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REPORT OF THE WORKSHOP ON SHORTCOMINGS OF CETACEAN TAXONOMY IN RELATION TO NEEDS OF CONSERVATION AND MANAGEMENT, APRIL 30 - MAY 2, 2004 LA JOLLA, CALIFORNIA

Edited by
R.R. REEVES, W.F. PERRIN, B.L. TAYLOR, C.S. BAKER and S.L. MESNICK

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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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Report of the Workshop on Shortcomings of Cetacean Taxonomy in Relation to Needs of Conservation and Management

April 30 – May 2, 2004
La Jolla, California

Edited by R. R. Reeves, W. F. Perrin, B. L. Taylor, C. S. Baker and S. L. Mesnick

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1. PRELIMINARIES

The Workshop took place at the Southwest Fisheries Science Center and the Scripps Institution of Oceanography, La Jolla, California, from April 30 to May 2, 2004, following a two-day open symposium, "Cetacean Systematics: Approaches in Genetics, Morphology, and Behavior." Participation in the workshop was by invitation and included 48 participants from 6 countries (Appendix 1).

The three-day workshop was convened jointly by Perrin, Taylor and Baker, with help from a steering committee that also included Brownell, Dizon, Jefferson, LeDuc, Mesnick, Morin, Reeves, and Waples, and a local organizing committee chaired by Mesnick. Taylor chaired the plenary sessions.

Understanding the structure of cetacean populations at the species, subspecies, and evolutionarily significant unit (ESU) levels is pivotal to conservation at global and regional levels. For example, consideration of whether to add the "southern resident" killer whales of the eastern North Pacific to the U.S. Endangered Species List hinged on poorly understood evolutionary relationships between this population and killer whales globally (LJ/04/KW10). In the absence of a fundamental understanding and agreement on the number of species and subspecies of killer whales, consensus could not be reached on whether this whale population was significant to the taxon to which it belongs. That example raises a series of questions: What data are sufficient or necessary to define species and subspecies? Must taxonomic decisions be based on skull morphology, or are genetic differences sufficient? If genetic data are sufficient, what standards apply for the different levels of differentiation? If morphology is required, how can one overcome the frequent difficulty of gaining access to adequate samples of mature specimens?

A related problem is that of identifying market samples (e.g., whale meat) or stranded cetaceans. Being able to identify such specimens can lead to important conservation benefits, sometimes exposing problems related to bycatch or directed catch. At a minimum, researchers should be able to assign an uncertain specimen to a species, if not (ideally) to a subspecies or regional population. The development of an agreed molecular species taxonomy is a feasible and necessary first step. A validated ("ground-truthed") database at the species level would form the basis for future development below the species level, eventually permitting assignment of specimens to their geographical origins.

The main purpose of the conference (including symposium and workshop) was to address those and related questions by bringing together experts from the fields of morphological, behavioral, and molecular systematics and related fields. The workshop itself was organized around specific tasks and proposals.

1.1 Adoption of draft agenda

The agreed agenda is given in Appendix 2.

1.2 Appointment of rapporteur

Reeves was appointed rapporteur for the plenary sessions. The working group reports were drafted and edited by the respective chairs and rapporteurs. The plenary report was drafted by Reeves and Perrin after the workshop, and the entire draft report (including the plenary report and all three working group reports as appendices) was circulated for review to all participants before being judged final.

1.3 Available documents

Background documents prepared for the workshop are listed in Appendix 3. In addition, participants had the benefit of the presented papers and posters from the symposium immediately preceding the workshop (listed in Appendix 4).

2. WORKING GROUP REPORTS AND DISCUSSION

2.1 Working Group on Species- and Subspecies-level Taxonomy

2.1.1 Report

Perrin summarized the working group report (Appendix 5). Briefly, the report includes the following:

1) Examples of how taxonomy is important to conservation, e.g., in relation to the management of cetacean exploitation and international trade, in evaluating calls for the culling of cetacean populations, and in setting conservation priorities.
2) A review of the shortcomings of current cetacean taxonomy in terms of management needs, e.g., its piecemeal and intrinsically conservative nature; the great difficulty of assembling and gaining access to large, representative samples for comparative morphological analyses; the lack of consensus on standards for designating species and subspecies; the shortage of bonafide taxonomists; the fact that for most cetaceans, we do not have enough morphological data to meet an evidentiary standard for establishing (or rejecting) additional species; and the traditional tendency to err in the direction of avoiding designating too many taxa rather than making sure that all potentially recognized taxa have been designated.
3) An overview of the recognized species and subspecies, and a brief review of those known or suspected to have associated taxonomy- and/or conservation-related issues (see agenda item 5, below).
4) Extensive discussions of species and subspecies concepts, with proposed guidelines for delimitation at these two taxonomic levels (see agenda items 3 and 4, below).
5) Elaboration of a scheme for ranking cetacean species and subspecies in order of priority of need for taxonomic research, according to a combination of taxonomic uncertainty and conservation risk (see agenda item 5, below).
6) Recommendations for addressing logistical and other constraints on progress in cetacean taxonomy, e.g., in relation to cataloguing of material, collection and storage of specimens, access to and study of specimen material, laboratory techniques and analysis, and development of additional genetic resources.

2.1.2 Points of clarification

Portions of the plenary discussion are incorporated under the appropriate substantive items elsewhere in this report (especially see agenda items 3 and 4, below).

In developing its species guidelines, the working group had effectively rejected all formal species concepts that do not require at least two independent lines of evidence. The agreed guidelines were noncommittal in regard to specific types of evidence required for species delimitation. No type of evidence was seen as essential, nor were any completely dismissed as irrelevant. However, some kinds of evidence were considered secondary and not suitable as primary support for species-level decisions, e.g., behavioral and distributional data. In cases of conflicting evidence, e.g., where morphology and genetics point in different directions, or where a difference is present at mtDNA loci but not at nuclear loci, an argument for species status would be rejected pending additional evidence for adjudication.

The working group was prepared to accept as a practical, unavoidable reality that different standards for species delimitation are being, and will continue to be, applied to different taxonomic groups (e.g., birds vs. cetaceans vs. other mammals).

Palsbøll queried whether it might be necessary to appoint an individual or a team to advance the working group's recommendation for a complete genome sequence for a cetacean (Appendix 5, Section 7, Item 11). He noted that the University of California is part of the Joint Genome Facility in Walnut Creek and that this facility would be quite open to such a project. Baker pointed out that previous offers by the National Institutes of Health to develop genome sequences for the humpback whale and the bottlenose dolphin had been rejected, with the explanation that these species "evolve too slowly."

2.2 Working Group on Killer Whales as a Case Study

2.2.1 Report

Waples summarized the working group report (Appendix 6). The working group contained a diversity of opinions concerning killer whale taxonomy, and these are clearly set forth in the group's report (Appendix 6). An overall conclusion was that, globally, killer whales exhibit relatively shallow divergence at mtDNA loci, and the fossil record has been interpreted to signify a 5 million year history of a monotypic lineage. Although Hoelzel interpreted the global genetic data to be consistent with a population bottleneck a few hundred thousand years ago, many biologists familiar with killer whales find the idea of a global-scale bottleneck difficult to envisage.

Killer whales worldwide do not appear to be distinguishable along ecotype differences defined from research in the eastern North Pacific (ENP) (i.e., "residents," "transients," and "offshores," with their respective foraging specializations). It therefore seems that at least some of their typical traits have evolved multiple times.

Differences in point of view are rooted partly on how much emphasis an individual investigator puts on learned ("cultural") characteristics such as social structure and acoustics. Some participants regard such features as too ephemeral to have value in taxonomy, regardless of their importance to conservation and management decision-making, Other participants consider these characteristics to be associated with reproductive isolation and therefore taxonomically relevant.

The working group had the benefit of "strawman" proposals prepared in advance by different teams of investigators, one arguing for a single species and the other for multiple species. The arguments are laid out in Appendix 6. A straw poll within the working group indicated little support for the premise that one or more new species could be described on present evidence. Nevertheless, a majority of participants expressed the opinion that more than one species of killer whale exists and may eventually be described and named.

Strong agreement existed within the working group that Soviet data and analyses proposing multiple killer whale species in the Antarctic were only suggestive and not convincing by themselves. Additional data need to be collected in a rigorous fashion and subjected to modern quantitative analysis. Nuclear genetic evidence may prove informative in this process.

In the North Pacific, the split between "resident" and "transient" whales is supported by a number of lines of evidence, and some investigators are comfortable with concluding that the two ecotypes are separate species. However, establishment of the species boundaries quickly becomes a major sticking point. Among other things, it is unclear how to resolve the relationships between the Antarctic ecotypes and the northeastern Pacific ecotypes.

The working group made little progress on the question of killer whale subspecies. Those who thought that more than one species exists also felt that, until the species question can be resolved, it would be appropriate to recognize a series of subspecies to reflect clear differences among types of killer whales. Overall, a majority of participants felt that Resident- and Transient-type killer whales in the ENP probably merit at least subspecies status, although questions of how to delineate sympatric subspecies would remain (see agenda item Subspecies below).

2.2.2 Points of clarification

In response to a question from Baker as to how the strength of a particular line of evidence (e.g., microsatellites) might be assessed (e.g., as high vs. low, or enough vs. not enough), Waples stated that no specific cut-off was identified (e.g., for F_{ST} values). Microsatellite results are sometimes expressed as number of migrants per generation. Hey cautioned against citing specific programs (e.g., MIGRATE) as results for defining degrees of strength for genetic evidence.

Berta queried the working group's basis for estimating 5 million years ago as the divergence time for killer whales. This information had been provided by Heyning, who confirmed the existence of a 5 million year old fossil, clearly identified as belonging to *Orcinus*.

2.3 Working Group on Achieving a Validated Molecular Taxonomy and Global Phylogeography of the Cetaceans

2.3.1 Report

The report of this working group was not available in draft form for review by participants until midday on 2 May, and therefore it did not get the same degree of scrutiny as did the other two working group reports. Baker briefly summarized the report (Appendix 7).

Most of the group's time was spent considering the representativeness of data and discussing issues of provenance and validation. Due to time constraints, the concept of a "molecular taxonomy," how it has been applied to cetaceans, and how it relates to phylogeography were addressed only superficially, although greater detail was provided in background papers by Baker et al. (LJ/04/phylo2, summarized in Attachment 3 to Appendix 7) and Dalebout (LJ/04/Phylo3).

2.3.2 Points of clarification

A number of points were made in the truncated plenary discussion of the working group report. A statement of one view of how species should be delineated was given by Sherwin (see below under agenda item 6.1).

3. SPECIES

3.1 Species concepts

This item was considered in depth by the working group on species- and subspecies-level taxonomy, and only limited discussion occurred in the plenary. Rather than reiterating the summary here, readers are directed to the appropriate section of the working group report (Appendix 5, Section 5.2.1).

The workshop acknowledged that both major species concepts – the Biological Species Concept (BSC) and the Phylogenetic Species Concept (PSC), as well as their various sub-approaches – have merit and should be considered relevant and useful in cetacean taxonomy. It was agreed that the different approaches to species delimitation should be employed in a flexible and pragmatic way, with the basic aim of using proxies to identify irreversible divergence. Multiple lines of evidence are essential, and what ultimately matters is that a convincing argument is provided demonstrating irreversible divergence.

As indicated above (Item 2.1.2), the processes of developing and selecting criteria for species delimitation are likely to remain in flux, both through time and across taxa. For example, according to M. Ford, fish systematists remain largely devoted to the BSC, but they are increasingly giving attention to the PSC as well. Although some groups of experts (e.g., the British Ornithological Union *in* Helbig et al. 2002) have prescribed protocols, the balance of opinion at this workshop was toward a less prescriptive and more advisory approach. Hey pointed out that the guidelines developed here could prove influential, as few, if any, similar expert groups have been so forthcoming about the underlying uncertainty of species delimitation or about the hypothetical nature of the species concept.

Baker noted that when Cracraft (1983, 1989) first articulated the PSC, there was an expectation that a great deal of revision in taxonomy was about to take place. He (Baker) queried whether the guidelines adopted at this workshop did or did not signal that cetacean systematists were prepared to countenance extensive changes to the traditional taxonomy. Perrin's answer was that the workshop was stepping back from a prescriptive approach and therefore that wholesale change was unlikely. Proposed changes in cetacean taxonomy will continue to depend upon peer acceptance or rejection, within an essentially informal framework.

3.2 Criteria

The guidelines developed by the Taxonomy working group (Appendix 4, Section 5.2.1) were generally accepted, and they are repeated here, with a few revisions or additions based on the plenary discussion.

Both morphological data and genetic data can be taken as proxies for reproductive isolation and irreversible divergence. It is possible, however, for individual morphological characters to be convergent, and for the data from one genetic locus to not reflect phylogenetic history because of homoplasy or natural selection. Therefore, a finding of congruent divergence for each of multiple distinct kinds of data should be taken as strong support for species designations. Such distinct kinds of data could include morphological data together with genetic data, or data from multiple independent genetic loci. In the case of morphological data, any phenotypic character is acceptable. Ideal data sets, including both morphological data and data from multiple loci, can provide not only a large amount of information for decisions regarding species, but also the information necessary to assess the uncertainty associated with that decision.

Data on geographical ranges and on behavior (e.g., feeding behavior and vocalizations) can complement morphological and genetic data and serve as useful lines of evidence in species delimitation. Given the difficulties of knowing the degree to which geographical distribution and behavior actually reflect genetic divergence, however, these kinds of data should not be the primary basis of such delimitations.

The workshop participants emphasized that taxa, including species, are best viewed as hypotheses about evolutionary history rather than as rigidly fixed or sacrosanct entities. Thus, species are subject to revision as new data or new analytical techniques become available. Individual taxa are necessarily associated with support from the data and evolutionary theory that were used to define them. In this light, we appreciate that species designations have some uncertainty and may be subject to revision as more data become available.

3.3 Case study: killer whales

The intent under this item was to consider whether the agreed species delimitation guidelines would change anything for killer whales. According to LeDuc, who spoke for the multiple-species side in the debate, the main effect is to reinforce the need for more data because of the emphasis on requiring multiple lines of evidence. In his view, the molecular evidence for splitting northeastern Pacific whales is solid, but the morphological and ecological evidence needs strengthening. Although the morphological and ecological evidence for multiple species in the Antarctic is even stronger overall, the picture there is still incomplete.

According to Hoelzel, who represented the single-species position, both the mtDNA and nuclear DNA evidence from the North Pacific is equivocal and hard to interpret (see Appendix 7).

There was extensive discussion as to whether the North Pacific evidence from mitochondrial and nuclear markers was discordant, and no agreement could be reached in the time available. The discussion led, however, to a broader consideration of whether nuclear markers were useful for helping to resolve species delimitation issues. A statement on this subject was prepared jointly by Sherwin, Lavery, Baker, and Krüetzen under the leadership of Morin, as follows: Development and application of nuclear markers has been accepted as an important direction for further phylogenetic analysis. Choice of markers will be predicated on a variety of issues, including rate and mode of evolution, reproducibility, orthology, technical considerations, and cost. For example, there is general agreement in the literature that microsatellites are most appropriate for genetic studies below the species level, because of increasing complications of variable mutation rates and increasing homoplasy with evolutionary time.

In order to pursue such issues further, Morin offered to convene a nuclear markers working group (see 7.1, below).

Another issue that arose in discussion concerned data deficiencies in regard to the global extent of sampling for killer whales. The question of whether regional sampling of killer whales has been adequate for a global understanding of their taxonomy can only be addressed if the distribution and size of samples are clearly depicted. Although a compilation of all skeletal material available in museums between California and Alaska is available, the need remains for a comprehensive, global inventory of (a) where specimens (including biopsies and bones) have been obtained, and (b) where those tissues and bones are presently housed (see 7.5, below).

4. SUBSPECIES

4.1 Subspecies concepts

The subspecies has been and remains a difficult concept (see, in particular, Appendix 5, Section 5.2.2). Scientific opinion varies concerning the utility of designating subspecies. Some scientists insist that no compelling justification has been offered as to why subspecies are important, while others regard subspecies as meaningful in terms of both biology and conservation (see Appendix 5, Section 2).

Several participants stressed that taxonomic practice should not be changed simply to accommodate perceived political needs. All participants agreed, however, that using conservation concerns as a basis for focusing taxonomic effort and resources, e.g., on taxa considered endangered or threatened, was a legitimate endeavor. The idea is to make sure that priority attention is given to taxonomic issues that matter for conservation.

It was noted that some definitions of subspecies, specifically those that cite as a criterion the need for a population to be on an independent evolutionary trajectory, are little different from that of an evolutionarily significant unit (ESU). Waples pointed out that the lineages of separate ESUs are largely independent although some low-level genetic exchange can occur. In his view, a subspecies lies somewhere in between a species and an ESU.

Perrin stressed that a critical distinction between species and subspecies involves the question of reticulation, or reversibility. In the case of a subspecies, it may not be possible to demonstrate that the population is on an independent evolutionary trajectory with no reticulation, while such demonstration is a requirement for species status. Because subspecies (and ESUs) are on a continuum, it should be no surprise that distinctions are often problematic and require judgments by the investigator as to the strength of a given factor or suite of factors. Thus, the subspecies concept may be construed as broad enough to contain two types of entities: (a) populations that are not quite far enough along the continuum to be judged as species, and (b) populations that should be species but for which not quite enough evidence is yet available to justify their designation as such.

Thus far, cetacean subspecies have been geographical forms that are noticeably different. Therefore, designations have been based on a combination of morphology and distribution. In the context of this workshop, attention was drawn to the potential for bringing genetic evidence, including neutral markers, into the subspecies definition. It was suggested that for many cetacean species, the difficulty of bringing together, over a reasonable timescale, the large, representative series of osteological specimens needed for definitive morphological comparisons is effectively insurmountable. This is true, for example, for many of the elusive, offshore beaked whale species, the wide-ranging killer whales, and all of the large whales. Thus, for taxonomy at the subspecies level to be relevant for conservation, the range of evidence that can be used needs to be broadened to include genetic markers.

4.2 Criteria

The guidelines developed by the working group on species- and subspecies-level taxonomy (Appendix 5, Section 5.2.2) were generally accepted. Concerns were expressed, however, about the non-specificity in the guidelines as to what kinds of genetic evidence could be used as the basis for a subspecies. For example, there is some danger that dependence upon mtDNA alone could make female philopatry the sole basis for distinguishing subspecies, a practice that could lead to rampant splitting below the species level. It was agreed that reference to "*appropriate* genetic evidence " would adequately capture this concern and preclude misapplication. Thus the following guidelines for subspecies were adopted (from Appendix 5):

In addition to the use of morphology to define subspecies, the subspecies concept should be understood to embrace groups of organisms that appear to have been on independent evolutionary trajectories (with minor continuing gene flow), as demonstrated by morphological evidence or at least one line of appropriate genetic evidence. Geographical or behavioral differences can complement morphological and genetic evidence for establishing subspecies. As such, subspecies could be geographical forms or incipient species.

It was recognized that applying these standards could result in cases where subspecific status is given to entities that may later prove to be species, as has often happened in the past.

Further, the workshop wished to reiterate the importance of peer review and peer opinion in judging the validity of published subspecies designations. As noted in Appendix 5, criteria for delimiting subspecies can be chosen arbitrarily, and different workers might choose different levels of diagnosability or gene flow. Therefore, the onus is on individual investigators to explain their choice of criteria and make their case for designation accordingly. Scientific peer-review, publication procedures, and peer opinion after publication can be expected to help ensure the integrity, credibility, and legitimacy of the subspecies designation process. This explanation applies with equal force to the species designation process: peers are either convinced by an argument or they are not.

4.3 Unnamed subspecies

Designation of unnamed subspecies can provide a mechanism for allowing the recognition of a highly differentiated form without having to wait until its nomenclature is settled. Several examples exist, notably the dwarf minke whale (listed by Rice [1998] as *Balaenoptera acutorostrata* subsp.) and the Kerguelen Island form of Commerson's dolphin (listed by Rice as *Cephalorhynchus commersonii* subsp.). Resorting to this type of designation can reflect either nomenclatural difficulty (e.g., a need to resolve holotype identity as in the case of the "Bryde's whale" in the Calcutta Museum; see Appendices 5 and 7) or the fact that no individual scientist has yet taken the time to prepare and publish a formal description.

4.4 Case study: killer whales

A number of issues arose during the discussion of whether the above guidelines would be useful for designating killer whale subspecies. The guidelines do not make allopatry or parapatry a requirement for distinguishing subspecies. Therefore, the workshop participants agreed that the "resident" and "transient" killer whales in Washington/British Columbia, which are at least partially sympatric by any definition of the term (see Glossary), would qualify for consideration.

The "resident" (fish specialist) ecotype in the North Pacific is relatively easy to delineate spatially given its largely obligate association with salmonids. The "transient" (mammal-eating) and "offshore" (probably fish-eating) ecotypes are less easily delimited because transients, at least, are known to extend fairly far south and possibly offshore and the distribution of "offshores" is highly uncertain. The two ice-inhabiting forms in the Antarctic could be lumped into a single subspecies with a clear ecological/behavioral distinction between them and the open-water third form. It is unclear, however, whether a strong case could be made for splitting the ice forms into separate subspecies, given the limited amount and uncertain provenance of some of the data on their ecological differences. The strongest single line of evidence distinguishing them from each other is the size and configuration of the eye patch.

There was a brief discussion as to whether a holotype is needed to define a subspecies. Dalebout pointed out that a shrike species in Somalia had been described solely on the basis of a photograph and DNA sequences from feather pulp (Smith et al. 1991). Numerous named holotypes of killer whales are available (LJ/04/KW3) and it would be preferable, but not essential, for the nomenclature to be resolved from the outset (see discussion above of unnamed subspecies).

Hoelzel summarized his views concerning killer whale subspecies, as follows: In the North Pacific, the clearest distinction is behavioral (foraging specialization). With respect to morphology, although experienced observers can tell the ecotypes apart, diagnosability is not particularly well quantified. Differences in mtDNA between "residents" and "transients" are fixed within the populations, and nuclear data show only shallow degrees of divergence. Even though a full genetic profile of Antarctic killer whales is not yet available, the morphological differences there are strongly suggestive (albeit not well quantified), and subspecies designation could be appropriate.

It was noted that a blind study is underway (led by Wade) where multiple examiners attempt to distinguish "residents" and "transients" from photographs, with no prior knowledge of genotypes. The purpose is to provide a quantitative evaluation of external morphological difference between the two ecotypes.

5. REVIEW OF NEEDS FOR TAXONOMIC ATTENTION

This subject was addressed in detail by both the working group on species- and subspecies-level taxonomy (Appendix 5) and the working group on molecular taxonomy (Appendix 7), and their conclusions were largely consistent. Appendix 5 contains a review of the taxonomy of species or species groups about which there is ongoing disagreement, for which subspecies are recognized, or that present issues of particular conservation concern (Section 4 of Appendix 5). It also contains an explanation of how priorities were assigned, taking account of both taxonomic uncertainty and conservation risk (Section 6 and Appendix Table 5-1). Appendix 7 contains a summary of current data deficiencies (what is known vs. what is needed) in cetacean molecular taxonomy (main text as well as Attachment 4 of Appendix 7) that should be read in combination with the relevant sections of Appendix 5 as they are complementary.

Following a brief plenary discussion, it was agreed that the table drafted by the working group on species- and subspecies-level taxonomy encapsulating their collective views on species priorities should be adopted by the workshop as a whole (Table 1). Most of the substantive points raised in the plenary discussion were incorporated as additions or corrections to relevant portions of the text of the working group report; therefore they are not repeated here (see Appendix 5). Nonetheless, it is important to recognize that it would have been impossible, in the time available, to reach complete agreement on every point. Apart from the intrinsic complexity and difficulty of boiling down the collective opinions of so many individuals with varied expertise into a high-medium-low hierarchy, it must be acknowledged that composition of the workshop itself will have had a considerable influence on how priorities were assigned. A different mix of experts might have produced a different set of rankings.

5.1 First priority

The following specific issues stand out as needing particular attention. For additional details, see Appendix 5 (Section 6):

- With Norway continuing to hunt North Atlantic minke whales on the basis of a formal objection under IWC rules, and Japan taking hundreds of minke whales in the Antarctic and minke, Bryde's, sei, and sperm whales in the North Pacific each year under national permits for scientific research, three areas of taxonomic research on baleen whales need immediate clarification. One is resolution of the *borealis-edeni-brydei-omurai* complex. A second is the question of appropriate designations for North Atlantic and North Pacific minke whales, and in particular J-stock minke whales. Resolution of these questions would have direct and immediate relevance to management under the IWC and CITES. The third area relates to the blue whale. Although blue whales are no longer exploited, they were drastically depleted by commercial whaling during the 20th century. The current status of populations, both in terms of taxonomy at the subspecies level and of abundance and trends, is uncertain. Blue whales in the northern Indian Ocean are of particular concern; they appear not to migrate to the Antarctic in summer.
- Longstanding difficulties of determining the taxonomic status of inshore and offshore populations of bottlenose dolphins (often within ocean basins or seas and including *Tursiops truncatus* and *T. aduncus*) need to be resolved so that the deliberate, incidental, and mixed-intent "fisheries" for these animals (e.g., in western South America, southern Asia, and east Asia) can be assessed more rigorously and managed more responsibly. The importance of bottlenose dolphins in the live-capture industry creates a special need for taxonomic clarity, given the involvement of CITES in regulating trade and national agencies in stock assessment. Ultimate resolution of bottlenose dolphin taxonomy will require congeneric analyses (Funk and Omland 2003).
- The bottlenose dolphins are part of a wider taxonomic problem that involves the entire Delphininae/Stenoninae complex. Although external morphology makes field identification of these genera and most of the species within them relatively straightforward, paraphyly of their mtDNA lineages creates serious difficulties with genotypic resolution and forensic identification of specimens. Therefore, congeneric analyses (i.e. analyses that consider the full range of diversity within and across the species in this complex) are required to clarify this group's taxonomy. Many populations of these dolphin species/genera are either heavily exploited, subject to large-scale bycatch, or both.
- The taxonomic status of humpback dolphins (*Sousa* spp.) in the Indo-Pacific needs to be clarified (LJ/04/Taxo3). These animals are particularly vulnerable because of their near-shore distribution, tendency to occur primarily in or near estuaries, and apparently low numbers. Their discontinuous occurrence and morphological variability across the range from East Africa to southern China and eastern Australia strongly suggest that multiple taxa should be recognized.
- Like humpback dolphins, Irrawaddy dolphins (*Orcaella brevirostris* sensu lato) are neritic and occur discontinuously in brackish estuaries and near-shore marine waters of northern Oceania and parts of Southeast Asia, but they also occur far up some rivers and in certain lake or lagoon systems. Sev-

eral populations are classified as Critically Endangered by the IUCN as a result of incidental mortality in fisheries and various forms of habitat loss or degradation. In addition to a forthcoming proposed new species-level distinction within this genus, it is important to establish whether subspecies- and additional species-level differences exist (LJ/04/Taxo3).

- Taxonomy of the genera *Neophocaena* and *Platanista*, both of which are currently considered monotypic, needs to be addressed with a sense of urgency. Both genera may include two (or more) species, and at least some of these (putative) species occur in only one or a few countries (LJ/04/Taxo3). Their extremely coastal or riverine distribution and vulnerability to gillnet entanglement, exposure to toxins, and other potential threats mean that improved clarity with regard to systematics would have important implications for conservation and management.
- Two South American genera have long been in need of taxonomic revision. The obligate freshwater genus *Inia* contains three geographically distinct groups of dolphins that are regarded as either: (a) a single species with three subspecies, (b) two species, one of which consists of two subspecies, or (c) three separate species. Given the rapid deterioration of riverine habitat as a result of competing demands from humans, it is important to clarify the taxonomy of the *Inia* dolphins while they are still relatively abundant. The riverine form of *Sotalia* is sympatric with *Inia* throughout most of the Amazon and at least part of the Orinoco system. The species-level distinction between the two ecotypes of this small dolphin – riverine and marine coastal – is important to resolve while these animals are still relatively abundant (LJ/04/Taxo3). Large-scale gillnet mortality of *Sotalia* occurs in many areas.
- Although long considered safe from the effects of human activities, the pelagic, deep-diving beaked whales (Ziphiidae) are now known to be vulnerable to underwater noise (e.g., military sonar, geophysical seismic profiling) and entanglement in drift gillnets. Two widely distributed species (*Ziphius cavirostris* and *Mesoplodon densirostris*) and one North Pacific endemic (*Mesoplodon stejnegeri*) were identified by workshop paricipants as warranting special attention to resolve taxonomic uncertainty.
- Finally, as explained in previous sections of this report, the killer whales (genus *Orca*) have become a high priority for conservation management, and taxonomic clarification is a major need on the part of management agencies .

5.2 Second priority

No attempt was made to elaborate on this topic, which refers primarily to species and subspecies assigned a 2 (Medium) ranking in Appendix Table 7-1.

6. REVIEW OF VALIDATED DNA DATABASE

This topic was not addressed substantively in the plenary due to lack of time. The participants agreed that Appendix 7 adequately covered the ground and endorsed the conclusions reached there.

6.1 Species and subspecies level

Sherwin offered the following statement for inclusion in the report: Methods of species diagnosis could be judged by their level of α- and β- errors when analyzing specimens of known species. The absolute and relative error rates may depend upon multiple factors, such as the number of characters or taxa. Therefore, the performance of different methods would be re-evaluated at regular intervals as the database grows and changes.

6.2 Phylogeography of selected species complexes

Readers are referred to Appendix 7.

6.3 Virtual curation

Readers are referred to Appendix 7. Also see agenda item **7.6** below.

7. RECOMMENDATIONS

7.1 Species concepts and guidelines

The workshop **recommended** that the guidelines presented under Item 3.2 of this report be disseminated widely, promoted, and adhered to in cetacean taxonomy.

At present, there is not an accepted and clear choice of nuclear markers that should be used for taxonomic delimitation, but the advantage of using standardization among studies is recognized. The workshop therefore **recommended** the creation of a working group to evaluate nuclear genetic marker characteristics and applications, and to share information and resources that will facilitate standardized application of nuclear genetic markers for cetacean population genetics and taxonomy. Morin offered to take the lead in setting up and initiating such a group

7.2 Subspecies concepts and guidelines

The workshop likewise **recommended** that the guidelines presented under Item 4.2 of this report be disseminated widely, promoted, and adhered to in cetacean taxonomy.

7.3 Priority data for taxonomic attention

The workshop **recommended** that the rankings assigned in Table 1 (and discussed under Item 5, above) be regarded as guidelines for ordering taxonomic research in relation to conservation.

The workshop also **recommended** that special consideration should be given to taxonomic research in areas judged to be centers of endemism for cetaceans or where boundaries across groups of cetaceans are known (or suspected) to occur (see Appendix 5, Section 6).

7.4 Addressing logistical barriers

The lengthy series of recommendations prepared by the working group on species- and subspecies-level taxonomy (Appendix 5, Section 7) was agreed by the workshop participants and is included here. Note that some have relevance to issues other than “logistical barriers.”

Cataloguing of material

1. More of the world’s cetacean collections in museums and other institutions should be catalogued and made accessible through the internet. This effort is already underway by many major museums, but the contents of some smaller collections remain relatively unknown as to their content. To facilitate access and comparisons, catalogues should ultimately be linked and managed through a single centralized location. The information catalogued for each specimen should be standardized with the following minimum data: collection locality and date, age/sex class, material collected (including soft tissue samples), and total length. The inclusion of photographs of external appearance and skull morphology with records available online wherever possible is strongly encouraged. Existing comprehensive lists of specimens should be updated and new compilations should be produced for additional taxa. These should also be available on the internet. Centralized files of skull photographs, external body photographs, and sound recordings should be established. Such centralization (by individual institutions, with appropriate network links) is increasingly feasible with new digital technologies.
2. More databases and archives should be funded and developed to make tissues for genetic research, as well as genetic data for species identification purposes (e.g., GenBank), publicly available. In addition, a standardized minimum of information regarding the source specimen should be included in all Genbank records, e.g., collection location and date, full sample number designated by institution where sequence data were generated, whether a biopsy sample came from a free-swimming animal (and known individual ID# and photo) or the material was obtained from a museum specimen (including museum specimen number and full name of museum).

Collection and Storage

3. More emphasis should be placed on the collection and permanent museum preservation of adequate series of cetacean specimens as baseline material for taxonomic research. Intensified efforts should be made to obtain specimens (skulls, skeletons, biopsies) from remote regions and thus to amplify the geographic coverage of available samples, especially for species or genera of special conservation concern. Such sampling should emphasize the salvage of stranded carcasses and body parts, bycaught animals, and deceased captive individuals, supplemented with biopsies from free-ranging populations. To this end, stranding networks should be adequately supported and resulting specimens and data made available and accessible.
4. Adequate series should consist of at least 20-30 adult specimens of each species, including post-cranial material where at all possible, and accompanied by “voucher” material such as soft-tissue samples, photographs, and measurements of the whole animal. If a DNA extraction is made, a sample of that material should be curated with the specimen when feasible, or at least with clear links back to the specimen when that is not feasible. The taxonomic value of fully documented specimens is infinitely greater than piecemeal collections of unassociated material. Collection and permanent museum

preservation of adequate series of entire skeletons, including post-cranial bones, can be a special problem for the large whales, for the obvious reasons of collection and preparation logistics and space requirements. For large whales, where storage space is a problem, adequate sample sizes could be considered on an ocean-basin rather than institutional basis (equivalent to the likely scale of geographical variation).

5. Tissue samples and DNA extracts should be archived using the best long-term preservation methods available, recognizing that these will change and improve with time, as will the range of data that can be obtained from such material. At present, the types of data that can be derived from tissue samples include DNA, pollutant loads, and diet. Preservation requirements will differ depending on the type of data sought. A standardized minimum should be established – e.g., at least a skin or muscle sample preserved in ethanol or in a saturated saline solution of 20% DMSO at –20 deg C for DNA analysis. Support should be provided to improve procedures and infrastructure for the long-term preservation of DNA and soft-tissue samples. Because soft-tissue samples, even when stored in DMSO and refrigerated, may have a limited shelf life, curators should be encouraged to undertake DNA extraction and archiving as rapidly as possible after collection. Where DNA sequence data are obtained from specimens held in museums and other institutions, the specimen records should be updated in a timely fashion to indicate this, including citations of any publications using these data and Genbank accession number(s).
6. The value of tissue samples for DNA (and other) analyses, including biopsy samples collected from free-swimming animals, along with information on how to preserve such samples and where they can be sent, should be advertised more widely. This is particularly important for areas and species characterized by a high degree of taxonomic uncertainty. Specimens from which both osteological material (e.g., the skull) and a tissue sample have been collected are of greatest value for taxonomy. Next in value are specimens documented with photographs of diagnostic features (preferably including external appearance) and a tissue sample. In the event that no photographic documentation of the source animal is collected, a tissue sample (e.g., biopsy) may still be of some, though lesser, value.

Access and Study

7. More grants should be made available to allow researchers to travel to far-flung museums to examine, measure, photograph, and sample specimens. This is a special problem because of the size and rarity of many species. In some cases, researchers based in different geographical locations could establish cooperative agreements that allow, for example, two individuals to examine specimens for each other’s study, thus cutting their travel costs..
8. Longstanding obstacles to bonafide science caused by permit requirements (e.g., under the Convention on International Trade in Endangered Species [CITES] or imposed by nation-states to protect their “biological heritage”) should be addressed and, if possible, removed as they too often inhibit the sharing and free exchange of scientific specimens. Such sharing and exchange can be fundamental to resolving taxonomic problems of conservation importance. Member countries need to establish institutional permits to facilitate exchange of research specimens.

Laboratory Techniques and Analysis

9. The search for, sampling, and analysis of so-called “ancient” DNA from cetacean bone material, baleen, and other preserved tissues should be continued and expanded. Further development of techniques for extracting DNA from such materials should also be supported. It should be recognised that DNA extracted from historical (“ancient”) material such as bones and teeth may be unstable as well as degraded. Due likely to a combination of natural decomposition, build-up of bacteria and fungi, and museum preparation techniques, DNA extracted from such material may only allow successful PCR amplifications of fragments of any length for a limited window of time. The extent of this problem should be investigated, together with methods that may help overcome or at least alleviate it (e.g., additional DNA purification steps during the extraction process).
10. Analyses to address questions at the boundary between species and infraspecific enti-

ties should be congeneric, that is, they should include both a range of what are thought to be closely related species-level taxa and adequate geographic and sample-size coverage within what are thought to be species, to allow detection of incomplete lineage sorting and other types of paraphyly (Funk and Omland 2003) and to develop the resolution needed for forensic applications.

Development of Additional Genetic Resources

11. *Cell lines*. Molecular analyses are currently conducted using DNA made directly from tissue samples, which are expensive to obtain and of inherently limited amounts and longevity.

    a) Cell lines, established from tissues of living individuals, should be established from as many species as possible. Immortal cell lines provide indefinitely renewable DNA resources and thereby circumvent many of the limitations associated with tissue-based DNA preparations.

    b) Cell lines can also permit the assessment of simple molecular phenotypes, such as gene expression. Although they would not be expected to reflect exactly what is found within particular tissues of the living organism, such simple phenotypes are still useful for many purposes.

12. *Phylogenetically informative loci*. To date, cetacean molecular phylogenetic analyses have been limited largely to mitochondrial sequences. Because different loci can have different histories, ideally multiple loci should be used for phylogenetic assessment. Effort should be devoted to developing additional nuclear loci to complement the work on mitochondria. Two general categories of loci should be developed, as follows:

    a) Randomly selected neutral loci. Nonfunctional regions of the nuclear genome, such as introns of protein-coding genes, have been shown to be variable within and between closely related populations. Such loci often show evidence of incomplete lineage sorting or gene flow (e.g., in the Delphininae), but are still very useful for assessments of demographic history using population genetic models.

    b) Loci selected to have short intra-population gene trees. Like the mitochondria, some genes are expected to have shallow gene trees within populations or species. Y-chromosome genes, like the mitochondria, are expected to have shallow gene trees because of reduced effective population sizes. A separate category of such genes consists of the ribosomal RNA genes, which occur in long arrays and show little intraspecific variation because of high rates of concerted evolution. Finally, protein-coding genes, which are shown to evolve rapidly compared to other genes, may be good candidates for having short intraspecific gene trees because of recurrent selective sweeps.

    Initial effort to develop several loci of each category, for use in one species group, will be especially beneficial because once utility has been established, such loci can then be readily used by other researchers for work with other species groups.

13. *Genome sequence*. Complete, or nearly complete, genome sequences are rapidly becoming available for many mammals. Because cetaceans have evolved so rapidly at the morphological level, it is imperative that an odontocete and a mysticete be given priority for genome sequencing. Such sequences would lay the groundwork for identifying useful genes for phylogenetic and taxonomic research and would open up new areas of cetacean genetic research. Rapidly evolving structural and functional components of the genome would be revealed and could become the basis for functional and systematic evolutionary research.

7.5 Killer whales

The killer whale working group (Appendix 6) generated a list of needed future research. In addition to addressing those needs, it was proposed that the general recommendations given above (7.1-7.4) should be seen as applying to killer whales, as to other high-priority taxa.

It was **recommended** that more effort be given to sampling killer whales for fatty acid signature and stable isotope ratio analyses to illuminate differences (and similarities) in diet.

Further, the workshop specifically **recommended** that global inventories (maps) be prepared showing where killer whales have been sampled and where the materials (biopsies, bones, etc.) are currently housed.

Participants acknowledged that it was beyond the scope of this workshop to try to set up a cataloguing system for taxonomy-related data on killer whales. Nevertheless, the workshop wished to record its hope that such a system would be established, incorporating photographic data, tissue samples, sound recordings, and other relevant materials.

7.6 Instituting web-based approaches and nominating curators

As explained in Appendix 7, virtual databases of DNA sequences will be a necessary component of an improved and comprehensive molecular taxonomy for cetaceans. The workshop **recommended** that virtual species databases be encouraged, and that virtual curators (e.g., one or two people in charge of a database consisting of sequences from multiple contributors) be supported to design and construct a database that is applicable across species.

7.7 Other

Data on behavior can provide valuable supplemental evidence for species or subspecies delimitation, and can also help identify or clarify population boundaries, thereby helping to set the stage for focused morphological or genetic comparisons. The workshop therefore **recommended** that:

- Effort be increased to record cetacean vocalizations globally, and particularly in areas where data are lacking entirely or where other types of data appear to provide poor resolution of population differences. (To the extent possible, recording of vocalizations should be conducted in concert with the collection of biopsies.)
- An accessible archive of validated cetacean vocalizations, analogous to global DNA databases, be established.
- A study be conducted to elucidate aspects or components of cetacean vocalizations that contain phylogenetic or species-specific information.
- Expand efforts to collect data and samples to support studies of foraging specialization – e.g., fatty acids, stable isotopes, stomach contents, and direct observations.
- Expand efforts to collect data related to life history characteristics, such as timing of reproduction.

8. OTHER BUSINESS

A brief discussion took place concerning ways to ensure that the workshop recommendations are implemented. It was agreed that, in addition to being submitted to sponsoring agencies, the report would be made available as part of the Southwest Fisheries Science Center's internal technical memorandum series, thus making it generally available on-line. It was anticipated that no special effort would be needed to promote the workshop findings, beyond making them available in the normal manner.

9. ADJOURNMENT

The workshop completed its agenda and adjourned at 1730 hrs on 2 May 2004. Participants expressed their special appreciation to Mesnick and the many individuals from Scripps and the Southwest Fisheries Science Center who invested considerable time and effort.

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Table 1. Cetacean species and subspecies, with priority rankings for taxonomic research: 1 = high, 2 = medium, and 3 = low priority (see text and Appendix Table 5-1). Subspecies mainly from Rice (1998).

Species (Common Name) – Rank (1 High, 2 Medium, 3 Low)	**Species (Latin name)**	**Risk/Taxonomic Uncertainty**	**Subspecies (Common Name)**
Bowhead Whale – 3	*Balaena mysticetus*	(H,L)	
North Atlantic Right Whale – 3	*Eubalaena glacialis*	(H,L)	
North Pacific Right Whale –3	*Eubalaena japonica*	(H,L)	
Southern Right Whale – 3	*Eubalaena australis*	(M,L)	
Pygmy Right Whale – 3	*Caperea marginata*	(L,M)	
Gray Whale – 3	*Eschrichtius robustus*	(H,L)	
Blue Whale – 1	*Balaenoptera musculus*	(M,H)	
	2	(M,M)	Common Blue
	2	(M,M)	Pygmy Blue Whale
	1	(M,H)	Northern Indian Ocean Blue Whale
	2	(M,M)	Antarctic Blue Whale
Fin Whale	*Balaenoptera physalus*		
	3	(L,M)	Northern Hemisphere Fin Whale
	2	(M,M)	Southern Hemisphere Fin Whale
Sei Whale	*Balaenoptera borealis*		
	2	(M,M)	Northern Hemisphere Sei Whale
	2	(M,M)	Southern Hemisphere Sei Whale
Common Bryde's Whale – 1	*Balaenoptera brydei*	(M,H)	
Pygmy Bryde's Whale – 1	*Balaenoptera edeni/omurai?*	(H,H)	
Common Minke Whale – 1 or 2	*Balaenoptera acutorostrata*		
	3	(M,L)	North Atlantic Minke Whale
	1	(M,H)	North Pacific Minke Whale
	2	(M,M)	Dwarf-form Minke Whale
Antarctic Minke Whale – 3	*Balaenoptera bonaerensis*	(L,L)	
Humpback Whale – 2	*Megaptera novaeangliae*	(M,M)	
Sperm Whale – 3	*Physeter macrocephalus*	(L,L)	
Pygmy Sperm Whale – 3	*Kogia breviceps*	(L,M)	
Dwarf Sperm Whale – 3	*Kogia sima*	(L,H)	
Amazon River Dolphin (Boto) – 1 or 2	*Inia geoffrensis*		
	2	(M,M)	Amazon Dolphin
	1	(H,M)	Orinoco Dolphin
	1	(H,M)	Bolivian Dolphin
Gangetic Dolphin (Susu) – 1	*Platanista gangetica*		
		(H,H)	Ganges Dolphin
		(H,H)	Indus Dolphin
Franciscana – 2	*Pontoporia blainvillei*	(M,M)	
Yangtze River Dolphin (Baiji) – 3	*Lipotes vexillifer*	(L,H)	
Baird's Beaked Whale – 2	*Berardius bairdii*	(M,M)	
Arnoux's Beaked Whale – 3	*Berardius arnuxii*	(L,L)	
Northern Bottlenose Whale – 2	*Hyperoodon ampullatus*	(M,M)	
Southern Bottlenose Whale – 3	*Hyperoodon planifrons*	(L,M)	
Indo-Pacific Beaked Whale – 3	*Indopacetus pacificus*	(L,L)	
Shepherd's Beaked Whale – 3	*Tasmacetus shepherdi*	(L,L)	

Cuvier's Beaked Whale – 1	*Ziphius cavirostris*	(H,M)	
Hector's Beaked Whale – 3	*Mesoplodon hectori*	(L,L)	
True's Beaked Whale – 3	*Mesoplodon mirus*	(L,M)	
Gervais' Beaked Whale – 3	*Mesoplodon europaeus*	(L,M)	
Sowerby's Beaked Whale – 3	*Mesoplodon bidens*	(L,L)	
Gray's Beaked Whale – 3	*Mesoplodon grayi*	(L,L)	
Pygmy Beaked Whale – 3	*Mesoplodon peruvianus*	(M,L)	
Andrews' Beaked Whale – 3	*Mesoplodon bowdoini*	(L,L)	
Spade-toothed Whale – 3	*Mesoplodon traversii*	(L,L)	
Hubbs' Beaked Whale – 2	*Mesoplodon carlhubbsi*	(M,M)	
Ginkgo-toothed Beaked Whale – 3	*Mesoplodon ginkgodens*	(L,M)	
Stejneger's Beaked Whale – 1	*Mesoplodon stejnegeri*	(H,M)	
Layard's Beaked (Strap-toothed) Whale – 3	*Mesoplodon layardii*	(L,L)	
Perrin's Beaked Whale – 3	*Mesoplodon perrini*	(L,L)	
Blainville's Beaked Whale – 1	*Mesoplodon densirostris*	(H,M)	
Narwhal – 2	*Monodon monoceros*	(M,M)	
Beluga or White Whale – 3	*Delphinapterus leucas*	(M,L)	
Finless Porpoise – 1	*Neophocaena phocaenoides*	(H,H)	
		(H,H)	Indian Ocean Finless Porpoise
		(H,H)	Western Pacific Finless Porpoise
		(H,H)	Yangtze River Finless Porpoise
Harbor Porpoise	*Phocoena phocoena*		
	2	(M,M)	Black Sea Harbor Porpoise
	2	(M,M)	North Atlantic Harbor Porpoise
	2	(M,M)	Eastern North Pacific Harbor Porpoise
	2	(M,M)	Western North Pacific Harbor Porpoise
Spectacled Porpoise – 2	*Phocoena dioptrica*	(M,M)	
Vaquita – 3	*Phocoena sinus*	(H,L)	
Burmeister's Porpoise – 2	*Phocoena spinipinnis*	(M,M)	
Dall's Porpoise – 2	*Phocoenoides dalli*	(M,M)	
Commerson's Dolphin – 2	*Cephalorhynchus commersonii*		
	2	(M,M)	South American Commerson's Dolphin
	3	(L,M)	Kerguelen Commerson's Dolphin
Chilean Dolphin – 3	*Cephalorhynchus eutropia*	(M,L)	
Haviside's Dolphin – 3	*Cephalorhynchus heavisidii*	(M,L)	
Hector's Dolphin – 3	*Cephalorhynchus hectori*		
		(M,L)	South Island Hector's Dolphin
		(H,L)	North Island Hector's (Maui's) Dolphin
Short-beaked Common Dolphin – 2	*Delphinus delphis*	(M,M)	
Long-beaked Common Dolphin – 2	*Delphinus capensis*		
		(M,M)	Indo-Pacific Common Dolphin
		(M,M)	Long-beaked Common Dolphin
Pygmy Killer Whale – 3	*Feresa attenuate*	(L,M)	
Short-finned Pilot Whale – 2	*Globicephala macrorhynchus*	(M,M)	
Long-finned Pilot Whale – 3	*Globicephala melas*	(L,M)	

		(L,L)	North Atlantic Long-finned Pilot Whale
		(L,M)	Southern Hemisphere Long-finned Pilot Whale
Risso's Dolphin – 2	*Grampus griseus*	(M,M)	
Fraser's Dolphin – 2	*Lagenodelphis hosei*	(M,M)	
Atlantic White-sided Dolphin – 3	*Lagenorhynchus acutus*	(L,L)	
White-beaked Dolphin – 3	*Lagenorhynchus albirostris*	(L,L)	
Peale's Dolphin – 3	*Lagenorhynchus australis*	(L,L)	
Hourglass Dolphin – 3	*Lagenorhynchus cruciger*	(L,M)	
Pacific White-sided Dolphin – 2	*Lagenorhynchus obliquidens*	(M,M)	
Dusky Dolphin – 2 or 3	*Lagenorhynchus obscurus*		
		(M,M)	South American Dusky Dolphin
		(L,M)	South African Dusky Dolphin
		(L,M)	New Zealand Dusky Dolphin
Northern Right Whale Dolphin – 3	*Lissodelphis borealis*	(L,L)	
Southern Right Whale Dolphin – 3	*Lissodelphis peronii*	(L,M)	
Irrawaddy Dolphin – 1	*Orcaella brevirostris*	(H,H)	
Killer Whale – 1	*Orcinus orca*	(M,H)	
Melon-headed Whale – 2	*Peponocephala electra*	(M,M)	
False Killer Whale – 2	*Pseudorca crassidens*	(M,M)	
Tucuxi – 1	*Sotalia fluviatilis*		
		(M,H)	Marine tucuxi
		(M,H)	Freshwater tucuxi
Atlantic Humpback Dolphin – 1	*Sousa teuszii*	(H,M)	
Indo-Pacific Humpback Dolphin – 1	*Sousa chinensis*	(H,H)	
Pantropical Spotted Dolphin – 2	*Stenella attenuata*	(M,M)	
	3	(M,L)	Eastern Pacific Offshore Spotted Dolphin
	2	(M,M)	Hawaiian Spotted Dolphin
	3	(M,L)	Eastern Pacific Coastal Spotted Dolphin
Clymene dolphin – 3	*Stenella clymene*	(L,M)	
Striped Dolphin – 2	*Stenella coeruleoalba*	(M,M)	
Atlantic Spotted Dolphin – 2	*Stenella frontalis*	(M,M)	
Spinner Dolphin – 2	*Stenella longirostris*	(M,M)	
		(M,M)	Gray's Spinner Dolphin
		(M,L)	Eastern Spinner Dolphin
		(M,L)	Central American Spinner Dolphin
		(M,L)	Dwarf Spinner Dolphin
Rough-toothed Dolphin – 2	*Steno bredanensis*	(M,M)	
Common Bottlenose Dolphin – 1	*Tursiops truncatus*	(M,H)	
Indo-Pacific Bottlenose Dolphin –1	*Tursiops aduncus*	(M,H)	

APPENDIX 1

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APPENDIX 2

Workshop Agenda

1. Preliminaries
    1.1 Adoption of draft agenda
    1.2 Appointment of rapporteurs
    1.3 Available documents
    1.4 List of participants
2. Working group reports and discussion
    2.1 Working Group on Species- and Subspecies-level Taxonomy
        2.1.1 Report
        2.1.2 Points of clarification
    2.2 Working Group on Killer whales as a Case Study
        2.2.1 Report
        2.2.2 Points of clarification
    2.3 Working Group on Achieving a Validated Molecular Taxonomy and Phylogeography of the Cetaceans
        2.3.1 Report
        2.3.2 Points of clarification
3. Species
    3.1 Species concepts
    3.2 Criteria
    3.3 Case Study: killer whales
4. Subspecies (see Taxonomy report p24)
    4.1 Subspecies concepts
    4.2 Criteria
    4.3 Unnamed subspecies
    4.4 Case Study: killer whales
5. Review of needs for taxonomic attention
    5.1 First priority
    5.2 Second priority
6. Review of validated DNA database
    6.1 Species and subspecies level
    6.2 Phylogeography of selected species complexes
    6.3. Virtual curation
7. Recommendations
    7.1 Species concepts and guidelines
    7.2 Subspecies concepts and guidelines
    7.3 Priority taxa for taxonomic attention
    7.4 Addressing logistical barriers
    7.5 Killer whales
    7.6 Instituting web-based approaches and nominating curators
    7.7 Other
8. Other business
9. Adjournment

APPENDIX 3

List of Documents

Working Group on Species- and Subspecies-level Taxonomy:

LJ/04/Taxo1- A review of cetacean systematics in relation to conservation and management. **Randall R. Reeves & William F. Perrin**

LJ/04/Taxo2 - Draft annotated agenda for Working Group on Species- and Subspecies-Level Taxonomy.

LJ/04/Taxo3 - Systematics of coastal, tropical small cetaceans: a review. **Thomas A. Jefferson**

LJ/04/Taxo4 - Ecosystems management - structure, function and considerable compunction. **Timothy J. Ragen**

LJ/04/Taxo5 - A strawman proposal for a cetacean taxonomic designation scheme. **Barbara L Taylor**

LJ/04/Taxo6 - Beaked whale systematics: zoogeography, conservation issues and management. **Robert L. Brownell, Jr.** & **James G. Mead**

Working Group on the Killer Whale as a Case Study:

LJ/04/KW1- Influences of ecology, cultural traditions and social organization on the genetic population structure and systematics of killer whales. **L. Barret-Lennard & K. Heise**

LJ/04/KW2 - Draft workshop description and agenda: killer whales.

LJ/04/KW3 - Nomenclature of killer whales. **William F. Perrin**

LJ/04/KW4 - The role of acoustics in defining killer whale populations and societies. **John K. Ford**

LJ/04/KW5 - Reassessing the social organization of resident killer whales in British Columbia. **John K. Ford & G. M. Ellis**

LJ/04/KW6 - How old are the southern residents? **Michael J. Ford**

LJ/04/KW7 - Mitochondrial sequence variation in North Pacific killer whales. **Richard LeDuc & Barbara L. Taylor**

LJ/04/KW8 - Genetic and morphological evidence supports multiple species of killer whales in Antarctica. **Richard LeDuc & Robert Pitman**

LJ/04/KW9 - Social structure in eastern tropical Pacific killer whales. **Sarah L. Mesnick & Sergio Escorza-Treviño**

LJ/04/KW10 - Orcas and the U.S. Endangered Species Act. **Robin Waples**

Working Group on Achieving a Validated Molecular Taxonomy and Global Phylogeography of the Cetaceans:

LJ/04/Phylo1- Draft agenda for Working Group on Achieving a Validated Molecular Taxonomy and Global Phylogeography of the Cetaceans.

LJ/04/Phylo2 - An applied molecular taxonomy and phylogeography for conservation of cetacean species: universal access to a comprehensive, validated, and curated dataset**. C. Scott Baker et al**.

LJ/04/Phylo3 - Requirements of a molecular taxonomy for the identification & discovery of cetacean species: genetic distinctiveness, exclusivity, and concordance. **Merel L. Dalebout**

LJ/04/Phylo4 – Cetacean sequence data: what is and isn’t in GenBank. **Frank Cipriano**

APPENDIX 4

List of talks and posters presented at the Symposium on Cetacean Systematics: Approaches in Genetics, Morphology and Behavior – April 28-29, 2004 [immediately preceding the Workshop]

Arnold, P. W., A. Birtles, A. Dunstan, V. Lukoschek, and M. Matthews. Color patterns of the dwarf minke whale and use of coloration in assessing taxonomic relationships of the baleen whales.

Baker, C. S. www.DNA-surveillance: implementing a comprehensive and validated molecular taxonomy for cetaceans.

Barreto, A. S. *Tursiops* in Atlantic South America: is *Tursiops gephyreus* a valid species?

Caballero, S., C. S. Baker, L. M. González, F. Trujillo, J. A. Vianna, F. R. Santos, H. Barrios, M. G. Montiel, and S. Beltrán. Molecular Systematics of the South American Coastal and River Dolphin *Sotalia* sp.

Chivers, S. J., R. G. LeDuc, K. M. Robertson, N. B. Barros, and A. E. Dizon. Large inter-ocean genetic differences within *Kogia sima* indicate long-term isolation and possibly a new species.

Dalebout, M. L. Genetic distinctiveness, exclusivity and concordance: a molecular taxonomic approach to species identification and discovery.

Duffield, D. A., H. Zornetzer, E. O. Espinoza, and N. B. Barros. Use of biomarkers as species-level systematic and forensic molecular tools in the detection of cetacean hybrids.

Fajardo, L., A. Berta, R. L. Brownell, Jr., and C. C. Boy. Using polymorphic data and frequency analysis to infer the phylogenetic relationships and biogeography of porpoises (Cetacea: Phocoenidae).

Fleischer, R. Applications of ESU and subspecies concepts in birds.

Formica, P. M., F. Cipriano, and H. Markowitz. Differentiation of geographic stocks of rough-toothed dolphins, *Steno bredanensis*, using molecular techniques.

Fung, C. Does cranial morphology reflect adaptive evolutionary divergence of sympatric killer whale (*Orcinus orca*) ecotypes?

Gatesy, J. E. Combined versus separate analyses of systematic data sets for cetaceans.

Goode, M., H. Ross, S. Lavery, C. S. Baker, and A.G. Rodrigo. A maximum likelihood test of phylogenetic identification of species.

Hatch, L. T., S. M. Bogdanowicz, R. G. Harrison, and C. W. Clark. Male genes and male songs: fin whales as a case study for integrating genetic and acoustic data in defining baleen whale stocks.

Hatch, L., S. M. Bogdanowicz, and R. G. Harrison. Why Y? Chromosome–specific markers and their use for cetacean systematics.

Hey, J. New methods for measuring gene flow between closely related populations of species.

Higa, A. Geographic variation of the franciscana, *Pontoporia blainvillei* (Gervais & d'Orbigny, 1844) based on skull morphology.

Hoelzel, A. R., A. Natoli, M. E. Dahlheim, C. Olavarria, R. W. Baird, and N. A. Black. Low worldwide genetic diversity in the killer whale (*Orcinus orca*): implications for demographic history.

Jefferson, T. A. Systematics of coastal tropical small cetaceans: a review.

Johnson, W. E., E. Eizirik, W. J. Murphy, J. Pecon-Slattery, A. Antunes, and S. J. O'Brien. The origins and evolutionary history of modern felid species.

Krützen, M.and W. B. Sherwin. Does genetic differentiation imply speciation? Phylogenetic and paternity analyses show that this is not the case in West Australian bottlenose dolphins (*Tursiops* sp.).

Lavery, S., M. Dalebout, H. Ross, and C. S. Baker. Contrasting patterns of mtDNA diversity and molecular taxonomy of cetaceans.

LeDuc, R. G. Species: hard to define, but we know it when we see it…or do we?

Martinez-Vergara, M., A. J. Bohonak, S. Hildebrandt, and J. M. Afonso-López. Phylogeography of the Atlantic spotted dolphin (S*tenella frontalis*).

McDonald, J., W. B. Sherwin, J. Mann, M. Krützen, and R. Connor. Population forecasting and conservation unit definition in cetaceans.

Mead, J. Some observations upon the systematics of *Tursiops.*

Mesnick, S. L. and J. P. Barlow. Listen to my song: bioacoustical insights into cetacean taxonomy.

Morin, P.A. Incorrect and unresolved phylogenies from mtDNA: cautions for relying on one genetic marker for species designations.

Perrin, W. F. and R. R. Reeves. A review of cetacean taxonomy at the species and subspecies level.

Pitman, R. L. Are there new species of killer whales in the Antarctic?

Plater, B. Enfranchising populations under the ESA: the legal definition of "species."

Price, S. A. Composite species-level cetacean phylogeny.

Rosel, P. E., S. Kingston, A. Westgate, and L. Adams. Evolutionary relationships and species identification within Delphininae: a comparison of single-locus sequence data and multi-locus anonymous nuclear markers.

Rosenbaum, H. C., G. Amato, and R. DeSalle. A rigorous framework for assessing molecular genetic characters as indicators of species level conservation units.

Segura García, I., A. Rocha-Olivares, and L. Rojas Bracho. Genetic structure and differentiation of *Tursiops truncatus* ecotypes in the Gulf of California,

Seminoff, J. A. and W. J. Nichols. Trumping the need for taxonomic resolution with effective conservation actions: the case of green/black sea turtles in the Eastern Pacific Ocean.

Siciliano, S. and A. M. Di Beneditto. Present conservation and management status of the franciscana (*Pontoporia blainvillei*) along the Brazilian coast and the taxonomic status of its discontinous populations.

Stafford, K. M. and S. E. Moore. Variation in calling behavior in northeastern Pacific blue whales (*Balaenoptera musculus*.)

Taylor, B. How the holes in cetacean taxonomy are affecting conservation and management.

Viaud, K., A. J. Bohonak, and R. L. Brownell. Conservation Status of the black sea bottlenose dolphin (*Tursiops truncatus ponticus*): an assessment using morphology and genetic variation.

Waples, R. Application of alternative ESU concepts to a common problem in applied conservation biology.

Wayne, R. Adaptive genetic variation and units for conservation.

Yamada, T. Recognition of a new species *Balaenoptera omurai.*

Zornetzer, H. R. and D. A. Duffield. Morphological and photometric characterization of intergeneric hybrids between *Tursiops* and *Delphinus, Tursiops* and *Pseudorca.*

APPENDIX 5

Report of the Working Group on Species- and Subspecies-Level Taxonomy

Edited by W. F. Perrin and R. R. Reeves

Participants: Perrin (chair), Archer, Berta, Best, Brownell, Dalebout, Eagle, Fajardo, Gatesy, Hey, Jefferson, Knowlton, McGowen, Mead, Ragen, Reeves, Secchi, Taylor,

1. PRELIMINARIES

1.1 Review terms of reference

The terms of reference for this working group were as follows:

- *Review the importance of taxonomy in conservation* and its shortcomings for use in management.
- *Review the status of taxonomy* for each species/species group.
- *Methodology and logistics* – Identify general and specific natural features, logistical problems, and methodological issues that impede progress in cetacean taxonomy and in understanding geographical isolation.
- *Priorities* – Rank species according to the perceived need for research to resolve taxonomic uncertainty. This ranking should be at both the species and subspecies levels, and should integrate questions as to: (a) probability that structure at these levels is present, (b) whether or not uncertainty has already been resolved to a satisfactory degree, and (c) perceived level of immediate risk to species/subspecies conservation.
- *Recommendations* – Develop draft general and specific recommendations to improve understanding at species and subspecies levels, with emphasis on issues of immediate conservation relevance.

1.2 Arrangements for workshop

This working group limited its discussions to species and subspecies and the boundaries between them. Reeves acted as rapporteur. Jefferson drafted the glossary (Attachment 1).

The group's discussions were informed by and organized around the background paper by Reeves and Perrin (LJ/04/Taxo1), which was circulated to participants prior to the meeting. Much of the background information in this report was taken from LJ/04/Taxo1, supplemented by the discussions. The working group met for two days (30 April and 1 May 2004) and agreed on the main elements of its report before adjourning on the second day. The draft report was circulated and summarized verbally by Perrin at the 1-day workshop plenary session on 2 May. Minor corrections and additions were made following the workshop, based on comments from the participants.

1.3 Adopt agenda

The agreed agenda is given in Attachment 2.

2. REVIEW OF IMPORTANCE OF TAXONOMY TO CONSERVATION

Mace (2004) addressed this topic in some detail. The following summary emphasizes specific examples involving cetaceans (taken primarily from LJ/04/Taxo1).

Management of cetacean exploitation

To the extent that direct exploitation is managed for sustainability, defining the population unit being exploited is crucial. Although this requirement usually involves distinctions at the biological population or stock level rather than the species level, there are times when the latter becomes relevant. One example is provided by the bowhead whale (*Balaena mysticetus*) hunt in Alaska. The bowhead is considered monotypic, although a morphological variant called *ingutuk* has long been recognized by Inupiat whalers. During the 1978 hunt at Barrow, Alaska, the whalers exceeded the bowhead quota by one animal, and they insisted that this individual was an *ingutuk* and therefore should not have been counted against the quota (Braham et al. 1980). Scientists inferred from limited morphological and genetic-biochemical analyses that the *ingutuk* was not a separate species. Indeed, Rooney et al. (2002) have since concluded from more extensive morphometric and phylogenetic analyses that the *ingutuk* is a recently weaned bowhead whale and that female individuals may be more prone than males to express *ingutuk* features [see Right whales (Balaenidae), below].

Drive fisheries where bottlenose dolphins, *Tursiops truncatus* and *T. aduncus*, are (or were) taken provide another example. These species are at least partially sympatric around the Penghu Islands, Taiwan (Wang et al. 1999), where a drive fishery involving "mixed schools" of both species (Zhou and Qian 1985) was conducted until the early 1990s (Hammond and Leatherwood 1984; Reeves et al. 1994). Had there been any effort to manage the Penghu Islands fishery for sustainability (direct killing of cetaceans is now legally prohibited in Taiwan), it would have had to incorporate consideration for both *Tursiops* species. However, because of taxonomic uncertainty at the time (only one species, *T. truncatus*, was generally recognized until the late 1990s; see Curry and Smith 1990, Wang et al. 1999), it is unlikely that managers would have been inclined or equipped to require separate assessments for what were considered morphotypes of a single species. Moreover, according to Kishiro and Kasuya (1993; also see Kasuya et al. 1997:fig. 1), *T. aduncus* occurs along the Ryukyu Islands in the East China Sea while *T. truncatus* predominate elsewhere in Japanese waters. Drive fisheries in southern Japan, some of which continue (e.g., the reported direct catch of "bottlenose dolphins" in Japan in 2000 was 1,426; IWC 2003a), may take both species of bottlenose dolphins without consideration for the differences between them. Species or subspecies with allopatric distributions would be less likely to raise this kind of problem. The sympatric occurrence of the two morphologically similar species of *Tursiops* in East Asian seas creates the risk that both will be hunted without recognizing that two, rather than just one, species is involved.

Management of international trade

Live-capture and trade of small cetaceans have also aroused concerns related to designations of *Tursiops* species and subspecies [see Bottlenose dolphins (*Tursiops* spp.), below]. Traditionally, the live-animal industry has regarded the two forms (*truncatus* and *aduncus*) as morphological variants of a single species, with some tendency to regard the *aduncus* type as more desirable from a husbandry perspective (Reeves et al. 1994; Wang et al. 1999). Wang et al. (1999) concluded that for "proper protection to both species, conservation legislation must be amended to include *T. aduncus* and the impact of exploitation or other threats to each [*Tursiops*] species must be considered independently." Both species have often been displayed together in the same pools or tanks, and no distinction between them has been required in trade or other official records. It was only in 2003 that the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) began to recognize *T. aduncus* as a separate species for trade monitoring and regulatory purposes. This action was taken following a controversial shipment of *T. aduncus* from the Solomon Islands to Mexico (Ross et al. 2003).

A debate within CITES had taken place previously when it was proposed that the putative subspecies *Tursiops truncatus ponticus* should be uplisted from Appendix II (regulated trade permitted) to Appendix I (commercial trade prohibited) (see Reeves et al. 2003: table 1.2). The intent had been to curtail the international trade in live dolphins from the Black Sea, where *T. t. ponticus* is endemic. It is standard practice for CITES listing proposals to be reviewed formally by the IUCN Species Program through a process involving consultations with scientific experts. The IUCN analyses failed to validate *T. t. ponticus* as a bonafide subspecies, although they confirmed that the bottlenose dolphins in the Black Sea should be managed as a geographically distinct population (or series of populations) (e.g., see IWC in press). The "genetic distinctiveness" of bottlenose dolphins in this partially enclosed sea was a focal issue in the CITES deliberations (Simmonds 2003). It proved impossible to resolve that issue in a conclusive manner, and the parties finally agreed to leave "the bottlenose dolphin" in Appendix II but to set a "zero quota" for the trade in live specimens removed from the wild in the Black Sea. In the course of negotiating that outcome, the proponent (Georgia) "removed any mention of the population being a genetically distinct sub-species, although this may still be the case [*sic*]" (Simmonds 2003). In retrospect, it seems likely that if the experts who reviewed the proposal for the IUCN Analysis had been able to affirm that *T. t. ponticus* was a valid subspecies, the uplisting proposal would have been considerably less contentious.

International trade in the products from whaling has also presented challenges related to systematics and nomenclature. A series of "downlisting" proposals (from Appendix I to Appendix II) was considered by CITES for minke whales in 1997, 2000, and 2002 (Reeves et al. 2003). Although the existence of more than one species of minke whale had been recognized in the IWC Scientific Committee for some time (Perrin and Brownell 2002) and IUCN had listed *B. bonaerensis* separately in the 1996 Red List (Baillie and Groombridge 1996), the split between *B. acutorostrata* and *B. bonaerensis* was not formally recognized by the IWC until 2000 (Perrin and Brownell 2001; IWC 2001a) and not by CITES until 2002 (reported by Brownell). Besides the fact that species are generally perceived to be of greater importance to conservation than are populations or stocks (see below), there are other conservation-related reasons to clarify taxonomy. The CITES downlisting proposals referred to global abundance of minke whales as though there were only one species, and when estimates from the Antarctic (mainly *B. bonaerensis*) were added to those for the North Atlantic and North Pacific (*B. acutorostrata*), the aggregate number was considerably more impressive (i.e., less likely to generate interest in risk-averse decision-making) than if the individual ocean-basin estimates had been considered in isolation. Because the minke whale complex, however defined (see later), has a cosmopolitan range, includes relatively large numbers of individuals, and has been the numerically dominant target of commercial whaling over the last quarter-century (Gambell 1999; Perrin and Brownell 2002), getting its taxonomy clarified is both challenging and important.

Rationale for culling

The foregoing concern that abundance estimates used in the CITES context should be aligned with a solid understanding of species (and population) differences has an analogue in the international debate on the "need" to cull whale populations to protect fisheries. For example, Komatsu and Misaki (no date) provide photographs of stomachs of sei, minke, and Bryde's whales containing large quantities of fish and squid, without specifying which species of minke and Bryde's whales the stomachs came from. These authors argue that whale populations need to be culled to reduce competition with fisheries, using estimates of fish consumption by whale populations that may be, at least in some instances, biased upward by lumping multiple species (*B. bonaerensis* and *B. acutorostrata* subsp. in the Southern Ocean) and ignoring the existence of two or more species of Bryde's whales in the western Pacific (Yoshida and Kato 1999, Kato 2002, Wada et al. 2004) or by attributing assumptions about prey preferences to the wrong species.

A related issue concerns killer whales (*Orcinus* spp.). It has been suggested that these top predators have driven a cascade of collapses of marine mammal populations in the North Pacific and Bering Sea (Springer et al. 2003). Likewise, it has been suggested that their predation has been a contributing factor for recent declines in minke whale and certain pinniped populations in the Antarctic (Branch and Williams 2003). If it is assumed that more than one killer whale taxon were present in either region, survey data used to estimate killer whale numbers for incorporation in predator-prey models could be seriously confounded by a failure to distinguish between different species or subspecies of *Orcinus*.

Setting conservation priorities

To most scientists, biological populations need only be recognized as such to receive high priority for conservation. However, in the political and fiscal arena where decisions are made to allocate scarce resources and restrict human activities, non-scientists may need to be persuaded that a group of organisms is something more than "just" a population. As Mace (2004) noted: "Whether we like it or not, the species rank has a special resonance with the public and with policy-makers."

A clear and timely example of how much difference a name can make (in this case a subspecies name) is that of the so-called Maui's dolphin, a recently described subspecies of Hector's dolphin (*Cephalorhynchus hectori*). Already before Baker et al. (2002) published their description of the subspecies, the "North Island population" of Hector's dolphin had been formally recognized by IUCN as Critically Endangered (Reeves et al. 2003). Yet when this population was given its own common name, Maui's dolphin, it immediately acquired new standing as a *cause celélèbre* among advocacy groups and, in turn, in the eyes of government agencies. As WWF New Zealand trumpeted on 27 November 2002, immediately following the release of the description of the subspecies: "Maui's dolphin is now officially the world's rarest marine dolphin. Maui's dolphin can no longer be considered as one of four populations of Hector's dolphins; we expect to see more government effort directed towards protecting it."

Similar reasoning to that of WWF New Zealand is common. When the IWC, and then others (e.g., IUCN and CMS, the Convention on Migratory Species), decided to recognize North Pacific and North Atlantic right whales as separate species (see below), the perspectives of the general public, conservationists, and management agencies changed. For example, the Committee on the Status of Endangered Wildlife in Canada, the official body for listing species and populations under Canada's Species At Risk Act, commissioned separate status reports and species designations to replace the former unified reports and designations that addressed North Atlantic and North Pacific populations under one rubric – the "northern right whale." Separate recovery plans/strategies for the two species were developed by the Canadian Department of Fisheries and Oceans and WWF-Canada. Similarly, the recovery plan for the "northern right whale" under the U.S. Endangered Species Act (NMFS 1991) is being split into two separate plans, one for the North Atlantic and one for the North Pacific. From the narrow perspective of conservation biology, replacement of the traditional distinction between North Atlantic and North Pacific populations of one species ("northern right whale") with the recognition of each as a separate species was an arcane taxonomic decision and did not alter their status as evolutionarily significant units. From the wider perspective of those who make policy decisions and allocate conservation resources, however, it represented a shift in priorities, regardless of how subtle and difficult it may be to quantify or characterize that shift.

Consideration of higher-level taxonomy and variation below the subspecies level

While the group focused on species-level and subspecies-level questions, it recognized that it is also important to consider higher-level taxonomy in conservation (e.g., see Fajardo et al. 2004). For example, the Ziphiidae have come into prominence as a family in recent years because of their vulnerability to the lethal and debilitating effects of acoustic signals. Also, some species such as the gray whale, sperm whale, and South Asian river dolphin (*Platanista gangetica*) are the last representatives of ancient lineages at the family level. It is well to consider whether effort should be directed preferentially toward such groups, or instead, toward relatively young lineages with possibly greater evolutionary potential (e.g., delphinids). It was also acknowledged that conservation decision-making and action usually occur population-by-population, at levels far below those of species and other long-term lineages. Systematics below the species level is vital to conservation.

3. REVIEW OF SHORTCOMINGS OF CURRENT TAXONOMY IN TERMS OF NEEDS OF MANAGEMENT

A comprehensive revision of cetacean taxonomy at any point in time is practically impossible. Therefore, piecemeal revision is unavoidable and its undesirable side effects are inevitable. When a team of researchers has managed to obtain sufficient samples and complete a diagnosis, they cannot be expected to wait until similarly conclusive analyses are available for all other cetaceans before publishing their results. Therefore, taxonomic revisions will continue to occur as discrete events that accumulate over time and that are periodically assembled into a synthesis reflecting the current imperfect state of knowledge (e.g., Rice 1998). Progress in classification at both the species (*alpha*) and subspecies (*beta*) levels is unavoidably uneven and iterative.

The spinner dolphin, a pantropical species, provides an instructive example. This species has been broken down into three subspecies in the eastern Pacific, which represents less than half of the species' total range (Perrin 1990). Those subspecies were initially diagnosed as a series of management stocks in the context of very high mortality caused by the tuna purse seine fishery. Eventually, the large samples obtained as a result of that mortality made it possible to differentiate and describe the subspecies. This situation in the eastern tropical Pacific is exceptional. Few other populations of small cetaceans have been sampled so thoroughly over such a broad and continuous area. If comparable coverage existed for the rest of the Pacific and for the Indian and Atlantic Oceans, it is possible that dozens of additional subspecies of spinner and spotted dolphins could be described. Good hints at the existence of variants are already available for the Indo-Pacific region (where a dwarf spinner subspecies has been described – Perrin et al. 1989,1999) and the western Indian Ocean (Van Waerebeek et al. 1999).

The very large numbers of whales killed by the commercial whaling industry, and that industry's global reach, potentially would have provided large samples for analyses of geographical variation. However, the logistical constraints of transporting, curating, and housing skulls and skeletons have been a major impediment to the accumulation of such samples, and as a result the application of the biological species concept to whale populations in different ocean basins, using standard morphological and morphometric approaches, has been impractical. At least in part because of the relative ease and feasibility of gaining access to large samples of DNA over large spatial scales, the phylogenetic species concept has been increasingly used as a supplement to, if not a replacement for, the biological species concept.

Further shortcomings in cetacean taxonomy include the following:

1. There is a lack of consensus on standards for designating species and subspecies.
2. Taxonomy has remained a largely "ivory-tower" museum-based discipline whose priorities have had little or no relation to conservation or management needs.
3. The shortage of taxonomists is a longstanding and wide-ranging problem, causing "biases and under-representations in species lists compiled for monitoring and planning purposes" (Mace 2004:717).
4. For most cetaceans, we do not have enough morphological data to meet an evidentiary standard for establishing (or rejecting) additional species. (Caveat: In some cases, however, the material available in existing collections has not been exhaustively exploited.)

5. There has been a tendency to err in the direction of avoiding designating too many taxa rather than making sure that all potentially recognized taxa have been designated. In other words, the direction of precaution toward stability in traditional taxonomy has not been appropriate for conservation.
6. Cetacean taxonomy in the latter half of the 20th century was conservative in part as an over-reaction to the excessive splitting that occurred during the 19th century.

The killer whale in the northeastern Pacific provides an example in which, by some points of view, taxonomy is inappropriate and inadequate for meeting conservation needs. Not only is there genuine uncertainty about the taxonomy of killer whales within the region, but also data from all over the globe were thought to be needed before this could be resolved, and it was not possible to obtain such data in a timely way. The working group noted that although there had been reluctance in the case of killer whales to move ahead with taxonomic revision on a regional basis, this was done for common dolphins (*Delphinus*), which were split into two species based on data from only a relatively small portion of the genus's global distribution (Heyning and Perrin 1994).

The challenge facing taxonomy in relation to conservation is to focus on and find a way of dealing responsibly with low-data situations, with the goal of assuring that taxonomic designations are made in a more timely and relevant manner.

4. REVIEW OF TAXONOMY FOR CURRENTLY RECOGNIZED SPECIES/SPECIES GROUPS

Overview

Rice's (1998) comprehensive review of the systematics and distribution of marine mammals resulted in the recognition of 83 species of cetaceans. Subsequent authoritative lists have included several revisions of Rice's taxonomy in the light of new data or differing interpretations. Perrin et al. (2002) followed Rice faithfully except in the case of right whales, where they recognized three rather than one species, for a total of 85. Baker et al. (2003) disagreed, recognizing only one species of right whale. The most recent list published by the International Whaling Commission (IWC) includes 82 species, with a footnote indicating that one of the two "Bryde's whales" is missing because its "nomenclature is still unsettled" (IWC 2001a). The most recent list published by IUCN (World Conservation Union; Reeves et al. 2003) consists of 84 species, including two Bryde's whales, the recently described *Mesoplodon perrini* (Dalebout et al. 2002), and the resurrected *Mesoplodon traversii* in place of *M. bahamondi* (Van Helden et al. 2002). Most authorities agree that there are at least 84 living species of cetaceans.

Relatively few subspecies are recognized. Rice (1998) recognized 40, and they were listed in Reeves et al. (2003: table 1.1). Perrin (2002a) also listed 40 subspecies after combining two of Rice's (*Stenella attenuata* subsp. A and subsp. B, under *S. a. attenuata*) and adding another (*Stenella longirostris roseiventris*). IWC (2001a) did not include subspecies except in the case of *Platanista gangetica* where the Ganges and Indus subspecies (*P. g. gangetica* and *P. g. minor*, respectively) were listed separately.

The IUCN's Red List of Threatened Animals is the only recognized risk-based assessment tool available over much of the globe (see www.iucnredlist.org). A major effort was made in 1996 to assess all then-recognized species of cetaceans against quantitative criteria developed by IUCN (Baillie and Groombridge 1996). Although the first priority was to ensure that each species was assessed at the global level, some effort was also made to assess geographical populations and subspecies. Sixteen cetacean "stocks," "populations," or subspecies were assigned a threatened status in 1996, and a few additional ones have been added since then (see Reeves et al. 2003: Table 1.1, for a synthesis as of mid-2003).[1] The IUCN Red List Program updates the Red List annually, and the IUCN/SSC Cetacean Specialist Group is responsible for producing and evaluating assessments for the cetaceans. Highest priority for assessment is given species and populations thought to be at greatest risk of extinction. In practice, additional factors, notably the existence of one or more interested individuals who are willing to compile the data and analyses for the assessment, play a key role in determining which conservation units end up on the Red List.

Getting lists of threatened taxa aligned with the scientific consensus on systematics is a challenge that may never be met in a definitive or final way. Nevertheless, considerable improvement upon the status quo is both desirable and feasible. In some instances, the available data and analyses are adequate to support a listing decision for one or more "populations" but not for the entire species. Such populations may in fact be listable units at the subspecies or similar level, but lack of information or even criteria to determine their "separateness" can seriously impede listing decisions. In these circumstances, the entire

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[1] In the present report, when the terms Critically Endangered, Endangered, Vulnerable, Lower Risk, and Data Deficient are capitalized, it signifies that they are intended to refer to the official Red List status.

species often remains as Data Deficient, a category too often interpreted by managers, conservation organizations, and others who might be able to initiate or assist conservation efforts to mean that no serious risk exists.

The working group discussed those species or species groups about which there is ongoing disagreement, for which subspecies are recognized, or that present issues of particular conservation relevance. These discussions formed the basis for priority rankings (Section 6 below).

Right whales (Balaenidae)

This group has been the focus of long-standing disagreements about both nomenclature and taxonomy. Species-level differences based on morphology and ecology between the bowhead whale (*Balaena mysticetus*) and the temperate-region right whales (*Eubalaena* spp.) have been recognized and widely accepted since the 19th century. Rice (1998) rejected the generic distinction outlined by Allen (1908), which had enjoyed wide acceptance over the course of the 20th century, arguing that the morphological and molecular differences between right whales and bowhead whales were no greater than those between the various species of the genus *Balaenoptera*. Rice's position, that all living balaenids belong to the same genus, *Balaena*, was considered and rejected by Bannister et al. (1999), who cited "the customary usage of right whale biologists over many years" as their rationale. The IWC and most other authorities have also continued to use *Eubalaena* (IWC 2001a; Perrin et al. 2002).

The temperate-region right whales have been the source of much taxonomic uncertainty, as summarized by Rice (1998). Recognition of three rather than one or two species has clear implications for conservation (see above, under "Setting Conservation Priorities"). Perrin and Brownell (2001) outlined four alternative courses of action in the light of strong genetic evidence adduced by Rosenbaum et al. (2000) indicating long-term isolation of the populations in the North Atlantic, North Pacific, and Southern Hemisphere. Although Perrin and Brownell recommended recognition of three subspecies (*E. glacialis glacialis*, *E. g. australis*, and *E. g. japonica*) as the "most conservative" of the four options "in evolutionary biological terms," the IWC Scientific Committee chose to recognize the three populations as full species (*E. glacialis* in the North Atlantic, *E. australis* in the Southern Hemisphere, and *E. japonica* in the North Pacific). The stated rationale was: "The level of cladistic difference justifies species-level recognition under the *phylogenetic species concept* [PSC] (species are groups of organisms defined by a unique combination of character states, with a parental pattern of ancestry and descent, and are fully diagnosable)" (IWC 2001a). T he former term "northern right whale" has been rendered meaningless, replaced by Atlantic right whale (*E. glacialis*) and North Pacific right whale (*E. japonica*) (Perrin et al. 2002; Reeves et al. 2003).

Baker et al. (2003), however, rejected the application of the PSC to right whales, stating that the nucleotide substitutions described by Rosenbaum et al. (2000) "have no discernable phenotypic expression, and are probably selectively neutral; they cannot be construed as evidence of either prezygotic or postzygotic isolating mechanisms. No other consistent differences have been found between the three populations, so under the biological species concept all three must be regarded as members of a single biological species, *Eubalaena glacialis*." This controversy captures in a nutshell the disagreement between adherents of the biological and phylogenetic species concepts when dealing with morphologically similar allopatric forms. There is a caveat, however: these very large animals present a particular challenge to full-blown quantitative morphological comparisons of large series of specimens. No institution or set of institutions currently has the necessary series. Therefore, more effort should be devoted to collecting skulls and post-cranial skeletons from stranded right whales so that sufficiently large series will eventually be available to support morphological comparisons (and end inordinate reliance on phylogenetic differences as the basis for species designations) (see Section 7 below).

Gray whale (*Eschrichtius robustus*)

The gray whale in the North Pacific has generally been regarded as monotypic even though two "management stocks" have long been recognized and mtDNA haplotype frequencies showed them to be "geographically isolated and demographically closed population units" (LeDuc et al. 2002). The extinct North Atlantic population might have qualified as a subspecies, or possibly even as a separate species, but this question is moot and has no immediate relevance to conservation. Consideration should be given, however, to the possibility that eastern and western Pacific populations merit recognition as subspecies. As in the case of right whales (above), more effort should be made to collect skulls and post-cranial material from stranded gray whales in western North America so that sufficiently large series will eventually be available to support morphological comparisons with western Pacific gray whales (already reasonably well represented by collections from Korea early in the 20th century). Also, further analyses using non-neutral genetic markers should be conducted for evidence of isolation between eastern and western Pacific gray whales.

Finner whales (*Balaenoptera* spp.)

This diverse genus is the most speciose, and the most problematic, among the mysticetes. Until the 1990s, a fairly stable array of five species was generally accepted: blue whale, *B. musculus*; fin whale, *B. physalus*; sei whale, *B. borealis*; Bryde's whale, *B. edeni*; and minke whale, *B. acutorostrata*. Over the past 10-15 years, two additional species have come to be recognized.

Cetologists had long known that two well-defined morphotypes of minke whales existed – "white-shouldered" (*acutorostrata*-type) and "dark-shouldered" (*bonaerensis*-type) (Williamson 1975; Best 1985). Dizon et al. (1992), after considering various lines of evidence including enzyme electrophoresis on tissue proteins (Wada and Numachi 1991), concluded that "speciation, not just subspeciation, may be occurring in the minke whale populations." Indeed, two species came to be recognized in the late 1990s, the common minke whale (*B. acutorostrata*) and the Antarctic minke whale (*B. bonaerensis*). A third morphotype, the dwarf minke whale, was described by Best (1985), Arnold et al. (1987), and others. Provisionally, Rice (1998) designated it as one of three subspecies of *B. acutorostrata*: *B. a. acutorostrata* in the North Atlantic, *B. a. scammoni* in the North Pacific, and *B. a.* subsp., the Southern Hemisphere dwarf. The systematics and nomenclature of minke whales, a group that has been heavily exploited at least regionally and that continues to be exploited in the northeastern Atlantic, northwestern Pacific, and Antarctic, are a high priority. Of particular and immediate importance is the population known in IWC terminology as "J-stock" (for the Sea of Japan, this population's center of distribution), distinguished from the parapatric "O-stock" (for Sea of Okhotsk) on the basis of differences in the timing of reproductive events, body size, and genetic characteristics (Kato 1992; Goto and Pastene 1997). J-stock is at high risk because of past overhunting, continued mortality from entanglement/entrapment in fishing gear, and its inclusion in the ongoing Japanese whale hunt in the northwestern Pacific (e.g., Baker et al. 2000). This "stock" may well deserve recognition as a subspecies (if not a species).

Brownell pointed out that the subspecies name *B. a. scammoni* probably does not apply to the entire North Pacific (*contra* Deméré 1986) as it may refer only to a relatively isolated form of minke whale in the coastal northeastern Pacific.

Morphological (osteological) investigations are ongoing, as are studies of regional acoustic differences. Of all the baleen whales, minke whales are represented by relatively large series in museum collections. Also, particularly given the ongoing work on color-pattern differences among geographical populations (subspecies) of common minke whales (Arnold et al. 2004), photographs should be collected and made available from minke whales killed in Japanese scientific whaling and taken as bycatch in fishing gear in Japan and South Korea.

The second recently recognized species is a "Bryde's whale," i.e., it resides in what Best (1977) referred to as the *edeni-brydei* complex. While there is a broad consensus that at least two "Bryde's whale" species – an "ordinary" species and a "pygmy" species – exist within the Bryde's/sei complex (Wada and Numachi 1991; Dizon et al. 1996; Pastene et al. 1997; Rice 1998; Yoshida and Kato 1999), their taxonomy and nomenclature remain confused. In fact, another recently described "new" species, *B. omurai* (Wada et al. 2003), would mean that there are three rather than two species of "Bryde's whales," or perhaps looked at another way, four species in the *borealis-edeni-brydei-omurai* complex. A more detailed description of the *B. omurai* holotype is expected to be published in the next year or so (T. Yamada, pers. comm. to Perrin). The problem of determining species-level, and indeed subspecies-level, taxonomy for this group is particularly important to resolve, as Japanese whaling for "Bryde's whales" is ongoing under a nationally administered program of "scientific research" whaling, and strong support has been provided by some Japanese scientists for the concept of culling some of the larger whales, including Bryde's whales, to protect commercial fisheries (cf., Tamura and Ohsumi 2000; see above under "Rationale for Culling"). A global approach will be required for ultimate resolution as, for example, Best reported that three different forms of "Bryde's whale" occur in southern African waters alone.

An immediate and pressing need is to obtain a DNA sample from the holotype of *Balaenoptera edeni* in the Calcutta Museum. Any further taxonomic work on the "Bryde's whales" has to await genetic resolution of the *B. edeni* holotype's identity.

Of the other *Balaenoptera* species, all three have generally been regarded as irreducible except at the subspecies level. The blue whale has been the most problematic in this regard. A pygmy subspecies, *B. m. brevicauda*, has a distribution centered in subantarctic waters of the Indo-Pacific and southeastern Atlantic Oceans (Rice 1998) but its distinguishing features at sea and genetic identity need to be resolved (Kato et al. 2002; IWC 2003b). Rice (1998) listed three additional subspecies – *B. m. musculus* in the North Atlantic and North Pacific, *B. m. indica* in the northern Indian Ocean, and *B. m. intermedia* in the Antarctic. The distinctions among them are vague, beyond their presumed geographical separation. On a worldwide basis, blue whales exhibit a number of geographically distinct acoustic call types that may prove informative in delimiting subspecies (Stafford 2003) although there is some evidence that "calling behavior may be somewhat plastic" (Stafford and Moore 2004). Clarification of the subspecies taxonomy of blue whales would be useful for the purposes of Red List classification and, more generally, for assessing the global status of this species, which is presently listed as Endangered. The Antarctic subspecies (called "Antarctic stock" in the Red List) is also listed as Endangered, while the North Pacific and North Atlantic "stocks" (i.e., *B. m. musculus*) are listed respectively as Lower Risk (conservation dependent) and Vulnerable. The pygmy subspecies (called as such) is listed as Data Deficient.

Both the fin whale and the sei whale are divided into Northern Hemisphere and Southern Hemisphere subspecies by Rice (1998), citing Tomilin (1946). Although Tomilin provided some evidence of differences in body size between the two fin whale subspecies, the main basis for subdividing both species was (presumably) their disjunct geographical distributions. Ongoing work by Hatch et al. (2004a, 2004b) is intended to characterize genetic and acoustic differences between North Atlantic and North Pacific fin whales. Although there was insufficient time to discuss the matter in depth, the working group generally agreed that the recently described "pygmy fin whale" (*B. physalus patachonica*) (Clarke 2004) may not prove valid.

Humpback whale (*Megaptera novaeangliae*)

No disagreement exists concerning the single-species character of this genus. Subspecies have been proposed by various authors on the basis of regional differences in body length and coloration. Rice (1998) concluded that "the percent separability between them is not quite as high as is customarily required for division into subspecies." Clapham and Mead (1999) also expressed the view that the size and pigmentation variability among populations "does not warrant subspecific differentiation." Several members of the working group nevertheless wished to record their view that Rice's rejection of subspecies in the humpback whale was inconsistent with his treatment of other cosmopolitan baleen whale species, where similar types of morphological data and/or presumed geographical separation were accepted as the basis for recognizing subspecies in different ocean basins (e.g. sei whale, fin whale).

Pygmy and dwarf sperm whales (*Kogia* spp.)

Interesting though it is, this genus has received little attention from systematists since it was split into two species in the 1960s (Handley 1966). Rice (1998) described the two species as "well-differentiated and broadly sympatric." New genetic data suggest long-term isolation between populations of *K. sima* in the Atlantic and Indo-Pacific Oceans (Chivers et al. 2004). Consideration of these data, especially in the light of ongoing work in other parts of these animals' range, may eventually lead to recognition of a third *Kogia* species, or at least a series of subspecies.

Amazon dolphins or botos (*Inia*)

These river dolphins of northern South America have been the subjects of substantial taxonomic confusion. In an authoritative review of the state of knowledge, Best and da Silva (1989) rejected the arguments that had been made to date for multiple species, citing the limited scale of sampling and the questionable efficiency of geographical barriers that would have led to speciation. They recommended the continued "provisional usage" of a single species, *I. geoffrensis*, divided into three subspecies: *I. g. humboldtiana* in the Orinoco drainage, *I. g. geoffrensis* in the Amazon drainage except the upper Madeira system, and *I. g. boliviensis* in the upper Madeira River drainage. Best and da Silva considered such a configuration to be satisfactory for conservation purposes, noting that the three subspecies "encompass[ed] different geographical areas and countries and as such should permit the separate treatment of conservation problems as they pertain to each region." A further consideration is that although the species is listed by IUCN as Vulnerable (Baillie and Groombridge 1996), its aggregate abundance is large (possibly tens of thousands; A.R. Martin, pers. comm. to Reeves) and there is little evidence of major declines in numbers or range (IWC 2001b).

The primarily morphometric basis for recognizing two species of *Inia*, as set forth by Pilleri and Gihr (1977), has been strongly criticized and rejected over the years (see Rice 1998). However, recent studies employing different lines of evidence corroborate the argument for the existence of two species. Comparisons of cranial morphometrics (da Silva 1994), full-body morphology (Ruiz-García et al. 2002), and mtDNA (Banguera-Hinestroza et al. 2002) all indicate a marked divergence between the Bolivian dolphins (*I. boliviensis*) and those from the Amazon and Orinoco basins (*I. geoffrensis*). Assuming that nuclear genetic markers were to confirm the validity of the two *Inia* species, *I. geoffrensis* presumably would continue to be subdivided into Amazon and Orinoco subspecies. There is ongoing work on this genus by a number of investigators.

Ganges and Indus dolphins (*Platanista*)

This group of obligate freshwater dolphins has been the subject of considerable taxonomic confusion.

Because of the enormous scale of human demands on the rivers that they inhabit and the consequently severe degradation and loss of freshwater habitat, continued deliberate killing in spite of legal protection, and substantial incidental mortality, these dolphins are threatened throughout their range. Clarification of their taxonomy could play a useful role in shaping conservation strategies. For example, the development of an aggressive program to "rescue" dolphins from irrigation canals and return them to the Indus River (Braulik 2000), and efforts to influence national water policies for the benefit of the dolphins, have been premised upon the understanding that the Indus dolphin is an endemic species unique to Pakistan (Braulik et al. 2000). Although this would be difficult to document, it seems likely that the Indus dolphin's recently assigned status as a subspecies rather than a full species (see following) will diminish its perceived importance within Pakistan and perhaps also reduce its status as a priority taxon for international lending and aid institutions (see above under "Setting Conservation Priorities"). In the first synoptic review of the genus, Anderson (1879) essentially described a metapopulation of a single species, *P. gangetica*, distributed in a series of river systems from the Indus in the west to the Karnaphuli in the east. Based only upon rather flimsy morphological and biochemical evidence, the concept of two species [*P. minor* (= *indi*) and *P. gangetica*] gained acceptance during the 1970s (e.g., Rice 1977), with Kasuya's (1972) proposed alternative of two subspecies (*P. g. gangetica* and *P. g. indi*) being noted but largely ignored (see Reeves and Brownell 1989). In view of Rice's (1998) reevaluation of the same evidence, and based on the recommendation of Perrin and Brownell (2001), the IWC Scientific Committee reverted to Kasuya's position and rejected the two-species approach in favor of a single species divided into two subspecies (IWC 2001a). Perrin and Brownell (2001) contended that the present-day geographical isolation of the Indus population (*P. p. minor*) from the Ganges-Brahmaputra-Meghna population was likely secondary and caused by lowered water levels in the headwaters of "both drainages" and by the construction of "impoundment barriers to dispersal" (i.e., dams and barrages). The question of whether the Indus population is sufficiently different to warrant species status, or indeed subspecies status, nevertheless needs to be resolved in a timely manner. Comparative analyses should include samples from the possibly isolated dolphin population(s) in the Karnaphuli and Sangu river drainages of southeastern Bangladesh (Smith et al. 2001). Orogenic analyses are needed to determine whether the Indus and Ganges systems were connected in historical times (Hamilton et al. 2000).

The Indus and Ganges dolphins were assessed for the 1996 Red List as separate species (*P. minor* and *P. gangetica*, respectively) and both were listed as Endangered (Baillie and Groombridge 1996). Pending an updated assessment, Reeves et al. (2003) construed this to mean that the currently recognized single species (*P. gangetica*), as well as the two subspecies separately, should be considered Endangered.

Franciscana dolphin (*Pontoporia blainvillei*)

The single-species nature of this genus is well established, but there is also good evidence of structure within the species (Siciliano and Di Beneditto 2004, Higa 2004). Four management stocks have been established in different regions, called Franciscana Management Areas or FMAs (Secchi et al. 2003). Very low gene flow (i.e. < 1 migrant/generation) occurs between FMA I (the northernmost stock) and any other FMA (II to IV from north to south) (Ott 2002). Morphological data are consistent with genetic results (Ramos et al. 2002; Higa et al. 2002; Secchi et al. 2003). Individuals from FMA II are smaller than those from adjacent areas, excluding the possibility of clinal differences. Therefore, FMA I can be regarded as a potential candidate for subspecies status.

Beaked Whales, Ziphiidae

All the members of the **Ziphiidae**, the family of deep-diving whales are especially vulnerable to the effects of underwater noise (Hildebrand 2003), and in addition, these whales are susceptible to entanglement in drift gillnets set in deep water.

Giant bottlenose whales (*Berardius* spp.)

The two species in the genus *Berardius* were established on the basis of a substantial size difference between the giant bottlenose whales in the Southern Ocean and those in the North Pacific, the latter being some 20-25% longer. *Berardius* appear to be entirely absent in the tropical belt, suggesting a gap in distribution spanning approximately 60º of latitude. Rice (1998) questioned the species split and indicated that an option would be to reduce *B. bairdii* to a subspecies of *B. arnuxii*. However, Dalebout (2002) found fixed nuclear and mitochondrial differences between the two species. She reported that she is investigating potential differences between animals in the Sea of Japan and the Pacific Ocean.

No immediate or severe conservation problems are known to exist for the whales in this genus, although *B. bairdii* has been hunted in Japan since the early 17th century (Ohsumi 1983). Also, *B. arnuxii* is rarely observed and may be naturally rare, and newly developing fisheries in the Antarctic could represent a threat to this species.

Northern and southern bottlenose whales (*Hyperoodon* spp.)

The situation for these ziphiid whales is reminiscent of that for *Berardius*, except that in this case the Northern Hemisphere species (*H. ampullatus*) is endemic to the North Atlantic and absent from the North Pacific. The southern bottlenose whale (*H. planifrons*) is separated from its North Atlantic congener by at least 50º of latitude. No subspecies have been proposed and taxonomic work on this genus is not a high conservation priority. However, for *H. ampullatus*, the existence of apparently isolated centers of abundance, with uncertain exchange among them, and the lack of data regarding their recovery from intensive whaling, gives cause for concern. Dalebout reported that research is ongoing to address the degree of isolation of the small population in The Gully, a submarine canyon off the coast of Nova Scotia, Canada.

Indo-Pacific beaked whale (*Indopacetus*)

Having long represented a taxonomic conundrum, this genus has emerged over the past decade as likely being both valid (i.e., distinct from *Mesoplodon* and *Hyperoodon*) and monotypic (*I. pacificus*). Mitochondrial DNA analyses have been used in combination with morphological characteristics to identify specimens and describe the genus and species (Dalebout et al. 2003). There is no immediate possibility of obtaining enough samples to even begin investigating subspecific differences for *Indopacetus*.

Cuvier's beaked whale (*Ziphius cavirostris*)

Like killer whales, Cuvier's beaked whale has a worldwide distribution. No disagreement exists concerning its species-level taxonomy and no subspecies have been proposed. Heyning (1989) nevertheless cautioned that the species "exhibits a great deal of morphological variation" and that its systematics have not been reviewed in recent times. Dalebout (2002) found strong evidence for population structure, suggesting that there are isolated groups in at least some areas. A focused study of morphology is warranted but will require travel to numerous sites with cranial material. The species is of particular interest and concern because of its exceptional vulnerability to underwater noise from military sonar and seismic testing and its susceptibility to entanglement in drift gillnets.

Mesoplodon whales

Whales of this genus are extremely difficult to identify at sea, and that difficulty often extends to beach-cast specimens as well, especially females and juveniles. These whales are generally described as cryptic and elusive, and they occur predominantly in deep water and thus well away from most coastlines (Mead 1989). Of the 14 species currently recognized in this genus (Reeves et al. 2003), three have been discovered (or rediscovered) and described (or redescribed) within the past 15 years (Dalebout et al. 2002). Molecular genetic techniques have provided an important new dimension to the study of *Mesoplodon* systematics, and further major changes, including the discovery or recognition of additional species, can be expected (see Dalebout et al. 1998, 2002; Van Helden et al. 2002). Like Cuvier's beaked whales, *Mesoplodon* species appear to be exceptionally vulnerable to the effects of underwater noise from military sonar and seismic testing as well as to entanglement in drift gillnets.

Beluga or white whale (*Delphinapterus leucas*)

An extensive literature exists on the problem of stock discrimination within the species (e.g., O'Corry-Crowe and Lowry 1997). There is no disagreement concerning taxonomy at the species level. Rice (1998) acknowledged, but dismissed as unwarranted, various species and subspecies designations proposed by Soviet researchers in the past. The seriously threatened status of some isolated regional populations (e.g., Cook Inlet, Alaska; southern Ungava Bay, Canada; St. Lawrence River, Canada) gives cause for clarification of potential subspecific differences in this heavily exploited Arctic species.

Narwhal (*Monodon monoceros*)

This species, another heavily exploited Arctic endemic, is also well established at the species level. However, recent investigations using satellite telemetry and other lines of inquiry have provided evidence suggesting population structure (M.P. Heide-Jørgensen, pers. comm. to Reeves). The species' distribution is discontinuous, with major gaps between east and west Greenland and across parts of Eurasia.

Finless porpoise (*Neophocaena*)

The genus *Neophocaena* is well defined but the number of species and subspecies within it has been marked by uncertainty. Finless porpoises are limited to shallow coastal waters along continental and island coastlines of southern and southeastern Asia. Their total distribution has been depicted as almost continuous (Kasuya 1999a; Jefferson 2002a). Kasuya (1999a), however, gave a somewhat contradictory account, noting on one hand that the almost linear species distribution means that there is little chance of genetic exchange between "distant populations," yet on the other hand "there are no geographical barriers or habitat gaps that inhibit free interbreeding between nearby areas." Moreover, he noted that clinal variation was easily developed and "environmental gaps" in the species' range would be expected to accelerate the formation of "morphologically distinct local stocks." He concluded that available information was insufficient to establish more than one species of finless porpoise. Jefferson (2002a) placed a greater emphasis on the inadequacy of sampling and the possibility that further research would reveal species-level differences, particularly between the two principal morphotypes: *asiaeorientalis*-type with a narrow dorsal ridge and found primarily in temperate portions of the range, and *phocaenoides*-type with a wide dorsal ridge and found in more tropical areas. Amano (2002) indicated that five local populations have been clearly identified in Japanese waters on the basis of skull morphology and mtDNA variability. Mitochondrial DNA analyses by Yang et al. (2002) supported the possibility of migration and/or gene flow between the three putative finless porpoise populations in Chinese waters.

Because of their near-shore and partially riverine distribution, as well as their extreme vulnerability to capture in gillnets, finless porpoises are at risk throughout their range (Smith and Jefferson 2002). The Yangtze River population (subspecies *N. phocaenoides asiaeorientalis*) is Endangered (Baillie and Groombridge 1996) and numerous local populations are depleted if not extirpated. For example, in the eastern and central parts of the Inland Sea of Japan, the density of porpoises is only about 4% that of the late 1970s (Kasuya et al. 2002). Therefore, a geographically comprehensive review of the systematics of this genus, with particular attention to "the paucity of specimens and data available from very large portions of the range (e.g., the Persian Gulf area, the central Indian Ocean, and large portions of Southeast Asia)" (Jefferson 2002a), should be a conservation priority.

Phocoena porpoises

The species-level composition of this genus has been regarded as well settled (cf., Rosel et al. 1995a). There is considerable geographical variation within the circumboreal species *P. phocoena*, with at least three subspecies recognized (Rosel et al. 1995a; Rice 1998; Read 1999). The harbor porpoise is exceptional among the cetaceans in that large series of specimens have been available across much of its range, allowing a relatively large body of literature to amass on population structure from both morphometric (e.g., Yurick and Gaskin 1987; Amano and Miyazaki 1992; Gao and Gaskin 1996) and genetic analyses (e.g., Rosel et al. 1999; Tolley et al. 2001; Chivers et al. 2002).

The complete geographical separation of North Atlantic and North Pacific populations, in combination with the morphological and genetic evidence of isolation, easily justifies the subspecies distinction at the ocean-basin level and might even be considered as evidence to support separate species. The subspecies split is less clear-cut within the North Pacific, where Rice (1998) cited a supposed hiatus in the Aleutian Islands between Shemya (Near Group) and Unimak (Fox Group), a distance of approximately 1500km. This split was not recognized by Read (1999). In contrast, while Rice (1998) rejected the endemic Black Sea/Sea of Azov subspecies *P. p. relicta*, Read (1999) accepted it, citing Rosel et al. (1995b). Rosel et al. (1995b) concluded that "the morphological and genetic data, taken in combination, suggest that the original subspecies designations of *P. phocoena phocoena*, *P. phocoena vomerina*, and *P. phocoena relicta* for the Atlantic, Pacific, and Black Sea populations, respectively, are reasonable." Work is in progress using morphology and nuclear genetic markers to clarify the status of the Black Sea subspecies.

The harbor porpoise has been the focus of extensive management interest over the past several decades because of its susceptibility to gillnet entanglement. Therefore, the question of defining (and naming) units for conservation has become a major concern (Rosel 1997). The species is listed by IUCN as Vulnerable, and two "stocks" (Black Sea and Baltic Sea) are listed separately, also considered Vulnerable (see ASCOBANS 2002; IWC in press).

Brownell reported that observed morphological differences (e.g., dorsal fin shape) between Burmeister's porpoises (*P. spinipinnis*) from the Atlantic and Pacific coasts of southern South America make this species a candidate for taxonomic review, given that these porpoises are taken regularly in coastal gillnets in much of their range.

Dall's porpoise (*Phocoenoides dalli*)

This genus is non-controversial at the species level. The two subspecies (*P. d. dalli* and *P. d. truei*) recognized by Rice (1998) are separated by modal color pattern but no other phenotypic differences, and Jefferson (2002b) suggested that the two forms might be best considered color variants rather than subspecies. The single population of the *truei* form is genetically separated from the several populations of the *dalli* form, but no more than the *dalli* populations are separated from one another (Escorza-Treviño et al. 2004).

Catches (deliberate and incidental) remain high in Japanese and Okhotsk Sea waters, and it is important for assessment purposes to resolve the uncertainty about subspecies. Large series of specimens are available for most of the species' range, so investigations of morphology and genetics should be feasible without requiring new collections.

Cephalorhynchus dolphins

The four species in this genus are well differentiated and there is no reason to expect further splitting at the species level. However, subspecies are recognized for both Commerson's dolphin (*C. commersonii*) and Hector's dolphin (*C. hectori*).

In the case of Commerson's dolphin, a geographically disjunct population in coastal waters of the Kerguelen Islands of the southern Indian Ocean differs in body size, pigmentation, and skull size and shape from the South American/Falkland Islands Commerson's dolphins some 8500km distant (Goodall 1994). Although they have not been formally named and described as such, the two populations were recognized by Rice (1998) as unnamed subspecies (also see Pichler et al. 2001).

In the case of Hector's dolphin, which is endemic to New Zealand coastal waters and listed as Endangered by IUCN (Hilton-Taylor 2000), several geographically and genetically distinct groups have been identified, and the North Island population (classified by IUCN as Critically Endangered; Hilton-Taylor 2000) was recently described as a subspecies, *C. hectori maui* (Baker et al. 2002).

Pilot whales (*Globicephala* spp.)

Rice's (1998) scheme for subspecies of the antitropical long-finned species, *G. melas*, is unlikely to cause much controversy although it is important to recognize that the North Pacific subspecies (unnamed) is long extinct and rests solely upon skulls found at archaeological sites.

The circumtropical species, *G. macrorhynchus*, is subject to ongoing coastal whaling in at least Japan, Indonesia, and the West Indies, and also experiences incidental mortality in gillnets and longlines. In the northwestern Pacific, where sampling has been most extensive, two well-differentiated parapatric forms are recognized (Kasuya et al. 1988; Miyazaki and Amano 1994), and both are exploited in Japanese waters. Brownell reported that the southern form is similar to the pilot whales found around Hawaii and in the eastern tropical Pacific, while the northern form, which is associated with the cold Oyashio Current, resembles the pilot whales found in the cold California Current in the eastern North Pacific. The two forms off Japan are "genetically isolated" (Wada 1988) and probably deserve at least subspecies status. Broader sampling across the species' discontinuous global distribution could well provide evidence of additional subspecies-level (if not species-level) differences.

Lagenorhynchus dolphins

The species differences in this relatively diverse and widespread genus (which itself is not a coherent taxon – see LeDuc et al. 1999) are generally well accepted, as are the three subspecies of the dusky dolphin of the Southern Hemisphere (*L. obscurus*). Rice (1998) claimed that the North Pacific white-sided dolphin (*L. obliquidens*) was sufficiently similar morphologically to the dusky dolphin that it "could almost equally well be regarded" as a fourth dusky dolphin subspecies. However, while the two species are paraphyletic at the mitochondrial level, they are divergent at the nuclear level (Hare et al. 2002, Cassens et al. 2003). Members of the group noted moreover that pigmentation and skull differences between them are clear-cut.

The coastal and often disjunct distribution of these and other *Lagenorhynchus* species invites closer examination for further taxonomic (at least subspecies-level) differences. Although generally abundant, mortality levels in some areas are high enough to generate conservation concern (e.g., Peru: Van Waerebeek 1994; Van Waerebeek et al. 1997; IWC 1997). Some genetics work on the genus is underway in New Zealand.

Irrawaddy dolphin (*Orcaella*)

A consensus has long existed that there is only one species in this genus even though numerous disjunct populations are known, some of them confined to freshwater habitats and others to estuarine/marine habitats (Smith and Jefferson 2002). The extreme vulnerability of these dolphins, owing to their apparently narrow ecological niche, patchy distribution, and tendency to become entangled in fishing gear has made them a focus of conservation concern. Although the species *O. brevirostris* is listed by IUCN as Data Deficient, one local freshwater population (Mahakam River, Borneo) is Critically Endangered (Hilton-Taylor 2000) and Reeves reported that four additional local populations – three riverine (Mekong and Ayeyarwady Rivers; Songkhla Lake, southern Thailand) and one marine (Malampaya Sound, Philippines) – have been proposed for Critically Endangered status.

An initial examination of geographical variation in skull morphology led Beasley et al. (2002) to conclude that *Orcaella* in Australia and New Guinea are separable from those in southern Asia at the subspecies and possibly the species level. A formal description of a new species to contain the Australia/New Guinea animals is imminent. Clarification of *Orcaella* taxonomy at both the species and subspecies levels should be a conservation priority.

Killer whales (*Orcinus*)

This cosmopolitan genus was long regarded as monospecific (Rice 1998), even while researchers were beginning during the 1970s and early 1980s to establish the distinctiveness of two ecotypes in the northeastern North Pacific: resident and transient (Bigg 1982; Bigg et al. 1987, 1990; Fung and Barrett-Lennard 2004). Early attempts to distinguish different types of killer whales in the Southern Ocean met with a general reluctance to change the taxonomic status quo. Mikhalev et al. (1981) proposed that a "dwarf" form of killer whale in Antarctic waters should be recognized as a separate species (*O. nanus*), and Berzin and Vladimirov (1983) made an independent but similar proposal for a new species, *O. glacialis*. Evans et al. (1982) identified substantial and consistent geographical variation in color pattern at a global scale but made no explicit attempt to revise killer whale systematics. In the late 1980s, Heyning and Dahlheim (1988) concluded that, "Until more substantial data are presented, a conservative view of recognizing only one highly variable species probably is warranted."

By the early 1990s, hypotheses of multiple species of killer whales were gaining both plausibility and acceptance. Baird et al. (1992) likened the foraging specialization and sympatric isolation of killer whales in the eastern North Pacific to that observed in Galápagos finches, bluegill sunfishes, some insects, and possibly threespine sticklebacks. They described the resident and transient forms of killer whales as "incipient species." Baird (1994) went even further, arguing that the two forms already deserved species rank. An initial investigation of various genetic markers for killer whales globally was judged inconclusive, but "the current level of gene flow between sympatric residents and transients is low enough that incipient speciation is a possibility" (Hoelzel et al. 2002:343; also see Hoelzel et al. 2004). The recent availability of large series of photographically documented observations in the Antarctic have allowed reevaluation of earlier morphology-based analyses of variability, leading Pitman and Ensor (2003) to conclude that there are three sympatric or parapatric morphotypes there, with different habitat and diet preferences, color patterning, and average group sizes. A background paper submitted to this workshop presents genetic evidence congruent with the morphological data (LJ/04/KW4 by Leduc and Pitman).

Killer whales are not considered to be at risk of extinction on a global basis, but they are at the center of a major regional conservation controversy. The "Northeast Pacific southern resident population" is classified as "endangered," and the "northern resident" and "transient" populations in the same region as "threatened" under Canada's Species at Risk Act (COSEWIC 2003). These designations were established after intense debate, much of which would have been obviated by greater clarity about killer whale taxonomy. In the United States, an initiative to list the "southern resident" killer whales under the Endangered Species Act has caused heated, and still unresolved, controversy, hinging at least in part on the question of whether the resident, transient, and "offshore" forms represent different taxa (Krahn et al. 2002). Resolution of killer whale taxonomy is also important because of its implications related to ecological issues in the North Pacific and Southern Ocean (see under "Rationale for culling" above).

Tucuxi (*Sotalia*)

These small dolphins are distributed along the northeastern coast of South America and the Caribbean coast of Central America, and throughout much of the Amazon River system and at least the lower reaches of the Orinoco River system. Despite the fact that tucuxis are susceptible to large-scale bycatch in fisheries, they continue to be relatively common in large portions of their freshwater and marine range and are not known to be in immediate jeopardy anywhere. Although it has been customary over the past quarter-century to recognize a single species in the genus, it has also been acknowledged that the river and marine populations differ in at least mean body and skull size and possibly in certain ecological characteristics (IWC 1975; da Silva and Best 1994). The two "forms" have generally been designated subspecies: the freshwater *S. fluviatilis fluviatilis* and the marine S*. fluviatilis guianensis*. Recent morphometric analyses have led some researchers to again recognize them as separate species, *S. fluviatilis* and *S. guianensis* (Monteiro-Filho et al. 2002). However, the separation in individual morphological characters is modal rather than absolute. Ongoing genetic investigations are examining the issue of gene flow between the marine and riverine populations, which are genetically differentiated (Caballero et al. 2003, 2004).

Sousa-Stenella-Tursiops-Delphinus-Lagenodelphis Complex

The species in this group of genera are recently evolved, closely related, and notoriously confusing (they are referred to in the report of the Working Group on Achieving a Validated Molecular Taxonomy and Global Phylogeography of the Cetaceans (Appendix 7) as the "STDL complex.") Their taxonomy will ultimately be resolved only with congeneric analyses (see the framework provided by Funk and Ohman, 2003) that include for each of a series of putative taxa a large series of specimens from across its range.

Sousa -- The taxonomy and nomenclature of this reasonably well-differentiated genus have long been in a state of confusion. Humpback dolphins along the west coast of Africa are geographically disjunct and morphologically distinct and therefore generally regarded as a separate species, *S. teuszii*, the Atlantic humpback dolphin. Elsewhere in the genus' range, things are less clear-cut. Although many authorities have taken the "conservative" approach of regarding all of the animals from southeastern Africa to southeastern Asia (including southern China) and Australia as a single polytypic species, *S. chinensis*, the Indo-Pacific humpback dolphin (IWC 1975; Jefferson and Karczmarski 2001), others have argued that these animals should be divided into at least two species, one in the Indian Ocean sector (*S. plumbea*) and one in the Pacific Ocean sector (*S. chinensis*) (Ross et al. 1994; Rice 1998). Ongoing efforts to integrate genetic and other methods and to achieve broad geographical coverage should soon provide clarification. Although inconclusive, a recent review noted that "results from population genetic analyses suggest that strong population structuring occurs in this genus, both within and across ocean basins" (IWC 2003a). Rosenbaum reported that recent morphometric studies provide some support for the separation of *S. chinensis* and *S. plumbea*, although no formal taxonomic split was proposed, pending the results of ongoing molecular studies (Rosenbaum et al. 2002; Jefferson and Van Waerebeek 2004)

Dolphins in the genus *Sousa* are considered Data Deficient for the IUCN's Red List (Baillie and Groombridge 1996), in part because of the major uncertainties surrounding their systematics. Resolution of those uncertainties has long been acknowledged to be a high priority for conservation (Perrin 1988; Reeves and Leatherwood 1994; Reeves et al. 2003; IWC 2003a).

Stenella -- This group of pelagic dolphins is relatively stable at the species level (although the genus itself is not monophyletic; LeDuc et al. 1999). As noted earlier in Section 3, numerous additional subspecies may be added in the future to those already recognized for the pantropical spotted dolphin (*S. attenuata*; Perrin 2001) and spinner dolphin (*S. longirostris*; Perrin 1998) as more specimens and data become available. Some structure has also been suggested in preliminary results of ongoing work on *S. frontalis* in the North Atlantic (Martinez-Vergara et al. 2004).

Some populations are likely disjunct and small, centered on offshore islands or archipelagoes where they have been hunted extensively (e.g., around the Solomon Islands) and are subject to mortality from entanglement. The high mortality of spinner and spotted dolphins in the eastern tropical Pacific tuna fishery is especially well known, but large-scale mortality of these and other *Stenella* species has occurred in other areas including (but not limited to) Japan (*S. coeruleoalba*; Kasuya 1999), the Philippines (Dolar 1994), Sri Lanka (Leatherwood and Reeves 1989), and Taiwan (reported by Wang).

Tursiops -- In the mid-1970s, the IWC Scientific Committee's Subcommittee on Small Cetaceans stated (IWC 1975): "Although the necessary taxonomic work has not yet been done, it seems likely that there is only one species of *Tursiops* [*T. truncatus*], with sharply defined geographical races varying in body size and tooth size [count?] and distributed differentially relative to sea temperature and depth. There is great need to gather materials that will allow definitive examination of the nominal species *T. aduncus*, *T. gillii*, and *T. nuuanu* [and *T. gephyreus* and others], and materials from as many other populations as possible. These names are currently used by some workers." That consensus was challenged by Ross (1977), who proposed on the basis of morphometric comparisons that the two partially sympatric forms in southern African waters represented separate species, *T. truncatus* and *T. aduncus*. A morphological analysis of bottlenose dolphins in Australian waters, however, led Ross and Cockcroft (1990) to reject Ross's (1977) earlier position and propose a return to the earlier concept of one species with strong clinal differentiation caused by habitat variability. With the completion of extensive genetic analyses, and further morphological and ecological comparisons during the 1990s, however, a new consensus emerged that recognizes two *Tursiops* species (e.g., Rice 1998; Wang et al. 1999; Perrin and Brownell 2001; although see Krüetzen and Sherwin 2004). A major weakness in the current taxonomy is that *T. aduncus* may belong in another genus, as it is more closely aligned genetically with *Stenella frontalis* than with *T. truncatus* (LeDuc et al. 1999), albeit for a single mitochondrial marker. Moreover, high levels of differentiation in both mitochondrial and microsatellite markers between disjunct populations of *aduncus*-type bottlenose dolphins (in eastern Asian and southern African waters) have been interpreted as suggesting a third "*Tursiops*" species (Natoli et al. 2004).

Wells and Scott (2002) anticipated that further revision of the genus would prove necessary "to acknowledge significant differences between forms from different ocean basins, as well as differences between forms in inshore vs. offshore habitats within ocean basins" (e.g., Segura García et al. 2004). Coastal and offshore *T. truncatus* morphotypes in the North Atlantic were recently found to have greater nuclear genetic differentiation between them than exists between the short- and long-beaked common dolphins (Kingston and Rosel 2004). Thus, more species-level splitting may yet occur in the Atlantic (see also Mead and Potter 2004 and Barreto 2004). As indicated earlier under “Management of Cetacean Exploitation” and “Management of International Trade,” the taxonomy of bottlenose dolphins can have profound significance for certain aspects of management. Therefore, a comprehensive review of the systematics and population structure of this genus remains a high conservation priority (cf., Reeves and Leatherwood 1994; Reeves et al. 2003). In that regard, it is of interest that such a review has been perennially listed as a future “priority topic” for the IWC Scientific Committee’s Sub-committee on Small Cetaceans (IWC 1994 *et seq.*). The taxonomic status of the Black Sea subspecies *T. t. ponticus* has been the focus of management controversy in CITES (see above under “Management of International Trade” above), demonstrating the importance of work reported at this meeting by Viaud et al. (2004).

Delphinus **--** Biologists had long been aware of external morphological differences between partially sympatric long-beaked and short-beaked forms of common dolphins, but it was not until the early 1990s that the two forms were clearly described as separate species on the basis of morphology and ecology (Heyning and Perrin 1994) and genetics (Rosel et al. 1994). While Rice (1998) recognized these two species, he also chose to recognize a very long-beaked morphotype as a third species, *D. tropicalis*, even while acknowledging that it “may yet be shown to intergrade” with the long-beaked common dolphin, *D. capensis*, in several areas. Jefferson and Van Waerebeek (2002) concluded on the basis of morphological comparisons that the *tropicalis* form should be regarded as a subspecies of *D. capensis*. The population of common dolphins in the Black Sea has long been recognized as an endemic subspecies, *D. delphis ponticus*. This polytypic genus seems a good candidate for further taxonomic clarification and revision, at least at the subspecies level. *D. capensis* (and possibly also *D. delphis*) apparently exist in many isolated populations, and work is in progress to further investigate structure in both species.

5. FACTORS PRESENTLY RETARDING OR INHIBITING PROGRESS IN CETACEAN TAXONOMY

5.1 Logistical factors

The group noted the description of logistical factors given in LJ/04/Taxo1 and agreed that they should be addressed in specific recommendations (Section 7 below).

5.2 Methodological factors

Discussion concentrated on species and subspecies concepts.

5.2.1. Species concepts

Considerable discussion was devoted to consideration of the various species concepts, most of which have been characterized in the literature as variants of either the Biological Species Concept (BSC) or the Phylogenetic Species Concept (PSC). A table in Dalebout’s workshop background paper (LJ/04/Phylogeo1) summarizes a number of major species delimitation methods and the species concepts under which they operate (Attachment 3). The group agreed that this table offered useful examples of operational frameworks that are available for delimiting species. As a supplement to the table, the group asked Dalebout and Rosenbaum to prepare brief statements describing frameworks that they have employed to delimit species in two cases, one involving beaked whales (Ziphiidae) and the other right whales (Balaenidae).

The group agreed that both major species concepts, the BSC and PSC, as well as their various subapproaches, should be considered relevant and useful in cetacean taxonomy, and that the different approaches to species delimitation should be employed in a pragmatic way.

Hey provided a basic framework for considering species concepts (see Hey 2001), which the group generally accepted and is summarized in the following two paragraphs:

Biologists refer to species as groups of organisms that are distinct – genetically and morphologically – because of evolutionary divergence from other groups. Such evolutionary entities, or lineages, are the focus of many of the species concepts that have been proposed over the years (Mayden 1997; de Queiroz 1998). This is certainly true for general theoretical concepts, such as the evolutionary species concept (Simpson 1961), but also for species concepts that outline specific criteria for species identification. For concepts like the BSC and different versions of the PSC, the criteria are based partly on the recognition that entities to be identified as species are groups of related organisms that, by evolution, have diverged irreversibly from other groups.

Biologists also recognize that evolution is a usually gradual process, and that the origin and divergence of species can occur over very large numbers of generations. The slow evolutionary process is clearly observable when considering multiple populations of related organisms. In such contexts, some pairs of *populations are likely to be indistinguishable from others, while others are so distinct in multiple ways as to clearly merit identification as separate species. Necessarily, cases also arise where some divergence is apparent but it is not entirely clear that two species should be recognized. In some such cases, the criteria of two equally well-motivated but different species concepts lead to conflicting interpretations. Such discrepancies are expected simply as a consequence of application of different sets of criteria to real-world patterns that are at times truly intermediate. As observed by Mace (2004): "For the sake of having lists of species that are informative and useful, conservationists will need to adopt a pragmatic taxonomy and live with some of its biological inconsistencies."*

In recognition that divergence is found across the continuum, and of the need for guidelines for species delimitation in the midst of that continuum, the working group proposed a general, rather than a specific, protocol for species recognition. This protocol should be understood as advisory (guidelines) rather than prescriptive (criteria).

Both morphological data and genetic data, taken as proxies for reproductive isolation, can provide clear evidence of irreversible divergence. It is possible for individual morphological characters to be convergent, and for the data from one genetic locus to not reflect phylogenetic history because of homoplasy or natural selection. Therefore, a finding of congruent divergence for each of multiple distinct kinds of data should be taken as strong support for species designations. Such distinct kinds of data could include morphological data together with genetic data, or data from multiple independent genetic loci. Ideal data sets, including both morphological data and data from multiple loci, can provide not only a large amount of information for decisions regarding species, but also information necessary to assess the uncertainty associated with that decision.

Data on geographical ranges and on behavior (e.g., feeding behavior and vocalizations, such as in killer whales; also see Mesnick and Barlow 2004) can complement morphological and genetic data. Given the difficulties of knowing the degree to which geographical distribution and behavior actually reflect genetic divergence, these kinds of data should not be the primary basis of species delimitations, but can serve as useful lines of evidence.

Notwithstanding the rule of precedence, taxonomists have long recognized that species designations can be subject to revision as new data emerge. Similarly, present-day evolutionary biologists recognize that species designations must serve as hypotheses about evolutionary history (Hey et al. 2003). Individual taxa, e.g. species, are necessarily associated with support from the data and evolutionary theory that were used to define them. In this light, we appreciate that species designations have some uncertainty and may be subject to revision as more data become available.

5.2.2 Subspecies concepts

The subspecies concept has a perplexing and confusing history (e.g., Mayr and Ashlock 1991). Its inherently non-rigorous nature continues to plague taxonomic discourse and, by some views, hinders conservation (Zink 2004). No strict criteria for defining a subspecies have been applied in the past. Rice (1998) acknowledged that the amount of "morphological overlap" allowable for subspecies was up to the investigator, but he also cited a "rule" (attributed to Amadon 1949) that 75% of one population must be separable from all (99%-plus) members of "overlapping populations" to qualify as a subspecies. Alternatively, 97% of one of two "overlapping populations" must be separable from 97% of the other. Having stated these rules, Rice proceeded to recognize numerous subspecies, often founded on much looser criteria. Indeed, strict quantitative criteria for subspecies have never been applied to cetaceans.

Reeves and Perrin (LJ/04/Taxo1) considered the terms *race*, *geographical variant*, and *geographical form* essentially interchangeable with the term *subspecies*, except that this latter requires a formal, published description containing a defensible argument for morphological (or other) differentiation *and* evidence of allopatry or parapatry. In marine mammals, most geographical variation in morphology is due to differential selection (ecological divergence) rather than genetic drift (Perrin 2002). Cetacean subspecies, for the most part, have been geographical forms that have been formally described and given a Latin trinomial. Subspecies-hood has been the result of intensive research focus.

Dalebout (LJ/04/Phylogeo3) considered the discussion of subspecies offered in LJ/04/Taxo1) and encouraged the explicit recognition of the importance of historical separation, genetic heritability, and multiple sources of evidence for subspecies designations, citing Avise and Ball (1990).

During discussion, Taylor reported that the criterion of <1 breeding migration per generation has been used as genetic evidence for subspecies delimitation.

The naming of a subspecies involves steps similar to those required for naming a species, but the process is less rigid and formalized. For the tetrapods, the focus of subspecies delimitation tends to be on geographical separation, and diagnosis generally has rested on morphological differences (e.g., plumage in the case of birds, facial color patterns in the case of primates). Mammalian systematists tend to attribute evolutionary importance to subspecies and regard them as a way of recognizing incipient speciation.

Cetacean subspecies have traditionally been designated primarily on the basis of morphology. With cetaceans, for which collecting and preserving samples for morphological comparisons is exceptionally difficult, the group concluded that the allowable lines of evidence for subspecies designations should be extended to neutral genetic markers (much more readily attainable via biopsies). Genetic differences have already been used to some extent in defining and describing cetacean subspecies (e.g. Hector's dolphin). The group recommended that:

In addition to the use of morphology and genetics to define subspecies, the subspecies concept should be understood to embrace groups of organisms that appear to have been on independent evolutionary trajectories (with minor continuing gene flow), as demonstrated by morphological evidence or at least one line of genetic evidence. Geographical or behavioral differences can complement morphological and genetic evidence for establishing subspecies. As such, subspecies could be geographical forms, incipient species, or even actual species for which data are currently too poor to support their being elevated to the species level.

Although the group discussed the idea of using ocean-basin scale gaps in distribution enforced by physical barriers (e.g. continents) as a sole criterion for establishing subspecies, this idea was rejected by consensus.

The group noted that criteria for delimiting subspecies can be chosen arbitrarily, and that different workers might choose different levels of diagnosability or gene flow. Therefore, the onus should be left on individual investigators to explain their choice of criteria and make their case for designation accordingly. Scientific peer-review, publication procedures, and peer opinion after publication can be expected to help ensure the integrity, credibility, and legitimacy of the subspecies designation process. This explanation applies with equal force to the species designation process: peers are either convinced by an argument or they are not.

The group considered several examples to see how the general guidelines indicated above might work for designating species and subspecies. First, the species guideline of at least two independent lines of evidence was applied to the right whales, for which Rosenbaum et al. (2000), provided a single line of genetic evidence (mtDNA) to separate the three species. Distribution was a second line of evidence offered by Rosenbaum et al. (2000). These authors considered a number of morphological and physiological characteristics of right whales, but found only insufficient evidence or limited differences in pair-wise comparisons between ocean basins, rather than consistent differences among all three basins. By the guidelines for species as presented above, the Rosenbaum (2000) paper would not have been sufficient to carry the argument for three separate right whale species. At this workshop, however, Rosenbaum reported that there was now evidence from multiple nuclear genetic markers (submitted for publication) showing a similar degree of isolation, thus providing a second line of evidence, as required by the guidelines.

The guidelines were then applied to the spinner dolphin and blue whale. Perrin (1990) established the eastern spinner dolphin as a separate subspecies on the basis of morphological differentiation and differential distribution. The pygmy blue whale was established as a subspecies by Ichihara (1966) on the basis of a number of morphological characters (tail length, baleen length, body length at maturity, and pigmentation pattern) as well as geographical separation from the larger Antarctic blue whale in the Southern Hemisphere (Ichihara 1966). In both these cases, the subspecies designation met the guideline, that at least one line of evidence is needed to support major divergence.

5.2.3 Laboratory and field techniques

The group discussed options for improving techniques and incorporated these in recommendations (Section 7 below).

6. RANKING OF SPECIES AND SPECIES GROUPS FOR ATTENTION

In extensive discussions, the group attempted to rank all cetacean species according to the relative importance of resolving their systematics to inform conservation decision-making (table compiled here is presented as Table 1 in main text of workshop report). The rank assigned to each species was intended to incorporate consideration of both degree of taxonomic uncertainty (including at the subspecies level) and perceived seriousness and immediacy of threats to the taxon's persistence. Taxonomic uncertainty means the working group had reason to believe that additional splitting (rarely lumping) was likely to be justified, e.g., in instances when populations are disjunct and occur in different ocean basins. The group attempted to integrate the two distinctly different factors by reference to the matrix illustrated in Appendix Table 5-1 below. In regard to "taxonomic uncertainty," when problems of taxonomy related to distributional discontinuity had already been resolved to a satisfactorylevel (e.g., in the case of Hector's dolphin), the rank was downgraded accordingly.

It was agreed that special consideration should be given to centers of endemism or to regions where boundaries are known to occur across groups of species. Centers of endemism would include the Sea of Japan, northern Indian Ocean, Gulf of California, Baltic Sea, Mediterranean Sea, Black Sea, and Red Sea. Boundary areas would include the Cape of Good Hope and the Wallace Line in the central Indo-Pacific. Focusing research in these areas could be an efficient way to obtain data for recucing taxonomic uncertainty for multiple species.

The following specific issues stand out as needing particular attention:

- With Norway continuing to hunt North Atlantic minke whales on the basis of a formal objection under IWC rules, and Japan taking hundreds of minke whales in the Antarctic and minke, Bryde's, sei, and sperm whales in the North Pacific each year under national permits for scientific research, three areas of taxonomic research on baleen whales need immediate clarification. One is resolution of the *borealis-edeni-brydei-omurai* complex. A second is the question of appropriate designations for North Atlantic and North Pacific minke whales, and in particular J-stock minke whales (see earlier). Resolution of these questions would have relevance to management under the IWC, CITES, and perhaps the Convention on Migratory Species. The third area related to the blue whale. Although blue whales are no longer exploited, they were drastically depleted by commercial whaling during the 20th century. The current status of populations, both in terms of taxonomy at the subspecies level and with respect to abundance and trends, is uncertain. Of particular interest and concern is the population in the northern Indian Ocean that appears not to migrate to the Antarctic in summer.
- The longstanding difficulties of determining the taxonomic status of inshore and offshore populations of bottlenose dolphins (often within ocean basins or seas and including *T. truncatus* and *T. aduncus*) need to be resolved so that the deliberate, incidental, and mixed-intent "fisheries" for these animals (e.g., in western South America, southern Asia, and Japan) can be assessed more rigorously and managed more responsibly. The importance of bottlenose dolphins in the live-capture industry creates a special need for taxonomic clarity, given the involvement of CITES in regulating trade and national agencies in stock assessment. Ultimate resolution of bottlenose dolphin taxonomy will require congeneric analyses.
- The bottlenose dolphins are part of a wider taxonomic problem that involves the entire *Stenella-Tursiops-Delphinus-Lagenodelphis* complex. Although external morphology makes field identification of these genera and most of the species within them relatively straightforward, paraphyly of their mtDNA lineages creates serious difficulties with genotypic resolution and forensic identification of specimens. Therefore, congeneric analyses (i.e. analyses that consider the full range of diversity within and across the species in this complex) are required to clarify this group's taxonomy. Many populations of these dolphin species/genera are either heavily exploited, subject to large-scale bycatch, or both.
- The taxonomic status of humpback dolphins (*Sousa* spp.) in the Indo-Pacific needs to be clarified. These animals are particularly vulnerable because of their near-shore distribution, tendency to occur primarily in or near estuaries, and apparently low numbers. Their discontinuous occurrence and morphological variability across the range from East Africa to southern China and eastern Australia strongly suggest that multiple taxa should be recognized.
- Like humpback dolphins, Irrawaddy dolphins (*Orcaella brevirostris* sensu lato) are neritic and occur discontinuously in brackish estuaries and near-shore marine waters of northern Oceania and parts of Southeast Asia, but they also occur far up some rivers and in certain lake or lagoon systems. Several populations are Critically Endangered as a result of incidental mortality in fisheries and various forms of habitat loss or degradation. In addition to the forthcoming proposed new species-level distinction within this genus (see above), it is important to establish whether subspecies- and additional species-level differences exist.
- Taxonomy of the genera *Neophocaena* and *Platanista*, both of which are currently considered monotypic, needs to be addressed with a sense of urgency. Both genera may include two (or more) species, and at least some of these (putative) species occur in only one or a few countries. Their extremely coastal or riverine distribution and vulner-

ability to gillnet entanglement, exposure to toxins, and other potential threats mean that improved clarity with regard to systematics could have important implications for conservation and management.

- Two South American genera have long been in need of taxonomic revision. The obligate freshwater genus *Inia* contains three geographically distinct groups of dolphins that are regarded as either: (a) a single species with three subspecies, (b) two subspecies, one of which consists of two subspecies, or (c) three separate species. Given the rapid deterioration of riverine habitat as a result of competing demands from humans, it is important to clarify the taxonomy of the *Inia* dolphins while they are still relatively abundant. The riverine form of *Sotalia* is sympatric with *Inia* throughout most of the Amazon and at least part of the Orinoco system. The species-level distinction between the two ecotypes of this small dolphin – riverine and marine coastal – is important to resolve, while these animals are still relatively abundant. Large-scale gillnet mortality of *Sotalia* occurs in many areas.
- Although long considered safe from the effects of human activities, the pelagic, deep-diving beaked whales (Ziphiidae) are now known to be vulnerable to underwater noise (e.g., military sonar, geophysical seismic profiling) and entanglement in drift gillnets. Two widely distributed species (*Ziphius cavirostris* and *Mesoplodon densirostris*) and one North Pacific endemic (*Mesoplodon stejnegeri*) were identified by workshop participants as warranting special attention to resolve taxonomic uncertainty.
- Finally, as explained in Section 4 above, the killer whales (genus *Orca*) have become a high priority for conservation management, and clarification of their taxonomy is a major need on the part of management agencies (see Appendix 6 on the killer whale as a case study).

7. RECOMMENDATIONS

In addition to the needs outlined in the preceding section related to priority species and species groups, the working group identified the following items to address the logistical and other constraints that make cetacean taxonomy inadequate for conservation and management:

Cataloguing of material

13. More of the world's cetacean collections in museums and other institutions should be catalogued and made accessible through the internet. This effort is already underway by many major museums, but the contents of some smaller collections remain relatively unknown. To facilitate access and comparisons, catalogues should ultimately be linked and managed through a single centralized location. The information catalogued for each specimen should be standardized with the following minimum data: collection locality and date, age/sex class, material collected (including soft tissue samples), and total length. The inclusion of photographs of external appearance and skull morphology with records available on-line wherever possible is strongly encouraged. Existing comprehensive lists of specimens should be updated and new compilations should be produced for additional taxa. These should also be available on the internet. Centralized files of skull photographs, external body photographs, and sound recordings should be established. Such centralization (by individual institutions, with appropriate network links) is increasingly feasible with new digital technologies.
14. More databases and archives should be funded and developed to make tissues for genetic research, as well as genetic data for species identification purposes (e.g., GenBank), publicly available. In addition, a standardized minimum of information regarding source specimens should be included in all Genbank records, e.g. collection location and date, full sample number designated by institution where sequence data was generated, whether a biopsy sample came from a free-swimming animal (and known individual ID# and photo) or the material was obtained from a museum specimen (including museum specimen number and full name of museum).

Collection and Storage

15. More emphasis should be placed on the collection and permanent museum preservation of adequate series of cetacean specimens as baseline material for taxonomic research. Intensified efforts should be made to obtain specimens (skulls, skeletons, biopsies) from

remote regions and thus to amplify the geographic coverage of available samples, especially for species or genera of special conservation concern. Such sampling should emphasize the salvage of stranded carcasses and body parts, bycaught animals, and deceased captive individuals, supplemented with biopsies from free-ranging populations. To this end, stranding networks should be adequately supported and resulting specimens and data made available and accessible.

16. Adequate series should consist of at least 20-30 adult specimens of each species, including post-cranial material where at all possible, and accompanied by "voucher" material such as soft-tissue samples, photographs, and measurements of the whole animal. If a DNA extraction is made, a sample of that material should be curated with the specimen when feasible, or at least with clear links back to the specimen when that is not feasible. The taxonomic value of fully documented specimens is infinitely greater than piecemeal collections of unassociated material. Collection and permanent museum preservation of adequate series of entire skeletons, including post-cranial bones, can be a special problem for the large whales, for the obvious reasons of collection and preparation logistics and space requirements. For large whales, where storage space is a problem, adequate sample sizes could be considered on an ocean-basin rather than institutional basis (equivalent to the likely scale of geographical variation).
17. Tissue samples and DNA extracts should be archived using the best long-term preservation methods available, recognizing that these will change and improve with time, as will the range of data that can be obtained from such material. At present, the types of data that can be derived from tissue samples include DNA, pollutant loads, and diet. Preservation requirements will differ depending on the type of data sought. A standardized minimum should be established – e.g., at least a skin or muscle sample preserved in ethanol or in a saturated saline solution of 20% DMSO at –20 deg C for DNA analysis (see IWC 1991). Support should be provided to improve procedures and infrastructure for the long-term preservation of DNA and soft-tissue samples. Because soft-tissue samples, even when stored in DMSO and refrigerated, have a limited shelf life, curators should be encouraged to undertake DNA extraction and archiving as rapidly as possible after collection. Where DNA sequence data are obtained from specimens held in museums and other institutions, the specimen records should be updated in a timely fashion to indicate this, including citations of any publications using these data and Genbank accession number(s).
18. The value of tissue samples for DNA (and other) analyses, including biopsy samples collected from free-swimming animals, along with information on how to preserve such samples and where they can be sent, should be advertised more widely. This is particularly important for areas and species characterized by a high degree of taxonomic uncertainty. Specimens from which both osteological material (e.g., the skull) and a tissue sample have been collected are of greatest value for taxonomy. Next in value are specimens documented with photographs of diagnostic features (preferably including external appearance) and a tissue sample. In the event that no photographic documentation of the source animal is collected, a tissue sample (e.g., biopsy) may still be of some, though lesser, value.

Access and Study

19. More grants should be made available to allow researchers to travel to far-flung museums to examine, measure, photograph, and sample specimens. This is a special problem because of the size and rarity of many species. In some cases, researchers based in different geographical locations could establish cooperative agreements that allow, for example, two individuals to examine specimens for each other's study, thus cutting their travel costs..
20. Longstanding obstacles to bonafide science caused by permit requirements (e.g., under the Convention on International Trade in Endangered Species [CITES] or imposed by nation-states to protect their "biological heritage") should be addressed and, if possible, removed as they too often inhibit the sharing and free exchange of scientific specimens. Such sharing and exchange can be fundamental to resolving taxonomic problems of conservation importance. Member countries need to establish institutional permits to facilitate exchange of research specimens.

Laboratory Techniques and Analysis

21. The search for, sampling, and analysis of so-called “ancient” DNA from cetacean bone material, baleen, and other preserved tissues should be continued and expanded. Further development of techniques for extracting DNA from such materials should also be supported. It should be recognised that DNA extracted from historical (“ancient”) material such as bones and teeth may be unstable as well as degraded. Due likely to a combination of natural decomposition, buildup of bacteria and fungi, and museum preparation techniques, DNA extracted from such material may only allow successful PCR amplifications of fragments of any length for a limited window of time. The extent of this problem should be investigated, together with methods that may help overcome or at least alleviate it (e.g., additional DNA purification steps during the extraction process).
22. Analyses to address questions at the boundary between species and infraspecific entities should be congeneric, that is they should include both a range of what are thought to be closely related species-level taxa and adequate geographic and sample-size coverage within what are thought to be species, to allow detection of incomplete lineage sorting and other types of paraphyly (Funk and Omland 2003) and to develop the resolution needed for forensic applications.

Development of Additional Genetic Resources

23. *Cell lines*. Molecular analyses are currently conducted using DNA made directly from tissue samples, which are expensive to obtain and of inherently limited amounts and longevity.
    a) Cell lines, established from tissues of living individuals, should be established from as many species as possible. Immortal cell lines provide indefinitely renewable DNA resources and thereby circumvent many of the limitations associated with tissue-based DNA preparations.
    b) Cell lines can also permit the assessment of simple molecular phenotypes, such as gene expression. Although they would not be expected to reflect exactly what is found within particular tissues of the living organism, such simple phenotypes are still useful for many purposes.
24. *Phylogenetically informative loci*. To date, cetacean molecular phylogenetic analyses have been limited largely to mitochondrial sequences. Because different loci can have different histories, ideally multiple loci should be used for phylogenetic assessment. Effort should be devoted to developing additional nuclear loci to complement the work on mitochondria. Two general categories of loci should be developed, as follows:
    a) Randomly selected neutral loci. Nonfunctional regions of the nuclear genome, such as introns of protein-coding genes, have been shown to be variable within and between closely related populations. Such loci often show evidence of incomplete lineage sorting or gene flow (e.g., in the Delphininae), but are still very useful for assessments of demographic history using population genetic models.
    b) Loci selected to have short intrapopulation gene trees. Like the mitochondria, some genes are expected to have shallow gene trees within populations or species. Y-chromosome genes, like the mitochondria, are expected to have shallow gene trees because of reduced effective population sizes. A separate category of such genes consists of the ribosomal RNA genes, which occur in long arrays and show little intraspecific variation because of high rates of concerted evolution. Finally, protein-coding genes, that are shown to evolve rapidly compared to genomes of other mammals, may be good candidates for having short intraspecific gene trees because of recurrent selective sweeps.
    Initial effort to develop several loci of each category, for use in one species group, will be especially beneficial because once utility has been established, such loci can then be readily used by other researchers for work with other species groups.

13. *Genome sequence*. Complete, or nearly complete, genome sequences are rapidly becoming available for many mammals. Because cetaceans have evolved so rapidly at the morphological level, it is imperative that an odontocete and a mysticete be given priority for genome sequencing. Such sequences would lay the groundwork for identifying useful genes for phylogenetic and taxonomic

research and would open up new areas of cetacean genetic research. Rapidly evolving structural and functional components of the genome would be revealed and could become the basis for functional and systematic evolutionary research.

8. OTHER BUSINESS

The group agreed to delegate preparation of its report to the chair and the rapporteur.

9. ADJOURNMENT

The working group completed its discussions and adjourned at 1730 hrs on 1 May 2004.

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Appendix Table 5-1. Basis for integrating taxonomic uncertainty and conservation risk in order to rank species according to the importance of taxonomic research in relation to conservation (1 high, 2 medium, 3 low; see Table 1). Taxonomic uncertainty takes into account distributional discontinuities, especially between ocean basins.

			Taxonomic Uncertainty	
		High	*Medium*	*Low*
Conservation Risk	*High*	1	1	3
	Medium	1	2	3
	Low	3	3	3

ATTACHMENT 1

Glossary of terms

Allopatry – Geographic separation, such that members of two or more populations do not come into contact and cannot interbreed.

Control Region – A noncoding portion of the mtDNA molecule that functions in replication.

Cytochrome b – A mitochondrial gene involved in respiration and used in many studies of phylogenetic relationships at and above the species level.

*Distinct Population S*egment (DPS) – A concept used in vertebrate management in the United States, for which there seems to be little agreement on an exact definition. The NMFS considers that a DPS for Pacific salmonids must satisfy two criteria: 1) it must be substantially reproductively isolated from other conspecific population units, and 2) it must represent an important component in the evolutionary legacy of the species (Federal Register, Feb. 7 1996).

Evolutionarily Significant Unit (ESU) – A variously defined concept used in wildlife management and conservation. One definition is a group of individuals characterized by reciprocal monophyly at mtDNA loci and frequency differences at nuclear alleles. Other definitions are more qualitative, with the intent to designate what should be conserved in order to preserve potentially useful genetic variation.

Fixed Difference – Absolute difference in a character that diagnose 100% of specimens to a taxon, as opposed to simple frequency differences. In genetics, a sequence, position, site or allele present in all members of one population and lacking in all members of another.

Haplotype – A particular combination of alleles or nucleotides in a specific region of a chromosome or mtDNA molecule.

Homoplasy – The repeated appearance of similar features in two or more unrelated (i.e., not directly descendant) taxa.

Locus – The particular location on a chromosome or mtDNA molecule at which a gene for a particular trait or a particular marker resides.

Management Unit (MU) – Population with significant divergence of allele frequencies at nuclear or mitochondrial loci, implying restricted gene flow.

Microsatellites – Noncoding short tandem repeats in the nuclear genome; those having variable number of repeats used in population analyses.

Mitochondrial DNA (mtDNA) – Maternally inherited DNA contained in the mitochondrion, in a single, usually circular molecule. This is the most common type of genetic data used in marine mammal population analyses.

Monophyly – Relationship among two or more populations, containing all the descendants of a hypothetical common ancestor. As opposed to paraphyly (see below).

Nucleotide – The basic building blocks of nucleic acids, consisting of a sugar, a nitrogenous base, and a phosphate group.

Parapatry – Geographic contiguity, such that ranges abut one another (but do not actually overlap), and only members of populations at the edges have the opportunity to come into contact and interbreed.

Paraphyly – Relationship among two or more populations, containing the descendants of a hypothetical common ancestor that retain shared primitive characters, to the exclusion of those that have lost those characters. As opposed to monophyly (see above).

Phylogenetic – Relating to analyses based on inferred genealogical relationships among groups.

Polymerase Chain Reaction (PCR) – A biochemical laboratory procedure used to amplify DNA to levels useful in analyses.

Polymorphic – A character (gene or marker) with two or more distinct character states (alleles).

Polyphyly – Relationship among two or more populations which do not derive from a common ancestor.

Population Aggregation Analysis (PAA) – A formalized and expanded method of taxonomic investigation, in which all individuals in a local population are assumed to belong to the same species, and individuals that share identical character attributes (morphological or molecular) and are drawn from two different populations provide evidence that the populations are conspecific (Davis and Nixon 1992).

Population – A group of individuals of a species that are reproductively isolated to some degree from other such groups.

Race – Geographical form of a species, often using interchangeably with the term subspecies (the latter, however, can carry a formal designation and trinomial).

Reciprocal Monophyly - Relationship among two or more populations, each more closely related to to the other than to any other groups.

Species – The primary unit of biological evolution (see *Species Concepts* below). Although there is little consensus of exactly what a species is, all agree that the intent is to identify population entities on separate evolutionary pathways with little or negligible gene flow between them.

Species Concepts – A series of competing definitions of what a species is and how it is established by research. There are many different, but not mutually exclusive, species concepts (22 or more). The most commonly used ones in marine mammal systematics have been:

> *Biological Species Concept (BSC)* – A species is a group of interbreeding or potentially interbreeding natural populations separated from other such groups, by intrinsic (genetically fixed) barriers to gene flow (Mayr 1963, 2000).
>
> *Phylogenetic Species Concept (PSC)* – Two different species concepts are referred to by this name. In the one proposed by Mishler and Brandon (1987), a species is the least inclusive taxon recognized in a forma phylogenetic classification. In the one proposed by Hennig (1966) and clarified by Wheeler and Platnick (2000), species are the smallest diagnosable clusters of organisms, distinct from other such clusters, within which there are parental patterns of ancestry and descent (Cracraft 1989).
>
> *Genealogical Species Concept (GSC)* – This is similar to the PSC, but uses an explicitly history- or lineage-based approach and with greater emphasis on genetic data.
>
> *Genealogical Concordance Concept (GCC)* – This attempts to reconcile elements of the BSC and PSC. It defines a species when the following conditions are met: 1) concordance across sequence characters within a genetic locus leading to conclusive exclusion; 2) concordance in these genealogical patterns across multiple loci, both mitochondrial and nuclear; 3) concordance with biogeographical patterns; and 4) concordance with morphological characters.

Stock – A population of a species defined for the purposes of management (generally same as Management Unit).

Subspecies – The smallest unit used in formal taxonomy (subspecies when formally described are given a trinomial scientific name). The classical subspecies concept incorporates both morphological distinctiveness and geographical isolation. A rule of 75% separability from all members (99+%) of overlapping populations has been given (Amodon 1949) but rarely used explicitly. A more appropriate definition would be groups that appear to be on an independent evolutionary pathways but with still some significant gene flow between them and thus could be geographical forms or incipient species.

Sympatric – Having at least partially overlapping breeding ranges, such that most members of two or more populations have opportunities to come into contact and interbreed.

(Cited references listed in main subgroup report).

ATTACHMENT 2

Agenda for Working Group on Species- and Subspecies-Level Taxonomy

1. Preliminaries
   1.1 Review terms of reference
   1.2 Arrangements for workshop
   1.3 Adopt agenda
2. Review of importance of taxonomy to conservation
3. Review of shortcomings of current taxonomy in terms of needs of management
4. Review of taxonomy for currently recognized species/species groups
5. Factors presently retarding or inhibiting progress in cetacean taxonomy
   5.1 Logistical factors
   5.2 Methodological factors
      5.2.1 Species concepts
      5.2.2 Subspecies concepts
      5.2.3 Laboratory and field techniques
6. Ranking of species and species groups for taxonomic attention
7. Recommendations
8. Other business
9. Adjournment

ATTACHMENT 3

Species Delimitation Methods

Method[1]	*Biological criteria*	*Suitable data types*	*Species Concept*	*Assumptions/ Limitations*	*Nested?*[2]
PAA	Lineage isolation sufficient for fixation of character states	DNA sequence data, morphology	PSC	Character-fixation difficult to confirm statistically; individuals from same locality assumed to represent same population or species.	EXCL > CHA > PAA
CHA	Lineage isolation sufficient for coalescence to monophyly of haplotypes at one locus	Non-recombinant DNA haplotypes	PSC (+ some aspects of GSC)	*Non-phylogenetic* cladograms of haplotypes considered equivalent to species trees; individuals from same locality assumed to represent same	EXCL > CHA

				population or species.	
EXCL	Lineage isolation sufficient for allele coalescence to monophyly at unlinked loci	DNA haplotypes (alleles) for multiple loci	GSC	Unspecified number of independent genetic markers with divergence profiles.	GLC > EXCL
TTC	Lineage isolation sufficient for ecological/allopatric character divergence	Genetic, ecological morphological or physiological data with DNA haplotypes	CSC	H2 can never be completely falsified, choice of candidate traits may be subjective, inference keys can be misleading with insufficient sampling	EXCL > TTC
WP	Lineage isolation sufficient for geographical character divergence	DNA sequences, morphology	GSC/CSC	No gene flow between species; no recombination among DNA haplotypes	EXCL> WP > TTC
FFR	Recombination within nuclear loci is limited by the extent of geneflow	Co-dominant nuclear loci	BSC	All alleles segregating at a locus must be identified; no gene flow between species	EXCL > FFR
M2002	Combines aspects of PAA and EXCL with reference to traditional taxonomic groupings based on morphology	DNA sequences (with additional data from morphology, geography etc)	Aspects of PSC/GSC and GCC	As noted for PAA and EXCL	_

[1] CHA, cladistic haplotype aggregation; EXCL, exclusivity criterion; FFR, field for recombination; GLC; Genealogical/Lineage Concordance; HZB, Hybrid Zone Boundary; M2002, Milinkovitch et al. (2002) suite of criteria (see below); PAA, population aggregation analysis; TTC, Templeton's Tests of Cohesion; WP; Wiens and Penkrot (2002) method.

[2] In theory, could these methods be nested hierarchically within one another, and if so, how?

Example 1 (provided by Dalebout)

One approach to the delimitation of species units is through the application of the Genealogical/Lineage Concordance Concept (GCC; Avise 2000; Avise and Ball 1990). A group of organisms is considered to constitute a species under the GCC when the following evidence provides concordant support (Avise 2000; Avise and Ball 1990): 1) across-sequence characters within a genetic locus lead to conclusive exclusion; 2) genealogical patterns consistent across multiple loci, both mitochondrial and nuclear; 3) biogeographical patterns consistent; and 4) morphological characters consistent. The GCC approach was applied by Dalebout et al. (2002, 2004) in the discovery and description of *Mesoplodon perrini,* a new species of beaked whale.

To assist in species delimitation and routine identifications of beaked whales, a validated DNA reference database of control region and cytochrome *b* sequences was compiled for all 21 beaked whale species (Dalebout et al. 1998, 2004; Henshaw et al. 1997), together with a complementary nuclear DNA database of actin intron alleles for 17 of the 21 beaked whale species (Dalebout et al. 2004). Phylogenetic analyses of the mtDNA datasets confirmed the *alpha* taxonomy of all beaked whale species currently recognized. Reference sequences representing the species grouped together in species-specific lineages with high bootstrap support, distinguished from other such lineages by a series of synapomorphic nucleotide substitutions. All species also possessed fixed, diagnostic characters (*sensu* Davis and Nixon 1992) at one or both of the mtDNA loci (Dalebout 2002; Dalebout et al. 2002). For the nDNA actin intron, all beaked whale alleles were species-specific and, for the majority of species, grouped together in phylogenetic analysis to the exclusion of alleles representing other species (i.e., monophyly of alleles within species). While bootstrap scores for some species-specific clades were low, the overall consistency index of the tree was high, indicating little homoplasy in the data. Several internal branches received additional support from the presence of unique, diagnostic insertion-deletion substitutions.

Individuals of *M. perrini* in California were originally ascribed to a Southern Hemisphere species, *M. hectori,* from morphology (Mead 1981). Subsequently, genetic data indicated not only that these groups did not represent the same species, but also that they did not even belong to closely related sister species (Dalebout et al. 1998, 2002, 2004). Within the molecular taxonomic framework described above, the following lines of evidence were concordant and supported the validity of *M. perrini* as a distinct species (Dalebout et al. 2002, 2004): 1) phylogenetic patterns at the mtDNA – for both loci, sequences from representatives of *M. perrini* formed a monophyletic lineage, with $\geq$ 95% bootstrap support, distinguished from all other ziphiids by a series of fixed, diagnostic nucleotide substitutions; 2) phylogenetic patterns at the nuclear actin intron, including the presence of a unique 34-bp deletion distinguishing *M. perrini* from all other ziphiids; and, 3) the presence of fixed, diagnostic morphological differences (cranial and tooth morphology). Analyses using combined mtDNA control region and cytochrome *b* sequences for increased phylogenetic signals indicated that *M. perrini* is more closely related to at least four other species of *Mesoplodon* than to *M. hectori* (bootstrap score, 83%; Bremer support, 7; Dalebout et al. 2002). Those results confirm that the animals do not represent geographical variants or subspecies, and their apparent morphological similarity is likely due to shared ancestral features. *M. perrini* is known from five specimens from the eastern North Pacific. *M. hectori* is known from ~ 25 specimens from cold-temperate Southern Hemisphere waters.

(Cited references listed in main text of working group report)

Example 2 (provided by Rosenbaum)

The original Phylogenetic Species Concept (PSC) explicated by Cracraft (1983, 1989) and elaborated by Nixon and Wheeler (1990) relies on a character-based approach to delimit species. According to the PSC, a species is defined as "an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters and within which there is a parental pattern of ancestry and descent" (Cracraft 1989:35). The term "basal" here refers to "elemental" or "minimal" and is not intended as a reference to relative phylogenetic placement (J. Cracraft, pers. comm.). Character-based diagnosis gives the PSC its operational strength since all organisms have observable features (characters) and, so the argument goes, can be aggregated into phylogenetic species where appropriate, using either Population Aggregation Analysis (PAA; Davis and Nixon 1992) or analogous methods (such as Cladistic Haplotype Analysis, or CHA; Brower 1999). PAA characterizes populations as phylogenetic species if fixed differences are discovered. Although conceived before the upsurge in the use of molecular genetics in conservation, it should be noted that the PSC is agnostic with respect to the kind of character data it incorporates: Phylogenetic species may be delineated based on morphological, molecular, behavioral, or other characters with equal rigor.

The first step in a rigorous approach to identifying putative species is the physical construction of a database. All approaches to diagnosis are susceptible to sampling effects, so the primary consideration is to conduct focused taxonomic sampling around the species of interest. Considerable knowledge about the organisms in a study group is necessary to implement a reasonable and logical sampling strategy. An essential but commonly overlooked aspect of generating even a modest database is proper vouchering and verification of specimens and archiving of sequences. Each validation/verification and archiving procedure should be undertaken in such a way that diagnostic methods can be reproduced or re-tested if and when the need arises.

Phylogenetic trees are usually generated once terminals (OTUs) have been defined in a diagnostic framework. Tree-based methods help elucidate hierarchical relationships among OTUs and offer support to PAA once OTUs are defined. Knowledge of phylogenetic relationships becomes particularly important when the relationship in question shows paraphyly of defined OTUs but is not used as the primary means of species delimitation.

Rosenbaum et al. (2000) analyzed the genetics of the species boundaries between populations of right whales, *Eubalena* spp. (Balaenidae). Prior to their analysis, two nomenclatural units, based on very limited morphological information (summarized in Rosenbaum et al. 2000) were recognized – the northern right whale *Eubalena glacialis* Müller in the Northern Hemisphere and the southern right whale *Eubalena australis* Desmoulins in the Southern Hemisphere. Using mitochondrial control region sequences (D-loop), Rosenbaum et al. justified the resurrection of the North Pacific right whale *Eubalaena japonica* Lacépède as the third of three diagnosably distinct populations of right whales. PAA revealed at least three fixed nucleotide sites in each of the three distinct populations in the study. The same three entities appear well supported in a cladistic analysis. The resultant tree shows that the North Pacific and Southern Hemisphere right whales are sister groups, with the North Atlantic right whale immediately outside. The topology suggests that the North Pacific whales do not comprise a sister group to their erstwhile nomenclatural conspecifics. While this result was interesting, it was not definitive for the designation of the three groups of right whales – North Atlantic, North Pacific, and Southern Hemisphere – as independent, diagnosable units at the species level. However, the finding of a paraphyletic relationship constituted valuable evidence for differing evolutionary histories among the three groups. This conclusion is supported by recent additional evidence of additional diagnostic characters from multiple nuclear loci (Gaines et al., pers. comm.).

In the study by Rosenbaum et al. (2000), reciprocal monophyly and diagnosis coincide, but such agreement is not the only possible scenario that obtains when diagnosis and tree-building methods are used with the same data. Character fixation and the appearance of reciprocal monophyly in a phylogenetic analysis need not coincide, a seemingly trivial observation explicated by Goldstein and DeSalle (2000). Of significance is whether the results of PAA or phylogeographic analysis should be taken at face value when they disagree. Brower (1999) and Goldstein et al. (2000) illustrated some theoretical examples where two entities are found to be reciprocally monophyletic, and yet no diagnostics are identified for the two entities being scrutinized. Such an outcome is particularly likely when distance methods such as neighbor-joining are employed (Goldstein and DeSalle 2000). This underlies the difference between character-based and tree-based approaches to delimitation of putative species; monophyly is not necessarily coincident with character fixation. As Goldstein et al. (2000) state, “ If one adheres strictly to the Phylogenetic Species Concept, then whether or not some individuals within a particular phylogenetic species are more or less closely related to each other than to members of their own is simply irrelevant to the reconstruction of relationships among species.”

(Cited references listed in main working group report).

APPENDIX 6

Report of the Working Group on Killer Whales as a Case Study

Edited by R. Waples and P. Clapham

Participants: Waples (Chair), Baird, Barlow, Clapham, Dahlheim, Etnier, Fleischer, J. Ford, M. Ford, Fung, Hanson, Heyning, Hoelzel, LeDuc, Mesnick, Pitman, Wade, Wayne

SUMMARY

The overall goal of the killer whale workshop was to summarize the current state of knowledge concerning killer whale biology and taxonomy. Killer whales are among the most widely distributed of all mammals. Density of killer whales increases with latitude and is strongly associated with oceanic productivity. Currently, all killer whales are considered to be a single, cosmopolitan species, although this designation has been increasingly questioned in recent years. In the eastern North Pacific (ENP), three types are currently recognized: so-called "Residents" (which feed on fish), "Transients" (which feed on mammals) and "Offshores" (which may feed largely on fish).[2] The three types are distinguishable (in some cases unequivocally) through differences in many characteristics, including morphology, genetics, group size, social behavior, foraging specialization, range, dispersal, and call repertoires. Of the three putative types, the Offshore animals are the least well understood. Existing evidence suggests that there is no switching between ecotypes (although at present there is no way to determine whether this might happen over a timeframe of decades or longer).

In Antarctica, there is good evidence for the existence of three types which are also more or less distinguishable on the basis of morphology, genetics and ecology: Type A (a circumpolar specialist eating primarily minke whales), Type B (a mammal eater-taking mainly seals), and Type C (a fish-eater found primarily in eastern Antarctica).

Genetic analysis of mitochondrial DNA shows low diversity, no consistent worldwide geographical pattern, and no consistent correlation between mtDNA lineage and ecotype. The data are consistent with a fairly recent divergence of ecotypes, while lack of regional variation may reflect the matrilineal expansion of local populations. The distributional pattern of haplotypes implies that divisions in the mitochondrial phylogeny may have arisen as differentiation between ocean basins. There are fixed differences in the mtDNA control region between putative populations (among Resident populations, between Residents and Transients in the northeastern Pacific, and among geographical populations). Among the three Antarctic types, B and C are closely related, while Type A animals exhibited fixed differences from B and C whales.

Nuclear data do not discriminate unequivocally among the various killer whale ecotypes. For example, the Resident ecotype in the North Pacific shows the same genetic distance between the Kamchatka Peninsula (Russia) and Washington State (U.S.A.) populations (same mtDNA type) as between Resident and Transient types in the ENP.

Whether the different ecotypes of killer whales constitute a single species, multiple species or subspecies is not yet resolved. While there are clearly different ecotypes, it is not clear whether these represent a plastic and ephemeral response to changing habitat conditions, or the beginning of an irreversible process of speciation. Single-species advocates believe the genetic data are not strong enough to argue for long-term reproductive isolation, while proponents of the multiple-species view disagree; the latter contend that there are potentially two or three species of killer whales in Antarctica, and perhaps others in the North Pacific. The majority view among workshop participants was that multiple species probably exist at least in Antarctica, and that this might well be confirmed in the future, but that current data are limited (absent or insufficiently quantified) and therefore that separation at the species level is at this point premature. The working group agreed that it was not possible at this point to comment meaningfully on the relationship between Antarctic and ENP killer whales on the basis of existing data, except to note convergent similarities in summer feeding preferences be-

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[2] The working group acknowledged the long-held recognition among killer whale researchers that the terms "Resident", "Transient" and "Offshore" are misleading in that they do not strictly reflect the complex and sometimes overlapping habits, movements and distribution of the animals in these ecotypes. However, pending nomenclatural clarification (which is a recommendation of this working group), the terms have been retained here to reflect their continued wide use.

tween Antarctic Type B and ENP Transients, and Antarctic Type C and ENP Residents.

A majority of participants felt that Resident- and Transient-type killer whales in the ENP probably merited species or subspecies status. The relationship of Offshore-type killer whales to Residents and Transients (or any other killer whales in the world) is not clear.

INTRODUCTION

The working group met on April 30 and May 1, 2004 at the Southwest Fisheries Science Center in La Jolla, California. Clapham served as rapporteur. The principal goals of the working group were to review existing information on the characteristics, ecology and behavior of killer whales worldwide and attempt to resolve biological relationships within the genus *Orcinus* at all levels from species to local breeding populations. The hierarchy of biological diversity within the nominal species *Orcinus orca* can be partitioned in many ways to identify subspecific conservation units. These latter designations may be guided or dictated by legal mandates and may include (but are not necessarily limited to) Evolutionarily Significant Units (ESUs), Distinct Population Segments (DPSs), and stocks. The specific objectives were to:

1) review and summarize the current status of killer whale taxonomy at the level of species and subspecies; and

2) in light of the results from that endeavor, review biological relationships among different groups of North Pacific killer whales, focusing both on relationships among different groups of "Residents" and on relationships of Residents to other groups ("Offshores," "Transients").

It was expected that those exercises would be informed by the more general results and discussions that emerged from the symposium (Appendix 4) and the workshop as a whole.

This working group report is intended to summarize the existing state of the science on: a) global killer whale biology and taxonomy, b) biological relationships between North Pacific Residents and other groups of killer whales worldwide, and c) biological relationships between Puget Sound Southern Residents and other North Pacific Residents. The report identifies areas of scientific agreement as well as disagreement and suggests future work that could help resolve remaining uncertainties. A draft agenda circulated before the meeting proved inadequate to the aims and needs of the participants, and the report therefore follows instead the course of the discussions as they developed.

Background

Linnaeus (1758) described the species *Orcinus orca*, and the most recent formal taxonomic syntheses (Rice 1998; Baker et al. 2003) still considers all killer whales to be a single, cosmopolitan species. Killer whales are the most widely distributed marine mammal (Leatherwood and Dahlheim 1978; Heyning and Dahlheim 1988) and (except perhaps for *Homo sapiens, Rattus norvegicus,* and *Mus musculus*) may be the world's most widely distributed mammalian species. Hoelzel *et al*. (2002) analyzed samples of killer whales collected from selected locations around the world and found relatively low levels of genetic diversity at mtDNA and microsatellite loci; many local populations exhibited no mtDNA variation. In contrast to patterns seen in other cetacean species, they found little correspondence between geographical populations and genetic distance, and some mtDNA haplotypes were found in individuals from distant geographical regions. They suggested that these results could most plausibly be explained by a species-level bottleneck (perhaps in the later stages of the Pleistocene), followed by post-bottleneck expansion and local divergence among different matrilines. One limitation of the study by Hoelzel et al. was that although the samples included individuals from around the world, coverage was limited in some areas and for some morphological/life history types.

Some other lines of evidence suggest that the nominal species *Orcinus orca* may actually include multiple species. Soviet scientists (Mikhalev *et al*. 1981; Berzin and Vladimirov 1983) proposed two new species of dwarf killer whales from Antarctica, based on samples collected over a 20-year period. However, as discussed by Pitman and Ensor (2003), the paucity of descriptive detail and lack of a designated holotype in the former paper and the subsequent loss of type material designated in the second paper make it difficult to determine the validity of their proposals. Recently, Pitman and Ensor (2003) summarized existing information on Antarctic killer whales and concluded that, in addition to *Orcinus orca*, two different types of killer whales occur in Antarctic waters. It is unclear whether the two new types correspond to the species proposed by the Soviet scientists. The three types are distinguished by morphological and behavioral characteristics, and Pitman and Ensor (2003) suggested that they likely represent separate species *sensu* the Biological Species Concept. They cautioned, however, that this hypothesis should be tested with more information, particularly genetic data. Neither of the two new Antarctic forms was represented in Hoelzel et al.'s (2002) recent world-wide analysis of killer whale mtDNA and microsatellites.

SUMMARY OF KNOWLEDGE CONCERNING KILLER WHALES WORLDWIDE

Global overview

An invited paper by Barrett-Lennard and Heise (LJ/04/KW1) summarized influences of ecology, cultural traditions and social organization on population structure and systematics of killer whales worldwide. The paper (1) described the population complexity of *Orcinus orca* in the northeastern Pacific, (2) speculated about its causes and genetic consequences, (3) discussed evidence (or lack thereof) for population structure in the rest of the species' range, and (4) discussed the implications of known patterns of population structure for systematics of the species worldwide.

The paper included a short history of killer whale studies in the northeastern Pacific, including Michael Bigg's discovery of the Resident (fish-eating) and Transient (marine mammal-eating) ecotypes. At the present time, there is evidence for at least three populations of Residents, three populations of Transients, and at least one population of an "Offshore" type that also appears to eat fish. Genetically, these populations are diverged from each other at mitochondrial and nuclear microsatellite loci. The authors concluded that, based on observation and genetic information, the ecotypes appear to be largely reproductively isolated from each other.

The mechanism of isolation is speculated to be at least partially xenophobia (avoidance of non-population members), mediated by population-specific calls. The mechanism of new population formation is speculated to be allopatric or sympatric group fission, a process that may lead to highly structured, perhaps ephemeral populations; this may be at least a partial explanation for the low genetic diversity of the species worldwide.

The paper next discussed the evidence for population structure or ecological partitioning outside the northeastern Pacific. Areas with some evidence for genetically, behaviorally, or morphologically differentiated groups include the eastern tropical Pacific, the Russian far east, Norway, New Zealand and Antarctica. None of these areas is as well studied as the northeastern Pacific, however. The authors speculated that in areas of high marine productivity killer whale populations become more specialized to particular prey items, promoting the formation of populations and ecotypes.

With regard to systematics, the authors suggested that revisions should be based upon the identification of lineages that are relatively deep and upon ecological similarities. They noted that this pattern had not yet been reported in any published studies. Instead, the known patterns are consistent with either of two other scenarios: a recent adaptive radiation into a variety of new niches, or a species propensity to live in small xenophobic and ephemeral populations. If the former is correct, at least some of the currently diverged forms are probably incipient species and systematic revision may be useful. If the latter is correct, most forms are probably ephemeral and there is little to be gained in according them species status. The authors suggested that until the divergence process in killer whales is better understood the taxonomy should not be formally revised and killer whales should instead be described in terms of a species complex.

A recent review of killer whale abundance and density estimates worldwide (Forney and Wade, in review) found that density clearly increases with latitude (very low densities in tropical and mid-latitude waters, increasing densities above about 40-50 degrees, and densities peaking above 60 degrees). Given the reluctance of survey vessels to enter the ice in Antarctic waters, it is likely that existing data actually under-represent the true density of killer whales in the highest-latitude areas. Killer whale density was also strongly correlated with oceanic productivity as reflected in remotely sensed chlorophyll-α measurements.

Little is known about the densities of Offshore-type killer whales in most areas of the world, and observations by Pitman and others suggest that these animals are more common than may be thought; it should be noted that existing survey effort is heavily biased toward coastal areas. The often poor definition of the saddle patch in killer whales found in lower latitudes and the fact that animals with distinct saddles (as is typical of higher-latitude animals) are not observed there argues against seasonal migration of animals from high latitudes into warmer waters. However, the poorly defined saddle patch is not a universal characteristic, and the presence of southern elephant seal remains in the stomach of a killer whale (ecotype uncertain) taken by whalers off Durban (South Africa) indicates some migratory movement from at least the sub-Antarctic to temperate latitudes.

The working group noted that the current distribution of killer whales worldwide might not be representative of historic distribution, given the significant changes in the abundance and distribution of prey species (due to human exploitation or environmental changes). Furthermore, high directed takes of killer whales occurred in some locations (e.g. Japan, Norway, Iceland, Antarctica and Puget Sound), and frequent shooting by whalers of killer whales scavenging around large whale carcasses in at least some areas (notably in Antarctica); some populations may not have recovered from these large losses.

Summary of data relating to multiple ecotypes

There is clear evidence for the existence of multiple ecotypes with sympatric or parapatric distributions in the North Pacific and Antarctica. There is some anecdotal and other evidence that distinct ecotypes also exist in Norway and New Zealand, but currently available data are inconclusive. The suggestion has been made that the radiation of different ecotypes is more likely to have occurred in high-latitude areas characterized by high productivity (e.g. the northeastern Pacific and the Antarctic); however, it would be worthwhile to investigate this further in unstudied areas with similar oceanographic characteristics (e.g. the Benguela Current region off South Africa).

Antarctica

According to Pitman and Ensor (2003), three types of killer whales have been documented in Antarctica that do not strictly correspond to the three ecotypes found in the Eastern North Pacific (ENP) and Alaska. Type C is a fish-eater found primarily in eastern Antarctica, similar to the Resident-type in the ENP. Type B is a mammal feeder taking mainly seals, and is thus similar to the ENP Transient-type; its distribution appears to be circumpolar However, the Antarctic Type A is an open-ocean specialist on minke whales (also with a circumpolar distribution), and thus is not similar to the Offshore type in the ENP. However, it should be noted that categorization of feeding preferences was based upon observations made in a single Antarctic summer. These observations correspond roughly to descriptions by Soviet scientists (Berzin and Vladimirov 1983), whose data are very problematic in their selection and presentation and were analyzed without regard to possible biases; nonetheless, this earlier work stimulated the more recent observations by Pitman and Ensor (2003).

On current, rather limited evidence, there do not appear to be intermediate forms among the three Antarctic types, nor does it appear that any of the three represent an intermediate type between the other two. Observations made to date have not provided any evidence for intermediate forms. Animals with some of the morphological features of Types B and C have been observed outside Antarctica (e.g. off New Zealand and the Falkland Islands), but it is not known whether these few records are indicative of migration or occasional/extra-limital occurrence, or indeed whether the whales concerned were truly the Antarctic forms.

In summary, the evidence for reproductive isolation among the three Antarctic forms includes different morphology (color patterns and size), food specializations, habitat preferences and genetic groupings (see below). In addition, there appear to be no intermediate forms. One alternate view is that some or all of the three types might have arrived in Antarctica quite recently but there has not yet been sufficient time for measurable gene flow to occur. Another view is that the data (from Antarctica and from killer whale types worldwide) are currently inconclusive, with multiple (and sometimes poorly quantified) morphotypes, global distribution of some haplotypes, and insufficient information on gene flow; in this view, it would be premature to assign separate species status to different forms. More detailed discussion on the latter is given below.

Eastern North Pacific (Mexico to the Bering Sea)

J. Ford summarized characteristics of killer whales (with an emphasis on acoustic differences) from long-term, dedicated studies off the western coast of North America and the implications of this knowledge for population and social structure (LJ/04/KW4, KW5). Individual killer whales have repertoires of discrete (or stereotyped) calls. These calls are culturally inherited (indicating vocal learning), stable for more than one generation (about 25 years), and differ within and among populations. Such repertoires were first described in the northeastern Pacific, but similar regional distinctive repertoires have also been documented off Norway, Iceland, New Zealand, Russia and Patagonia.

Resident-type killer whales from the ENP live in highly stable groups based upon matrilines. Individuals stay in their group for life, with no dispersal having been detected. New groups are created by matrilineal fission, either gradually or quite abruptly upon the death of the senior female. Residents are typically found in clusters of 3-5 matrilines, and clusters mix to form what are termed “communities.” Each pod (closely related matrilines that travel together) emits about a dozen calls, shared by all pod members. All call types are used in all behavioral contexts. Calls are shared by some but not all pods in the community. Shared calls differ structurally at the level of the pod and matriline (= “dialects”). Pods that share calls form what is termed a clan. Thus, call-sharing closely reflects matrilineal heritage, and vocal similarity indicates relatedness. Acoustic distance is correlated with genetic distance in clans, and the probability of mating increases with acoustic distance; this appears to be an outbreeding mechanism. Clans may have had allopatric or sympatric origins, or both.

In the ENP, several Resident-type clans are currently recognized: Southern Residents (1 clan of about 83 whales, all sharing the same mtDNA haplotype), Northern Residents (3 clans, about 204 whales, all sharing the same mtDNA haplotype), and Southern Alaskan Residents (2 clans, one of which has about 190 whales and has the Northern Resident haplotype, and another of about 50 whales with the Southern Resident haplotype).

In contrast to Residents, Transient-type killer whales are wide-ranging and are found sporadically in any specific area, with less seasonality of occurrence. There is a variable social structure: some matrilines are stable, while others exhibit dispersal (Baird and Whitehead 2000). Like Residents, however, Transients form communities. Transients are acoustically cryptic; call repertoires are very stable, and these differ among the three documented Transient communities. Community-specific calls may correspond to mtDNA differences.

Offshore killer whales constitute the third "type", although there was some disagreement as to whether "Offshores" should be considered a separate population of "Residents." Offshores travel in large groups (50-75 whales) and are generally smaller animals with more rounded dorsal fins than those of Residents and Transients. The feeding ecology of Offshores is poorly known. They are found mostly on the outer continental shelf, but will visit inshore waters. The social structure is also unknown. Acoustically, Offshores have a rich repertoire of calls, with what appears to be extensive sharing among groups. They are acoustically quite distinct from Residents and Transients.

In addition, there is evidence for the existence of groups of killer whales that do not fit any of the three types above. The so-called "LA pod" (13 whales) and the Mexican "A" community (50+ whales) both appear to be acoustically different from Residents, Transients and Offshores.

Overall, in Ford's, view the evidence suggests that killer whale acoustic repertoires are cultural traditions that define identity and promote cohesion, but that on larger scales can also serve as an isolating mechanism that drives divergence among populations. Worldwide, one can think of killer whale communities as a mosaic of acoustically discrete and socially isolated populations that may not in themselves be ESUs, but that might instead be considered "culturally significant units."

Wade summarized the results of surveys conducted in Alaskan and Bering Sea waters. Animals observed during these surveys were assigned to ecotype through photographs showing distinct morphological differences, and through genetic analysis of biopsy samples. All three killer whale ecotypes were present in the Aleutians and the Bering Sea. Many Resident-type animals were observed around Kodiak Island and the Aleutians, but few in between. Transients were observed off the Alaska Peninsula and in the Aleutians but much less commonly to the east toward Kodiak. Abundance estimates derived from line-transect surveys for the area from Kodiak to the central Aleutians were: Residents 1675 whales (95% CI = 1166-2404); and Transients 543 whales (95% CI = 172-1712). There is evidence from genetic data that the central Aleutians region (notably in the area of Samalga Pass) represents a mixing zone for different populations; this is consistent with local oceanography and with known distribution breaks observed in other marine and avian species. Northern Resident haplotypes occur primarily to the east of the Pass, while haplotypes sampled on the western side are primarily of the Southern Resident type.

Dahlheim summarized what was known about the range and movement patterns of killer whales in the eastern North Pacific. Ranges of southern, northern and Alaskan Resident killer whales show some degree of overlap toward the extreme ends of their known ranges (and occasionally within the main portion of the range); however, while animals from different populations are sometimes seen in the same area, they do not appear to mix. A similar pattern of overlap is observed in Transient-type whales. Sasha Burdin has collected biopsy samples of killer whales off Kamchatka, and these are currently being analyzed.

Offshore killer whales appear to be capable of much more extensive movements, with matches recorded between the Bering Sea and locations as far afield as British Columbia and California. There is some evidence for a seasonal basis to these movements; for example, sightings of Offshores off California occur primarily in winter.

Mesnick summarized recent genetic insights into the social structure of killer whales observed in offshore waters, using samples obtained from the Eastern Tropical Pacific (LJ/04/KW9). Both mtDNA and microsatellites were used. Six of nine sampled groups had a single (Offshore) haplotype. Two other groups had at least two haplotypes, and one had at least three (not all groups were completely sampled). Mesnick cautioned that it was not clear what constitutes a "group," and that some samples may therefore have come from multiple (mixed) groups. Haplotypes in these groups were either the known Offshore type, or new types that were unassignable to ecotype; however, in an analysis the latter grouped more closely with known Resident types. One of the haplotypes (from a whale off Hawaii) had previously been recorded from a Type-A Antarctic whale. Overall, the mtDNA data show the existence of multiple haplotypes (and therefore matrilines) in killer whale groups in offshore waters. The preliminary microsatellite data showed a high degree of within-group relatedness (many shared alleles); in some cases, even animals with different mtDNA haplotypes were closely related, possibly suggesting shared paternities. A far lower rate of shared alleles was observed between groups. Mesnick cautioned that the data were preliminary, and that additional analyses involving more markers were required.

Summary of differences between Resident and Transient-type killer whales in the eastern North Pacific

Resident- and Transient-type whales in the ENP exhibit measurable differences in morphology (different dorsal fin and saddle patch shapes, Baird and Stacey 1988), group size (modal differences, with Transient groups being smaller, Baird and Dill 1996), dispersal (none for Residents versus some for Transients), range and distribution, contaminant burdens (generally higher in Transients) and acoustic repertoires and call types. Five known Transient mtDNA haplotypes were associated with Transient-type animals in all existing samples; these haplotypes do not appear in any other animals worldwide (although related haplotypes do).

Offshore-type killer whales are also different from Residents and Transients in several characteristics: morphology (the dorsal fin represents a third type in shape, and the saddle patch is more like that of Residents, though not identical and frequently much less defined); body size (generally smaller with less sexual size dimorphism), group size (probably larger but not certain), range (probably larger), dispersal (unknown), and contaminant burden (more similar to that of Resident-type whales). Only a single mtDNA haplotype has been assigned to confirmed Offshore-type animals, and is closer to the haplotypes of Residents than Transients. The acoustic characteristics of Offshore whales, and their relationship to Residents and Transients, are unclear.

Do killer whales ever switch ecotypes?

The question of whether killer whales of a particular ecotype ever switch to radically different prey at various times is important given the use of differing ecotypes as partial evidence in arguments for speciation. Soviet whalers operating in the Southern Ocean suggested the possibility that the same killer whale groups were exploiting very different prey (i.e. both fish and marine mammals) at different times, perhaps depending on seasonal availability, but the reliability of thsse reports is uncertain. In the ENP, data from field observations and from fatty acid analysis support the idea that the diet is consistent year-round (e.g., Resident-type whales always feed on fish and perhaps squid, with no indication that they take marine mammals). Stable isotope analyses (A. Abend and G. Worthy, pers. comm.) suggest trophic-level differences in prey between Resident- and Transient-type killer whales in this region, although since skin samples were used for those analyses, interpretation is constrained by the fast turnover of this tissue (and thus of the isotopic signatures therein).

Contaminant levels and patterns of detected congeners differ between Transient- and Resident-type killer whales along the western coast of North America, and also markedly by area. Mammalian prey of killer whales can metabolize organochlorine contaminants, which fish cannot; as a result, the pattern of contaminants in mammalian prey are passed on to Transient-type killer whales, and are distinguishable in contaminant profiles of the latter relative to those of Resident-type (fish-eating) animals. Because individual killer whales have not been repeatedly sampled, contaminant analysis cannot currently be used to assess whether prey switching occurs.

As noted above, vocalization patterns are quite different between Transient and Resident-type killer whales, which is consistent with different foraging patterns. Specifically, fish-eating whales are much more vocal than mammal-eating whales, which is presumed to relate to the greater ability of mammals to recognize (through hearing) imminent predation. In some cases (e.g. Norwegian killer whales, which appear to be herring specialists), sound may be used as a herding strategy. The lack of observed changes in vocalization patterns over the year in groups of one ecotype provides further support for the idea that there is no major prey-switching on a seasonal basis.

Overall, available evidence strongly points to a lack of dietary overlap between the fish-eating and mammal-eating types. However, it must be recognized that we do not know whether prey switching occurs on a much longer timescale (e.g. decades). Stable isotope analysis of museum specimens and of annual biopsies of individuals of known ecotype might provide insights into this question.

Genetic studies: implications for ecotype and population differentiation

In terms of phylogenetics, the relationship of killer whales to other cetaceans is not entirely clear. A cytochrome b analysis (LeDuc et al. 1999) did not show a clear relationship between this taxon and other cetaceans; Orcaella was the closest species, but the link was rather weakly supported. The fossil record for killer whales is poor, but one specimen dating to about 5 MYA is clearly a killer whale of some kind.

Hoelzel and colleagues (Hoelzel et al. 2002, Hoelzel unpublished data) analyzed samples from numerous locations worldwide including the ENP (Resident, Transient and Offshore types), the western North Pacific (Russia), the eastern and western North Atlantic, Argentina, New Zealand and Antarctica (a single Type A animal). Killer whale mtDNA (control region) exhibits low diversity and no consistent geographical pattern worldwide, which may be due to a bottleneck occurring some 150,000-300,000 years ago. Lack of regional variation may be due to the strictly matrilineal expansion of local populations.

Some working group participants expressed doubt that a species with such a widespread distribution could have undergone a bottleneck; interestingly, low diversity is also characteristic of some other abundant, cosmopolitan species (e.g. sperm whales and humans). It has also been suggested that a bottleneck may have occurred in sperm whales, but this suggestion raised extensive discussion in the literature (Whitehead 1998 and responses). Although humans have relatively low mtDNA diversity given their current distribution and population size, the absolute level of diversity is higher than in killer whales. The ratio between census population size and effective population size in killer whales is not clear, but is a factor that should be considered in such analyses.

Hoelzel's analysis of killer whales samples from the North Pacific indicated that all individuals in a single local community had the same mtDNA genotype, but some of the same types were found in different, widely separated communities (e.g. from Washington State and Russia). Resident and Offshore types are closely related in terms of mtDNA, and quite distinct from Transient types. Overall, Hoelzel considered that the genetic data provided no reason to reclassify the ecotypes as different species. There are fixed differences at three sites (sequence length = 995bp) between Resident-and Transient-type whales for mtDNA control region lineages, although these lineages are defined by few haplotypes (2 and 5, respectively). Overall, these findings, in association with data on cultural and foraging differences (recognizable differences between types) could be explained by a pattern of fairly shallow (i.e. recent) divergence of matrilines that invaded an area and subsequently underwent fission. Whether this is the beginning of a process of speciation, or an equilibrium process (with ongoing but low levels of gene flow), is not clear. It is possible that multiple ecotypes have evolved on multiple occasions over the evolutionary history of killer whales.

Microsatellite analysis showed significant differences among virtually all populations sampled, although the results could be heavily influenced by small effective population sizes in combination with kinship. Gene flow analyses of microsatellite data among Alaskan Transients, Alaskan Residents and Southern Residents produced results ranging from one to seven migrants per generation (a generation is estimated to represent 25 years). In light of the assumptions underlying the analytical method used, as well as the fact that the results are at odds with current knowledge (notably regarding lack of observed dispersal between Residents and Transients), some participants expressed skepticism regarding the reliability of these estimates. One general difficulty is that the moderate levels of nuclear genetic differentiation can be explained either by an equilibrium model involving low levels of ongoing gene flow, or by an isolation model involving recent divergence and no current gene flow. The methods available to date cannot reliably distinguish between these hypotheses, but new models (e.g. as described by Hey et al. – 2004) may be able to in the future.

Hoelzel presented an additional anaysis using the program STRUCTURE, which attempts to determine the number of gene pools in a mixed sample and assign individuals to the most likely gene pool. This analysis produced results generally consistent with currently hypothesized population structure in the North Pacific, but also identified some individuals that may be recent migrants. One of these might be explained by a sample taken in a probable mixing zone of two populations in the Bering Sea. Some members felt that another potential "migrant" may have been an artifact of the fact that there are likely unsampled populations in the North Pacific. Although the analysis was run allowing for the existence of one or more unsampled populations, the potential effect of unsampled populations on individual assignments is difficult to evaluate.

LeDuc and Taylor presented mtDNA control region sequence haplotypes from mid and low latitudes in the North Pacific, adding these to new and published data from higher latitudes and from other regions (LJ/04/KW7). The sequences from animals sampled in temperate and tropical waters, together with samples from Antarctica, added considerably to the number of haplotypes recorded globally from killer whales. The previously reported distinction between so-called "Resident" and "Transient" haplotypes was still maintained in a global phylogeny, but was not congruent with patterns of known ecotypes. However, distributional patterns of the haplotypes suggest that the Atlantic basin carries only haplotypes from the side of the phylogeny that contains the "Resident" and "Offshore" types, referred to as the "R" clade (in contrast to the "T" clade). Such a result implies that this division in the mitochondrial phylogeny may have arisen as differentiation between ocean basins. The observed haplotype distribution, together with the latitudinal limits of known fish specialists in the Northern Hemisphere, leads to a hypothesis of killer whale biogeography and evolution. Specifically, Northern and Southern Residents are hypothesized to be recent arrivals to the North Pacific from the North Atlantic, with subsequent character displacement leading to the ecological specialization seen today between fish and mammal specialists in the North

Pacific. Habitat differences in lower latitudes suggest that killer whales in these areas tend to be generalists. The possibilities of comparable specialization in other regions, as well as the possibility of a rassenkreis (species circle), cannot be ruled out.

In the Pacific, the largest gap in current sampling (relative to the distribution of killer whale sightings) is off Central America and northern South America. Also, given that the deep-water zone between 40 and 50 degrees North is known to be a high-productivity area and has not been covered well by sighting surveys, it is possible that killer whales exist there, and samples from that area would be very useful.

LeDuc and Pitman summarized mtDNA analyses of 49 samples from Antarctica (LJ/04/KW8). They believed the results supported the contention that two or three species of killer whales exist in that region. The 49 samples yielded 16 haplotypes. The Type B and C killer whales were closely related and constituted what appeared to be a monophyletic clade, although it was noted that firm conclusions could not be drawn until the tree was rooted. There were fixed differences between Type A whales and the other two types, indicating female reproductive isolation and thus (in the authors' view) a situation consistent with separate species status. Evidence for reproductive isolation between Types B and C was weaker, although the authors noted that, unless intermediate types exist, the existing data were suggestive of separate species status under the Biological Species Concept. This might also be consistent with marked differences in morphology and prey preferences between these two forms.

Some other participants disagreed with LeDuc and Pitman's conclusions, citing similar-level genetic differences among populations of single species of terrestrial taxa (e.g., jackals, ravens), as well as similarities with some human populations. It was noted that the existence of different ecotypes in killer whales, showing very short mtDNA branch lengths, is not dissimilar to some other taxa (e.g. wolves), and that it is possible that these forms evolve repeatedly and quite quickly over evolutionary time. This apparent plasticity suggests that such forms could be relatively ephemeral in evolutionary time. In wolves, animals raised in certain habitats and feeding on certain prey tend to colonize similar habitats when they disperse; this tendency appears to be the major axis of genetic differentiation in wolves, and it does not mean that different ecotypes represent different species. African canids such as wild dog packs in Kruger National Park show high F_{st} values (e.g. 0.25, as large or larger than values found between killer whale ecotypes), but dispersal is mediated by kinship (when packs break up they form new groups based on same-sex siblings); these are not unlike clans in killer whales. Some participants disagreed with this argument, and suggested that the degree of foraging specialization in killer whales is fundamentally greater than in other mammals. Mayr (1996) stated, "...there are no niches of mammal species that would be suitable for sympatric speciation"; however, this was not the case with killer whales, in which Baird et al. (1992) suggested disruptive selection for prey type as a potential mechanism for sympatric divergence.

As noted above, Hoelzel's estimates for divergence of ecotypes worldwide, following a possible bottleneck in the late Pleistocene, was on the order of 150,000 years, based upon mtDNA control region data. M. Ford addressed the question of divergence time of Southern Resident killer whales using simple models applied to published genetic data (mtDNA and microsatellites) (LJ/04/KW6). Both types of markers are consistent with a broad range of divergence times, from hundreds to hundreds of thousands of years, depending on the assumptions. Assuming a complete isolation model, the microsatellite data suggest a divergence time of less than 3000 years, but even a small amount of migration would make the data consistent with an ancient divergence. The mtDNA data clearly indicate that female gene flow does not occur regularly even at low levels, but this does not rule out the possibility of male-mediated gene flow. Like the microsatellite data, the mtDNA results are consistent with a very broad range of divergence times, depending on the assumptions made. For example, estimates of divergence time are affected by values used for effective population size. In addition, some of the haplotypes might be ancient, predating any divergence. Overall, the genetic data on killer whales are open to several interpretations regarding the date of the divergence and the nature of subsequent radiation. For example, the broad distribution of some haplotypes worldwide could reflect stochastic events following an ancient divergence and population expansion, while the much tighter genetic pattern observed in the Antarctic Types B and C suggests a single founder event.

Some participants felt it was important to recognize that genetic data reveal patterns on a long-term historical timescale but that, in contrast, we are attempting to interpret these differences in light of present-day observations. Such interpretations are questionable given the fact that the ecosystem was very different hundreds of years ago. It could be speculated that the existence of much larger fish prior to overexploitation by human fisheries meant that killer whales now feeding on large mammalian prey were once exploiting fish. However, there is obviously no way at present to assess the likelihood of this.

Other participants noted that, although "lost" ecotypes in killer whales might eventually be replaced by reappearance of the type in question, this would likely not occur on a human management timeframe (decades or centuries), and therefore such replacement should not be anticipated as a the basis for present-day management.

Other information relating to ecotypes

Fung presented data to address the question of whether different foraging specializations (ecotypes) were reflected in anatomical differences (Fung 2004). Various measurements of skulls and associated features tentatively suggested anatomical differences between Residents and Transients. For example, the data could be taken as suggesting that Transients have larger skulls and more massive jaws, possibly indicating the development of more powerful musculature for dealing with larger (mammalian) prey. However, this was based upon small sample sizes with little associated information about the animals concerned; thus it was not clear whether age and size differences in the samples could account for these (and similar) results. Genetic analysis of the sampled specimens should be undertaken to determine their ecotype; some of this work is currently underway.

Pitman noted a Soviet observation that fish-eating killer whales in Antarctica supposedly had significantly smaller flukes than killer whales preying upon mammals. Aerial photogrammetry in this and other areas would be a useful way to assess whether such morphological differences truly exist among ecotypes.

Sexual size dimorphism in killer whales may be more related to foraging specialization (i.e. different roles within a group) than to the mating system. Data on testis size in mature male killer whales are sparse, which is regrettable given that this information might be very informative with regard to the mating system; different mating systems can be reliable indicators of reproductive isolation among species.

Are different killer whale ecotypes separate species?

The working group recognized at the outset that there was no way to select an approach to species designation in killer whales that would be consistent with such designations for all other taxa, since there is no consistency in this regard across the animal kingdom (including in cetacean taxonomy).

In general, the participants recognized that it was not currently possible to discriminate between a single species that was capable of plastic, ephemeral adaptations (i.e. foraging specializations = ecotypes) and the early stages of a true speciation event (i.e. adaptive radiation on an irreversible evolutionary path).

It could be argued that killer whales are not typical mammals. For example, they constitute a rare mammalian example of sympatric divergence of different types, and possess a complex social system that likely promotes isolation among groups. Looking to taxa that are ecologically or culturally similar might represent a way forward, but such taxa were not identified. It could also be argued that considerable value should be placed on the cultural uniqueness of local killer whale groups, and that this should be given strong consideration in conservation. However, an alternative view is that cultural traditions are ephemeral and are therefore relatively unimportant for consideration with respect to species-level questions.

One approach to assessing species status would be to take all of the available information on killer whales, including data on morphology, acoustics, distribution and genetics (etc), and test it against criteria for different species concepts. This approach might well yield different conclusions depending on the concept used.

The working group also recognized that, in general, significant and reliably quantified morphological differences between groups of animals provide strong evidence for separate species, and that such differences may or may not be accompanied by genetic differentiation. Similarly, cryptic species (those showing no obvious morphological differences but which are genetically and/or ecologically distinct) may exist. Whether either of these cases applies to killer whales is the topic of much debate.

It was suggested that our inability to entirely delineate differences among types of killer whales should not stop us from defining reproductive isolation in cases where it clearly exists. However, there is currently no agreement on this issue.

Several participants felt strongly that the way in which taxonomic classification is conducted should not be changed to suit management purposes. It should continue to attempt to classify taxa based upon objective scientific observations rather than political considerations relating to conservation needs.

Summary of arguments

Overall, a number of divergent views on how to classify killer whales were expressed. Arguments for *Orcinus orca* being a single species, several species or several subspecies can be summarized as follows (caveats to some of the supporting contentions are noted in earlier sections of this report).

Single-species argument -- The proponents of the idea that killer whales constitute a single global species argued as follows:

- The mtDNA data could be explained by remnant variation from an ancient divergence, and these data therefore are not very informative in regard to higher-level structures. There is evidence that some populations are extended family units that were founded relatively recently from an oceanic population, when the current habitat became available (post-glaciation). The mtDNA data do not identify different lineages that correlate to ecotypes; instead, they suggest that trophic specialization may have evolved multiple times within the genus.

- The nuclear data do not discriminate unequivocally among ecotypes. For example, the Resident ecotype in the North Pacific shows the same genetic distance between the whale off Kamchatka (Russia and) Washington State (same mtDNA type), as between Resident and Transients in the ENP.
- Genetic data can be taken as indicative of a fairly recent divergence. This could mean that we are witnessing the early stages of a unique divergence, with insufficient time having elapsed to establish strong genetic differences. Alternatively, the ecotypes may be ephemeral phenomena that appear and disappear over relatively short evolutionary timescales.
- Foraging specializations and acoustic repertoires are likely learned and therefore might be ephemeral, and as such they are not good indicators of species difference.
- Morphological differences are observed in other taxa that are not necessarily considered to indicate separate species (although not so much in mammals).
- While there are some intriguing and suggestive observations on possible morphological differences among killer whale ecotypes, little quantification of these purported differences exists at present, and until better data become available it is premature to conclude that multiple species exist.

Multiple-species argument -- The proponents of the idea that killer whales constitute multiple species argued as follows:

- A congruence exists between patterns of genetic variation, acoustics, color patterns and ecological specialization between Residents and Transients, at least in the eastern North Pacific.
- Within those groups, mtDNA haplotypes are shared across a geographic range, but there is no evidence of movement across ecological space (i.e. no Transient animal has been observed to switch to the Resident ecotype, or vice versa). Haplotype sharing can be historical and does not necessarily imply recent movement.
- The variation within ecotypes does not negate the differences among them.
- The mtDNA data, as well as the lack of interaction among Residents and Transients in the North Pacific, provide evidence for female philopatry. It is unclear how other killer whales elsewhere should be placed relative to these groups.
- The data on morphology and genetics, and on trophic and habitat specialization (and the absence of intermediate forms) in Antarctic killer whales suggests that there are at least two, and possibly three species in this region. Types B and C are separate from other types elsewhere in the world, while Type A may or may not be the same species as the ENP Transient type.
- Overall, in the above view there may be four species: ENP Residents, ENP Transients (possibly including Antarctic A), Antarctic B/C (possibly two species, with the caveat that the separation of these types is currently based upon morphology, not genetics).

Subspecies argument -- Discussion of whether different types of killer whales represent subspecies became mired in disagreements about the validity of the subspecies as a taxonomic unit, and how it could be defined as something different from a discrete population.

A brief review in the working group of sub-species designations in odontocetes indicated that these have usually been based upon morphological differences with known or presumed genetic differentiation. Most such designations have involved allopatric or parapatric groups; in the latter, there are sometimes intermediate forms in areas of overlap. In some cases (e.g. inshore/offshore bottlenose dolphins), no subspecies designation has been made despite the existence of evidence that is consistent with that used for recognizing other cetacean subspecies.

Some participants felt that it was not wise to discuss subspecies without an explicit definition of the term, and no agreement could be reached on such a definition. A further complication was the uncertainty among participants regarding the conventions of zoological nomenclature conventions, specifically how subspecies trinomials would be assigned to (for example) ENP Residents and Transients, and how these ecotypes relate to the original designation of *Orcinus orca*.

Synthesis -- Overall, participants were divided over whether or not different killer whale ecotypes constituted separate species. The range of views can be broadly characterized as follows:

- Of the 17 participants in the working group, six felt that there was only a single species of killer whale worldwide, and that this designation will remain valid when additional data become available.
- Only one participant felt that multiple species definitely exist and that existing data support this.
- The majority of participants (ten) felt that multiple species probably exist, at least in Antarctica, and that this might well be confirmed in the future, but that current data are limited (absent or insufficiently quantified) and therefore that full species designation is at this point premature. In some cases, subspecies or ESU designations might be more appropriate until better data become available.
- The working group agreed that it was not possible at this point to comment meaningfully on the relationship between Antarctic and ENP killer whales on the basis of existing data, except to reiterate nominal similarities between Antarctic Type B and ENP Transients, and Antarctic Type C and ENP Residents.
- All 11 participants who felt that there are (or probably are) multiple species of killer whales based this belief upon the Biological Species Concept. Those who supported only one species based this opinion on either the Biological Species Concept, the Phylogenetic Species Concept, or both; some of this latter group felt that subspecies designations might be appropriate for the ENP, Antarctica, or both. Others in the same group felt that subspecies designations were based largely upon geographic distinctions and thus were not appropriate for use in killer whales.
- Overall, a majority of participants felt that Resident- and Transient-type killer whales in the ENP probably merited species or subspecies status.
- The relationship of Offshore-type killer whales to Residents and Transients (or any other killer whales in the world) is not clear.
- Insufficient time was available to consider in more detail proposed agenda items related to Puget Sound Southern Residents, their historic population size and distribution, and their relationships to other ENP killer whales.

FUTURE WORK

The following topics for future work were considered high priorities to help resolve outstanding taxonomic issues (note that these are not listed in order of importance):

- The current nomenclature systems for ecotypes (“Residents,” “Transients,” etc.) and for haplotypes are very confusing, especially to those who do not work directly with killer whales, and a new standardized system should be developed to clarify the situation. E-mail correspondence groups were formed under Baird (ecotypes) and J. Ford (haplotypes) for this purpose.
- Microsatellite data should be obtained for all ENP whales, and pedigrees should be established.
- Genetic researchers should coordinate their activities, pool samples, and standardize analyses.
- Additional analyses should be conducted using stable isotopes and fatty acids to elucidate dietary preferences of different ecotypes.
- Morphological differences among ecotypes should be better quantified, using oblique photographs, aerial photogrammetry, or other methods.
- Better information should be obtained on reproduction and mating systems, using recently developed methods for assessing pregnancy from skin biopsies, as well as anatomical examination of dead animals, or other techniques.
- Biopsies should be obtained from killer whale calves for paternity analyses.
- Additional genetic markers (e.g., Y chromosome, other autosomals) should be developed.
- The effect of kinship on genetic analyses should be assessed.
- Biopsy sampling by different individuals should be coordinated to standardize collection and preservation techniques and thus maximize the use of each sample for multiple analyses. Similarly, protocols for necropsy of stranded animals should be widely distributed so that the maximum amount of information can be obtained from each recorded death.

- Additional acoustic sampling from other populations is needed.
- Greater genetic sampling within populations would give a better idea of how genetic variation has changed over time. This should include sampling of Southern Residents, with priority given to the oldest animals so that they are sampled before they die.
- Greater sampling of different populations worldwide is needed.

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APPENDIX 7

Report of the Working Group on Achieving a Validated Molecular Taxonomy and Global Phylogeography of the Cetaceans

Participants: Baker (chair), Cipriano, Dizon, Chivers, Escorza-Treviño, Krützen, Lavery, Martien, Morin, Palsbøll, Rosel, Rosenbaum, Sherwin, Wang

1. OVERVIEW OF AN APPLIED MOLECULAR TAXONOMY FOR IDENTIFICATION OF CETACEAN SPECIES

The working group met on April 30 and May 1, 2004, with the following terms of reference:

1. Discuss and make progress toward development of an orderly system of molecular taxonomy based on a comprehensive and validated dataset of sequences and a web-based system of access for phylogenetic species identification of specimens.
2. Discuss and make progress toward a web-based system of species-level databases for describing range-wide phylogeographic variation and identifying origin of specimens.
3. Draft recommendations on the above, directed at taxonomists, managers and research agencies.

The agenda is given as Attachment 1. Cipriano and Dizon acted as rapporteurs. The working group began with a discussion of the role of taxonomy and systematics and how molecular data have been used to identify species and assess higher order relationships. The role and objectives of a molecular taxonomy for cetaceans were considered in terms of the following components (Dalebout et al. 2004, LJ/04/Phylo3).

i) *Comprehensiveness* – DNA sequences of a chosen locus representing all described species of Cetacea should be included. Multiple representatives from different geographical locations should be included for each species to reflect the full range of genetic diversity. The number of specimens required will differ among taxa, depending on levels of intra-specific genetic diversity and divergence from other closely related species. Where databases are to be established for several loci, the same suite of reference specimens should ideally be used to generate all sequences.

ii) *Validation* – DNA sequences of the chosen locus should be obtained from holotype specimens wherever possible. Otherwise, DNA sequences should be obtained only from validated specimens, e.g., those examined by experts for that group and from which diagnostic skeletal material or photographs have been collected (Dizon et al. 2000).

iii) *Genetic distinctiveness and exclusivity* – Molecular phylogenetic identification of species is straightforward when reconstruction of gene trees from individual organisms within a given taxon (i.e., species) forms monophyletic lineages reflecting divergence and independent evolutionary trajectories. Under some species concepts (e.g., genealogical lineage/concordance concept, see LJ/04/Phylo3), lineages representing the same species are expected to group together to the exclusion of lineages representing other described species, with synapomorphic nucleotide substitutions distinguishing the lineages from one another. Other species concepts or delimitation criteria are not dependent on genealogical concordance and might not be amenable to this approach.

iv) *Concordance* – Phylogenetic analyses of multiple loci, including standardized nuclear loci, together with assessment of morphological features, behavior or geographic distribution, should yield concordant results for nominal species. Within this framework, molecular taxonomy can lead to and accommodate the discovery of new species.

v) *Universal accessibility and curatorship* – Databases of DNA reference sequences and information on validated source specimens should be easily updateable and accessible universally, together with standardized phylogenetic programs to assist in species identification with appropriate caveats (Ross et al. 2003). Such universal access can be facilitated through the World-Wide Web, with molecular and morphological data under the curatorship of species-specialists.

2. REVIEW PROVISIONAL DATASET OF CETACEAN MTDNA CONTROL REGION AND CYTOCHROME B SEQUENCES FOR SPECIES-LEVEL IDENTIFICATION

The working group reviewed the databases currently available for cetaceans on GenBank (Attachment 2) and in the web-based program *DNA Surveillance*. The former includes 1,165 sequences (variable lengths) of the mtDNA control region and 260 sequences of the cytochrome *b* gene. For the latter, the reference dataset provides nearly complete coverage of cetacean species and contains a total of 450 sequences from 87 species in 14 families (Version 3.1, Attachment 4). For the mtDNA control region, there are 285 sequences representing 78 species, and for the mtDNA cytochrome *b* gene, 165 sequences representing 83 species (Appendix Table 7-1). In most cases, species are represented by several reference sequences obtained from different populations, allowing potential assignment of user-submitted test sequences to geographical origin. Species classification follows Rice (1998) with the following exceptions: for the Balaenidae, four species are recognized following Rosenbaum et al. (2000); for the Balaenopteridae, Antarctic, North Pacific, North Atlantic and dwarf minke whales are recognized as distinct taxa [the latter three are recognized as subspecies of *Balaenoptera acutorostrata* by Rice (1998) and confirmed to be phylogenetic species by Baker et al. (2000)]; for the Ziphiidae, 21 species are recognized following Dalebout et al. (2002); and for the Platanistidae, two species are recognized following Hamilton et al. (2001). The terminology (rather than nomenclature) for the sei whale/Bryde's whale complex follows Yoshida and Kato (1999) for the "common" pelagic form, the coastal "Kochi" form and the pygmy "Solomon Islands" form. These forms and their mtDNA sequences conform to *B. brydei, B. edeni,* and *B. omurai*, respectively in the proposed taxonomic revision of Wada et al. (2003).

The working group considered the need to document reference sequences for molecular taxonomy in a manner that allows subsequent validation of species assignment. Preferably, a reference sample should originate from a morphologically and photographically documented specimen. However, observations from an experienced scientist might be the only information available to document a biopsy sample collected from a free-ranging whale or dolphin. In such cases, a measure of the degree of confidence of species identification should be associated with the reference sequence, as is typically the case with photographic identifications from natural markings (Dizon et al. 2000). Recognizing that some species require a larger reference set of sequences for identification than do others, and that we likely have on assembled those sets of sequences from a variety of sources, the working group recommended that information to assess the verifiability of each sequence in the database be included as part of each record. This information would include whether the sequence is from a sample collected from the holotype, a museum specimen, a free-ranging whale or dolphin (i.e., biopsy), an animal killed accidentally in a fishery, or a stranded animal. Further, the associated information should include whether skull and or post-cranial material is available, photograph(s), geographical information about where the sample was collected, the name and contact information of the sample collector or the person who made the initial species identification, how the species was identified (e.g., field observation only, post-field examination of morphological, photographic or genetic data), who made the final species identification, and who holds the data. If the species was identified from genetic data, the following should be addressed: what marker was used, were multiple markers typed, is there evidence of consistency by loci, and who conducted the genetic analysis and in which laboratory.

3. REVIEW METHODOLOGICAL AND STATISTICAL ISSUES IN SPECIES IDENFICATION USING MOLECULAR CHARACTERS

Although the working group did not discuss this item explicitly, aspects were covered under other agenda items.

4. CONSIDER THE RELIABILITY OF SPECIES IDENTIFICATION BY CONCORDANCE OF THE TWO PROVISIONAL DATASETS OF MTDNA LOCI; REVIEW RESULTS OF INTERNAL VALIDATION EXERCISE FOR *DNA-SURVEILLANCE*

Given the time constraints, the working group chose to omit any detailed discussion of this agenda item.

5. REVIEW SPECIES OR SPECIES COMPLEXES FOR WHICH PHYLOGENETIC IDENTIFICATION IS COMPLICATED BY KNOWN OR SUSPECTED PARAPHYLY OF MTDNA LINEAGES (E.G., SUBFAMILY DELPHININAE); RECOMMEND IMPROVEMENT TO SAMPLING OF POPULATIONS OR GENETIC LOCI, INCLUDING NUCLEAR LOCI, TO IMPROVE IDENTIFICATION

Although the working group did not discuss this item explicitly, aspects were covered under agenda item 6.

6. REVIEW AVAILABLE DESCRIPTIONS OF PHYLOGEOGRAPHY OF CETACEANS FOR

PURPOSES OF IMPROVED TAXONOMIC IDENTIFICATION OF ACCEPTED SPECIES

Sources of uncertainty

The working group identified the following sources of uncertainty associated with the present molecular taxonomy of cetaceans:

Sampling limitations

In some cases, the reliability of reliable molecular identification could be improved through increased sampling (increasing either the overall number of samples or their geographical distribution).

Shortcomings in analytical and/or molecular methodologies

For many species, substantial improvement might be achieved through the incorporation of additional (particularly nuclear) loci or the application of alternative analytical approaches. In this context, differences were noted between tree-based and character-based approaches to delimitation of putative species. Time did not allow full discussion, but see Appendix 5.

Inadequate taxonomic representation in phylogenetic analyses

For some species, analyses incorporating a full suite of genetic diversity within the family or sub-family (at both the species and below-species levels) will be required.

Shortcomings in the conventional taxonomy

In other cases, difficulties in identification to species are likely due to unrecognized partitions within currently accepted nominal species. In these cases, appropriate revision of the accepted taxonomy is likely to resolve some of the apparent difficulties in routine molecular identification of species.

Potential problems with field identification

Given the known difficulties with field identification of some species (particularly in the *Sousa/Stenella/Tursiops/Delphinus* and possibly *Lagenodelphis* complex, hereafter referred to as the "STDLs"), the true species identity of published sequences attributed to those species is in doubt. This reinforces the need for additional validated samples (linked to morphological specimens).

Biological reality

In some cases, the true organismal phylogeny might be difficult to resolve because of evolutionary history (e.g., low inter-specific divergence relative to high intra-specific diversity, incomplete lineage sorting, ongoing hybridization). In these cases, reliable species identification using molecular methods is likely to remain problematic regardless of the level of sampling, number of loci examined, analytical approaches employed, or improvements in the conventional taxonomy.

Criteria for identifying data deficiencies

As an initial basis for selecting those species for which data deficiencies might reduce the reliability of molecular species identification, the working group reviewed the 16 species showing <90% bootstrap species-specific monophyly for the internal robustness trial conducted with *DNA Surveillance* (see LJ/04/Phylo2). An additional 23 species had only 1 or 0 sequences available. Other species were added to the list if the collective knowledge of the working group indicated that there might be molecular identification difficulties. The working group discussed each species in turn (Attachment 3), and summarized the potential causes of difficulty, what additional but unpublished molecular data exist, and what new molecular evidence might soon be brought to bear on the issue. It was pointed out by some members that this list is obviously not exhaustive and that it reflects only the collective knowledge of those present.

The working group noted the potential in some cetacean groups for multiple coastal forms to arise independently from a widely distributed parent species (cf. Funk and Omland's [2003] "peripheral isolates speciation"). As an important general principle, molecular analyses of individual cetacean taxa should include consideration of the full range of species and within-species diversity within the appropriate family or subfamily and the geographic variation within each. The working group **recommended** that analyses involving members of the STDL complex should be performed with reference to the full range of species and within-species diversity, including the geographical distribution of within-species diversity, across the family or subfamily.

7. CONSIDER REQUIREMENTS TO EXTEND MOLECULAR TAXONOMY TO NOMINAL SUBSPECIES THROUGH GLOBAL PHYLOGEOGRAPHY

Given the time constraints, the working group was unable to discuss this agenda item.

8. DISCUSS IMPLICATIONS OF CURRENT INFORMATION ON PHYLOGEOGRAPHY FOR RECOGNITION OF ADDITIONAL GENETIC PARTITIONS THAT MIGHT REFLECT NESTED TAXA

The working group noted the earlier discussion of potential for further partitioning below the species level (under items 5 and 6 above, Attachment 3). For example, recent molecular evidence of substantial genetic divergence within *Inia geoffrensis* suggests partitioning at the species or sub-species level (Banguera-Hinestroza et al. 2002). In other cases, structure at the subspecies level has been suggested by phylogeographic analysis (e.g., *Cephalorhynchus hectori mauii*, Pichler et al. 2001).

Under either a tree-based or character-based analysis based on currently available data, new or revised taxonomic partitioning might also be expected in the following groups:

Tursiops spp*., Balaenoptera acutorostrata, Kogia sima, Cephalorhynchus commersonii, Sotalia* sp(p)., *Sousa* sp(p)., *Orcaella brevirostris,* and *Phocoena phocoena*

Potential partitioning in killer whales was not discussed as this was covered by another working group.

The working group did not discuss synonymizing any currently recognized taxa on the basis of available molecular information.

9. RECOMMENDATIONS FOR PROGRESS WITH AN IMPROVED MOLECULAR TAXONOMY

Comprehensive and "evaluated" dataset for cetaceans

The working group recognized the need for a comprehensive and fully validated set of DNA reference sequences for the 87 described cetacean species (see Attachment 4). At this point, a fully validated dataset (mtDNA control region, cytochrome *b*, and a nuclear intron) exists only for the family Ziphiidae (see Dalebout et al. 2004). The working group noted Gatesy et al.'s (2004) large, multiple-locus (mtDNA and nuclear) dataset, but the question of coverage for one or more loci across all 87 species and the validation of source specimens were not reviewed. However, the review of data deficiencies (Attachment 3) indicated that a mtDNA dataset with all described cetacean taxa, with a minimum of 2-6 representatives for each species, could now be compiled by the addition of available unpublished sequences to Version 3.1 of *DNA Surveillance.* Such a dataset would not be fully validated but could be "evaluated" by species specialists to reduce the likelihood of errors. The working group **recommended** that the individuals or laboratories with these sequences collaborate in a joint publication of the sequences and provide accompanying documentation of provenance.

Virtual curation and species specialists

The working group recognized that, for some widely distributed species, a global phylogeny will only be possible through large multi-investigator collaborations. The genus *Tursiops* is one such taxon. It is distributed worldwide, and its taxonomy remains confused. Numerous researchers worldwide are working on *Tursiops* systematics and phylogeography. A number of specialists in *Tursiops* genetics and morphology met during the symposium and workshop and initiated a plan to establish virtual curation of DNA sequences from bottlenose dolphin specimens, particularly mtDNA control region sequences. These specialists agreed that validated sequences are a critical part of the database.

Once compiled, the control region sequences will be used to construct an initial global molecular phylogeny. Analyses using only validated sequences as well as using the entire database of sequences will be performed and evaluated collaboratively by the virtual curators. Other topics of importance that were discussed included the need for calibration of morphometric measurements so that datasets can be combined and the need for a matched morphological and genetic study. The working group recognized that establishment of additional teams of virtual species curators would greatly accelerate progress toward resolution of problematic taxa. It therefore **recommended** that the Plenary Workshop consider ways to encourage the formation and operation of such teams.

Proprietary databases

The working group also recognized the need for proprietary databases, and noted that their curation has associated issues including authorship, priority, availability, transparency, maintenance and financial support. Recognizing also that such databases limit the utility of privately held data, including limitations on the types of analyses that can be conducted and limitations on publication, the group **encouraged** individuals to publish and submit their data to accessible databases (such as GenBank) as soon as possible.

Holotypes

The use of holotypes for evaluating and revising taxonomy and nomenclature was discussed. The working group recognized institutional concerns related to, and policies limiting destructive sampling, given the critical role of holotypes. Nevertheless the working group **recommended** that institutions maintaining holotypes allow access to holotype material for genetic analysis, following the example of the National Museum of Natural History of the Smithsonian Institution (Dalebout et al. 2004). An example is the need for genetic analysis of the holotype from *B. edeni* in Calcutta (Wada et al. 2003).

GenBank The working group briefly discussed the potential for structural improvements that would enhance development of a molecular phylogeny for cetaceans. The working group agreed that it would be helpful if GenBank provided better direction and more standardized data fields for individual specimen identification codes and geographical origins (if known) of individuals. The working group nominated Palsbøll to establish a dialogue with GenBank representatives to investigate how and by whom taxonomic decisions are made, and to determine how best to provide advice to GenBank personnel on cetacean nomenclature and on ways to improve the fields mentioned above.

Sample preservation

The working group recommended that hard and soft tissues from valuable specimens should be stored under conditions that are appropriate for long-term preservation and in ways that ensure the usefulness of such tissues for genetic analyses.

Genetic markers

Mitochondrial DNA markers are currently used in several DNA taxonomy databases for a variety of animal taxa, including cetaceans. The working group noted several times in discussion, that mitochondrial DNA sequences might not be sufficient for identification purposes for all currently recognized cetacean taxa, and **recommended** that a suite of genetic loci, appropriate for different taxonomic groups within the order, and combined analysis, should be considered for accurate and robust identification of all specimens.

10. IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Due to insufficient time, this item was not discussed.

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Appendix Table 7-1. Cetacean families and species represented in the mtDNA control region and cytochrome *b* datasets (Version 3.1) implemented in *DNA Surveillance*.

		CONTROL REGION		CYTOCHROME B	
Suborder	Family	No. of species represented/total	No. of sequences[a]	No. of species represented/total	No. of sequences
Mysticeti	Balaenidae (right & bowhead whales)	4/4	9	2/4	3
	Neobalaenidae (pygmy right whale)	1/1	2	1/1	1
	Eschrichtiidae (gray whale)	1/1	3	1/1	2
	Balaenopteridae (rorquals)	10/10	21	8/10	15
Odontoceti	Physeteridae (sperm whale)	1/1	2	1/1	2
	Kogiidae (pygmy & dwarf sperm)	2/2	3	2/2	4
	Ziphiidae (beaked whales)	21/21	42	21/21	42
	Monodontidae (beluga & narwhal)	2/2	4	2/2	5
	Phocoenidae (porpoises)	6/6	44	6/6	12
	Delphinidae (oceanic dolphins)	27/36	146	34/36	66
	Pontoporiidae (franciscana)	1/1	2	1/1	3
	Iniidae (Amazon River dolphin)	1/1	3	1/1	4
	Lipotidae (Yangtze River dolphin)	1/1	4	1/1	2
	Platanistidae (Ganges & Indus dolphins)	0/2	0	2/2	4
Total		78/89	285	83/87	165

[a] Does not include sequences available in the humpback whale populations dataset (mtDNA control region only)

ATTACHMENT 1

Agenda of the Working Group on Achieving a Validated Molecular Taxonomy and Global Phylogeography of the Cetaceans

1. Overview of an applied molecular taxonomy for identification of cetacean species.
2. Review provisional dataset of cetacean mtDNA control region and cytochrome *b* sequences for species-level identification..
3. Review methodological and statistical issues in species identification using molecular characters.
4. Consider the reliability of species identification by concordance of the two provisional datasets of mtDNA loci. Review results of internal validation exercise for DNA-surveillance.
5. Review species or species complexes for which phylogenetic identification is complicated by known or suspected paraphyly of mtDNA lineages (e.g., subfamily Delphininae). Recommend
6. Review available descriptions of phylogeography of cetaceans for purposes of improved taxonomic identification of accepted species.
7. Consider requirements to extend molecular taxonomy to nominal subspecies through global phylogeography.
8 Discuss implications of current information on phylogeography for reflection of additional genetic partitions that might reflect nested taxa.
9. Recommendations for progress with an improved molecular taxonomy.
10. Implications for conservation and management.

ATTACHMENT 2

Cetacean sequence data: What is and isn't in GENBANK

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"GenBank" is an annotated collection of all publicly available nucleotide and amino acid sequences held and administered by the National Center for Biotechnology Information (NCBI). Established in 1988 as a national resource for molecular biology information, NCBI creates public databases, conducts research in computational biology, develops software tools for analyzing genome data, and disseminates biomedical information (http://www.ncbi.nlm.nih.gov/).

A review of the 2,723 cetacean sequences lodged in GenBank (as of mid-April 2004) reveals a lack of depth and breadth in coverage across genes, species, and geographical populations/stocks (Appendix Table 7-2). Four putative species have no sequence data available; another 17 lack even a single control region sequence, the main locus used for forensic identification (e.g. see working group report references section); 20 total lack a cytochrome *b* sequence, also used for forensics and species level taxonomic diagnosis; and 34 are represented by only one control region or cytochrome *b* sequence.

Understanding of cetacean systematics and evolutionary relationships, taxonomic descriptions, and forensic analysis are all hampered by the dearth of sequence data in GenBank. More sequence information is privately held, without publication in GenBank, than is currently available publicly. For example, southern minke whales and dwarf minke whales, central in the controversy over Japanese "scientific whaling" in the Southern Ocean, are not represented by either a control region or cytochrome *b* sequence in GenBank. Little information is provided in annotation fields concerning the geographical sources of sequences currently held. Some of the taxonomy used in the [organism] field is incorrect or out of date, and several misidentified (to species) sequences have been archived uncorrected for several years.

Appendix Table 7-2. Summary of cetacean GenBank sequences in broad categories, sorted by source species in general taxonomic groupings (sequences from specimens diagnosed only to genus not included).

		mitochondrial genes					nuclear genes			
Species	total	12S	16S	ctrl	cyt*b*	compl. mtDNA	actin	SINE	SRY	any MHC
Baleen whales										
Balaena mysticetus	111	1	1	72	2	2				
Balaenoptera acutorostrata (North Pacific/North Atlantic)	122			71	5	2	8	13	1	1
B. acutorostrata sp. (dwarf)	0									
Balaenoptera bonaerensis	30							22	1	6
Balaenoptera borealis	14			4	1					
Balaenoptera brydei	1			1						
Balaenoptera edeni	26			16	5					
Balaenoptera musculus	56			16	2		20		1	1
Balaenoptera omurai	3			3						
Caperea marginata	10			2	1	2				
Eschrichtius robustus	129	1	1	92	2	2				17
Eubalaena australis	19			16					1	1
**Eubalaena glacialis*	22			19	1					
Megaptera novaeangliae	181	4	3	91	2		8	18	1	
Beaked whales										
Berardius arnuxii	1									
Berardius bairdii	23	1	1	3	1	1		14		
Hyperoodon ampullatus	8			4	1	2				
Hyperoodon planifrons	2			2						
Indopacetus pacificus	10			5	5					
Mesoplodon bidens	10	1	1	4	1					
Mesoplodon blainvillei	0									
Mesoplodon bowdoini	1			1						
Mesoplodon carlhubbsi	2			1						1
Mesoplodon densirostris	3			1	1					
Mesoplodon europaeus	8	2	2	1	2					
Mesoplodon ginkgodens	0									
Mesoplodon grayi	6			6						
Mesoplodon hectori	2			2						
Mesoplodon layardii	4			4						
Mesoplodon mirus	1			1						
Mesoplodon perrini	11			6	5					
Mesoplodon peruvianus	11	2	2	1	2					
Mesoplodon stejnegeri	5			2				1	1	1
Mesoplodon traversii	3			3						
Tasmacetus shepherdi	7	1	1	4	1					
Ziphius cavirostris	18	1	2	8	2					
Monodontids										
Delphinapterus leucas	85	2	3	20	3				1	14
Monodon monoceros	28	1	1	5	2	2		11		4
Sperm whales										
Kogia breviceps	28	2	2	1	3	2				
Kogia sima	11	1	2		2				1	
Physeter macrocephalus	115	3	2	4	3	2		45	1	1

*Includes both *E. glacialis* and *E. japonica*

		mitochondrial genes					nuclear genes			
Species	total	12S	16S	ctrl	cyt*b*	compl. mtDNA	actin	SINE	SRY	any MHC
Dolphins										
Cephalorhynchus commersonii	9			8	1					
Cephalorhynchus eutropia	20	2	2	12	2					
Cephalorhynchus heavisidii	54			53	1					
Cephalorhynchus hectori	12			11	1					
Delphinus capensis	12			8	4					
Delphinus delphis	64	2	2	20	15				1	1
Delphinus tropicalis	2				1					
Inia geoffrensis	58	5	5	14	14	2		13		
Lagenodelphis hosei	2				2					
Lagenorhynchus acutus	13			2	3		4			
Lagenorhynchus albirostris	14	2	2	1	5	2				
Lagenorhynchus australis	3			2	1					
Lagenorhynchus cruciger	2			1	1					
Lagenorhynchus obliquidens	40			4	3		6		1	2
Lagenorhynchus obscurus	86	2	2	5	41					
Lipotes vexillifer	55	1	2	20	2			11	1	15
Lissodelphis borealis	3	1	1		1					
Lissodelphis peronii	7	2	2	1	2					
Pontoporia blainvillei	34	2	3	7		2		11		
Sotalia fluviatilis	7	1	1		2					
Sousa chinensis	5	1	1		2					
Sousa teuszii	0									
Stenella attenuata	5			1	5					
Stenella coeruleoalba	39	3	1	13	2					
Stenella clymene	1				1					
Stenella frontalis	2				2					
Stenella longirostris	14			1	7					
Steno bredanensis	5	1	1		2					
Tursiops aduncus	41			31	4					
Tursiops truncatus	156	4	3	56	5			11	1	1
Blackfish										
Feresa attenuata	1				1					
Globicephala macrorhynchus	41			5	4			24	1	3
Globicephala melas	28	2	2	3	4				1	
Grampus griseus	8	1		1	2				1	1
Orcaella brevirostris	5				3				1	1
Orcinus orca	14	1	1		3				1	
Peponocephala electra	3			1	1				1	
Pseudorca crassidens	4	1	1		1					
Porpoises										
Neophocaena phocaenoides	142	1	1	124	2				2	8
Phocoena dioptrica	2			1	1					
Phocoena phocoena	192	2	2	128	17	2			1	1
Phocoena sinus	12			1	2					8
Phocoena spinipinnis	12	2	2	6	2					
Phocoenoides dalli	149			121	7			12		
Asian river dolphins										
Platanista gangetica	54	2	3	13	21			11		
Platanista g. indi	1									
Platanista g. minor	5	1	1		1	2				
totals	2565	65	65	1166	260	27	46	217	22	88

ATTACHMENT 3

Notes from review of current data deficiencies for molecular taxonomy of cetaceans

Abbreviations: n = no. of control region sequences currently in *DNA-surveillance* dataset; GB = no. of control region sequences currently in GenBank; BS = *DNA-Surveillance* species-specific bootstrap value (see LJ/04/Phylo2)

Delphininae + Stenoninae (STDLs):

Particular difficulties in molecular identification have been noted within this group (see main text). This reinforces the need for more validated samples (linked to morphological specimens) in this group.

Steno bredanensis - rough-toothed dolphin (n=1, GB=0)

- New sequences becoming available (P. Formica, San Francisco State University, pers. comm.). Appears to have phylogeographic divergence by ocean, but this has not been tested in full context with other members of the sub-family.

Stenella coeruleoalba - striped dolphin (n=1, GB=13)

- (NB. Two indistinguishable sequences in GenBank, AY046549 916 bp labeled *Stenella coeruleoalba* and AY185142 366 bp labeled *Delphinus capensis,* from the same laboratory.)
- There do not appear to be any diagnostic mtDNA control region characters for this species.
- With somewhat larger data sets (18-20, reported by Rosel), still difficult to identify (not monophyletic clades). Even larger data sets, encompassing a greater proportion of the genetic diversity within this species might provide better resolution.
- Additional sequences available: NW Atlantic (Rosel); worldwide coverage (Archer 1996); E. Valsecchi (pers. comm. - unpublished sequences). Krützen reported teeth available from Australia, from well identified carcasses.

Stenella attenuata - pantropical spotted dolphin (n=1, GB=1)

- Escorza-Treviño reported 100 Pacific haplotypes available. Distinct from *S. longirostris*, but have not been analyzed in full context of sub-family diversity.
- Rosel reported ~30 Atlantic samples

– 10 fixed mitochondrial differences from other Atlantic STDLs, but have not been analyzed in full context of sub-family diversity.

Stenella frontalis - Atlantic spotted dolphin (n=1, GB=0)

- Rosel reported ~200 from North Atlantic and Gulf of Mexico with phylogeographic differences between them – group together at low bootstrap levels.

Stenella longirostris - spinner dolphin (BS<50%, n=2, GB=1)

- More sequences coming from French Polynesia (M. Poole, pers. comm..) – highly diverse sequences relative to other areas.
- Worldwide sequences in Galver (2002) – some phylogeographic structure, especially with dwarf spinner *S. rosiventris.*

Sotalia fluviatalis – tucuxi (n=2, GB=0)

- Partitioning suspected.
- Riverine samples are lacking; more marine samples are coming – (S. Caballero, University of Auckland, pers. comm..).

Tursiops truncatus - bottlenose dolphin (*truncatus* form) (BS<50%, GB=56)

- Wide geographical distribution, high diversity and strong phylogeographic patterns.
- Despite large samples, still sampling problems and taxonomic issues.
- Even with good data, probably still difficult to identify due to high intra-specific diversity and low inter-specific divergence.
- Currently no diagnostic molecular characters.
- Work on these issues is currently underway by multiple investigators through the coordinated efforts of a team of specialists.

Tursiops aduncus - bottlenose dolphin (*aduncus* form) (GB=31)

- Comments for *truncatus* form also applicable here.
- S African *T. aduncus* samples currently being analysed (A. Natoli, University of Durham, pers. comm..).

Delphinus delphis - common dolphin (short-beaked) (BS<50%, GB=20)

- Paraphyletic with respect to *D. capensis.*
- All comments for *T. truncatus* also applicable here, except that no team has yet been formed to specifically address this species.

Delphinus capensis - common dolphin (long-beaked) (BS<50%, GB=8)

- All comments for *T. truncatus* also applicable here, except that no team has yet been formed to specifically address this species.

Delphinus tropicalis (n=0, GB=0)

- Genetic taxonomic status uncertain.
- Diversity over range unknown.

Lagenodelphis hosei - Fraser's dolphin (n=0, GB=0)

- Samples now collected by V. Little (pers. comm.); analyzing Philippine and Hawaiian samples.

Stenella clymene - Clymene dolphin (n=0, GB=0)

- Rosel reported that ~30 W Atlantic samples, analyzed with Atlantic *S. coeruleoalba,* were paraphyletic.

Sousa **spp.** - humpback dolphins (n=0, GB=0)

- Morphology shows two clear species, with evidence suggestive of a third.
- Rosenbaum reported samples now taken throughout range; evidence for genetic partitions below currently recognized species level.

Globicephalinae + Orcininae:

Globicephala macrorhynchus - short-finned pilot whale (BS<50%, GB=5)
- Chivers reported that longer control region sequences better resolve within-species phylogeographic diversity.
- There is some evidence for further geographical partitioning between oceans.
- Recent morphometric and genetic study in Japan (T. Kasuya, pers. comm.) – within-species diversity not deep, has not been analyzed in the context of full sub-family diversity.

Peponocephala electra - melon-headed whale (n=1, GB=1)
- Baird reported new samples from Hawaii, more samples coming from ETP biopsy samples, and Krützen reported 9 biopsy samples from Arafura Sea.

Orcaella brevirostris - Irrawaddy dolphin (n=0, GB=0)
- Isabel Beasley (pers. comm. James Cook University, Townsville) has some genetic and morphological evidence for further partitioning.

Lissodelphininae:

Lagenorhynchus albirostris - white-beaked dolphin (n=1, GB=1)
- Amaral thesis analyzed eastern Atlantic specimens.
- Cipriano has more Newfoundland sequences and tissue samples from east coast of US.

Cephalorhynchus commersonii (BS<70%, GB=8)
- Shallow divergence, appear easy to identify.
- Likely sub-species level partition between Kerguelen Island and So. America.

Cephalorhynchus hectori (BS<90%, GB=11)
- Partitioning between N & S Island , New Zealand – sub-species recognised.

Lagenorhynchus obscurus (BS<70%, GB=5)
- Recent study by Cassens et al. 2003 (Peru, Africa, Argentina) indicates partitioning.

Lagenorhynchus obliquidens (GB=4)
- Newly-apparent paraphyly reported by Cipriano.
- More samples and genes should be sequenced.

Lagenodelphis hosei (n=0, GB=0)
- More sequences available from Dizon – to be added to DNA-Surveillance soon.

Mysticetes:

Balaenoptera acutorostrata (BS<70%, GB=71 but does not include dwarf form)

Balaenoptera bonaerensis (GB=0)
- Control region sequences to be published soon (L. Pastene, pers. comm..).

B. brydei/edeni/omurai/borealis complex (recent taxonomic revision, GB=20)
- Few sequences available – some evidence (ecological and genetic) for more geographic partitioning.
- Representation of some forms poor – need for further sampling due to continuing confusion and evidence for additional partitioning.

Balaenoptera musculus - blue whale and pygmy blue (BS<70% separation from pygmy blue, GB=16 but does not include pygmy blue)
- No problem with species identification, but subspecies identification difficult.
- Conventional taxonomy confused and no diagnostic differences.
- Some geographical partitioning; LeDuc reported that a worldwide description of blue whale diversity is in progress.

Ziphiidae:

Hyperoodon ampullatus – northern bottlenose whale (BS<90%, GB=2)
- Might be partitions below accepted species level for southern bottlenose.
- Suggestive data in Dalebout thesis, but not sufficient to resolve this.

Ziphius cavirostris - Cuvier's beaked whale (GB=8)
- Very widespread, might be partitioning.

Phocoenidae:

Phocoena dioptrica - spectacled porpoise (n=1, GB=1)
- More samples are needed.
- No evidence of problems.
- Morphological study underway.

Neophocaena phocaenoides - finless porpoise (raised due to potential geographic partitioning)
- More samples needed from greater geographical range (GB=124, all from same area).
- Might be further geographic partitioning.
- Clear morphological differences, probably two species (reported by Jefferson) – only one currently included in database.
- Many additional samples soon available from Wang.

Phocoena phocoena - harbour porpoise (BS<50%)
- Evidence for partitioning below species level.
- Many samples and sequences available that could be included.
- Accepted taxonomy might need revision, especially in the Black Sea.

Other Odontocetes:

Some taxa were not discussed given time constraints and limited expertise within the working group, including *inter alia*: *Kogia* spp., Asian river dolphins and franciscana; discussion of killer whales was deferred to the working group on killer whales.

[Cited references included in Literature Cited above]

ATTACHMENT 4

Progress on an applied molecular taxonomy of cetacean species

C.S. Baker, H. Ross, S. Lavery, A. Rodrigo and M.L. Dalebout

Introduction

DNA sequences of homologous loci provide universal characters for taxonomic identification. Such genetic characters are particularly useful for groups such as many cetaceans, in which morphological features are subtle and difficult to compare because of rarity of specimens or widespread distributions. The use of genetic databases to identify cetacean products for purposes of monitoring of trade and investigating illegal hunting or for identifying ambiguous beach-cast specimens, has become common (e.g., (Baker et al. 1996, Baker and Palumbi 1994, Dalebout et al. 1998, Dizon et al. 2000, Grohman et al. 1999, Henshaw et al. 1997, Simmonds et al. 2002). More recently, there has been an explosion of interest in the systematic application of these techniques to basic organismal taxonomy (Baker et al. 2003, Blaxter 2004, Hebert et al. 2003, Ross et al. 2003, Tautz et al. 2003). Proposals to implement a molecular-based or 'DNA taxonomy' have met with both unbridled enthusiasm and fierce criticisms (see *Trends in Ecology and Evolution* 2003, volume 18, issue 6; *Philosophical Transactions of the Royal Society, London Biology* 2004, volume 359, March).

Here we review progress with operational implementation of *DNA Surveillance*, a Web-based system of molecular identification of species for the order Cetacea, with particular emphasis on improving the standards of organismal taxonomy and aiding conservation. We describe the structure and methodology of the Web-based program itself, the status of the 'comprehensive database' of DNA sequences used by the program, our efforts to evaluate the reliability and robustness of species identification with the current database and the requirement to 'validate' the DNA database with voucher specimens. Finally, we discuss future plans to incorporate species-specific or 'congeneric' phylogeographic datasets, including GIS, into the program, and the need to delegate authority of validation and expansion of datasets to 'virtual' curators. A review and discussion of genetic distinctiveness, exclusivity and concordance, in relationship to species concepts, species delimitation criteria and the application of *DNA Surveillance* are considered in a companion background document by Dalebout (LJ/04/Phylo3).

Molecular phylogenetic identification of species

Phylogenetic identification of specimens of known species differs from the usual goal of organismal or molecular phylogenetics, which is more concerned with hierarchical relationships above the species level. Given a database of 'reference' sequences, unknown 'test' specimens can be identified to species based on their phylogenetic grouping with sequences from recognized species to the exclusion of sequences from other species (Baker et al. 1996). The phylogenetic identification is represented as a 'tree', with closely related sequences forming neighboring branches. This allows an hierarchical comparison to establish, first, the suborder and, second, the family or subfamily derivation using a small number of reference sequences from a large number of species. A close relationship or match with a 'reference' sequence provides evidence for species-level identification of a product. One or more 'out groups' (i.e., distantly related species) are used to protect against a misclassification error. The strength of support for an identification or phylogenetic grouping is evaluated by 'bootstrap' resampling of the sequence data. The relative support for a grouping or branch in the tree is shown as the percentage agreement from a large number (>1,000) of bootstrap simulations.

Problems in phylogenetic identification can occur if taxon sampling is incomplete (missing species) or within-species sampling is not sufficiently representative of diversity. In cases of deep intra-specific diversity or shallow inter-specific divergence, an unknown test sequence could group with the next most closely related species. For this reason, it is important that levels of genetic diversity within and divergence between species in a group of interest are assessed as part of the development of a molecular taxonomy. It was also noted that recently diverged species might not be reciprocally monophyletic at both mtDNA and nuclear loci (e.g., (Hare et al. 2002, Palumbi et al. 2001).

More problematic are accepted species that appear to be paraphyletic for mtDNA lineages in respect to other species, such as some species of the family Delphininae, particularly the genera *Stenella, Tursiops* and *Delphinus* (the STDLs, (Dizon et al. 2000). As a conservative approach, Baker et al. (1996) suggested that identification of test sequences should be considered conclusive only if they nest within the diversity of reference sequences for a species. If species or species complexes were paraphyletic, identification by standard phylogenetic methods can only to be made to a higher taxonomic rank within which mtDNA lineages are monophyletic (e.g., genus or subfamily).

Components of a molecular taxonomy of cetaceans

Early experience with molecular phylogenetic identification of market samples, bycatch and beachcast, provided some general principles for a more comprehensive molecular taxonomy of cetaceans. First, as described above, unknown 'test' specimens can be identified to species based on their phylogenetic grouping with sequences from recognized species to the exclusion of sequences from other species. Second, identification of a test sequence should be considered conclusive only if it nests within the diversity of reference sequences for a species (Baker et al. 1996). In practice, this is less crucial if phylogenetic support for the species-level grouping is strong and the taxonomic sampling is known to be complete. Third, agreement is expected among the results from molecular markers, morphology, and geographic distribution (genealogical/lineage concordance concept; (Avise and Ball 1990). Lastly, DNA reference sequences should be derived only from validated or voucher specimens - animals examined and identified by experts for which diagnostic skeletal material or photographs of such features are collected (as discussed by (Dizon et al. 2000).

From consideration of these principles Dalebout et al. (Dalebout et al. in press) suggested the following as crucial minimum components of a more general molecular taxonomy:

vi) *Comprehensiveness* – All described species of Cetacea should be represented. Multiple representatives from different geographic locations should be included for each species to reflect the full range of genetic diversity.

vii) *Database validation* – DNA sequences of the chosen loci should be obtained from holotype specimens wherever possible. Otherwise, DNA sequences should be obtained only from validated specimens; those examined by experts for that group and from which diagnostic skeletal material or photographs have been collected (Dizon et al. 2000).

viii) *Locus sensitivity* - The locus or loci selected for species identification should be appropriate to the taxa of interest.

ix) *Genetic distinctiveness and exclusivity* – Sequences from specimens assumed to represent a given taxa should form monophyletic lineages.

x) *Concordance* – Phylogenetic analyses of multiple loci, including standardized nuclear loci, together with assessment of morphological features, behavior or geographic distribution, should yield concordant results for nominal species.

xi) *Universal accessibility and curatorship*– Databases of DNA reference sequences and information on validated source specimens should be easily updateable and accessible universally, together with standardized phylogenetic programs to assist in species identification with appropriate caveats (Ross et al. 2003).

Implementing the components of www.DNA-surveillance

To assist in the genetic identification of whales, dolphins and porpoises, an interactive application for phylogenetic identification, referred to as *DNA Surveillance*, has been developed and is accessible through the website, www.DNA-surveillance. *DNA Surveillance* implements phylogenetic methods for identification of species within a particular taxonomic group, such as the currently available datasets for whales, dolphins, and porpoises (Order: Cetacea). The application aligns a user-submitted gene sequence of unknown origin against a set of validated reference sequences. The evolutionary distances between the unknown or 'test' sequence and each of the reference sequences is computed and a phylogenetic tree displays the affinity of the unknown sequence to the reference sequences (Ross et al. 2003).

DNA Surveillance differs in several important ways from the BLAST search options available on the website of the international genetic database, GenBank. The problems associated with using GenBank for species identification are particularly relevant to cetaceans, where the primary taxonomic identification of the specimen can be ambiguous or incorrect (e.g., Henshaw et al. 1987, Dalebout et al. 1998). Sequences entered in GenBank are not curated and often are not associated with identifiable reference or voucher specimen material. The taxonomic representation of a BLAST search is difficult to judge because of the large number of redundant gene sequences for some species, the absence of sequences from other closely related species and the nature of the pairwise alignment and search algorithm. The taxonomic distribution of sequences in GenBank reflects the sampling protocols of individual research programs rather than phylogenetic diversity. BLAST and related search engines seek only locally maximal matches in pairwise comparisons. The extreme (E) value associated with each sequence hit in a BLAST search is not a rigorous measure of evolutionary distance or genetic similarity, and depends on the size of the database being searched (Karlin and Altschul 1990). Inconsistent application of keywords also reduces the power of searching GenBank by fields, impeding effective data mining. By contrast, *DNA Surveillance* is designed specifically for species identification. The reference sequences in *DNA Surveillance* are pre-aligned at each hierarchical level of the database, using a mixture of algorithmic and manual methods, to create an optimized alignment. The sequences in *DNA Surveillance* were chosen to reflect known phylogenetic diversity at the species and population level (where available). The genetic distances and trees in *DNA Surveillance* are calculated using standard phylogenetic algorithms, as implemented in the Phylogenetic Algorithms Library (Drummond and Strimmer 2001).

The reference datasets mounted on www.DNA-surveillance comprise sequences from the highly variable control region and more conserved cytochrome *b* mitochondrial DNA (mtDNA). Both have proven to be effective for the species identification of test specimens and for differentiating intra- and inter-specific relationships among species (see below, *Progress on a Comprehensive Dataset*). Reference sequences were selected to reflect the generic, specific, or geographic diversity observed at a taxonomic level and to maximize the discriminatory power of the analysis. Most sequences were included only if the specimen had been expertly identified and diagnostic skeletal material or photographic records were collected (Dizon et al. 2000) (see below, *Dataset validation*). Datasets are arranged hierarchically, allowing initial family-level identification of cetaceans, and subsequently more detailed analysis within the suborders Mysticeti (baleen whales) and Odontoceti (toothed whales). The diverse (21 species) odontocete family Ziphiidae (beaked whales) is represented by a comprehensive validated data set (Dalebout et al. in press). The phylogenetic trees are rooted using an appropriate out group: the sperm whale (*Physeter macrocephalus*) for the mysticete, odontocete, and general cetacean reference data sets, and the pygmy sperm whale (*Kogia breviceps*) for the ziphiid reference data set. The latter out group was chosen to reduce out group branch length in the resultant trees[3].

Progress on a comprehensive dataset--Version 3.1 of the reference datasets implanted on www.DNA-surveillance provides nearly complete coverage of the taxonomic diversity of cetaceans and comprise a total of 450 sequences from 87 species in 14 families (Dalebout et al. 2003); mtDNA control region, 285 sequences representing 78 species, and mtDNA cytochrome *b*, 165 sequences representing 83 species. In most cases, species are represented by several reference sequences obtained from different populations, allowing potential assignment of user test sequences to geographic origin. Species classification follows Rice (1998) with the following exceptions: for the Balaenidae, four species are recognized following Rosenbaum et al. (2000); for the Balaenopteridae, Antarctic, North Pacific, North Atlantic and dwarf minke whales are recognized as distinct taxa (the latter three are recognized as subspecies of *Balaenoptera acutorostrata* by Rice (1998) and confirmed to be phylogenetic species by (Baker et al. 2000b); for the Ziphiidae, 21 species are recognized following Dalebout et al. (2002); and for the Platanistidae, two species are recognized following Hamilton et al. (2001). Given the confused taxonomy of the sei whale-Bryde's whale complex, we have used the terminology (rather than nomenclature) of Yoshida and Kato (Yoshida and Kato 1999) for the 'common' pelagic form, the coastal 'Kochi' form and the pygmy 'Solomon Islands' form. These forms and their mtDNA sequences conform to *B. brydei, edeni* and *omurai*, respectively in the proposed taxonomic revision of Wada et al. (2003). We are also aware of the problems associated with the apparent lack of genetic differentiation among some members of the *Stenella-Tursiops-Delphinus* complex of species (as discussed in Dizon et al. 2000). The program includes a caution message for test sequences identified as originating from some species of the subfamily, Delphininae. Species missing from version 3.1 of both databases are *Sousa teuszii* and *S. plumbea* (Atlantic and Indian Ocean humpbacked dolphins). Specimens representing these have now been made available through a loan from the tissue archive of the Southwest Fisheries Science Center, La Jolla, and sequences will be added to the release of an updated and expanded dataset (proposed Vs 4.0).

Progress on a validated dataset -- The 1999 workshop on *Molecular genetic identification of whales, dolphins, and porpoises* recommended that reference sequences should be documented in a manner that allows subsequent validation of species assignment. Preferably, a reference sample should originate from a morphologically and photographically documented specimen. In some instances, however, observations by an experienced scientist might be the only information available, e.g., a biopsy sample collected from a free-ranging whale or dolphin. In such cases, a measure of the degree of confidence of species identification should be associated with reference sequences, as is typically done in the case of photographic identifications by natural markings (Dizon et al. 2000).

Based on these criteria, reference sequences in Vs3.1 of the *DNA Surveillance* database vary in the extent to which they can be considered fully validated remains variable. At present, the most completely documented dataset is for the beaked whales (Family Ziphiidae) as reported in Dalebout et al (in press) and Dalebout (2002). This dataset has the ad-

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[3] Reliance on the topology of the phylogenetic tree in identification of the sperm whale is problematic at present. Given its distinctiveness, this species is used as the outworking group for trees constructed using the cetacean, mysticete, and odontocete databases. The tree-building algorithm forces all sequences except the outworking group into a monophyletic clade. This has the consequence of separating a submitted sperm whale sequence from the reference sperm whale sequences. A family-level data set for the Physeteridae, which is under development, should solve this problem.

vantage (and disadvantage) of being based largely on beachcast samples, including three holotype specimens, held in museums or institutions around the world. The large majority of other sequences in Vs3.1 were taken from GenBank sequences associated with peer-reviewed publications that included cetacean specialists as authors or generated from samples in the tissue archives of the Southwest Fisheries Science Center and the University of Auckland. Thus, most sequences have the potential to be better documented but most are internally consistent in grouping with other fully documented or validated sequences.

Reliability of program operation -- The operational or internal reliability of *DNA Surveillance* was tested by submitting an unaligned copy of each reference sequence as a test sequence to each data set in which it occurs. The test was judged a success (1) if the test sequence was the shortest evolutionary distance to a member of the same taxon and (2) if it was monophyletic with respect to the other sequences of the same taxon. The latter analysis considered only the topology of the neighbor-joining tree, not bootstrap simulations. The relevant taxonomic level for comparison was the family for the cetacean database, the species for the various mysticete, odontocete, and ziphiid databases, and the population for the humpback database.

The results showed a high level of reliability for self-testing using both control region and cytochrome *b* databases. The shortest distance and correct species branching relationship was returned at 100% for the following ranking in the specified hierarchical datasets: to family for All Cetaceans; to species for mysticetes; to subfamily for odontocetes; to species for Ziphiidae; to species for Phocoenidae; to species for Globicephalinae+Orcininae (noting one Irrawaddy dolphin sequence forms a long branch that pulls towards the killer whale); and to species for Lissodelphininae. Only for the Delphininae+Stenoninae was the success reduced slightly to 93% (27 of 29 reference sequences). The population-level reliability for the humpback phylogeographic dataset was low, as expected from the overlapping distribution of some clades in different oceans (Baker and Medrano-Gonzalez 2002). The reliability test also showed small errors in the true evolutionary distance and branch placement of a sequence as a result of the profile alignment. The homology of some individual nucleotide positions in the control region sequences is problematic and multiple alignments are plausible. To help overcome some of this uncertainty, the advanced search options provide the ability to perform a full alignment of the test and reference sequences.

Robustness of phylogenetic identification -- Although the results of the operational reliability test are encouraging, they do not provide information on the confidence or robustness of a phylogenetic identification, only its correct topological placement. Even for operational reliability, the rate of success could be biased upwards by the small number of specimens representing some of the problematic species (e.g., pantropical spotted and striped dolphins). For example, the two failures in the Delphininae+Stenoninae were among the short- and long-beaked common dolphin, which are represented by a relatively large sample from Rosel et al. (1994). From our experience with market samples, some of the other commonly hunted dolphins can be difficult to identify with confidence based on bootstrap simulations (Dalebout et al. 2001, Lavery et al. 2004).

To evaluate the confidence of identification, given the current reference dataset, we undertook an internal robustness test by scoring the bootstrap support for species nodes in the phylogenetic trees provided for each hierarchical dataset (Appendix Table 7-3; Lavery, this meeting). The results were consistent with previous observations of genetic distinctiveness and diversity of cetacean species. High bootstrap support (approaching 100%) was found using either control region or cytochrome *b* datasets for all beaked whales and all mysticete species, except the North Atlantic right whale, which tended to collapse down into the southern right whale, and the North Atlantic minke whales. It was also difficult to evaluate the robustness of identification for the North Atlantic, North Pacific and southern dwarf form minke whales, which are represented by only a small number of reference sequences in Version 3.1. For both of these taxa, however, more careful reconstruction with parsimony method shows phylogenetic distinctiveness of each oceanic populations or form (Baker et al. 2000a, Rosenbaum et al. 2000). High support was also found for species of Phocoenidae, with the exception of the control region for the harbor porpoise. Moderate (>75%) to high support was also found for most Globicephalinae+Orcininae and Lissodelphininae. Exceptions included one of the Irrawaddy dolphin sequences, which was placed with <50% support, and the short- and long-fin pilot whales. For the latter two species, it is clear that divergence between the species is low but that intra-specific diversity is also low, giving high consistency but low branch support. This pattern is also found in the genus *Cephalorhynchus*, although bootstrap support for these species is higher (> 75%). Low levels of support (<50%) are found for several of the species from Delphininae+Stenoninae and a full evaluation was not possible because some are represented by only a single reference sequence. Some interesting discrepancies were noted between results of the control region and cytochrome *b* datasets for this species. For example, *T. truncates* is well supported (>90%) in the cytochrome *b* analysis but poorly supported in the control region analysis (<50%). The situation was reversed with *T. aduncus*. The reasons of this have not been explored fully but are likely to be the result of differences in the number of samples (much greater for control region) or the geographic distribution of samples of the two datasets, as well as differences in the nature of variation in the loci themselves. Some errors in the taxonomic identification of samples in either dataset cannot yet be excluded.

Future developments

Improved statistical methods for species identification -- The statistical issues of species delimitation or species identification by molecular taxonomy have received relatively little attention (Sites and Marshall 2003). At present, DNA Surveillance implements only a Neighbor Joining reconstruction and bootstrap simulations to judge confidence in a species-level groupings. These are unlikely to be sufficiently sensitive to reliably identify some taxa distinguished by low levels of divergence or high levels of variation. An option for use of maximum parsimony and representation of the Bremer support index would be desirable but is problematic because of computation time. However, neither the nonparametric bootstrap nor the Bremer support index is a true statistical tests. Another option suggested by Goode et al. (2004) this meeting) is to attach the test sequence at all possible positions in a pre-defined reference tree and apply a maximum likelihood analysis to the alternative topologies. This uses a general statistical framework for assessing alternative hypotheses of species identity but the sensitivity of the test has not yet been investigated. The ability to download an alignment of the test and reference datasets as a NEXUS file would allow the user more freedom to explore their own preferred methods.

Database validation -- A full review of the assembled reference databases, including an effort to document fully the provenance of all GenBank sequences, is still required for validation. A joint publication from all major contributors would be desirable to confirm the validation exercise (e.g., Dalebout et al. 2003). Ultimately, an effort should be made to access the required genetic information from all existing cetacean holotype specimens. Where no holotype specimen is available or where the DNA has been destroyed by age or handling, Dalebout et al (in press) suggest that an official 'DNA neotype' should be formally designated for the purposes of molecular taxonomy. Such a designation would seem to be allowed by the International Code of Zoological Nomenclature (ICZN)[4] but might require a ruling by the Commission on a case-by-case basis (J. Mead, pers. comm.).

Delegated authority, virtual curation and proprietary datasets-- DNA Surveillance was developed with the intent to delegate administration of reference datasets to species specialists anywhere in the world. These specialists would be delegated as 'virtual' curators to maintain the integrity of species- or genus-specific datasets and provide regular updates of the datasets. A virtual Secretariat would maintain responsibility for updating the program. To prevent confusion, updates of both the application and datasets have been given accession numbers (e.g., the software is now Version 2.0 and the control region and cytochrome b datasets are now both Version 3.1).

At present, DNA Surveillance protects the privacy of all reference datasets while allowing their use for identification of test sequences. Beyond the tables of information on the sequences displayed through the Website, details of reference sequences are revealed to users at the discretion of the data administrator or owner. In recognition of the proprietary nature of some user-submitted test sequences, these are neither captured nor stored, except in temporary caching. The intent is to lift the proprietary protection of the primary validated datasets once all of these have been published or submitted to GenBank. This will be accompanied by an option to download the aligned test and reference sequences in the NEXUS format for subsequent analysis by the user. However, the option for proprietary protection could be useful in the future for extensive phylogenetic databases held by species specialist or virtual curators. Holders of these datasets might be willing to have them used for identification of test sequences but not prepared to make the datasets fully public.

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[4] A neotype can be designated in the following circumstances: "The single specimen designated as the name-bearing type of a nominal species or subspecies when there is a need to define the nominal taxon objectively and no name-bearing type is believed to be extant. If stability and universality are threatened, because an existing name-bearing type is either taxonomically inadequate or not in accord with the prevailing usage of a name, the Commission might use its plenary power to set aside that type and designate a neotype".

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Appendix Table 7-3. Internal robustness test of phylogenetic identification of cetaceans using the mtDNA control region and cytochrome *b* datasets (Version 3.1) implemented in *DNA Surveillance*. The null hypothesis is that the mtDNA sequences were paraphyletic unless species-specific monophyly is supported at some chosen level of bootstrap support. For example, a species might be considered paraphyletic for a chosen bootstrap value of >90% but not for a chosen bootstrap support of >75% (i.e., monophyly is supported by >75% but not >90% bootstrap support). Paraphyly at three specified levels marked by the letter 'Y'. The exact bootstrap support at which a species was considered monophyletic and the number of sequences representing the species are shown in the column to the right for each locus. Species considered paraphyletic at <50% bootstrap support are marked with a gray block. Bootstrap support cannot be calculated for species represented by only a single sequence, although these singletons contribute to the phylogenetic analysis of other species in the dataset.

		Dlp Paraphyly			Mono		CytB Paraphyly			Mono	
		<50%	<75%	<90%	%	N	<50%	<75%	<90%	%	N
Mysticetes:											
Pmac	sperm				100	2				?	1
BacDW	dwarf minke				?	1				-	0
Bacu	North Atlantic minke		Y	Y	69	2				?	1
Bacu	North Pacific minke				?	1				-	0
Bbon	Antarctic minke				100	2				?	1
Bbor	sei				100	3				?	1
Bede	Bryde's (Kochi)				?	1				?	1
Bede	Bryde's (common)				90	3				98	2
Bede	Bryde's (Solomon Is.)				?	1				100	2
Bmus	blue		Y	Y	52	2				100	2
Bmus	blue (pygmy?)				?	1				-	0
Bphy	fin				100	2				100	3
Mnov	humpback				100	2				100	2
Bmys	bowhead				100	3				100	2
Egla	North Atlantic right	Y	Y	Y	90*	2				?	1
Eaus	southern right		Y	Y	71	2				?	0
Ejap	North Pacific right			Y	80	2				?	0
Erob	gray				100	3				100	2
Cmar	pygmy right				100	2				?	1
Ziphiidae:											
Barn	ArnouY's beaked				100	2				98	2
Bbar	Baird's beaked				100	2				95	2
Zcav	Cuvier's beaked				100	2				100	2
Tshe	Shepherd's beaked				100	2				100	3
Hamp	northern bottlenose				100	2				100	2
Hpla	southern bottlenose			Y	84	2				100	2
Ipac	Longman's beaked				100	2				?	0
Mbid	Sowerby's beaked				100	2				100	2
Mbow	Andrews' beaked				99	2				100	2
Mcar	Hubbs' beaked				99	2				100	2
Mden	densebeaked				100	2				100	2

Meur	Gervais' beaked				98	2				100	2
Mgin	ginkgo-toothed beaked				100	2				?	1
Mgra	Gray's beaked				100	2				100	2
Mhec	Hector's beaked				100	2				100	2
Mlay	straptooth				100	2				100	2
Mmir	True's beaked				100	2				100	2
Mper	lesser beaked				100	2				100	2
Mste	Stejneger's beaked				100	2				100	2
Mtra	spade-toothed				100	2				99	2
Mpir	Perrin's beaked				99	2				100	2
Ipac	Indopacetus pacificus				-	0				97	2
Phocoenidae:											
Adio	spectacled porpoise				?	1				?	1
Npho	finless porpoise				98	11				100	2
Pdal	Dall's porpoise				100	6				100	2
Ppho	harbour porpoise	Y?	Y?	Y?	<50?	19				96	3
Pspi	Burmeister's porpoise				99	6				100	2
Psin	vaquita				?	1				91	2
Delphininae + Stenoninae:											
Sbre	rough-toothed				?	1				?	2
Scoe	striped				?	1	Y	Y	Y	56*	2
Satt	Pantropical spotted				?	1	Y	Y	Y	<50	3
Sfro	Atlantic spotted				?	1		Y	Y	52	2
Slon	pantropical spinner	Y	Y	Y	<50	2				91	3
Sflu	tucuYi				96	2				100	2
Ttru	bottlenose (*truncatus*)	Y	Y	Y	<50	20				93!	2
Tadu	bottlenose (*aduncus*)				97	11		Y	Y	74	2
Dcap	common (long-beaked)		Y	Y	51	10	Y	Y	Y	57*	2
Ddel	common (short-beaked)	Y	Y	Y	<50	18	Y	Y	Y	<50	3
Lhos	Fraser's				-	0				99	2
Schi	Indo-pacific humpbacked				-	0		Y	Y	74	2
Dtro	Delphinus tropicalis				-	0				?	1
Scly	Clymene				-	0				?	1
Globicephalinae + Orcininae:											
Gmac	short-finned pilot	Y	Y	Y	<50?	7		Y	Y	65	2
Gmel	long-finned pilot				99	5				92	2
Ggri	Risso's				99	3				100	3
Pele	melon-headed				?	1				?	1
Pcra	false killer				?	1				?	1
Oorc	killer				100	7				100	3
Obre	Irrawaddy				-	0	Y	Y	Y	<50?	3
Fatt	pygmy killer				-	0				?	1

Lissodelphininae:									
Lacu	Atlantic white-sided			100	2			100	2
Lalb	white-beaked			?	1			100	3
Ccom	Commerson's	Y	Y	68	8			?	1
Ceut	Chilean			93	4		Y	80	2
Chea	Heaviside's		Y	76	7			?	1
Chec	Hector's		Y	77	8			?	1
Lcru	hourglass			?	1			?	1
Lobl	Pacific white-sided			91	5	Y	Y	67	3
Lobs	dusky	Y	Y	51	15		Y	87	3
Laus	Peale's			99	2			?	1
Lper	southern right			97	2			100	2
Lbor	northern right			-	0			?	1

Y = sp. is paraphyletic at this criterion
? = only 1 sequence for sp.
- = not in data set
* = paraphyletic

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