

# Annex I

## Report of the Working Group on Stock Definition

**Members:** Bravington (Chair), Andersen, Baker, Brandão, Butterworth, Danielsdóttir, Donovan, George, Givens, Gong, Goto, Hammond, Youn, Kanda, Kitakado, LeDuc, Palsbøll, Pastene, Perrin, Polacheck, Pomilla, Punt, Rosenbaum, Schweder, Skaug, Song, Tiedemann, Víkingsson, Walløe, Wang, Waples.

### 1. ELECTION OF CHAIR AND APPOINTMENT OF RAPPORTEURS

Bravington was elected Chair. Perrin and Givens acted as rapporteurs.

### 2. ADOPTION OF AGENDA

The adopted agenda is given as Appendix 1

### 3. REVIEW OF DOCUMENTS

The documents discussed were SC/57/SD1, SD2 and SD5.

### 4. STATISTICAL AND GENETIC ISSUES RELATING TO STOCK DEFINITION

SC/57/SD1 described the initial development and testing of a model for analysing population structure in the absence of source population information, based on pairwise microsatellite allele matching probabilities. The approach is intended for cases where the existence of subpopulations is uncertain and *a priori* assignment of samples to hypothesised subpopulations is difficult or unappealing. The model allows one to distinguish two separate sources of genetic correlation (or excess homozygosity): a portion associated with covariates such as time, space, and age and a second constant portion not associated with covariates but instead attributable to the existence of non-interbreeding substocks. Hypothesis tests can be carried out using permutation methods. A variety of examples illustrated how the model could be potentially informative and effective, and compared its results to those from other published analysis methods. Within the next year, the authors plan to apply the approach to the case of Bering-Chukchi-Beaufort Seas bowhead whales (*Balaena mysticetus*).

During the discussion of SC/57/SD1, a variety of methodological suggestions were made. In summary, the Working Group noted the potential promise in this approach, strongly encouraged its continued development and application and looked forward to seeing progress and results at the 2006 meeting.

SC/57/SD2 presented an analysis in which the Norwegian minke whale DNA-register was screened for pairs of apparently closely related individuals. The most closely related pairs were then screened at 15 additional micro-

satellite loci, and these loci were used to test the hypothesised relatedness. This resulted in the detection of 27 pairs of related individuals. In some pairs, the two relatives were captured a long way apart, with many pairs crossing a *Small Area* boundary, and two pairs crossing a *Medium Area* boundary. The observed number of parent-offspring pairs was higher than its expected value, based on the current abundance estimate of 107,000 animals. The results in SC/57/SD2 were preliminary.

In discussion, the Working Group first noted that the general approach to genetic sampling is very cost-effective; only a small proportion of animals need to be screened at the extra loci. In terms of the modelling, it was noted that the expected number of parent-offspring pairs in SC/57/SD2 was sensitive to assumptions about demographics, in particular to the assumed mortality rate (here 0.1). Given the preliminary nature of the results, it was not yet possible to say whether the observed excess of parent-offspring pairs was statistically significant. Sensitivity analyses on mortality rate and biological parameters were proposed. The author commented that more complex analyses making fuller use of the data are possible, for example in more precise modelling of the link between genetic distance and spatial distance. In summary, the Working Group welcomed SC/57/SD2 and strongly **encouraged** further developments of the technique.

SC/57/SD5 presented the effect of increasing the sample size (from 220 to 22,000) in a simulation exercise to explore the performance of the Boundary Rank (BR) algorithm (Martien and Taylor, 2001) when an underlying cline may be present. Despite the much larger sample size, the previous conclusions of Butterworth and Brandão (2004) remain unchanged: although the algorithm provides unbiased results for uniform sampling of the region, non-trivial bias becomes evident when sampling is preferentially to one side of the optimal dividing line. Furthermore the distribution of boundary placement about this optimum is quite wide and this width appears to decrease only rather slowly as sample size increases. These further analyses thus serve to support previous advocacy of the need for close inspection of results from application of the BR technique if a cline structure is suspected, rather than automatically accepting its outputs.

In discussion, the Working Group concurred that close scrutiny of automatic boundary-setting methods is always important. However, although SC/57/SD5 certainly does reveal an underlying bias independent of sample size, the implications for practical use of BR with whales are not clear. The extent of bias is not enormous (up to about 10% of population range for the scenarios in the paper), although the large random variability in boundary placement may be of more concern. The scenarios in SC/57/SD5 have very low haplotypic diversity; at higher and more realistic diversities,

other effects may swamp this particular bias. It was also suggested that the centre may not in fact be the best place to put a management boundary in a cline, if harvesting (and sampling) is skewed towards one end.

Of course, it is desirable to keep simulations simple, and it would be a big task to address all such complications directly in a one-off simulation model. Fortunately, the TOSSM project provides exactly the framework needed for the most meaningful tests of Boundary Rank (and other algorithms). More complex simulations along the lines of SC/57/SD5 can be done fairly easily within the existing package RMETASIM; in simple exploratory cases, it will not even be necessary to use the harvesting and demographic extensions in Testing of Spatial Structure Models (TOSSM). The Working Group **recommended** that those thinking about doing simulation tests of boundary-setting should explore the possibility of using TOSSM/RMETASIM.

## 5. TESTING OF SPATIAL STRUCTURE MODELS (TOSSM)

### 5.1 Update on intersessional progress

At the 2003 IWC meeting, the Scientific Committee and the SD Working Group instigated the TOSSM project, following a Workshop in La Jolla, USA, January 2003. The main aim of TOSSM is to develop simulation tools that can be used to examine the performance of current and future genetic population structure techniques. The focus is on a management context, where the genetic techniques are used to suggest management boundaries, which in turn are used to set or subdivide catch limits according to some rule; the performance of different genetic methods is ultimately to be assessed in terms of how well a simulated management regime performs if the suggested boundaries are used. The Scientific Committee's experience of studying population structure, e.g. in developing *Implementation Simulation Trials (ISTs)* for common minke whales (*Balaenoptera acurostrata*) in the North Pacific, has shown that genetic data does not usually provide unequivocal evidence for specific boundaries for use in management. Furthermore, few boundary-placement techniques have been subject to any form of simulation testing. Even those that have, cannot be considered to have undergone the level of extensive simulating testing to incorporate uncertainty that has been a feature of, for example, the IWC's work on the RMP and AWMP. This is perhaps not surprising, given the scope and complexity of developing suitable genetically-specified simulation datasets.

The Report of the TOSSM Workshop (IWC, 2004) identified the following six work modules, each of which has to be completed before the simulation performance testing can actually begin.

- (i) Genetic simulation.
- (ii) Biology and population dynamics.
- (iii) Sampling.
- (iv) Catch strategy.
- (v) Adaptation of boundary-settings methods for testing.
- (vi) Integrating all the above to allow a complete test to be run.

Considerable progress on these was made before the 2004 IWC meeting. At that stage, the SD Working Group identified the following priority tasks for intersessional work before the 2005 meeting:

- (a) working with the developer of RMETASIM to fix a bug uncovered during TOSSM testing;

- (b) incorporation of coalescence into step (i) to speed up the simulations, which are currently very slow; and
- (c) incorporation of whale-like density dependence into step (ii).

The TOSSM developers (Martien, Tallmon, Tiedemann) made good progress intersessionally. Tasks (a) and (b) are complete, and (c) should be complete by 1 July 2005. However, there were delays beyond the control of the developers, and it has not been possible to take the project through to generating the first simulated datasets, as was hoped last year.

The Working Group warmly thanked Martien, Tallmon, and Tiedemann for their efforts. Modules (i) and (ii) are now basically complete (at least for the simple population archetype proposed for the first round of tests). Modules (iii), (iv) and (vi) should be easier than (i) and (ii) were, because of the RMETASIM framework and the availability of code for the *Catch Limit Algorithm (CLA)*. The hardest remaining work is in module (v). The WG noted that detailed documentation is vital in complex simulation models, and requested that the developers maintain a 'living document' describing *inter alia* the demographic model and parameters.

### 5.2 Directions for further work

The IWC has extensive experience of complex simulation exercises similar to TOSSM. To avoid costly back-tracking, it is important to do some 'full runs' early on – that is, to make sure that the entire set of steps can be completed together for a fairly simple scenario – before spending too much attention on polishing individual details. Although some background work is still needed, TOSSM has now reached the 'full run' stage. Once a few 'full run' results are in hand, it will be time to discuss preliminary results with non-IWC developers of population structure models, who form an essential part of the TOSSM process.

The most efficient way forward would be to hold an intersessional Workshop after completing the background work and some 'full runs'. Holding the Workshop in March 2006 would leave enough time to (i) complete the background work beforehand and (ii) implement some of the Workshop recommendations before IWC 2006, so that a more useful set of test results can be considered at that meeting. Tiedemann offered to host the meeting at University of Potsdam, including free meeting facilities and the provision of computing power for generating extra datasets during the meeting. The WG thanked Tiedemann for his offer and **strongly endorsed** the Workshop proposal, which is given in full in Appendix 2. The workshop objectives are:

- (1) present results of preliminary runs using existing adapted methods;
- (2) discuss adjustments to the first sets of simulated data;
- (3) discuss how to better adapt existing boundary-setting methods, specifically via:
  - (a) tunable 'back-end' rules for deciding how many boundaries;
  - (b) 'front-end' rules for preliminary sample grouping, etc;
- (4) discuss other boundary-setting methods that might be tested in TOSSM; and
- (5) decide on priorities for further simulated datasets, e.g. more complex population archetypes, more realistic genetics, simulation of physical tags.

The intersessional background work needed before the Workshop is listed in Table 1, together with timelines and lead personnel.

**6. UNIT-TO-CONSERVE**

The point of this agenda item is to allow consideration of various possible definitions of unit-to-serve, and their corresponding implications for management; see IWC (2003, p.49). No papers were received this year, but the Working Group discussed recent academic thinking on this point as summarised in Waples and Gaggiotti (In press). In Waples' summary, the term 'population' is used in a somewhat similar way to 'stock' in IWC pre-2002, the year when the Stock Definition WG decided not to use the term 'stock' except in its own name.

When faced with a case where two randomly-mating groups are linked by migration, two fundamental questions arise.

Question 1. Given that the magnitude of departure from panmixia occurs along a continuum, how does one define a point along that continuum at which subunits are differentiated enough to be considered 'populations'?

Question 2. Assuming one has defined a point along the continuum that corresponds to the concept 'population', how can one in practice determine whether units of interest

are populations? This is a quantitative question that requires developing population metrics that can be evaluated for power and sensitivity.

Biological definitions of 'population' can be sorted into two different paradigms (Andrewartha and Birch, 1984): the ecological paradigm (which emphasises demographic cohesion) and the evolutionary paradigm (which emphasises reproductive cohesion). A suite of definitions is shown in Table 2.

Waples noted that none of the definitions in Table 2, with the possible exception of number 6 (McElhany *et al.*, 2000), is operational in the sense of being able to unambiguously answer Question 1. This lack emphasises the importance of a process such as TOSSM to bridge the gap between empirical data related to population structure (estimates of migration and gene flow; characterising relationships among population groups) and the management objectives, such as avoiding local depletions.

Despite the absence of an operational definition of 'population,' it is possible to identify a number of criteria that might be used to make the definition quantitative and operational. Some possibilities are:

Evolutionary paradigm. Reproductive cohesiveness is determined by levels of gene flow, and the evolutionary consequences of gene flow scale with the absolute number of effective migrants,  $N_e m$ . First, one might consider that

Table 1  
Timetable for intersessional work.

Population dynamics model	RMETASIM	RMP	Methods
1/7/05 Finish specification of movement	Finish density dependence KM/DT	Write RMP	Adapt ~4 existing methods (SAMOVA,
1/11/05 and mutation rates for 'gray whale	Add data generation for RMP + catch-	blackbox	Spagedi, etc.); add rules for initial grouping and
with stepping stones' RT/AP/PP	setting via calling RMP MB/KM	(AP/CA)	for deciding number of stocks RT/KM/NK/TK
1/1/06	Generate dataset(s) KM/HS		
1/2/06 Preliminary 'full run' test of methods	(including harvesting under RMP) and feedback to non-IWC developers RT		

TK=Kitakado; NK=Kanda; MB=Bravington; KM=Martien; DT=Tallmon; HS=Skaug; PP=Palsbøll; CA=Allison; AP=Punt; RT=Tiedemann.

Table 2  
Some suggested definitions of 'population' in the ecological literature.

Definition	Ref
<b>Ecological paradigm</b>	
A group of organisms of the same species occupying a particular space at a particular time.	1,2
A group of individuals of the same species that live together in an area of sufficient size that all requirements for reproduction, survival and migration can be met.	3
A group of organisms occupying a specific geographic area or biome.	4
A set of individuals that live in the same habitat patch and therefore interact with each other.	5
A group of individuals sufficiently isolated that immigration does not substantially affect the population dynamics or extinction risk over a 100-year time frame.	6
<b>Evolutionary paradigm</b>	
A community of individuals of a sexually reproducing species within which matings take place.	7
A major part of the environment in which selection takes place.	8
A group of interbreeding individuals that exist together in time and space.	9
A group of conspecific organisms that occupy a more or less well defined geographic region and exhibit reproductive continuity from generation to generation.	10
A group of individuals of the same species living close enough together than any member of the group can potentially mate with any other member.	11
<b>Variations</b>	
Stock: a species, group, or population of fish that maintains and sustains itself over time in a definable area.	12
Demographic units: those having separate demographic histories.	13
Demes: separate evolutionary units.	13
Interaction group – based on distance an individual might travel during the non-dispersive stage of its life.	14
Natural population: can only be bounded by natural ecological or genetic barriers.	15
Local population: (a) individuals have a chance to interact ecologically and reproductively with other members of the group; and (b) some members are likely to emigrate to or immigrate from other local groups.	15

**References:** <sup>1</sup>Krebs (1994); <sup>2</sup>Roughgarden *et al.* (1989); <sup>3</sup>Huffaker *et al.* (1984); <sup>4</sup>Lapedes (1978); <sup>5</sup>Hanski and Gilpin (1996); <sup>6</sup>McElhany *et al.* (2000); <sup>7</sup>Dobzhansky (1970); <sup>8</sup>Williams (1966); <sup>9</sup>Hedrick (2000); <sup>10</sup>Futuyma (1998); <sup>11</sup>Hartl and Clark (1988); <sup>12</sup>Booke (1981); <sup>13</sup>Brown and Ehrlich (1980); <sup>14</sup>den Boer (1977, 1979); <sup>15</sup>Andrewartha and Birch (1984).

separate populations exist when any departure from panmixia is found, i.e. when there are no restrictions to gene flow. Another possible criterion is:  $N_e m < 1$ . With gene flow below this level, the random process of drift dominates and population allele frequencies tend to behave independently. This latter criterion might be too stringent, because substantial differences in subpopulation allele frequency can occur when  $N_e m > 1$ . Choice of any particular values is somewhat arbitrary, but some possibilities include  $N_e m < 5$  (which generally implies  $F_{ST} < 0.05$ ) and  $N_e m < 25$  (which generally implies  $F_{ST} < 0.01$ ).

Ecological paradigm. Demographic cohesiveness scales with the fraction of the subpopulation that immigrates from other subpopulations ( $m$ ). A key question under this paradigm is: how small must  $m$  be before the subpopulations are demographically independent? Surprisingly, this question has received little formal study. One study (Hastings, 1993) suggests that transition to demographic independence occurs when  $m$  falls below about 10%. This suggests a possible criterion:  $m < 0.1$ .

With respect to Question 2, a wide variety of analytical methods are available to test whether these or any other population criteria have been met. Published studies provide some insight into likely results, and TOSSM will provide more detailed information of direct relevance to cetaceans. Waples summarised his own preliminary simulation results in terms of the quantitative criteria above:

- (1) using sample sizes and numbers of polymorphic markers that are routinely attainable using current methods, power to detect departures from panmixia can be very high (~100%) even with high gene flow ( $N_m=25$ );
- (2) power to test specific hypotheses about restricted gene flow can also be high; however, developing the appropriate test criterion requires assumptions about several key parameters that are difficult to estimate in most natural populations;
- (3) the ecological paradigm is difficult to evaluate using genetic markers, because the transition from demographic dependence to independence occurs in a region of high migration where traditional equilibrium genetic methods have reduced power. This may change in the near future as a result of recent theoretical developments and continued advances in computational power, both of which will make it easier to detect contemporary migration using genetic markers.

The high power to detect very weak population structure has a potential downside: care must be taken not to confuse small artifacts (e.g. non-random sampling, family structure, data errors) with a true signal of population differentiation (Waples, 1998). This emphasises the need for careful attention to experimental design, sampling protocols and data quality control, as well as the importance of understanding the biology of the target species.

Waples' summary triggered an extensive discussion. As identified in previous IWC meetings, it is clear that the evolutionary paradigm provides information in units (number of migrants per generation) that are not always directly applicable to IWC management issues (IWC, 2001, p.230). In addition, there are persistent population structures that clearly are of management and conservation interest, such as matrilineal philopatry e.g. in feeding stocks of humpback whales (*Megaptera novaeangliae*), but that do not correspond to breeding stocks or 'populations' (see also Avise, 1995). Within the more relevant but also more difficult ecological paradigm, the IWC's focus is on

population dynamics, i.e. on per-capita exchange rates rather than more typical genetic measures such as absolute migrants-per-generation. There is a wide variety of possible time and space scales that could be of interest for management; hence the aim of the Committee has been, through the Stock Definition Working Group, to get to a point where it can provide advice to the Commission about likely levels of depletion on a whole range of different time and space scales. This has been the principle underlying TOSSM.

One feature of performance testing through a process like TOSSM, is that every automatable boundary-related method – whether it proposes boundaries, tests significance of differences across boundaries, or estimates animal or gene flow rates across boundary – will need some kind of 'decision statistic' and associated 'tuning parameter' which will together determine how many boundaries are proposed (if any). For example, the decision statistic in a model that estimates demographic parameters might be chosen to be something like 'upper 70<sup>th</sup> percentile of posterior distribution of animal flux per generation'; in a hypothesis-testing framework, on the other hand, the decision statistic would be a  $p$ -value. The tuning parameter is simply some fixed reference value to be compared with the observed decision statistic; depending on which side the observed decision statistic falls, a boundary will or will not be set. The choice and computation of decision statistic for a given boundary-setting method can vary from simple to very complex, depending on the method, and forms a major part of the TOSSM work program (module (v)).

There is no general conclusion yet in the IWC about which types of decision statistic might be appropriate in different circumstances, let alone about appropriate values of the corresponding tuning parameters. The Working Group noted the desirability of establishing comparable measurement scales, while recognising the need for flexibility in particular cases. Without some idea of what the decision statistic and tuning parameter might be, it could be difficult for geneticists to do experimental design. Since one part of TOSSM will be to experiment with different decision statistics and to tune the tuning parameters, it is to be hoped that the Committee will gain some insight into sensible choices. In the meantime, from a design perspective, it might be fruitful to aim for something like a target CV on  $N_e m$  (which, given abundance estimates and biological information, might be directly informative about animal flux rates), instead of strict statistical power with respect to a particular (but likely arbitrary) significance level and alternative hypothesis.

The Working Group noted the increased power for detecting differences provided by new analysis methods and more data in recent years. With big enough sample sizes and numbers of loci, there is now a realistic possibility for some whale species of detecting significant genetic differences that, while genuine, are actually not important in demographic terms: i.e. where the migration rate is too high to warrant separate management (Waples, 1998; Hedrick, 1983). This is a considerable change from the position a few years ago, where the data and methods very typically lacked the power to detect demographically-low (and therefore important) but genetically-high rates of migration.

Finally, the Working Group noted the importance of regular and repeated communication with population geneticists, to bridge the evident gap between academic methods development and the practical conservation/management issues that the IWC perpetually faces.

## 7. DRAFT AGENDA FOR 2006

- (1) Review statistical and genetic issues relating to stock definition.
- (2) Review progress on TOSSM.
- (3) Unit-to-serve.
- (4) Genetic quality issues [Palsbøll to compile list of relevant published papers].

## 8. ADOPTION OF REPORT

The report was adopted at 12:09 on Monday 6 June 2005.

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## Appendix 1

### AGENDA

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|---|---|
| 1. Election of Chair and appointment of rapporteurs.            | 5. Testing of Spatial Structure Models (TOSSM). |
| 2. Adoption of agenda.  | 6. Unit-to-serve.                               |
| 3. Review of documents.   | 7. Draft agenda for 2006.                       |
| 4. Statistical and genetic issues relating to stock definition. | 8. Adoption of report.                          |
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## Appendix 2

### PROPOSAL FOR AN INTERSESSIONAL TOSSM WORKSHOP IN MARCH 2006

As for many years, the IWC is currently grappling with a number of difficult questions about setting management boundaries in the presence of possible population structure. Some of the most pressing cases include: West Greenland fin (*B. physalus*) and minke whales; Bering-Chukchi-

Beaufort Sea bowhead whales; North Pacific minke whales; and Antarctic minke whales. The TOSSM project is designed for simulation-testing of methods that set management boundaries in realistic cases. A key difference from other genetic simulation tests is that TOSSM explicitly

checks the performance of proposed boundaries under harvesting, in terms of monitoring subsequent local depletion.

There are broadly two parts to TOSSM: generation of simulated data, and adaptation/testing of management boundary algorithms. The focus to date has been on the first part, in particular through adapting RMETASIM to cope with demographic and genetic structures relevant to whales. This has been a big task, but most of the hard work is complete, at least for the fairly simple genetic and demographic archetypes that we propose to consider first. The crucial harvesting 'module' still needs doing, but the amount of work involved is not great and we expect to complete it intersessionally. We will then be able to simulate test datasets from a simple population archetype (three population stepping-stone, gray whale (*Eschrichtius robustus*) demographics), both with and without spatially structured harvesting.

As yet, there has been no testing of boundary-setting methods (the second vital part of TOSSM). This is partly because the RMETASIM changes are not quite finished, and partly because it is not trivial to adapt existing boundary-setting methods to the TOSSM framework, since they are generally designed for somewhat different problems. With a little more intersessional work, we will be able to adapt and run variants of several existing genetic population structure tools such as SAMOVA and Spagedi. It may also be possible to run several methods currently being developed inside IWC. At that stage, we will need to bring in the non-IWC developers of genetic population structure tools to provide feedback and discuss future developments. We propose doing this at an intersessional Workshop, leaving us with enough time to make some adjustments to the simulations and boundary-setting algorithms, and to make further runs, before reviewing progress at IWC 2006. Experience with other IWC simulation-testing exercises (RMP and AWMP) is that such intersessionals are essential to making timely progress; and since the IWC unavoidably has to make management recommendations based at present on incompletely-tested models, it is important to make swift progress with thorough testing.

The focus of the Workshop will not be on exhaustive testing or detailed comparisons between methods, but rather on completing a 'full run' with all the essential TOSSM elements (i.e. making sure everything 'works' together), and

on checking which methods can get over the first and lowest hurdles, i.e. the easiest cases for boundary setting. In subsequent phases of TOSSM, we will subject candidate boundary-setting methods to a succession of ever more severe trials, reflecting greater realism, less informative data, and greater departures from the assumptions of the methods under test.

#### **Terms of Reference**

To progress the testing of genetic methods for setting management boundaries, with the involvement of non-IWC population geneticists.

#### **Draft agenda**

1. Overview of the TOSSM project.
2. Results of preliminary runs using existing adapted methods.
3. Adjustments to make to the existing simulations.
4. How to better adapt existing boundary-setting methods.
5. Other boundary-setting methods to consider in TOSSM.
6. Priorities for future simulated datasets.
7. Recommendations for priority work within TOSSM.

#### **Participants (provisional list only)**

Punt, Donovan, Martien, Palsbøll, Tiedemann, Bravington, Skaug, Taylor, Kitakado, Kanda, Baker, Hammond, Danielsdóttir + (non-IWC), Tallmon and four from E. Andersen, Waples, Luikart, Jorde, Excoffier, Rannala [Total expected ~15].

#### **Timing and venue**

University of Potsdam (Berlin) for four days in March 2006.

#### **Estimated cost**

£9,000, covering travel and subsistence for five non-IWC people (US and Europe), six IWC people requiring funding and six IWC people not requiring funding. On behalf of Potsdam University, Tiedemann has kindly offered to provide all meeting and computation facilities free of charge.

#### **Steering group**

Tiedemann (Convenor), Martien, Donovan, Bravington, Kitakado, Kanda and Skaug.