

SC/67B/REP/09

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Report of the SM SD Joint Intersessional  
Workshop: resolving Tursiops taxonomy  
worldwide

International Whaling Commission



INTERNATIONAL  
WHALING COMMISSION

## Report of the SM/SD Joint Intersessional Workshop:

### Resolving *Tursiops* Taxonomy Worldwide

**Summary** An intersessional workshop was convened to evaluate taxonomy and population structure of bottlenose dolphins (*Tursiops* spp.) worldwide. This followed priority topic review in the SM sub-committee over three years (2015-2017), divided into broad geographic regions. More than 20 different *Tursiops* species have been described historically but only two - *T. truncatus* (Montagu, 1821) and *T. aduncus* (Ehrenberg, 1832) - are currently recognised. Bottlenose dolphins are known to show morphological and genetic divergence throughout their range, raising issues for recognition of discrete units needed for effective conservation and management. Summary data were compiled for studies presented at the Scientific Committee reviews and at the workshop; these summaries were tabulated (see Annex D), and formed the basis for discussions concerning taxonomic and population distinction issues in each geographic region during the workshop.

The workshop considered the distribution of research efforts to date, identified data-deficient regions, **recommended** those areas as priorities for *Tursiops* research (see details in item 3.2, priority recommendations in item 6.2), continued compilation of specimen, study, and researcher details, and concentrated effort to improve our understanding of *Tursiops* in data-deficient areas.

The workshop considered unresolved species, sub-species and population questions in each region and what would be required for more confident recognition of such distinctions, and **recommended** that guidelines for recognition of cetacean species, subspecies, and DIPs be followed for proposing taxonomic and population-level distinctions and for assessing the information used to support such distinctions. The workshop **strongly emphasized** that such distinctions be examined within an appropriately wide and inclusive geographic context, using of multiple lines of evidence.

Further priority **recommendations** included: (1) Collect additional data to better characterize divergence between coastal and offshore forms in the western South Atlantic Ocean to help resolve whether *T. t. gephyreus* might more accurately be elevated to species status, (2) Investigate *T. aduncus* lineages in the Indian Ocean and western South Pacific to assess potential subspecies recognition, (3) Continued study of animals associated with the "*T. australis*" mtDNA lineage in the context of both *T. truncatus* and *T. aduncus*, (3) Examine the level of male-mediated gene flow between the coastal and offshore forms in the western North Atlantic Ocean to determine whether the coastal form should be elevated to species or subspecies status, (4) Conduct comprehensive morphometric analyses comparing *Tursiops truncatus* in the Mediterranean, Black Sea, and eastern Atlantic to evaluate whether any regions may harbour a taxonomic unit above the level of population, (5) Conduct comprehensive morphometric analyses of coastal and offshore *Tursiops truncatus* in the eastern North Atlantic Ocean and compare results to those from western North Atlantic to evaluate potential taxonomic differences, (6) Morphometric analyses of Gulf of California coastal and offshore dolphins relative to those from California and the eastern tropical Pacific, with a particular focus on the level of divergence of coastal dolphins in the upper Gulf of California to other areas, (7) Collect additional genetic and

morphological data throughout the eastern South Pacific Ocean and further studies to investigate coastal versus offshore forms throughout the region, including coastal and offshore waters from Central America to Mexico, and if possible around the southern tip of South America to Argentina.

The workshop was kindly hosted at NOAA Southwest Fisheries Science Center (SWFSC), La Jolla, California, 12-14 January 2018. The list of participants is given as Annex A.

## **1. INTRODUCTORY REMARKS**

### **1.1. Convenor's opening remarks**

Natoli welcomed the group and the participants were introduced. The workshop participants expressed their gratitude to SWFSC for providing the venue, and to Aimee Lang and Julie Creek for organization and logistics support.

### **1.2. Election of Chair**

Natoli was appointed as Chair and Rosel was appointed as co-chair of the meeting.

### **1.3. Appointment of rapporteurs**

Cipriano, Rosel and Lang served as rapporteurs. The report was coordinated by Cipriano, with the support of Rosel, Lang, Natoli.

### **1.4. Adoption of the Agenda**

The agenda was reviewed, updated, and adopted by the workshop participants. The adopted Agenda is provided as Annex B.

### **1.5. Available Documents**

A list of documents reviewed during the workshop and cited in the text is given in Annex C.

## **2. TERMS AND A STRATEGY FOR ASSESSING TAXONOMIC AND POPULATION-LEVEL DISTINCTIONS IN *TURSIOPS***

### **2.1. Summary: Context and Motivation for the 2015-2017 Scientific Committee Review and 2018 Workshop on Resolving *Tursiops* Taxonomy Worldwide**

At SC/65b the sub-committee on small cetaceans (hereafter, the sub-committee) identified as its next priority topic a review of the taxonomy and population structure of the genus *Tursiops*, to be conducted in stages over three annual Scientific Committee meetings. Understanding whether there is consistency in the recognition of the taxonomic and/or population status of various local forms across the distributional range, and to which taxonomic or population unit(s) they should be assigned, has been challenging; the status of many forms worldwide is still unresolved. An additional aim of this exercise was to develop a widely applicable taxonomic-assessment framework for small cetaceans.

Bottlenose dolphins are among the most widely distributed cetaceans. Factors contributing to taxonomic uncertainty in this genus include the wide distribution across highly variable environments, variability among locally-adapted populations, sympatry of various forms in some regions, a lack of specimens from many regions, differences in research methods and designs, and a long and complex nomenclatural history in the taxonomic literature (Hershkovitz, 1966; Rice, 1998; Wang and Yang, 2009). Relationships among members of the entire family *Delphinidae*, and in particular the subfamily *Delphininae* (*Sousa*, *Sotalia*, *Stenella*, *Tursiops*, *Delphinus* and *Lagenodelphis*), are poorly resolved, and the systematics of these species and genera is still unclear (Perrin *et al.*, 2013). Worldwide, more than 20 different *Tursiops* species have been described historically but only two - *T. truncatus* (Montagu, 1821) and *T. aduncus* (Ehrenberg, 1832) - are currently recognised (Society for Marine Mammalogy Committee on Taxonomy 2017). *T. truncatus* has a worldwide distribution from temperate to tropical waters in both hemispheres, whereas *T. aduncus* is confined to the Indo-Pacific region and is principally found in near-shore waters. In many regions where bottlenose dolphins occur, different forms have been described, based on distribution, morphology, and genetic profiles. Among the *T. truncatus* forms in the Atlantic and Pacific, two geographically and (to varying degrees) morphologically and genetically differentiated types have often been described as e.g. ‘coastal morphotype’ and ‘offshore morphotype’. The morphological differentiation between coastal and offshore forms has raised questions about whether these forms represent different populations, subspecies or subspecies. However, the correlation of morphotype with preferred habitat is not consistent across regions - for example, in the eastern North Atlantic the coastal and offshore forms are not morphologically distinct (Louis *et al.*, 2014), whereas in the western North Atlantic coastal animals are smaller than offshore animals (Mead and Potter, 1995). (See section 2.6 Distribution-Related Terminology below for an explanation of the terminological conventions for names ascribed to these different types that we use here). Relatively high levels of genetic differentiation have been observed among coastal *T. truncatus* populations in areas where detailed analyses have been conducted (e.g. Florida, Gulf of Mexico, western North Atlantic, Mediterranean - Natoli *et al.*, 2005; Rosel *et al.*, 2009; Sellas *et al.*, 2005; Vollmer and Rosel, 2017).

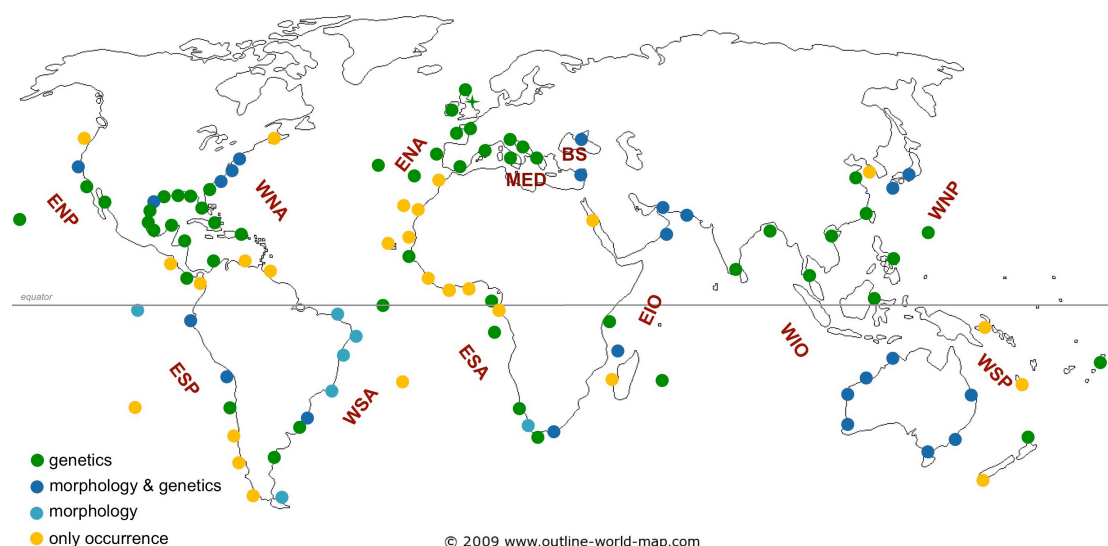
Over the course of three years (2015-2017), the sub-committee reviewed all relevant morphological, genetic and occurrence information available for *Tursiops* worldwide according to the following regional subdivision (Fig.1):

- SC/66a: Indian Ocean, adjacent western Pacific/Oceania
- SC/66b: Atlantic Ocean, Mediterranean and Black Sea
- SC/67a: eastern Pacific Ocean and western North Pacific Ocean

After reviewing the available information, the sub-committee then focused on evaluating the support provided for taxonomic (subspecies, species) and population-level distinctions proposed in the publications we reviewed. This included, *inter alia*, proposals for the recognition of new species and/or subspecies, and evidence for population-level divergence significantly strong to warrant recognition of the bottlenose dolphins in particular areas as worthy of designation as distinct ‘management units’ (see

detailed discussions below of the various names given to such units, and the criteria used to identify them).

Detailed summaries of available evidence and conclusions from each of the 2015-2017 reviews are included in the sub-committee reports for that year (IWC 2016, IWC 2017, IWC 2018). It should be noted that in all of the regions considered during the three-year review, sizeable areas have almost no information, thus presenting significant challenges in understanding bottlenose dolphin diversification worldwide.



**Fig.1** Map showing the regional subdivisions considered throughout the review: eastern Indian Ocean (EIO), western Indian Ocean (WIO), eastern North Atlantic (ENA), eastern South Atlantic (ESA), Mediterranean Sea (MED), Black Sea (BS), western North Atlantic (WNA), western South Atlantic (WSA) eastern North Pacific (ENP), eastern South Pacific (ESP), western North Pacific (WNP), western South Pacific (WSP). Dots of different colours identify the locations where published information was available for review.

At SC/66a taxonomic and population distinctions for bottlenose dolphins in the Indian Ocean (EIO and WIO), adjacent western South Pacific Ocean (WSP) and Oceania regions were addressed. In the Indian Ocean and western Pacific, *T. aduncus* and *T. truncatus* are clearly distinguishable, and the differences between them are consistent across many different areas for both genetic and morphological analyses (e.g. Ross and Cockcroft 1990; Wang *et al.*, 1999, 2000). Some population structure has been documented for *T. truncatus* in the WNP (e.g., Chen *et al.*, 2017), but few such studies have been performed in this area. Reciprocally monophyletic genetic differentiation and some morphological differentiation was documented among at least three forms of *T. aduncus* across the region including distinct forms in South Africa, Pakistan and Australia (see Natoli *et al.*, 2004; Gray *et al.*, 2018). It was difficult to resolve the taxonomic status of "*T. australis*" (recently described from south Australian waters, Charlton-Robb *et al.*, 2011), in part because of discordance in results between morphometrics

and different genetic markers (Hale *et al.*, 2000; Kemper, 2004; Charlton-Robb *et al.*, 2011; Jedensjö *et al.*, 2013).

At SC/66b, the Atlantic Ocean (WNA, WSA, ENA, ESA), Mediterranean (MED) and Black Sea (BS) regions were reviewed. Only one species, *T. truncatus*, is recognised to be present throughout these regions, with the Black Sea population recognised as a subspecies, *T. truncatus ponticus* Barabash-Nikiforov, 1940. Significant population structure has been found for this species throughout the Atlantic and Mediterranean (e.g., Natoli *et al.*, 2005; Rosel *et al.*, 2009; Fruet *et al.*, 2014; Louis *et al.*, 2014a, b). Ecological differences have been documented between coastal and offshore forms in both the eastern North Atlantic (ENA) and western North Atlantic (WNA) (Mead and Potter, 1995 ; Louis *et al.*, 2014 a, b). Molecular genetic analyses revealed significant genetic differentiation for a wide range of molecular markers between coastal and offshore forms in the WNA (Kingston and Rosel, 2004; Kingston *et al.*, 2009; Rosel *et al.*, 2009; Vollmer and Rosel, 2017; Moura *et al.*, pers. comm.) and also in the ENA (Natoli *et al.* 2004; Louis *et al.*, 2014 a, b; Moura *et al.* pers. comm.). *Tursiops truncatus* appears to occur throughout both coastal and offshore areas in the African east Atlantic (Queroil *et al.*, 2007; Van Waerebeek *et al.*, 2016), but there are too few data to determine whether there is inshore/offshore differentiation of bottlenose dolphins in that region. In the western South Atlantic (WSA), significant morphological differentiation exists between coastal and offshore forms which may be indicative of species or subspecies-level differences (Costa *et al.*, 2016; Wickert *et al.*, 2016); the two types are parapatric along the coast of southern Brazil and possibly sympatric in northern Argentina (Costa *et al.*, 2016). Although molecular genetic studies have been hampered by small sample size, but see Fruet *et al.* (2017), and further molecular genetic analysis is ongoing, the significant morphological differentiation between the large coastal form and smaller offshore form (a single, but strong line of evidence) is consistent with and supportive of subspecies-level distinction. However, it was difficult to draw firm conclusions about whether the coastal form should be elevated to species status, pending additional molecular genetic analysis to evaluate levels of male-mediated gene flow. The review of bottlenose dolphins in the Atlantic, Mediterranean and Black Sea further illustrated the need to standardize and widen the types of evidence (morphological, genetic, ecological and behavioral/acoustic) used to diagnose and delimit population-level differences and recognise taxonomic (species, subspecies) distinctions.

At SC/67a, the subcommittee considered published information on bottlenose dolphin distribution and potential taxonomic distinctions in the eastern North Pacific (ENP), eastern South Pacific (ESP) and portions of the western North Pacific (WNP) not covered at SC/66a. Newly available information on *Tursiops* from areas covered in SC/66a (2015) and SC/66b (2016) was also reviewed.

Well-differentiated forms of *T. truncatus* are present in the eastern North Pacific; both morphological and genetic data provide convincing evidence for the presence of two distinct forms of *T. truncatus*. In California, a coastal form (originally described as *T. gilli* Dall, 1873) is restricted to waters within 1 km of the coast from at least Ensenada, Mexico to San Francisco, California while an offshore form (originally described as *T. nuuanu* Andrews, 1911) is also found off California. There is significant genetic differentiation between the Gulf of California and California coastal populations (of the same

magnitude as between coastal and offshore populations), but a comprehensive morphological analysis comparing the two has not yet been performed. In the Gulf of California, there was significant differentiation between offshore populations in the central and southern regions, and a coastal form restricted in range to the upper portion of the Gulf is of conservation concern given documented numbers of stranded dolphins observed in that area.

Both *T. aduncus* and *T. truncatus* appear to co-exist throughout much of the western North Pacific although this area has not been thoroughly examined. Existing data do not support the presence of multiple forms of either species in the western North Pacific, although population-level differentiation in some areas has been documented (Chen *et al.*, 2017)

In the eastern South Pacific, comprehensive skull morphometry studies have not been conducted to date. Some studies suggest the presence of two forms in Peru, Ecuador and Colombia based on dorsal fin shape, tooth width and some qualitative differences in skull characters (Van Waerebeek *et al.*, 1990, Santillan *et al.*, 2008, Felix *et al.*, 2017), but sample sizes have been relatively small. Only an offshore type and a small, possibly hybrid group are documented in Chilean waters. Further work is needed to determine whether a coastal type is present in Chile. The review of bottlenose dolphins conducted at SC/67a concluded that sample sizes for most of the studies in this region have been relatively low and increased sampling throughout the region is needed so that the distinctions between the different types in the eastern South Pacific can be better resolved; a wide range of data (morphological, genetic and other) from the eastern North and eastern South Pacific should be compared, so that the distributions of any potentially distinct units can be fully explored.

## **2.2. Review: A Practical Example of Approaches for Stock Delineation Used by U.S. Government Agencies**

Lang presented a brief summary of the report of a 2014 NOAA Fisheries workshop (Martien *et al.*, 2015) that focussed on how multiple lines of evidence could be used to delineate demographically independent populations (DIPs) of marine mammals - historically referred to as "stocks" or "population stocks" for management purposes under the U.S. Marine Mammal Protection Act (MMPA). The MMPA defines population stock as "a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature." Under the MMPA, "population stock" is the fundamental unit of legally-mandated conservation (Martien *et al.*, 2015). A set of guidelines (GAMMS) has been developed that includes guidance for how DIPs should be delineated under the MMPA (<http://www.nmfs.noaa.gov/pr/sars/guidelines.htm>). Although these guidelines indicate that many types of evidence may be used to delineate DIPs, most delineations have relied heavily on genetics, and there is little guidance on how other lines of evidence should/can be used. These guidelines are updated occasionally, the latest update was in 2016 (<http://www.nmfs.noaa.gov/pr/sars/pdf/gamms2016.pdf>).

Distinct Population Segments (DPSs) are a similar "below-species" unit recognised as eligible for protection under the U.S. Endangered Species Act (ESA) (U.S. Department of the Interior, 1996). The

criteria for identifying DPSs under the ESA and DIPs under the MMPA are not identical, as the levels of divergence described by these two categories relate to different time scales (Wood and Gross, 1998).

The 2014 NOAA Fisheries workshop was convened to examine ways to improve delineation of DIPs of marine mammals under the MMPA, particularly for cases where genetic data are unavailable. Prior to the workshop, discussion groups considered the strength and weaknesses of a suite of different potential lines of evidence that can be used to delineate marine mammal stocks, including acoustics, movements, stable isotope ratios and fatty acids, contaminants, morphology, life history characteristics, trends in abundance, physiographic and oceanographic data, distributional data, and behavioral association data. The 2014 workshop participants then used the discussion group summaries to evaluate and rank the strengths and weaknesses for each line of evidence with respect to different marine mammal groups. Differences in genetics, morphology, and movement patterns between two groups were ranked as strong lines of evidence for delineating DIPs. The workshop participants agreed that there was no quantitative way to combine different lines of evidence in order to delineate DIPs and that, where (only) two or three weak lines of evidence were available, considerations had to proceed on a case-by-case basis. The 2018 *Tursiops* Taxonomy Workshop participants recognised that the process used by US government agencies in such deliberations is sensible and informative, and noted that such a clear and consistent approach is not used routinely elsewhere - the effort to delimit DIPs eligible for protected status independent of alpha-taxonomy status was seen as particularly valuable.

### **2.3. Review: Species Concepts and Approaches for Assessment of Proposed Species, Subspecies, and Population-level Distinctions**

In order to address the objectives of this workshop, participants briefly reviewed and discussed species and subspecies concepts, and criteria proposed for recognizing taxonomic distinctions at the species and subspecies levels, especially as proposed by the Workshop on Cetacean Taxonomy held in 2004 (Reeves *et al.*, 2004) and further developed in the series of papers in a recent Special Issue of Marine Mammal Science on delimiting cetacean subspecies using primarily genetic data (Taylor *et al.*, 2017a; Martien *et al.*, 2017; Rosel *et al.*, 2017a; Rosel *et al.*, 2017b; Archer *et al.*, 2017; Taylor *et al.*, 2017b). Although these efforts were not reviewed in detail during the 2018 *Tursiops* Taxonomy Workshop, they represent the context that participants shared while conducting deliberations on the strength of the evidence supporting the species-, subspecies-, and population-level distinctions we considered.

The 2004 workshop considered a variety of species concepts and approaches to species and subspecies delimitation, and concluded that both major species concepts, the Biological Species Concept (BSC) and Phylogenetic Species Concept (PSC), as well as their various sub-approaches, could be considered relevant and useful in cetacean taxonomy, and that the different approaches to species delineation should be employed in a pragmatic way (Reeves *et al.*, 2004). The workshop also recognised that levels of divergence observed range across a continuum, and thus for recognizing species within that continuum a general (guidelines), rather than specific (criteria) approach was more appropriate. With regard to species-level distinctions, the 2004 workshop agreed that species are "groups of organisms that are distinct - genetically and morphologically - because of evolutionary divergence from other



groups" and also that "such evolutionary entities, or lineages, are the focus of many of the species concepts that have been proposed..." The workshop concluded that "a finding of congruent divergence for each of multiple distinct kinds of data should be taken as strong support for species designations" and also that "such distinct kinds of data could include morphological data together with genetic data, or data from multiple independent genetic loci". The 2004 workshop also concluded that additional kinds of data, such as geographical range, feeding behaviour, and vocalization repertoires, should not be used as the primary basis for species delineations, but could serve as useful lines of evidence (Reeves *et al.*, 2004).

With regard to subspecies distinctions, the 2004 workshop recognised that cetacean subspecies have primarily been designated on the basis of morphology, that no strict criteria for defining cetacean subspecies had been used historically, and that cetacean subspecies recognised to date had been geographically-distinct forms that had been given a Latin trinomial. The workshop 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 behavioural differences can complement morphological and genetic evidence for establishing subspecies." These conclusions of the 2004 workshop are now often quoted as a requirement that species-level distinctions be supported by multiple lines of evidence, while subspecies-level distinctions could be based on a single line of evidence - in both cases morphological or genetic divergence was considered primary, while geographical range and behavioural differences were considered secondary (Reeves *et al.*, 2004).

De Queiroz (2007) attempted to simplify the many long-standing disputes surrounding the "species concept" by separating the idea of "species conceptualization" from methods for inferring the boundaries and numbers of species ("species delimitation"). De Queiroz (2007, and a series of preceding papers cited therein) recognised that most species concepts have a "common element" - they all treat "existence as a separately evolving metapopulation lineage" (in essence, using a variety of terms and descriptions) as the primary defining property of the species category, but the various species concepts (including BSC and PSC) differ in the importance they ascribe to specific properties acquired by lineages during the course of divergence (intrinsic reproductive isolation, diagnosability, reciprocal monophyly, etc.). De Queiroz refers to these properties as "secondary species criteria" and argues that they should not be considered relevant to species conceptualization but only as operational criteria used in the process of species delimitation, as they provide evidence for lineage separation. Similar to the pragmatic approach recommended by the 2004 cetacean taxonomy workshop, de Queiroz (2007) also concluded that the presence of any one of the "properties acquired by lineages during the course of divergence" is evidence for the existence of a species, and that "more properties and thus more lines of evidence are associated with a higher degree of corroboration."

Building further on the "lines of evidence" criteria proposed by the 2004 workshop (Reeves *et al.*, 2004) and the "properties acquired by lineages" evidence described by de Queiroz (2007), a Special Issue series of six papers in Marine Mammal Science (Volume 33, summarized in Taylor *et al.*, 2017a)

proposed a set of guidelines and standards for delimiting subspecies and species using (mainly) genetic evidence. Taylor *et al.* (2017a) developed the following subspecies definition: "A *subspecies* is a population, or collection of populations, that *appears to be* a separately evolving lineage with discontinuities resulting from geography, ecological specialization, or other forces that restrict gene flow to the point that the population or collection of populations is diagnosably distinct". The "Guidelines and Standards" chapter of the Special Issue (Taylor *et al.*, 2017b) pointed out that this definition is consistent with the subspecies concept discussed in Reeves *et al.*, (2004), but is more explicit in requiring *diagnosability* - as defined in another Special Issue chapter (Archer *et al.*, 2017) "diagnosability is a measure of the ability to correctly determine the taxon of a specimen of unknown origin based on a set of distinguishing characteristics." Diagnosability and its applicability for making subspecies-distinctions are discussed in detail by Archer *et al.* (2017).

Martien *et al.* (2017), recognizing the increasingly important role of genetic data in cetacean species and subspecies delimitation, reviewed seven categories of analytical methods and focussed on the ability of each to distinguish subspecies from populations and species, the degree of diagnosability between putative taxa, and the extent to which the putative taxa have diverged along separate evolutionary pathways. Martien *et al.* (2017) recognised that two types of metrics are needed to evaluate taxonomic 'cases' (i.e., proposed taxonomic distinctions being reviewed to determine consistency with species-, subspecies-, or population-level divergence). These include the degree of genetic differentiation (which varies along a continuum from population-level divergence to subspecies to species) and the degree of diagnosability (useful for distinguishing subspecies vs. population-level divergence). They concluded that "diagnosability is best estimated with either assignment tests or multivariate methods, while evaluating the degree of divergence requires a synthesis of multiple lines of evidence derived from different analytical methods and different data types, including nongenetic data" (Martien *et al.*, 2017).

Rosel *et al.* (2017a) reviewed 32 peer-reviewed articles for methodology, consistency of markers and analytical methods used, and overall quality of arguments used, when genetic data were employed to delimit new species and subspecies of marine mammals. A mixture of both sound and inadequate practices for use of genetic data for cetacean taxonomy was found in these studies; limitations often included lack of basic background material such as distribution maps and sampling records, and inadequate geographic coverage for broadly-distributed taxa. These common limitations suggested that improvements could be made for use of genetic data in cetacean taxonomy by developing standardized guidelines for a minimum set of information to be included in such efforts, clear articulation of the taxonomic question being investigated, adequacy of sampling, choice of genetic markers used, and analytical methods and strength of evidence required to support taxonomic conclusions reached (Rosel *et al.*, 2017a). A separate Special Issue paper then went on to explore, using pairs of well-recognised cetacean populations, subspecies, and species, a suite of metrics measuring molecular genetic differentiation to examine which best categorized those three levels of divergence when using the mitochondrial DNA control region as the genetic marker; Nei's estimate of net divergence ( $d_A$ ) and percent diagnosability performed best for making such distinctions. Most species-level distinctions were unambiguously supported by use of these two metrics with this gene region, and subspecies-level

distinctions were generally supported by intermediate levels of divergence, but some recognised subspecies were more consistent with population-level divergence (Rosel *et al.*, 2017b). These results were combined with the description of a measure of diagnosability (Archer *et al.*, 2017) and recommendations in Rosel *et al.* (2017a), and culminated in a description of "Guidelines and Standards" for delimiting cetaceans subspecies (Taylor *et al.*, 2017b). However, as pointed out in Rosel *et al.* (2017a) and Taylor *et al.* (2017b) and during discussion at the 2018 workshop, there are risks with relying on a single gene tree; confirmation from multi-locus genotyping should follow particularly for delimiting species. In addition, species identification of dolphins based only on mtDNA control region sequence similarity can be imprecise or misleading due to homoplasy in the recent delphinid radiation (Dizon *et al.*, 2000).

Schwartz and Boness (2017), in the introductory remarks to the Special Issue papers, provide a concise and thoughtful summary of the challenges involved in dividing up the genetic divergence "continuum" into discrete species, and point out that those working for natural resource agencies are charged with delimiting subspecies and other "units" at and below the species level when such entities are eligible for protection under a legal framework, such as the U.S. Endangered Species Act (1973) and Marine Mammal Protection Act (1972) - both of which give protected status to units below the species level. The current workshop's consideration of the taxonomic and population-level distinctions proposed for bottlenose dolphins within each of the major geographic regions should be viewed within this context - resource managers in those regions need help in deciding whether such distinctions are warranted, and whether the proposed population-, subspecies- and species-level distinctions are supported by sufficiently strong and diverse lines of evidence.

Workshop participants discussed the various recommendations in Reeves *et al.* (2004), Taylor *et al.* (2017a), Martien *et al.* (2017), Rosel *et al.* (2017a and 2017b), Archer *et al.* (2017), and Taylor *et al.* (2017b), focusing on how the current workshop could make practical use of the criteria, standards, and guidelines therein for making informed judgments about the population-, subspecies- and species-level distinctions proposed for *Tursiops* within each of the geographic regions we reviewed. The workshop recognised that attempting to impose discrete categories on the continuum of genetic divergence is problematic, but accepted (at least in principal) the proposed species and subspecies definitions (as outlined above) and also that the "Special Issue" proposed guidelines are useful for both proposing taxonomic and population-level distinctions and for assessing the information used to support such distinctions. The 2018 workshop participants agreed to use these general guidelines: 100% diagnosability is not required for populations or subspecies; subspecies and species cannot be clinal; subspecies do not have to be reproductively isolated from other subspecies; reproductive isolation of species can be incomplete even when introgression is rare; phylogenetic analyses can be informative as they demonstrate evidence for independently evolving lineages, but should be cautiously interpreted whether or not reciprocal monophyly between the focal groups is found; the type of markers used for monophyly distinctions is important and such evidence must be considered cautiously; contradictions between evidence for lineage separation from nuclear and mitochondrial markers must also be thoroughly evaluated; and, the context for differences found for such markers should take into account potentially confounding factors such as gender, sex-biased dispersal, effective population size, social

structure, the potential for environmental plasticity, the different 'response time' of nuclear vs. mitochondrial markers, etc.

#### **2.4. Review: Distribution-Related Terminology**

The earliest geographic distinctions proposed for bottlenose dolphins that we reviewed (Ross, 1977; Walker, 1981; Van Waerebeek *et al.*, 1990; Ross and Cockroft, 1990) were usually characterized as "coastal" vs. "offshore" and these authors carefully used the neutral term "forms" to describe the types found in different areas while marshalling the evidence to (potentially) recognise them as different populations, subspecies, or species. Occasionally there are references to "inshore" (e.g. Chen *et al.*, 2017) or distinctions between "coastal" vs. "pelagic" (e.g. Louis *et al.*, 2014). For consistency, our usage here typically contrasts "coastal" vs. "offshore"; we use the terms "types", "forms", and "units" as neutral descriptors while assessing the evidence supporting potential distinctions. Some authors recognise apparent differences in feeding ecology between the dolphins found in different areas as "coastal ecotype" vs. "offshore ecotype" (e.g. Felix *et al.*, 2017), morphological differences have similarly been recognised as "morphotypes" - we choose not to use either of these terms here. The definition of the term "population" is hard to pin down and has widely different meanings for different disciplines (see Waples and Gaggiotti, 2006 for a full discussion); in our usage "population-level distinctions" refers to populations that exhibit significant differentiation (primarily genetic), but below that expected for subspecies, and satisfy the criteria found useful for delineating units deserving separate-management recognition (such as DIPs).

#### **2.5. Strategy for Objective Recognition of Taxonomic and Population-level Distinctions for *Tursiops***

The approach summarized below was developed over the course of the 2015-2017 *Tursiops* review, as we considered (a) existing and proposed population, subspecies, and species distinctions, (b) the evidence supporting each distinction, (c) species and subspecies "concepts" and definitions, and (d) the criteria and guidelines for delimiting these taxonomic units that have been suggested by previous workshops and in publications we reviewed. This strategy is an update of the 'objectives' originally drafted in the proposal for holding the 2018 workshop.

##### **1. Use established criteria and guidelines for objective assessment of taxonomic and population-level distinctions in *Tursiops***

Using established and more recently proposed criteria and guidelines for the types of data, analyses, and supplementary information that should be included:

- identify key "taxonomic" (sub-species, species) and population-level distinctions proposed for bottlenose dolphins within each of the major geographic regions that were reviewed previously by the sub-committee and at the 2018 workshop
- consider the relative importance of morphology, behaviour, mitochondrial and nuclear genetic data for consideration of differences at the species, subspecies and population levels

- consider also the use of established and new genetic markers, morphological analyses, behavioural and ecological evidence, and their integration towards a consistent classification for the genus
  - summarize evidence in support of or against the proposed distinctions, including sample sizes, amount of sequence data and diversity of genetic markers used, geographic coverage of specimens used, and supplementary information (life history, parasites, ecology, etc.)
2. *Evaluate the strength of evidence for recognition of *Tursiops* forms identified in various regions*
- Using the information compiled in the sub-committee's three-year review of *Tursiops* together with any additional information available to:
- review the evidence supporting proposed distinctions (morphological differences, genetic divergence/connectivity, behavioral differences, ecological/habitat differences)
  - determine whether proposed population-, subspecies- and species-level distinctions are supported by sufficiently strong and diverse lines of evidence
3. *Identify poorly known regional populations that are data deficient and highlight important outstanding areas for further research*

### **3. REVIEW OF AVAILABLE EVIDENCE FOR TAXONOMIC AND POPULATION-LEVEL DISTINCTIONS OF *TURSIOPS* IN EACH REGION**

Intersessionally, the participants worked in groups, each group on specific assigned geographic regions (see Fig. 1) to summarise all the information reviewed during the SC meetings and relevant to the population, subspecies, and species distinctions proposed in publications we reviewed. Proposals came from publications we reviewed during the 2015-2017 Scientific Committee meetings and supporting information came from those reviews plus any new information available to the workshop. The Summary Table is available in Appendix C.

#### **3.1. Review of the Intersessional Summary Table**

The groups reviewed the Summary Table information, updated it where necessary, and prepared concise summaries for their assigned regions aiming to highlight the key issues. Each region's information was presented in a PowerPoint presentation addressing the following questions:

- 1) What are the population, subspecies, and species distinctions at issue in this region?
- 2) What lines of evidence have been used?
- 3) What analyses have been performed to address the validity of the proposed distinctions?

Based on the Summary presentations, workshop participants discussed the status of the existing taxonomy in each region, support for or against additional taxonomic (sub-species, species) and population-level distinctions, and what information, data, or additional analyses are still needed for final conclusions. Participants also identified data-deficient areas for which no decisions on *Tursiops* taxonomy and population structure could be made (see item 6 below). A synopsis of each regional summary presentation and following discussions are given below and include: (a) newly-available

information, (b) reviews of information compiled during 2015-2017 sub-committee reviews, (c) the 2018 workshops evaluation of the strength of the evidence, (d) our conclusions regarding the support for and against proposed population, subspecies and species distinctions, recommendations, and (e) suggestions for future work (Workshop Agenda items 3, 4, 5).

### **3.2. Summary of Information Available and Evaluation of Taxonomic and Population-level Distinctions of *Tursiops* in each Geographic Region**

#### **3.2.1. Indian Ocean / Western South Pacific**

Both *Tursiops truncatus* and *Tursiops aduncus* are found throughout the Indian Ocean and western South Pacific. Numerous studies of bottlenose dolphins in this region have been conducted, but there are large areas where data remain sparse and would be potentially very useful, especially most of the eastern coast of Africa and the region from Pakistan through to Indonesia and Papua New Guinea. Questions to address within this region include the resolution of multiple lineages of *T. aduncus*, the magnitude of the divergence between *T. truncatus* and *T. aduncus* (which exceeds that between some delphinid genera), and further assessment of a recently described new species from southern Australia, "*T. australis*" (Charlton-Robb *et al.*, 2011).

Data pertinent to these issues were available from South Africa, Tanzania, Eritrea, Oman, Pakistan, India, Bangladesh, many locations around Australia, the Solomon Islands, New Caledonia and New Zealand. Relatively high resolution data, including mitogenomes (Moura *et al.*, 2013) and RADseq phylogenies from a manuscript in preparation made available to the 2018 workshop (Moura *et al.*, pers. comm.) allowed comparison between South African, Oman, Pakistan, India and Australia, together with mitogenome data for further regions around Australia, Indonesia and New Zealand (Cornaz, 2015). The ddRAD data (~4 million bp sequence data) confirmed a relatively deep level divergence between *T. truncatus* and *T. aduncus* and suggested a monophyletic *Tursiops* genus, with fairly extensive reticulation (especially between coastal and offshore populations in the North Atlantic). Within the *T. aduncus* lineages there were three well-defined lineages separating a South African through Oman named 'Holotype lineage', samples previously identified as "*T. australis*" from South Australia (Charlton-Robb *et al.*, 2011), and a lineage comprised of samples from eastern Australia. An extended mitogenome analysis (see Moura *et al.*, 2013; Gray *et al.*, 2018; Cornaz, 2015) identified at least five *T. aduncus* lineages with relatively deep nodes: the Holotype lineage, a newly identified 'Pakistan' lineage (see Gray *et al.*, 2018), western Australia, eastern Australia, and samples previously identified as "*T. australis*" from South Australia.

Samples from Bangladesh sequenced for the mtDNA control region also formed a distinct lineage (Amaral *et al.*, 2015; Gray *et al.*, 2018), which should be compared with the Pakistan lineage at higher resolution when possible. Further sampling in Indonesia, Taiwan, and China may reveal a further lineage associated with the eastern Australia lineage. An earlier study with limited samples within regions compared South Africa and Australia *T. truncatus* and *T. aduncus* body lengths and skull lengths. This study showed almost no overlap between species but no differentiation in relative skull length within species among regions (Hale *et al.*, 2000). A comprehensive study comparing cranial

measurements among Oman and Pakistan specimens showed significant differentiation between the *T. truncatus*, *T. aduncus* Holotype, and Pakistan *T. aduncus* lineages (most strongly differentiating *T. truncatus* and *T. aduncus*; Gray, 2017). The data for *T. truncatus* in the Indian Ocean are relatively few, mostly from Oman, where the mtDNA lineage fits into the broader lineage found worldwide (Gray *et al.*, 2018).

Low but significant population genetic structure was found for *T. aduncus* in South Africa and Tanzania (Natoli *et al.*, 2008; Sarnblad *et al.*, 2011). Populations of *T. aduncus* and *T. truncatus* around Australia have been intensively studied, using microsatellite DNA, mtDNA and in some locations Y-markers (at low resolution; Gross, 2014). Strong genetic differentiation between *T. aduncus* and *T. truncatus* is seen throughout this range, where *T. aduncus* is consistently coastal and *T. truncatus* consistently offshore in distribution. Population structure is seen for both species throughout Australia, sometimes at a fine geographic scale (e.g. Ansmann *et al.*, 2012; Wizniewski *et al.*, 2010; Allen *et al.*, 2016; Moller *et al.*, 2007), and including *T. truncatus* lineages along the southern coast for which the geographic distribution is not fully known (Krützen *et al.*, pers comm.).

In southern Australia, samples from two regions (near Port Lincoln and near Melbourne) have been identified previously as a putative new species: "*T. australis*" (Charlton-Robb *et al.*, 2011). The samples from near Port Lincoln were those identified within the *T. aduncus* lineage in the ddRAD phylogeny (Moura *et al.*, pers. comm.) and have a mitogenome haplotype that is basal to the rest of the samples within the genus (Moura *et al.*, 2013). Those near Melbourne have this same mtDNA haplotype, but greater autosomal affinity to *T. truncatus* (based on microsatellite DNA data). It is possible that the 'Melbourne' population represents a population with *T. truncatus* ancestry introgressed with mtDNA from the 'Port Lincoln' lineage. Morphological studies for samples from throughout Australia and including the southern Australian range clearly differentiated *T. aduncus* from *T. truncatus* skulls, but did not find the differentiation between the "*T. australis*" and *T. truncatus* skulls reported in an earlier study (Jedensjö *et al.*, 2015; Charlton-Robb *et al.*, 2011).

In summary, both *T. truncatus* and *T. aduncus* are found in the Indian Ocean and western South Pacific, and both morphological and molecular genetic data provide strong evidence that their taxonomic rank as two separate species is valid. Little research has been conducted on intraspecific variation within *T. truncatus* in this region, and the workshop **agreed** that this should be investigated further, especially the potential for coastal/offshore differentiation. In contrast, numerous genetic and morphological studies of *T. aduncus* have been conducted and several distinct lineages have been observed. The workshop **recommended** that these lineages be investigated further, using both morphological and molecular genetic data to assess possible subspecies classification. It was **noted** that extensive areas are lacking sample coverage (eastern Africa, throughout Indonesia and eastern Australia), and that the analysis of samples from those areas is critical to clarifying the species and subspecies classifications. Workshop participants concurred with conclusions of the Society for Marine Mammalogy's Committee on Taxonomy that the basis for the taxonomic status of "*T. australis*" is questionable due to discordant results using different genetic markers and from different studies of morphological differences between "*T. australis*" and *T. truncatus* specimens. The apparent mixture of

multiple-species-lineages in mitochondrial and autosomal data of "*T. australis*" samples does not meet the criteria for species designation. The workshop **encouraged** continued and more collaborative studies of animals associated with the "*T. australis*" mtDNA lineage in the context of both *T. truncatus* and *T. aduncus*.

### 3.2.2. Eastern North Atlantic

*Tursiops truncatus* is the only species recognised in the eastern Atlantic. Data from the region are not homogeneous, with a large portion (south of the Strait of Gibraltar along and off the entire African Atlantic east coast) almost totally unrepresented, except for some data from oceanic islands. Occurrence of *Tursiops truncatus* in the coastal waters of most west African states is reported, including records from western Morocco, Western Sahara, Mauritania, Senegal, The Gambia, Guinea-Bissau, Sierra Leone and Liberia, Cote de Ivoire, Ghana, and Sao Tome/Principe (summarized in Weir *et al.*, 2010; Van Waerebeek *et al.*, 2008; Van Waerebeek *et al.*, 2016). There are clearly also bottlenose dolphins farther offshore observed around the Cape Verde (Hazevoet *et al.*, 2010) and Madeira archipelagos (Queroil *et al.*, 2007), and many records from the Canary Islands (e.g. Arbelo *et al.*, 2013; Garcia-Alvarez *et al.*, 2014).

The main questions in the eastern North Atlantic are the extent of structure among coastal populations and whether the degree of differentiation between coastal and offshore forms warrants sub-species or species classification, or is more consistent with population-level divergence. For samples collected north of the Strait of Gibraltar, multiple lines of evidence have been considered. Nuclear (microsatellite) and mtDNA (control region) analyses identified significant differentiation between coastal and offshore forms, with further structure detected within each type (Natoli *et al.*, 2004; Natoli *et al.*, 2005; Louis *et al.*, 2014a), but shared mtDNA control region haplotypes have been found between the two forms (Louis *et al.*, 2014b). Stomach contents analysis confirmed differences in the dominant fish prey between offshore (bycatch) and coastal (beachcast) individuals, and stable isotope analysis also showed significant differences between the two groups (Louis *et al.*, 2014b). However, morphological data including total body length and measurement of different body parts failed to identify any significant differentiation between coastal and offshore individuals (Louis *et al.*, 2014b), corroborating results of the population demographic history analysis based on genetic data that suggested a recent divergence between coastal and offshore forms. Thus, some genetic differentiation between coastal and offshore *Tursiops* is observed in the ENA, but a lack of significant morphological divergence does not provide a strong second line of evidence supporting a change to the current taxonomy.

At the population level, dolphins along the Britain, Ireland, and European coasts tend to be found in isolated units with high levels of site fidelity (Fernandez *et al.*, 2011, Mirimin *et al.*, 2011, Louis *et al.*, 2014a). A now-extinct population in the North Sea was distinct from the Scottish and English Channel populations (Nichols *et al.*, 2007). No population structure was detected among the oceanic islands of the Azores and Madeira and *Tursiops* sampled from Madeira were placed within the 'global' Atlantic mtDNA lineage (Queroil *et al.*, 2007).



In summary, based on the data available *T. truncatus* is the only bottlenose dolphin species recognised in the ENA. Although strong morphological differences between coastal and offshore forms of *T. truncatus* have been found in the western North and western South Atlantic, there is no evidence to date that multiple diagnosable morphological forms exist in the eastern North Atlantic. Moderate genetic differentiation has been recorded between offshore and coastal populations off the coast of Europe, and in concert with stable isotope data, indicate at least some ecological habitat partitioning among populations in the eastern North Atlantic. However, a comprehensive morphological study has not yet been conducted in the region and workshop participants **recommended** such a study should be undertaken. Population structuring has been identified within the coastal animals, but molecular genetic comparisons across island-associated offshore dolphins have not revealed significant population structure. Studies of bottlenose dolphins in coastal and offshore waters of the African continent north of the Equator are lacking and this represents one of the data-deficient areas identified by the workshop. Participants **recommended** collaborative efforts to be encouraged to examine *Tursiops* in the region, including sample collection for morphological and molecular genetic analyses.

### 3.2.3. Mediterranean and Black Seas

In the Mediterranean and Black Sea (and adjacent North Atlantic) only *Tursiops truncatus* is found, with the Black Sea population recognised as a distinct subspecies, *Tursiops truncatus ponticus*. This subspecies distinction was based principally on morphological data (Barabasch-Nikiforov, 1960; Geptner *et al.*, 1976) and evident geographical isolation. Conservation status of *Tursiops truncatus ponticus* was assessed by the IUCN (Birkun, 2012) and designated Endangered. The main taxonomic questions for this region are: 1) should the Black Sea bottlenose dolphin continue to be recognised as a subspecies? and 2) is the Mediterranean bottlenose dolphin also eligible for subspecies recognition?

Recent genetic and morphological studies (Natoli *et al.*, 2005; Viaud-Martinez *et al.*, 2008; Moura *et al.*, 2013; Moura *et al.*, pers. comm.) have assessed divergence of the Black Sea bottlenose dolphin and confirmed recognition as a distinct subspecies. Genetic data for this population included nuclear DNA markers (Natoli *et al.*, 2005; Moura *et al.*, pers. comm.) and mitochondrial DNA (Natoli *et al.*, 2005; Viaud-Martinez *et al.*, 2008; Moura *et al.*, 2013); all these analyses compared Black Sea bottlenose dolphins with the neighboring Mediterranean and Atlantic populations. Significant genetic differentiation at both nuclear and mtDNA was detected, but no complete lineage sorting (reciprocal monophyly) was observed at the mtDNA level (haplotypes were shared between the Black Sea, eastern and western Mediterranean, and eastern North Atlantic). However, high-resolution nuclear DNA sequence data (ddRAD, Moura *et al.*, pers. comm.) resolved the Black Sea samples as monophyletic, suggesting therefore that such high-resolution genetic analysis is needed to identify and confirm lineage divergence in *Tursiops*. That resolving the divergence of Black Sea bottlenose dolphins is challenging might reasonably be expected, as the radiation can only be recent given the young age (about 8000 years) of the Black Sea (see discussion in Moura *et al.*, 2013).

New morphological studies have reinforced the original morphological data and supported the observed genetic differentiation. Principal component analysis based on cranial morphology and total

body length (Viaud-Martinez *et al.*, 2008) confirmed the smaller cranial and body size of *T. t. ponticus* versus other populations. A more recent morphological study compared body length of Black Sea bottlenose dolphins with the original data of Barabasch-Nikiforov (1960) and suggested the possible presence of offshore (bigger) and inshore (smaller) forms within the Black Sea (Gol'din *et al.*, 2015).

Genetic analyses, utilizing both nuclear and mtDNA markers, showed significant genetic differentiation between the Mediterranean population and the neighboring Atlantic populations (Natoli *et al.*, 2004; Natoli *et al.*, 2005). However, at the mtDNA level no lineage sorting is apparent, with haplotypes shared between the two basins (Natoli *et al.*, 2005; Moura *et al.*, 2013); ddRAD analysis clusters all the Mediterranean samples within the same lineage (Moura *et al.*, pers.comm.). No dedicated comprehensive morphological studies comparing the Mediterranean and Atlantic populations have been conducted, except for comparison of secondary data of total body length (Gol'din *et al.*, 2015). Stomach content comparisons between Mediterranean and Atlantic samples showed clear difference in diet (Blanco *et al.*, 2001).

Both nuclear and mtDNA genetic data suggested clear population structure within the Mediterranean Sea with genetically different populations (Natoli *et al.*, 2005; Gaspari *et al.*, 2015) distinguishable from east to west and within basins (*i.e.* Adriatic Sea), that well mirrors the environmental complexity and habitat variability of the Mediterranean Sea, and the tendency of this species for philopatry and adaptation to local habitats. This is supported by observed estimated low migration rates between different regions (Natoli *et al.*, 2005). In the Alboran Sea, comparisons across the Oran-Almeria thermal front showed differentiation consistent with that reported for various other species in this region (see Natoli *et al.* 2005, Natoli *et al.*, pers. comm). One morphological study investigated the total body length and skull morphology across the Mediterranean basin (but with no comparisons to the Black Sea animals) also identified the Levantine population as significantly smaller size animals than the rest of the Mediterranean samples, suggesting the existence of a form of dwarfism in that region (Sharir *et al.*, 2011).

In summary, only *T. truncatus* is recognised across the Mediterranean and Black seas. *Tursiops* in the Black Sea have been isolated from those in the Mediterranean and Atlantic long enough to exhibit unique morphological and genetic characteristics. The workshop **agreed** that multiple data types provide strong support for recognition of the Black Sea bottlenose dolphin as a separate subspecies *T. t. ponticus*. Within the Mediterranean Sea molecular genetic data provide strong evidence for population structure within the Mediterranean basin, but do not provide evidence to date for any higher taxonomic divisions. Few morphological studies have been conducted. There is some evidences suggesting a genetically distinct population characterised by a smaller morphotype in the Levantine area has also been considered. The workshop **recommended** comprehensive morphometric analyses comparing *Tursiops truncatus* throughout the Mediterranean to those in the Black Sea and those in the eastern Atlantic to evaluate whether any regions may harbour a taxonomic unit above the level of population. It was also noted that large areas of the basin are data deficient and participants **stressed** the importance of gathering genetic and morphological specimens from those areas including offshore waters for a more comprehensive understanding of the population structure within the basin.

### 3.2.4. Eastern South Atlantic

This is perhaps the most under-represented area with respect to information on *Tursiops*. Little is known from this region along the west African coast south of the Equator. As with the African coast north of the equator, the occurrence of *Tursiops truncatus* in the coastal waters of most west African states is likely, including reports from Gabon, Namibia and South Africa (summarized in Weir *et al.*, 2010; Van Waerebeek *et al.*, 2008; de Boer, 2010; Van Waerebeek *et al.*, 2016). The main question in this region is the degree of differentiation between coastal and offshore forms. It appears that *Tursiops* are found in the coastal zone throughout the west African region, but only a few scattered samples are available; a few samples from Senegal and Namibia have been subject to genetic analysis, which fall into the global lineage (Hoelzel *et al.*, 1998).

In summary, only *T. truncatus* is expected to be present in the eastern South Atlantic Ocean. The workshop identified the eastern South Atlantic as the region with the least available information on bottlenose dolphin diversity. The lack of available information hampered the ability to draw conclusions about *Tursiops* taxonomy and population structure in this region. Workshop participants **recommended** comprehensive information be compiled on active researchers in the region, numbers and locations of morphological and molecular genetic samples that have been collected to date. This process has already started intersessionally by the workshop participants (see Annex E); the workshop **recommended** progressing it forward. The workshop also **noted** that coordinated efforts in needed to improve our understanding of *Tursiops* in the region. In addition, as with the eastern North Atlantic region, collaborative efforts to examine *Tursiops* throughout the region should be encouraged and facilitated, and it would most informative if these efforts were extended to include west African waters north of the equator so that the full African coast is considered.

### 3.2.5. Western North Atlantic

A single species, *T. truncatus*, is recognized in the western North Atlantic. However, multiple lines of evidence support the existence of sympatric or parapatric coastal and offshore forms in this region, including morphology, genetics, parasite loads, habitat and prey preferences and biochemical markers (Hersh and Duffield, 1990; Mead and Potter, 1995; Hoelzel *et al.*, 1998; Kingston *et al.*, 2009; Rosel *et al.*, 2009; Costa and Rosel, 2016; Rosel and Wilcox, 2016; Vollmer *et al.*, 2017). The taxonomic question addressed for this region was: do available data support elevating the coastal form in the western North Atlantic to subspecies or species status?

Genetic data for the region include mitochondrial DNA (mtDNA) control region sequences, full mitogenome data, microsatellite data, anonymous fragment length polymorphism data, and ddRAD sequence data (e.g., Kingston *et al.*, 2009; Rosel *et al.*, 2009; Caballero *et al.*, 2012; Richards *et al.*, 2013; Moura *et al.*, 2013; Moura *et al.*, pers comm.). All marker types indicate significant genetic differentiation between the coastal and offshore forms and the mitogenome and ddRAD data suggest the coastal form is sister to all other *T. truncatus* samples included in the analyses (Moura *et al.*, 2013;

Moura *et al.*, pers comm.). All datasets reveal reciprocal monophyly between the two forms and control region haplotype networks indicate 8 mutations between them. The amount of genetic differentiation between the two forms is greater than that found between offshore and coastal forms elsewhere in the world (i.e., ENP, WSA) and meets the Taylor *et al.* (2017) mtDNA control region threshold for species distinction. At the population level, significant genetic differentiation and fine-scale population structure have been found within the coastal ecotype in both the western North Atlantic and the Gulf of Mexico (Sellas *et al.*, 2005; Parsons *et al.*, 2006; Rosel *et al.*, 2009; Rosel *et al.*, 2017; Vollmer and Rosel, 2017). Within the offshore form, population subdivision has been detected in the northern Gulf of Mexico (Vollmer *et al.*, 2017).

Morphological data corroborate the genetic studies. Mead and Potter (1995) found significant separation between coastal and offshore forms using a differential relationship between specific cranial measurements. More recently, a principal components analysis of 19 cranial measurements in 101 physically mature skulls from the western North Atlantic revealed two well-separated groups corresponding to the coastal and offshore forms (Costa and Rosel, 2016). Offshore animals tend to be larger than coastal animals and have larger skulls. The level of difference between skulls of the two forms meets the diagnosability criterion of Patten and Unitt (2002) for at least subspecies (Costa and Rosel, unpublished). A principal components analysis of vertebral measurements also found significant differentiation between the two forms. The offshore form has more vertebrae than the coastal form, although sample sizes are relatively low (Costa and Rosel, 2016). While there is significant morphological and genetic differentiation between the two forms in the western North Atlantic, Costa and Rosel (2016) did not find significant differences in cranial morphology between the offshore forms in the western North Atlantic and western South Atlantic, suggesting the offshore animals in both hemispheres are members of a more broadly distributed pelagic form.

Overall, the genetic and morphological data provide strong support for recognition of the coastal ecotype in the western North Atlantic as at least a separate subspecies. Additional genetic analysis to rule out significant levels of male-mediated gene flow between the two forms and to put the level of divergence of the coastal animals in a worldwide context is needed in order to identify the appropriate taxonomic rank of the coastal bottlenose dolphins in the western North Atlantic.

In summary, only *T. truncatus* is present in the western North Atlantic Ocean, but two morphologically distinct forms are documented. These two forms, a smaller coastal form and a larger offshore form, also differ in habitat, prey preferences, and parasite loads, and exhibit significant molecular genetic divergence at multiple genetic markers. The degree of morphological and molecular genetic divergence meets their respective criteria for at least subspecies status for the coastal form. Workshop participants **noted** that an evaluation of male-mediated gene flow between the two forms is needed to complete the studies necessary to accurately assess and finalize the taxonomic status of the coastal form. Significant fine-scale population structuring and evidence for multiple demographically-independent populations has been found among the coastal animals in the western North Atlantic. Morphological and molecular genetic analyses of the offshore form in the western North Atlantic suggest it is a member of the more broadly distributed *Tursiops truncatus truncatus* subspecies.

### 3.2.6. Western South Atlantic

Two subspecies of *Tursiops truncatus* are recognised in the western South Atlantic, *T. t. truncatus* (offshore) and *T. t. gephyreus* (coastal). The taxonomic questions addressed here were: 1) do available data support subspecies status for *T. t. gephyreus*, and 2) do available data support elevating *T. t. gephyreus* to the species level.

Genetic data for the region include mtDNA control region sequences and microsatellite data (Fruet *et al.*, 2014; Costa *et al.*, 2015; Costa *et al.*, 2016; Costa and Rosel, 2016; Fruet *et al.*, 2017). Despite reasonable sample sizes, these studies found no shared haplotypes between offshore and coastal forms. However, Costa (pers. comm.) reports finding one shared haplotype between the forms - the haplotype of a specimen morphologically identified as *T. t. gephyreus* was shared with offshore animals. Based on the network in Fruet *et al.* (2017), reciprocal monophyly would not be expected in a phylogenetic analysis of the control region data.

Fruet *et al.* (2017) collected samples in oceanic waters > 150 meters deep and > 103 km from shore from the state of Paraná (PR), in southern Brazil to Uruguay (~23°-34°S) representing *T. t. truncatus*, and compared them to samples collected in nearshore coastal waters and lagoons from ~23°-54°S, representing *T. t. gephyreus*. Microsatellite analysis (11 loci) indicated the two sample sets were strongly differentiated. One individual biopsied in the offshore waters exhibited evidence of co-ancestry (~25%) with the coastal animals. However, Oliveira *et al.* (2016), using 7 microsatellite loci, provided some evidence for introgression between samples morphologically identified as *T. t. truncatus* and *T. t. gephyreus*. This result may be due to the small number of microsatellite loci used. Further work is necessary to determine whether there is any substantial male-mediated gene flow between the two subspecies.

Fine-scale population structure has been exhibited in the coastal form from southern Brazil down to Bahia San Antonio, Argentina (Fruet *et al.*, 2014). Oliveira *et al.* (2016) reported evidence for population structure, likely for the offshore form, *T. t. truncatus*, between northern and south-central Brazil using stranded samples. Fruet *et al.* (2014) also suggested, based on microsatellite data, that the coastal *T. t. gephyreus* population in Bahia San Antonio was an evolutionarily significant unit, separate from *T. t. gephyreus* in Uruguay and Brazil.

The results of osteological comparisons of coastal and offshore specimens from the waters of Brazil, Uruguay, and Argentina strongly support the presence of two taxa at least at the subspecies level, if not full species. Skulls from coastal dolphins are significantly larger than those offshore (Costa *et al.*, 2016; Wickert *et al.*, 2016) as well as other regions around the world (Hohl *et al.*, 2016). Up to six fully diagnostic skull characters have been described (Costa *et al.*, 2016; Wickert *et al.*, 2016). Skulls are also fully diagnosable using standard morphometric measurements (Costa *et al.*, 2016; Wickert *et al.*, 2016), or nearly so (98% - 100%) using 2-dimensional geometric morphometrics (Hohl *et al.*, 2016). As demonstrated in Costa *et al.* (2016), in a small number of samples for which complete data were available (n = 17), the forms are also fully diagnosable using a combination of vertebral formula

and vertebral shape characters. Overall, the genetic and morphological data provided strong support for recognition of the subspecies *T. t. gephyreus*; in fact, the morphological differences observed are on par with those distinguishing other small cetacean species (e.g., *Neophocaena* spp., Jefferson and Wang 2011). Additional genetic analysis to rule out significant levels of male-mediated gene flow between the two subspecies and estimate a divergent date between them is needed before species status can be robustly evaluated.

In summary, as in the western North Atlantic, only *T. truncatus* is recognised in the western South Atlantic Ocean, but here again two morphologically distinct forms have been identified. In this region, however, the coastal form is larger than the offshore form, in contrast to what is seen in the western North Atlantic. The degree of morphological differentiation between the two forms in the western South Atlantic recently lead to the coastal form being elevated to subspecies status, *T. t. gephyreus* while the offshore form appears to be a member of the more broadly distributed *Tursiops truncatus truncatus* subspecies. Workshop participants **agreed** that the morphological data strongly support the recognition of the coastal form as a separate subspecies, if not a full species. Molecular genetic divergence at mtDNA is less than that seen between the coastal and offshore forms in the western North Atlantic. At least one shared mtDNA control region haplotype has been reported between *T. t. truncatus* and *T. t. gephyreus*, and nuclear microsatellite data suggest the possibility of some interbreeding between the two forms, although the number of nuclear markers examined to date has been low. The workshop **recommended** that additional nuclear DNA data be collected to more fully characterize the degree of divergence and potential for ongoing male-mediated gene flow between coastal and offshore forms in the western South Atlantic to aid in determining whether *T. t. gephyreus* might more accurately be elevated to species status. Molecular genetic data support multiple demographically-independent populations within *T. t. gephyreus*, while there are insufficient data to establish whether there is population structure within the offshore form in this region.

### 3.2.7. Eastern North Pacific

Bottlenose dolphins within the eastern North Pacific are considered to be *Tursiops truncatus*; no subspecies are currently recognised within the region. Coastal and offshore forms have been recognised, largely on the basis of morphology and genetics. The main question in this region regards the magnitude of the coastal/offshore divergence and some latitudinal differences between coastal forms - in each case the question is whether the divergence is consistent with population-level distinction; should the coastal vs. offshore bottlenose dolphins in the Southern California Bight, northern Gulf of California vs. mainland Mexico vs. southern Baja Pacific coast, and eastern tropical Pacific dolphins be recognised as distinct population units? Should any of the populations be considered to comprise subspecies?

Initial studies by Walker (1981) found two clusters in a multivariate analysis of skull measurements, one comprised of offshore animals, most of which were captured off the Channel Islands, and the other comprised of beach-cast animals from California and Mexico, including the Gulf of California. Subsequent analysis of cranial characters in larger samples of skulls collected from offshore and

coastal dolphins (as verified genetically) in California waters were consistent with the earlier results, showing differences between the two forms primarily in characters associated with feeding (Perrin *et al.*, 2011). Coastal animals exhibited larger and fewer teeth and generally larger, more robust cranial features, and the diagnosability based on these skull characteristics was high (96.4% for adults) (Perrin *et al.*, 2011). Genetic analyses comparing the coastal and offshore forms in California waters supported the recognition of the two types, with significant genetic differences observed in both mitochondrial and nuclear analyses (Lowther-Thieleking *et al.*, 2015). Only a single haplotype was shared; this haplotype was common among the coastal form but found in only a single offshore individual. Long-term photo-identification studies of these coastal dolphins have shown that they range from northern California at least as far south as Ensenada, Baja California, with little mixing with the coastal dolphins photographed only 150 km to the south, off San Quintin, Mexico (Defran *et al.*, 1999a, 2015; Hwang *et al.*, 2014). Within this range, coastal dolphins are typically found within 1km of shore, while offshore bottlenose dolphins generally use waters 4km or more from the coastline (Defran *et al.*, 1999b).

Genetic analyses of the coastal and offshore forms off the coast of Mexico and within the Gulf of California revealed less clear patterns. In general, mitochondrial and nuclear genetic differentiation were observed between types in most areas, and some genetic differences were identified within types (Segura *et al.*, 2006; Segura *et al.*, 2018). In particular, dolphins representing the coastal form within the Gulf of California as well as coastal animals sampled south of the Baja Peninsula along the Mexican coast were genetically differentiated from the coastal population sampled (Lowther-Thieleking *et al.*, 2015) in the Southern California Bight/Channel Islands/San Diego areas. Analysis of stable isotopes also revealed differences between the nearshore and offshore types within the Gulf of California and along mainland Mexico, as well as between the animals on either side of the Baja Peninsula (Segura *et al.*, 2018).

Offshore-type bottlenose dolphins are also found in the Eastern Tropical Pacific (ETP). Comparison of cranial parameters revealed differences between these animals and the coastal form in Walker's (1981) study. Some differences in cranial measures and reproductive data were also found between the ETP and the California offshore dolphins, suggesting that the ETP dolphins reach reproductive maturity at a smaller size. However, the number of samples representing both the ETP offshore stratum (n=20, most of which were collected from animals bycaught in tuna purse-seine fishery) and the California offshore stratum (n=12) was small. Comparison of stomach contents and parasite loads revealed differences between the ETP offshore and coastal dolphins.

In the waters surrounding the main Hawaiian Islands, island-associated populations of *T. truncatus* are found close to shore while pelagic *T. truncatus* are found in deeper offshore waters (Baird *et al.*, 2009; Martien *et al.*, 2012). Two samples collected from dolphins off Kauai showed evidence of *T. aduncus* ancestry (Martien *et al.*, 2012).

Relationships among the offshore dolphins of the SCB, Hawaii and the coast of Mexico and those involved in the tuna fishery of the eastern tropical Pacific should be examined with morphological and molecular approaches. The relationship between upper Gulf of California coastal dolphins and the California/ mainland Mexico coastal dolphins should be examined more closely. The specimens, tissue

samples and data needed for these comparisons exist; the studies only need to be done. For each comparison, the question of population status vs. subspecies also needs to be addressed. Where existing life history samples and data exist, life history parameters should be included in the comparison of putative populations.

In summary, evidence to date indicates that only *T. truncatus* is present in the eastern North Pacific although two dolphins sampled in Hawaii showed molecular genetic evidence for mixed ancestry with *T. aduncus*. Morphologically distinct coastal and offshore forms are documented along the coast of California south to at least Ensenada, Mexico. Molecular genetic analyses using mtDNA and microsatellite data revealed significant differentiation between the coastal and offshore forms off California, although one shared mtDNA haplotype was identified and the level of genetic differentiation was lower than that seen of the coastal and offshore forms in the western North Atlantic. Further south along the Pacific coast of the Baja Peninsula, within the Gulf of California and along the mainland coast of Mexico, *T. truncatus* are also found in both coastal and offshore waters. Molecular genetic data provide evidence for population structure within and between both coastal and offshore animals the Gulf of California and between this area and the coastal animals found along the California coast. Morphological data are sparse and workshop participants **recommended** morphometric and further genetic analyses of coastal and offshore dolphins throughout Mexican waters be conducted and compared to those from California and the eastern tropical Pacific, with a particular focus on the relationship of coastal dolphins in the upper Gulf of California to other areas.

### **3.2.8. Eastern South Pacific**

*Tursiops truncatus* is found in both coastal and offshore waters along the coastlines of Columbia, Ecuador, Peru, and Chile (see summary of records reported in Van Waerebeek *et al.*, 1990). To date, there is no evidence for the presence of *T. aduncus* in the region. The main question in this region is potential coastal/offshore differentiation. Five different groups have been proposed in this region: (2 offshore, 3 coastal): Colombia-Ecuador Offshore stock (probably = ETP Offshore), Peru-Chile Offshore, Ecuador Coastal, Peru Coastal and an unique community (Pod-R) on the north-central coast of Chile (Van Waerebeek *et al.*, 2017). Evidence for these distinctions is based on several data types including differences in tooth width (Van Waerebeek *et al.*, 1990), skull morphology (Santillan *et al.*, 2008), dorsal fin proportions (Felix *et al.*, 2017), parasite prevalence (Santillan *et al.*, 2008; Van Bressem *et al.*, 2007; Van Bressem *et al.*; 2015), and genetics (Bayas-Rea *et al.*, 2017; Sanino *et al.*, 2008). Resolution and power of these analyses was hampered by small sample sizes, limited sampling along this immense geographic area, use of low-resolution genetic markers, and use of a limited range of analytical methods. The 2018 workshop concluded that compared to many other regions, there are insufficient morphological and genetic data available to examine potential differences between dolphins found in this area; and that more specimens and analyses are needed before the existence of separate forms of *Tursiops truncatus* in this region can be assessed and their taxonomic and population-divergence status determined.



In summary, only *T. truncatus* is recognised in the eastern South Pacific. A few regionally local studies suggest the presence of offshore and coastal forms, but a broad-scale synthesis of morphological or genetic data has not been conducted. This region ranked high in the assessment of data deficient areas and workshop participants were unable to draw conclusions concerning distinctions between offshore and coastal animals. Participants **concluded** that more genetic and morphological specimens and studies are needed throughout this region before assessment of taxonomic or population-level distinctions will be possible. They also **recommended** this work be conducted in a broader geographic context that would include coastal and offshore waters of Central America to Mexico, similar to the recommendation made for the eastern South Atlantic. It would also be useful to expand comparisons around the southern tip of South America to Argentina to examine relationships between dolphins in these two regions

### 3.2.9. Western North Pacific

Both *Tursiops aduncus* and *Tursiops truncatus* are found in the western North Pacific. Recognition of the two species within this region is supported by morphological and genetic differences. Analysis of available genetic samples of *T. aduncus* from the WNP has shown that they are more closely related to *T. aduncus* found in Australian waters than they are to *T. aduncus* from the Red Sea and the western Indian Ocean (Natoli *et al.*, 2004; Sarnblad *et al.*, 2011; Moura *et al.*, 2013). The key outstanding issues in this region include the occurrence and distribution of these two species in regions where genetic and/or morphological data are currently limited or unavailable, and the potential for significant population-level divergence within them in, e.g. island-associated groups.

The differences between the two species are best described for the waters off China and Taiwan. Genetic analyses revealed the presence of seven fixed differences in mtDNA control region sequences between *T. aduncus* and *T. truncatus* (as identified based on morphology) within this range; sequence divergence at the mtDNA control region was estimated at 4.4% (Wang *et al.*, 1999). Differentiation in external morphology and osteological characters also exists between the two species, with non-overlapping distributions of several cranial proportions, total number of vertebra, and rostral length characters (Wang *et al.*, 1999, 2000). Of note, the majority of samples utilized in these studies were collected from Taiwanese waters, with only a few samples collected from areas off mainland China. Samples representing *T. truncatus* were primarily collected from the northeastern and southern coasts of Taiwan and the Taiwan Strait, with a few samples collected from the waters of mainland China. Samples representing *T. aduncus* were collected in the Taiwan Strait, off mainland China, and in the Gulf of Tonkin; no *T. aduncus* samples were collected from the northeastern or southern portions of Taiwan.

Principal components analysis of cranial measurements of skulls collected along both coasts of Japan revealed the presence of two groups within this region (Kurihara and Oda 2006, 2007). When compared with cranial measures from the type specimens, skulls collected from island-associated dolphins in Japanese waters grouped with *T. aduncus*. Reports of *T. aduncus* indicate that this species is found (1) within the Sea of Japan (Notojima, Mori, 2013; Kunda Bay, Morisaka *et al.*, 2013), (2) in

the western and southern waters off Kyushu (Amakusa-Shimoshima Island, Shirakihara *et al.*, 2002; Kagoshima Bay, Nanbu *et al.*, 2006; Hirose 2013), (3) around Amami Island between Kyūshū and Okinawa (Funasaka *et al.*, 2016), and (4) in coastal waters of the Izu Island chain (Mikura Jima, Kakuda *et al.*, 2002; Koji *et al.*, 2013; Tori Shima, Morisaka *et al.*, 2013) and south to the Ogasawara (Bonin) Islands (Mori, 2005; Mori and Okamoto, 2013), ~1400 km north of the Marianas. Genetic and acoustic differences between islands have been reported (Hayano, 2013; Morisaka *et al.*, 2005).

Skulls collected from the waters surrounding mainland Japan, including those collected off Taiji on the eastern coast and a single skull collected from Joetsu on the Sea of Japan coast, grouped with *T. truncatus*. Genetic studies also indicate that the bottlenose dolphins caught off of Taiji are *T. truncatus* (Kita *et al.*, 2013). Analyses using both mtDNA control region and microsatellites (n=20 loci) suggested at least two populations of *T. truncatus* are found off Taiwan and Japan, one with a distribution corresponding the shallow continental shelf waters and another inhabiting deep continental slope habitat (Chen *et al.*, 2017). Comparison of mtDNA control region sequence data from these populations with published data derived from *T. truncatus* off the Hawaiian Islands and Palmyra (Martien *et al.*, 2014) revealed statistically significant differences between all strata (Chen *et al.*, 2017).

Examination of bycaught individuals in Korean waters suggest that *T. truncatus* is found in the Sea of Japan (=East Sea), Yellow Sea, and East China Sea (unpublished data, referenced in Kim *et al.*, pers. comm.). Evaluation of external morphology from photographs as well as cranial measures from the skull of a stranded animal indicate that the bottlenose dolphins found off Jeju Island, in the southwestern sea of the Korean Peninsula, are *T. aduncus* (Kim *et al.*, 2010; Kim *et al.*, pers. comm.). Published genetic data from these regions is not currently available.

Limited morphological and genetic data exist for bottlenose dolphins in the Phillipines. Dolar *et al.* (pers. comm.) notes that both *T. truncatus* and *T. aduncus* are found in Philippine waters, with the former being widely distributed but the latter being found in only a few areas (Balabac Strait, Tanon Strait, and the South China Sea). Photographic verification of the occurrence of *T. aduncus* in the Tanon Strait is provided in Tiongson and Karczmarski (2016). Two samples of *T. truncatus* from the Phillipines were included in the microsatellite analysis in Chen *et al.* (2017); although the small sample size precluded drawing any conclusions, it was noted that these two samples formed a cluster distinct from those identified off the coasts of Japan.

Only limited data on *Tursiops* spp. in Vietnam waters exist. A small number of samples (n=3, genetics; n=4, morphology) from the Tonkin Gulf have been analyzed and were identified as *T. aduncus* based on both morphology and genetics (Wang *et al.*, 1999, 2000). Smith *et al.* (1997) collected tooth count data from nine *Tursiops* spp. skulls found in Vietnamese temples; at least eight of the skulls were considered to be *T. aduncus* based on small skull size.

Bottlenose dolphins are generally poorly documented in Micronesia. Sightings of *T. truncatus* have been reported in the Mariana Islands (Hill *et al.*, 2014), and samples were collected from 14 individuals (Martien *et al.*, 2014). Nine of the sampled individuals had haplotypes consistent with *T. truncatus*, including two haplotypes that had also been found in bycaught animals from the

Philippines. The remaining five samples had haplotypes that were very similar to those collected from Frasier's dolphins in the Philippines, suggesting that introgressive hybridization of Frasier's dolphins mtDNA has occurred into the *T. truncatus* population found near the Marianas (Martien *et al.*, 2014). No morphological or genetic data collected from *Tursiops* spp. in other regions of Micronesia are available.

In summary, morphological and molecular genetic data support the presence of both *T. truncatus* and *T. aduncus* in the western North Pacific. The *T. aduncus* in this region appear to be more closely related to those found in Australian waters than those found in the western Indian Ocean.

Morphological and molecular genetic data collected to date do not indicate the presence of intra-specific variation above the population level for either species in this region; mtDNA data do provide evidence for population structure within *T. truncatus*. A major outstanding issue in this region is the need for more comprehensive sampling of both species to better delineate their geographic distributions of both species within and throughout the region. Workshop participants **noted** that large areas are underrepresented in terms of sampling and analyses (e.g., Philippines, Vietnam, Micronesia) and therefore **encouraged** more comprehensive sampling for morphological and molecular genetic analyses

#### **4. IMPORTANT OUTSTANDING AREAS FOR FURTHER RESEARCH AND POORLY KNOWN REGIONAL POPULATIONS THAT ARE DATA DEFICIENT**

Throughout the review process, areas in each regions where data and samples were lacking were identified. An effort was made to identify and connect with people operating in these regions, gather further published or unpublished information of the presence of *Tursiops*, obtain information about morphologic (skulls) and genetic samples available. A detailed list of these data deficient areas and corresponding countries, whether a person contact was identified and approximate type and number of samples potentially available for future analyses is given in Annex E.

Below, a summary of the data deficient areas identified in each region:

**Indian Ocean and western South Pacific:** most of the eastern coast of Africa, the Arabian/Persian Gulf, the Red Sea, the region from Pakistan throughout Indonesia, and oceanic islands (Papua New Guinea, Micronesia, Polynesia, Melanesia), eastern Australia.

**Western North Pacific:** including Japan South Korea, northern China, Vietnam and Philippines.

**Eastern North Pacific and eastern South Pacific:** including Oregon (U.S.A.) and all the central Pacific area from Mexico to Colombia, Ecuador, Peru and Chile.

**Western North Atlantic:** more samples from morphological analysis would be useful from the Caribbean area, lack of data from Colombia through Suriname.

**Western South Atlantic:** Need to better define limits of the distribution of *T. t. geophyreus* by sampling in Argentina and in Brazil, north of Santa Catarina and Parana states. An effort to sample both coastal and offshore waters should be also made (Fruet el al., 2017 workshop report).

**Eastern North Atlantic and eastern South Atlantic:** the entire Atlantic African coast is data deficient. A limited number of dedicated surveys have been conducted, data available are sparse and occasional, and only reporting the occurrence of *Tursiops*.

**Mediterranean and Black Sea:** the whole southern portion of the Mediterranean delimited by the African coast, the eastern Mediterranean (Aegean Sea) including main islands (Crete, Cyprus) and the Dardanelle/Bosphorus Strait System. In the Black Sea efforts should concentrate on gathering a more comprehensive samples sets from different areas including offshore regions.

## **5. STANDARDIZATION OF GENETIC AND MORPHOLOGICAL DATA AND ANALYSES FOR *TURSIOPS* TAXONOMY**

### **5.1. The Use of Genetic Data for Understanding Odontocete Diversity**

Use of multiple markers and/or multiple lines of evidence is recommended for a molecular genetic analysis of taxonomy as a single genealogy alone can be misleading. Neutral and selected markers have different utilities, and attention should be paid to the type of markers being used to address particular questions.

As high resolution markers (SNPs, RAD-Seq, ddRAD, etc.) become more accessible, future studies will likely go beyond use of microsatellites and mtDNA sequences. More markers generally equate with an increased power to detect differences. Paired with coalescent-based analyses, even based on only a few samples initially, such studies can help determine a useful level of effort (sampling and marker choice) for the likely level of divergence being tested and that information can be used to design a more complete study. Given enough molecular genetic markers, however, samples can be placed into different clusters that may represent social groups rather than taxonomic entities, so it is critical to have an understanding of the appropriate amount of difference that accurately reflects species-level, subspecies-level and population-level divergences before drawing conclusions concerning taxonomic distinctions. New analytical tools for species delimitation using multi-locus genomic data continue to be developed (e.g. Pei *et al.*, 2018). Finally, more traditional markers like mtDNA for taxonomic studies and mtDNA and microsatellite markers for population-level studies still retain utility and should not be discounted.

The marker system, analytical approach, number of samples and coverage of potential range should all be designed for relevance to the hypotheses to be tested (population structure, subspecies-level differences, species-level differences). Rosel *et al.* (2017a) and Taylor *et al.* (2017b) provide information and guidelines appropriate for making strong taxonomic arguments, irrespective of genetic marker type. Martien *et al.* (2015) discuss the strength of evidence different types of data provide for studying population -level distinctions. The Waples *et al.* Genetic Analysis Guidelines (in Press) also provides detailed information on which approaches and analytical methods are applicable for different sorts of questions. Since the level of divergence is likely not known *a priori*, an open mind and willingness to expand the study methods, objectives, sample sources and sample types (morphological, genetic, behavioral, parasite loads, etc.) is recommended.

Collaborative analyses where samples are already available (e.g. bottlenose dolphins around Australia) can allow progress to be made more quickly. Finally, it is extremely important to place local taxonomic studies in a broader geographic context. Without a broader context, determinations concerning taxonomic status will remain unresolved.

## **5.2. The Use of Morphology for Understanding Odontocete Diversity**

Prior to the 21<sup>st</sup> Century, odontocete taxonomy was accomplished with the use of morphological characters. If adequate series of specimens differed absolutely in at least one character, separate species were inferred, e.g. in the differentiation of two species in *Kogia* (Handley, 1966), revision of the spotted dolphins (Perrin *et al.*, 1987), and confirmation of the existence of Fraser's dolphin, *Lagenodelphis hosei* (Perrin *et al.*, 1973) and the Clymene dolphin, *Stenella clymene* (Perrin *et al.*, 1981). Distribution was also used in addition to morphology in the differentiation of subspecies. If large geographical series differed modally to the extent that most specimens could be assigned to one or the other form, they were adjudged to represent subspecies, e.g. of the pantropical spotted dolphin, *S. attenuata* (Perrin, 1975) and the spinner dolphin, *S. longirostris* (Perrin *et al.*, 1999). Where absolute differences were many and/or very large (large effect size), smaller series were believed adequate to differentiate species, e.g. for the mesoplodont beaked whales (Moore, 1968).

Morphological features include cranial and postcranial osteology, external size and shape, and color pattern. The most used characters in taxonomic morphology have been metric and meristic features of the skull (measurements and tooth counts). Advantages of these include repeatability and large amounts of data from individual specimens. One disadvantage is that different workers may vary in exactly how they take measurements and count teeth, although this can and should be addressed by intercalibration using the same skulls. Another drawback is the difficulty of obtaining adequate series of specimens to sufficiently characterize individual variation. Finally, because most analyses of skull metric characters are limited to adults and skulls with complete sets of measurements, sample sizes can often be drastically reduced. However, modelling allometric growth of features with respect to total skull length can sometimes allow for use of entire series (Bookstein, 1982). Additionally, although they should be used carefully, there are several missing data imputation schemes that can fill out data sets and permit use of samples only represented by partial measurements.

Studies using metric features have predominantly used similar lists of individual landmark-to-landmark measurements across multiple surfaces of the skull. There have been several 2-dimensional and 3-dimensional geomorphometric studies, which create a representation of the skull based on measurements among sets of linked landmarks. These methods are likely better able to quantify and describe differences in shape among forms. However, they are more reliant on having entire skulls on which all landmarks can be recorded (but see Churchill *et al.*, 2018) - and of course, analysis of skull metric characters must be limited to adult specimens. Postcranial meristic features, e.g. total vertebral count, number of ribs, or position of particular neural foramina, often vary between species, but sample size is usually a problem because few complete skeletons make their way to museums, and further, postcranial elements are often lost in specimen preparation. The same disadvantages apply to the use of

external size and shape, to an even greater degree. Here it is well known that different workers may vary greatly in how they take measurements, e.g. of the dorsal fin and flukes, and it is difficult to intercalibrate because very few dolphins and porpoises are preserved in the whole; nearly all wind up as osteological specimens, usually as skulls only. In addition, size and shape vary with attitude of the body, e.g., length differs between a beached dolphin and a fresh carcass in rigor mortis; body length may continue to increase beyond sexual maturity; growth only stops when physical maturity has been attained (when the vertebral epiphyses have all fused with the centra). For these reasons, measurements of external size and shape have not been considered very reliable or useful in taxonomy.

Color pattern is subject to similar disadvantages; it can change with age (e.g. degree of spotting in the two spotted dolphin species (Perrin *et al.*, 1987)) and even ecophenotypically (e.g., darkening induced by increased exposure to the sun in captive dolphins). A beached carcass also quickly darkens, often obscuring color pattern completely. If a color pattern element is well marked in adults and easily observed, it can be useful in delineating species, e.g. the obvious shoulder blaze that differentiates the Atlantic spotted dolphin from the pantropical spotted dolphin (Perrin *et al.*, 1987). Care should be taken in descriptions of color patterns from photos of live animals as angle, lighting conditions, sea state, and even habitat can influence how they appear in an image.

Simple bivariate analyses or ratios have been useful for identifying diagnostic differences, e.g. for differentiating between the skulls of *Stenella clymene* and *S. coeruleoalba* (Perrin *et al.*, 1981), while multivariate analyses have been effectively used to delimit subspecies and stocks of odontocetes for dolphins of the genus *Stenella* (Perrin, 1975) and *Tursiops truncatus* in California waters (Perrin *et al.*, 2011). Ordination based approaches such as Principal Components Analysis (PCA) are useful for reducing the dimensionality of the data set and more easily visualizing the degree of differentiation across all characters. To address taxonomic questions, classification approaches are common as they are designed to identify features or combinations of features useful for separating *a priori* defined sets of voucher specimens. The models thus defined can then be used to assign specimens of unknown origin. For example, Discriminant Analysis (DA) was used to assign holotype specimens of nominal species to species of spotted dolphins (Perrin *et al.*, 1987) and to assign the type specimen of *T. aduncus* to one of the two species of the genus delimited on the basis of molecular data (Perrin *et al.*, 2007), based on multiple skull dimensions. Machine learning and ensemble-based methods such as Random Forest (Breiman, 2001; Berk, 2006) have been shown to produce more robust classification models. With classification models, it is critical to consider how voucher specimens used to train them have been selected and ground truthed, as inappropriate *a priori* designations (e.g., based on features where overlap may occur such as geographic location) can degrade the effectiveness of classification models. Conversely, designations based on features which are used in building the model or heavily correlated with them can lead to inflated estimates of classification ability.

In general, multivariate analyses can be a sharp tool for delineation of species. However, with enough characters, any two arbitrary groups of specimens can be completely separated. Multiple, correlated, minor modal differences can interact to produce apparent significant differentiation. Thus, ordination approaches should be used in conjunction with classification models to gain a complete understanding

of the number of functionally independent features in a set of measurements. Characters exhibiting high diagnosability should be closely examined for biological significance and validated with samples not used in model construction.

## 6. CONCLUSIONS, FUTURE WORK AND WORKSHOP RECOMMENDATIONS

Due to their worldwide distribution in temperate and tropical waters, remarkable ability to adapt to local conditions, adopting unique feeding strategies for different habitats, and complicated social structures, including strong tendencies for strong site fidelity, bottlenose dolphins (*Tursiops sp.*) exhibit significant habitat partitioning throughout their range. Some adaptations to different environments have been accompanied by morphological differentiation as well. These characteristics have led to the naming of more than 20 nominal species of *Tursiops*. Whether the currently accepted *Tursiops* species accurately represent separate taxa and whether there are more *Tursiops* subspecies and/or species than are currently recognized was the focus of this workshop. The highly complex nature of the question required three-years of review within the 2015-2017 Scientific Committee meetings and culminated with this workshop to collate all the information on a global scale and make recommendations. The opportunity to bring researchers and experts together from around the world to discuss this single topic during the three year and at the workshop was a very successful aspect of the review. It also spurred research forward in some areas and promoted future collaborations among scientists. The Small Cetaceans Subcommittee annual priority topic reviews program provide this unique opportunity to take a global view on issues related to small cetaceans.

Overall, the workshop participants **agreed** that the current taxonomy provided by the Society for Marine Mammalogy's Committee on Taxonomy (2017) is well supported by morphological and molecular genetic data, as well as ecological and distributional data. This taxonomy includes the common bottlenose dolphin *T. truncatus* and the Indo-Pacific bottlenose dolphin *T. aduncus*. Three subspecies are recognized within *T. truncatus*: the nominate subspecies, *T. t. truncatus*, the Black Sea bottlenose dolphin, *T. t. ponticus*, and Lahille's bottlenose dolphin, *T. t. gephyreus*. Participants thoroughly reviewed the available support for the more recently described species *T. australis* and **concluded** that discordance in results from morphometric analyses and across different genetic markers call into question the basis for describing this new species at this time.

Several important outstanding taxonomic questions remain. In the Indian Ocean and western South Pacific, genetic and some morphological data support the existence of multiple, distinct lineages of *T. aduncus* with considerable, i.e., above the population level, amounts of genetic divergence among them. The evolutionary relationships among them remain unresolved and geographically comprehensive morphological and molecular genetic analyses will help determine whether some of these lineages should be elevated to subspecies status. In the western North Atlantic, multiple lines of evidence support significant differences, again above the population level, between coastal and offshore bottlenose dolphins and workshop participants **agreed** the level of divergence meets criteria for at least subspecies status for the coastal form. Future work will concentrate on examining the degree of male-mediated gene flow between the two forms. In the western South Atlantic,

morphologically diagnosably-distinct coastal and offshore forms of *T. truncatus* are present and the coastal form has been recognized as a distinct subspecies, *T. t. gephyreus*. Participants discussed whether it warranted elevation to species status and **concluded** that additional molecular genetic data examining the potential for male-mediated gene flow are needed before this question could be resolved. Finally, the taxonomy of coastal and offshore forms of *Tursiops truncatus* off the U.S. California coast and down to the central Baja Peninsula remains unresolved. Workshop participants **agreed** that there is strong evidence for morphological and genetic differences between these two forms. But genetic data from the Pacific coast of Baja California, the Gulf of California and further south in Mexican waters suggest a complicated population structure, and whether the structure observed to date is sufficient to warrant any taxonomic changes is still unclear. Given a significant conservation concern for the dolphins in the upper Gulf of California, future genetic and morphological studies throughout this region are essential.

Discussions at the workshop **identified** several data deficient regions (in samples/specimens, data and publications) within the distribution of *Tursiops* (see below 6.2.1 and Section 4) and highlighted the importance of increased communications and collaborations in these regions.

Recognizing molecular genetic techniques are advancing at a lightening pace, new analytical tools are being developed for delimiting species from these molecular genetic datasets and even new morphometric analytical tools, such as 3D geomorphometric analyses, are being incorporated into studies, participants **noted** there are still some general guidelines and standards that can and should be followed in taxonomic studies. Reeves *et al.*, (2004), Taylor *et al.*, (2017b) and Waples *et al.*, (in press) all provide important background on, and useful advice for designing research plans and presenting data and arguments when delimiting new subspecies or species. Participants **strongly encouraged** that these resources be considered in future studies. Several points highlighted during discussions include the importance of using multiple lines of evidence and the critical importance of placing local taxonomic studies in a broader geographic context. Without that context, new taxonomic proposals will remain unresolved.

## 6.2 Summary of Recommendations

### 6.2.1 Data-deficient areas

Participants identified geographic regions where data on *Tursiops* are sparse. In particular, there is poor coverage of the eastern South Atlantic, the African coast of the eastern North Atlantic, the southern and eastern Mediterranean Sea, the eastern South Pacific, eastern North Pacific north of California and the Mexican mainland and Central American coasts of the eastern North Pacific, eastern Australia and in the western Pacific islands of Micronesia, Melanesia, Polynesia, the Philippines and Vietnam.

The workshop **recommends** these areas as priorities for *Tursiops* research and **recommends** compilation of regional information on active researchers, numbers and locations of morphological and molecular genetic samples collected to date, and effort to complete work initiated during the workshop



(see Section 5). Collaborative efforts should be encouraged and facilitated to examine *Tursiops* throughout these regions.

#### 6.2.2 Standardization, guidelines and future studies

The workshop **recommends** the guidelines in Reeves et al. (2004) for the assessment of species status, and in Taylor et al. (2017b) for the assessment of subspecies, and in Martien et al. (2015) for DIPs. Participants **strongly emphasized** that future taxonomic questions be examined within an appropriately wide and inclusive geographic context and that multiple lines of evidence are necessary when positing taxonomic changes.

#### 6.2.3 Recommendations for future research

As described above, several important taxonomic questions remain unresolved at this time and the workshop participants provided a series of recommendations for addressing these outstanding issues. These recommendations are:

- (1) Collect additional nuclear DNA data to more fully characterize the degree of divergence between coastal and offshore forms in the western South Atlantic Ocean to aid in determining whether *T. t. gephyreus* might more accurately be elevated to species status.
- (2) Extend the geographic coverage, especially including eastern Africa, the region between Pakistan and Indonesia, and the region between Australia and China to more fully investigate *T. aduncus* lineages in the Indian Ocean and western South Pacific Ocean using genetic and morphological data. This should build on already available data suggesting multiple distinct lineages and assess potential subspecies recognition. Participants also **encouraged** continued study of animals associated with the "*T. australis*" mtDNA lineage in the context of both *T. truncatus* and *T. aduncus*.
- (3) Examine the level of male-mediated gene flow between the coastal and offshore forms in the western North Atlantic Ocean and determine whether the coastal form should be elevated to species or subspecies status.
- (4) Conduct comprehensive morphometric analyses integrated with extensive existing molecular data comparing *Tursiops truncatus* throughout the Mediterranean to those in the Black Sea and those in the eastern Atlantic to evaluate whether any regions apart from the Black Sea may also harbour a taxonomic unit above the level of population.
- (5) Conduct further morphometric analyses of coastal and offshore *Tursiops truncatus* in the eastern North Atlantic Ocean and compare results to those from western North Atlantic, integrating existing genetic data with the morphological data.
- (6) Perform morphometric analyses of coastal and offshore dolphins throughout Mexican waters compare data to those from California and the eastern tropical Pacific, with a particular focus on the relationship between coastal dolphins in the upper Gulf of California with other areas.

(7) Collect additional genetic and morphological data throughout the eastern South Pacific Ocean to augment those in hand and conduct studies addressing taxonomic hypothesis concerning the relationship between coastal and offshore dolphins throughout the region. This work should include coastal and offshore waters from Central America to Mexico, and extend if possible around the southern tip of South America to Argentina.

## **7. ADOPTION OF REPORT**

The report was adopted by emailed consensus on the 21<sup>th</sup> April 2018.

## **Annex A**

### **List of Participants**

**Ada Natoli**

UAE Dolphin Project, United Arab Emirates

**Aimee Lang**

SWFSC, La Jolla, CA USA

**Eric Archer**

SWFSC, La Jolla, CA USA

**Frank Cipriano**

San Francisco, CA USA

**Michael Krützen**

Zurich University, Switzerland

**Patricia Rosel**

NOAA Fisheries, SEFSC, Lafayette, LA USA

**Robert Brownell**

SWFSC, La Jolla, CA USA

**Rus Hoelzel**

University of Durham, UK

**William Perrin**

SWFSC, La Jolla, CA USA

**Annex B**  
**Workshop Agenda<sup>1</sup>**

**AGENDA**

**1. INTRODUCTORY REMARKS**

- 1.1. Convenor's opening remarks
- 1.2. Election of Chair
- 1.3. Appointment of rapporteurs
- 1.4. Adoption of agenda

**2. DISCUSS TERMS AND A STRATEGY FOR TAXONOMIC AND POPULATION-LEVEL DISTINCTIONS FOR THIS GENUS**

- 2.1. Review of existing proposed classifications of *Tursiops*: context and motivation for the 2018 workshop on resolving *Tursiops* taxonomy worldwide
- 2.2. Review of a practical example of approaches for 'stock' delineation used by US government agencies
- 2.3. The use of morphology for understanding odontocete diversity
- 2.4. Review of species and subspecies concepts
- 2.5. Distribution-related terminology

**3. REVIEW OF NEW AVAILABLE DOCUMENTS**

- 3.1. Overview: WP on the RAD phylogeny worldwide
- 3.2. Area IO: Gray *et al.*, 2017. Cryptic lineage differentiation among indo-pacific bottlenose dolphins (*Tursiops aduncus*) in the Northwest Indian Ocean
- 3.3. Area IO: WP on the morphometrics of the Pakistan lineage
- 3.4. Area ENP: Segura *et al.*, 2018. Eco-evolutionary processes generating diversity among bottlenose dolphin, *Tursiops truncatus*, populations off Baja California, Mexico.
- 3.5. Relevant WPs presented to the IWC meetings (Each presented by the author/regional responsible)

**4. DISCUSS SUMMARY DATA AVAILABLE FROM INTERSESSIONAL ACTIVITIES AND EARLIER SC SM SUBCOMMITTEE SESSIONS**

- 4.1. Review Intersessional table providing data summary
  - 4.1.1. IO/WSP (Australia)
  - 4.1.2. ENA
  - 4.1.3. MED & BLACK SEA
  - 4.1.4. ESA
  - 4.1.5. WNA
  - 4.1.6. WSA
  - 4.1.7. ENP
  - 4.1.8. ESP
  - 4.1.9. WNP

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<sup>1</sup> This agenda was followed during the workshop, but discussions during the workshop lead to rewording of some items relative to the original agenda in the workshop proposal, and including agenda items 3, 4, 5, 6 for each regional summary (section 3 of the report) so that each regional summary was complete

**5. EVALUATE THE STRENGTH OF EVIDENCE FOR TAXONOMIC AND POPULATION-LEVEL DISTINCTIONS OF *TURSIOPS* IN EACH GEOGRAPHIC REGION**

- 5.1. Consider types of evidence and relative value
- 5.2. Build consensus taxonomy for the genus (or higher level classification as appropriate) based on available data and highlight areas of poor resolution or uncertainty
- 5.3. Discuss life history, environmental and evolutionary history characteristics in the context of what is known about other delphinid genera and consider inference

**6. IMPORTANT OUTSTANDING AREAS FOR FURTHER RESEARCH AND POORLY KNOWN REGIONAL POPULATIONS THAT ARE DATA DEFICIENT**

- 6.1. Geographic regions
- 6.2. Morphological data deficiencies
- 6.3. Genetic data deficiencies
- 6.4. Inventory of available samples and other resources: Review and update of the Underrepresented area database

**7. STANDARDIZATION OF GENETIC AND MORPHOLOGICAL DATA AND ANALYSES FOR *TURSIOPS* TAXONOMY**

**8. FUTURE WORK AND RECOMMENDATIONS**

**9. ADOPTION OF REPORT**

## Annex C

### Information Sources Used in the Subcommittee Review and Cited in the Workshop Report

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**Annex D**  
**Tursiops Summary Table**

Summary table reporting information available and reported in the literature, organized by geographic region, that was evaluated by the sub-committee over the three years of review. Information has been classified and broken down in different sections (materials used and quantities, genetic markers, genetic analysis, morphological markers, feeding ecology, parasite data, behaviour) and correlated with general environmental characteristics of the region. Regions are identified as follow: eastern Indian Ocean (EIO), western Indian Ocean (WIO), eastern North Atlantic (ENA), eastern South Atlantic (ESA), Mediterranean Sea (MED), Black Sea (BS), western North Atlantic (WNA), western South Atlantic (WSA) eastern North Pacific (ENP), eastern South Pacific (ESP), western North Pacific (WNP), western South Pacific (WSP). Abbreviations used in the table as follows:  $F_{ST} = F_{ST}$ ,  $Rho_{ST} = Rho_{ST}$ ,  $\Phi_{ST} = \Phi_{ST}$ , mtDNA= mitochondrial DNA, msat = microsatellite, cr = control region (mtDNA), Cytb = cytochrome b gene, DPCA = Differential Principle Component Analysis, AFLP = Amplified Fragment Length Polymorphism, PCA = Principal Component Analysis, DFA = Discriminant Function Analysis.



## Annex E

### Outstanding Areas for Further Research ad Poorly Known Regional Populations that are Data Deficient

Geographic regions	Location	Species/form reported	Background information	Contact availability	Samples available/type of samples	Notes
EIO	Mozambique	T. truncatus & aduncus?	aduncus is known in coastal waters whereas truncatus offshore is not everywhere confirmed	contact		
	Madagascar			contact	a handful of samples and some teeth from Madagascar (north and south). Sequences from Mayotte. 4 aduncus skulls and 14 truncatus skulls	working on different manuscripts on the genetic population structure of T. aduncus in the western Indian Ocean region, including samples from Zanzibar, Oman, Madagascar, Mayotte, La Réunion and Mauritius
	Tanzania	T. aduncus and truncatus confirmed		contact		
	Kenya			contact		
	Somalia				published	
	Yemen			contact		
	Oman			contact	5-7 skulls plus some samples in University	
EIO (Red Sea)	Qibuti	T. aduncus and truncatus?		contact	two skulls	Checked two universities and Museum of Chennai, Bhubaneswar and Mumbai
	Pakistan			contact		
	India			contact		
EIO (Arabian/Persian Gulf)	Sri Lanka			contact	none	
	Eritrea	T. aduncus and truncatus?		contact		
	Egypt			contact		
EIO (Arabian/Persian Gulf)	Saudi Arabia	T. aduncus	unconfirmed truncatus offshore	contact	skin samples, two skulls	
	Saudi Arabia			contact	no samples available	
	Qatar			contact	no samples or information available	
WIO	Kuwait			contact		
	Iraq			contact		
	Iran			contact		
WIO	Myanmar					
	Malaysia					
	Indonesia					
WSP	Indonesia					
	Papua New Guinea					
	Polynesia					
WNP	Melanesia					
	Micronesia					
	Vietnam			contact?		
ENP	Philippines			contact?		
	China (north)					
	Japan					
ENP	South Korea			contact?		
	Oregon USA	T. truncatus	inshore/offshore?			
	Mexico		limited information in Gulf of California only	contact	genetic samples and skulls	
ESP	Guatemala			contact		
	El Salvador			contact		
	Costa Rica			contact		
ESP	Nicaragua			contact		
	Panama			contact	maybe 2-3 skulls	
	Colombia			contact	submitted	
WNA	Ecuador			contact	several dozen + few tissues samples	skulls in two private collections (CEPEC) and (Acorema)
	Peru			contact	left	
	Chile			contact	very few specimens, scattered geographically and all held in private hands	
WNA	throughout the Caribbean	T. t. truncatus	need skulls	contact?		
	Panama			contact		
	Costa Rica			contact		
WSA	Colombia			contact		
	Venezuela			contact		
	Guyana			contact		
WSA	Suriname					
	Brazil	T. t. truncatus and T. t. gephyreus	need to better define limits to distribution of T. t. gephyreus by sampling in Argentina and in Brazil in north Santa Catarina and Paraná states. Coastal and offshore waters should be sampled (Fruet et al., 2017 workshop report)	contact		
	Argentina			contact		
ENA	Morocco	T. truncatus		contact		
	Mauritania			contact	Skulls are available in Nouadhibou, Mauritania at the Institut Mauritanien de recherche océanographique et des Pêches (IMROP). 1 skull with Aguilas	
	Senegal			contact	Senegal Stranding Network, periodic surveys, genetic samples collected, collaborations with Smithsonian Institute and prior 2017 University of Western Brittany. If skulls in good condition stored at the museum of Cheikh Anta Diop, University in Dakar.	
ESA	Gambia			contact		
	Guinea Bissau			contact		
	Liberia			contact		
ESA	Cote d'Ivoire			contact		
	Ghana			contact		
	Nigeria			contact	few skull samples	
ESA	Guinea			contact		
	Cameroon			contact		
	South Africa (Atlantic)			contact		
ESA	Gabon	T. truncatus coastal		contact	10 biopsy samples + 1 skull	
	Republic of Congo	T. truncatus coastal		contact	5 skin samples stranding + 3 skulls and bones	
	Democratic Republic of Congo			contact	at least 2 skin samples from bycatch	
MED/BS	Angola			contact	few skull specimens, check also Cape Town Peter Best "collection"	
	Namibia			contact		
	South Africa (Atlantic)			contact		
MED/BS	Georgia	T. truncatus ponticus	information is limited to the analysis of samples from Azov Sea.	contact	31 + 5 skulls	31 samples from BS + 45 from other eastern MED regions in process for mtDNA. Intention to run dRAD. Skull number to determined.
	Ukraine	T. truncatus ponticus	Indications of offshore/inshore populations and other areas of BS would help	contact		
	Russia	T. truncatus ponticus		contact		
MED/BS	Romania	T. truncatus ponticus		contact		
	Bulgaria	T. truncatus ponticus		contact		
	Turkey	T. truncatus ponticus		contact		
MED/BS	Monaco	T. truncatus		contact		
	Algeria	T. truncatus		contact		
	Tunisia	T. truncatus		contact		
MED/BS	Libya	T. truncatus		contact		
	Egypt	T. truncatus		contact		
	Israel	T. truncatus		contact		
MED/BS	Lebanon	T. truncatus		contact		
	Cyprus	T. truncatus		contact		
	Greece (Aegean)	T. truncatus		contact		

Table summarising data deficient areas, species reported, whether a contact person has been identified and if available type and number of samples.