores were then averaged to produce a single score for each statement.

It took several rounds of discussion to get the wording of the questions and associated statements to the point where all experts understood and agreed on the meaning/intent of each statement. The Team considered eight questions: three that pertained to how similar Sea of Okhotsk beluga whales were to Alaska beluga whales (to give insight to how evidence used to delineate stocks within Alaska could be used by analogy in the Sea of Okhotsk), four that pertained to different lines of evidence about the demographic independence of Sakhalin Bay-Amur River beluga whales with respect to beluga whales elsewhere in the western Sea of Okhotsk, and a final statement that pertained to the plausibility of demographic independence of Sakhalin Bay/Amur-River beluga whales when all lines of evidence were taken together.

**Responses to questions concerning similarities between Alaska and Okhotsk beluga whales**

**Question 1.** Allot plausibility points to the following statements considering DNA evidence:

<table>
<thead>
<tr>
<th>Option</th>
<th>AVG</th>
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<tbody>
<tr>
<td></td>
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</table>
The pattern of differentiation in mtDNA observed among beluga whales in areas within the western Sea of Okhotsk is similar to the pattern observed in beluga whale aggregations defined as the Bristol Bay and Norton Sound stocks within Alaska 82.5

The pattern of differentiation in mtDNA observed in beluga whales among areas within the western Sea of Okhotsk is not similar to the pattern observed in beluga whale aggregations defined as the Bristol Bay and Norton Sound stocks within Alaska 17.5

**Interpretation:** There was a high level of agreement that the pattern of mtDNA differentiation observed among beluga whales in the western Sea of Okhotsk is similar to that seen in beluga whale stocks delineated in Alaska (82.5% agreement with no expert strongly supporting the alternative). The Team agreed the term “pattern” did not refer to the magnitude of genetic differentiation, which depends on effective population size, but rather meant finding strong statistical frequency differences between the strata. Bristol Bay and Norton Sound were chosen to be most similar to the western Sea of Okhotsk with respect to geography and behavior.

**Question 2.** Allot plausibility points to the following statements considering evidence about movement patterns including summer site fidelity:

<table>
<thead>
<tr>
<th>Option</th>
<th>AVG</th>
</tr>
</thead>
<tbody>
<tr>
<td>Movement patterns observed in the western Sea of Okhotsk are similar to movement patterns observed in beluga whale aggregations defined as stocks within Alaska</td>
<td>80.0</td>
</tr>
<tr>
<td>Movement patterns observed in the western Sea of Okhotsk are not similar to patterns observed in beluga whale aggregations defined as stocks within Alaska</td>
<td>20.0</td>
</tr>
</tbody>
</table>

**Interpretation:** There was a high level of agreement that telemetry-based movement patterns observed in western Sea of Okhotsk beluga whales are similar to movement patterns observed in beluga whale aggregations defined as stocks within Alaska (80.0% agreement with no expert strongly supporting the alternative).

**Question 3.** Allot plausibility points to the following statements considering the cumulative evidence from questions 1 and 2 about the similarity of western Sea of
Okhotsk beluga whales to stocks of beluga whales in Alaska:

<table>
<thead>
<tr>
<th>Option</th>
<th>AVG</th>
</tr>
</thead>
<tbody>
<tr>
<td>The overall mtDNA and movements data observed in western Sea of Okhotsk beluga whales are similar to mtDNA and movements data observed in beluga whale aggregations defined as stocks within Alaska such that they can be considered analogous</td>
<td>83.1</td>
</tr>
<tr>
<td>The overall mtDNA and movements data observed in western Sea of Okhotsk beluga whales are not similar to mtDNA and movements data observed in beluga whale aggregations defined as stocks within Alaska such that they cannot be considered analogous</td>
<td>16.9</td>
</tr>
</tbody>
</table>

**Interpretation:** There was a high level of agreement that both mtDNA data and studies of movements of beluga whales in the western Sea of Okhotsk are similar to the finding of similar studies of mtDNA and movements conducted on beluga whale aggregations defined as stocks within Alaska such that they can be considered analogous (83.1% agreement with no expert strongly supporting the alternative).

1.1.1.1 Responses to questions regarding the support of separate lines of evidence for alternative areas that delimit the stock to which Sakhalin Bay-Amur River beluga whales belong

**Question 4.** Allot plausibility points to the following statements considering mtDNA evidence:

<table>
<thead>
<tr>
<th>Option</th>
<th>AVG</th>
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</thead>
<tbody>
<tr>
<td>Beluga whales in Sakhalin Bay-Amur River are demographically independent from other western Sea of Okhotsk beluga whales</td>
<td>54.4</td>
</tr>
<tr>
<td>Beluga whales in Sakhalin Bay-Amur River and Nikolaya Bay together are demographically independent from other western Sea of Okhotsk beluga whales</td>
<td>39.4</td>
</tr>
<tr>
<td>Beluga whales in Sakhalin Bay-Amur River, Nikolaya Bay, and Ulbansky Bay together are demographically independent from other western Sea of Okhotsk beluga whales</td>
<td>4.4</td>
</tr>
<tr>
<td>There are no demographically independent groups within the western Sea of Okhotsk (i.e., the western Sea of Okhotsk is one demographically independent population)</td>
<td>1.9</td>
</tr>
</tbody>
</table>
**Interpretation:** There was strong agreement that the mtDNA evidence suggests there are multiple demographically independent populations of beluga whales in the western Sea of Okhotsk and that Sakhalin Bay-Amur River beluga whales are demographically independent from beluga whales in Ulbansky Bay and the bays to the west. Members were less certain whether Sakhalin Bay-Amur River beluga whales belong to a stock that summers only in the Sakhalin Bay-Amur River region or in a larger area that includes Nikolaya Bay.

**Question 5.** Allot plausibility points to the following statements considering evidence about nuclear DNA:

<table>
<thead>
<tr>
<th>Option</th>
<th>AVG</th>
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</thead>
<tbody>
<tr>
<td>There is complete random mating within beluga whales in the western Sea of Okhotsk</td>
<td>25.4</td>
</tr>
<tr>
<td>There could be some non-random mating within the western Sea of Okhotsk that is either too recent or at too low a level to be detected given current sample sizes and marker numbers</td>
<td>52.9</td>
</tr>
<tr>
<td>Sakhalin Bay-Amur River beluga whales mate primarily with each other</td>
<td>21.8</td>
</tr>
</tbody>
</table>

**Interpretation:** Conclusions concerning demographic independence among locations with the western Sea of Okhotsk that could be drawn from nuclear DNA evidence were less certain overall, with the greatest support (53%) for the potential for some non-random mating within the western Sea of Okhotsk.