

Review of Alaskan Harbor Seal Stock Assessment

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Executive summary

In 1995 the National Marine Fisheries Service (NMFS), in its Alaska Marine Mammal Stock Assessment Report, defined three stocks of harbor seals (*Phoca vitulina*) in Alaska. This was based primarily on broad-scale geographic differences in trends in abundance. However, it was recognised that considerable uncertainty about these stocks remained, and therefore NMFS initiated genetic studies of harbor seal stock structure in Alaska in the fall of 1994. The report resulting from these studies, “The Analysis of Population Genetic Structure in Alaskan Harbor Seals, *Phoca vitulina*, as a Framework for the Identification of Management Stocks,” is the subject of this review.

The review consisted of the assessment of documents provided to the review panel and a three-day site visit, which included presentations by and discussions with the principal scientists involved in the genetic study. An extensive survey of genetic diversity among putative populations from the Pribilof Islands to Southeast Alaska confirmed stock structure over this range, and further suggested that more than the initial three designated stocks will be appropriate for the effective management of this species in Alaska under the Marine Mammal Protection Act (MMPA).

I concurred with the conclusions outlined in the report, that finer stock division is needed, and that more inclusive sampling will be required to clearly identify these stocks. At the same time, I would recommend further analysis of the available data towards a clearer assessment of possible stock boundaries. This should incorporate data based on both mtDNA and microsatellite DNA markers. The data should also be more clearly interpreted in the context of earlier studies on the population genetics of this species. Those studies typically identify stock structure on a finer geographic scale than currently recognised in Alaska.

Introduction

Previous studies on the population genetics of the harbor seal have consistently shown evidence of population structure. On a world-wide scale, Stanley et al. (1996) used mitochondrial DNA sequence data (435bp of the control region) to compare 227 seals from 24 localities in the North Pacific and North Atlantic oceans. Applying a measure of population structure that reflects both haplotype frequency and genetic distance (Φ_{ST}), they provide a hierarchical assessment of genetic structure. This statistic describes the proportion of the genetic variance that accounts for among as opposed to within population diversity. On a global scale, 77% of the variance was explained by diversity among populations. This remained high for large-scale comparisons within ocean basins (72% in the North Pacific for populations spanning from Japan to California, and 60% in the North Atlantic over a population range from Sable Island to the Baltic Sea). On a finer scale in the North Pacific, comparing San

Francisco and the Channel Islands in California, this statistic still explained 17.8% of the variance, and was significant at $p < 0.05$. Some finer scale comparisons in the North Atlantic showed significant differentiation by this measure (e.g. comparisons between the Baltic and the North Sea, and comparisons between the British Isles, Norway and the Baltic), while others did not (e.g. comparing several colonies around the coast of Scotland). In both oceans, these authors consistently found structure over a geographic range of about 500 kilometers (km), but not over ranges of 100 km for some comparisons. However, the sample size was small for some of these comparisons, and this will limit the power of the test.

Mitochondrial DNA (mtDNA) is highly variable, and therefore provides good resolution, but it is inherited only from mother to offspring, and therefore only provides information on the movement of females. Nuclear microsatellite DNA loci are also highly variable, but are inherited bi-parentally, and so provide information on the movement of both males and females. Goodman (1998) used microsatellite DNA loci to compare 1,029 harbor seals from 12 geographic areas in the eastern North Atlantic, North Sea and Baltic Sea. He used a statistic related to F_{ST} (similar to Φ_{ST} but based only on allele frequency data, not genetic distance) to compare putative populations (the statistic used was RHO_{ST} , which takes into account the most likely 'step-wise' evolutionary model for microsatellite loci). The 12 areas were refined down to six differentiated regional populations, consistent with the work done by Stanley et al. (1996) using mtDNA. Together the data indicated that harbor seal philopatry operates over a range of about 300 km in the North Atlantic, North Sea region, and that both males and females are philopatric over this range. Both studies showed a significant correlation between geographic and genetic distance, with a slope that suggested some resolution over a geographic range of about 100 km.

In Alaska three putative stocks have been defined by NMFS, primarily on the basis of broad-scale patterns of population dynamics (Small & DeMaster 1995). These stocks range in size from approximately 800-1,000 km from end to end, following the distribution along the coast. However, more recent data on trends in abundance and movement patterns (based on radio telemetry) suggest the possibility of structure on a finer geographic scale. Studies on trends in abundance have suggested different trajectories for putative populations within both Southeast Alaska and the Gulf of Alaska (Frost et al. 1999, Small et al. 2003). Radio telemetry studies tend to suggest predominant movement for foraging over a range of about 50 km, although foraging range need not be informative about dispersal range, and harbor seals are capable of much longer excursions (Lowery et al. 2001). The data on Alaskan movement and population dynamics, together with the data on population genetic structure from the North Atlantic and elsewhere in the North Pacific, suggest the possibility of finer-scale population structure in Alaska and the consequent need for smaller geographic stock designations.

This was the basis for the study currently under review. The site visit for the review was undertaken over three days (16-18 March, 2004) at the Southwest Fishery Science Center (SWFSC) in La Jolla, California. The review panel included Kathy Frost and Brent Stewart, and I. We were provided with relevant documentation in advance, and given oral presentations on the first day of the site visit. The subsequent two days of the site visit were based on discussions with the scientists involved in the research, and an interactive exchange of ideas during which the scientists undertook some specific further analyses to help us clarify some points. The reports will be based on both the documents provided for the review, and the discussions and

presentations from the site visit. Each panel member will provide a separate, nonconsensus report. The focus of my report will be on the population genetics.

Summary and Review of Information used in the Assessment

The primary focus of the work undertaken at SWFSC towards the assessment of genetic stock structure among Alaskan harbor seal populations was based on the analysis of DNA sequence data from the mtDNA control region locus.

Documentation provided reviewed the basis for the definition of stocks under the guidelines of the MMPA, the methodology used in the analysis of the mtDNA data, and the results of those analyses. During the site visit some preliminary data on the analysis of Alaskan stocks using microsatellite DNA loci was also presented, though these data were not presented in any of the documentation. The review considered all of these materials, and my assessment is based on the rationale, the methods, the treatment of the results, and the interpretation provided.

Review of methodology

Samples were collected across a very broad geographic range from the Aleutians to Southeast Alaska, and over a period of years. Samples came from animals killed in subsistence hunts, animals found dead, and from scientific collections from individually tagged animals. A total of 881 samples were collected from 180 different locations. The distribution was sufficient for an excellent initial assessment of structure over this geographic range. The DNA was extracted, amplified, and sequenced using standard methods.

The first part of the study (Westlake & O'Corry-Crowe 2002) identified five centers of concentration for harbor seals in Alaska, and compared these using conventional F_{ST} and Φ_{ST} statistics (see introduction). These centers were the Pribilof Islands, Bristol Bay, Kodiak Island, Prince William Sound, and Southeast Alaska. This study also used a Mantel test to compare geographic and genetic distances, a minimum spanning network phylogeny to investigate the evolutionary history of genotypes at this locus across this geographic range, and a mismatch distribution analysis (Rogers and Harpending 1992) to assess the possibility of historical population expansion. In a preliminary study presented only as a conference poster (Campbell & O'Corry-Crowe 2003), 340 samples over a similar geographic range were compared for diversity at 11 microsatellite DNA loci using F_{ST} and Mantel tests. All of these data are directly comparable to data presented in earlier studies of harbor seal population genetics (e.g. Stanley et al. 1996, Goodman 1998, and Burg et al. 1999).

A separate analysis, attempting to define stock units on a finer geographic scale, employed clustering algorithms. Two of these were established methods (UPGMA and Neighbor Joining analyses), each of which produce a phylogram based on phenetic (distance) measures. UPGMA is the simplest method, generating a tree based on joining the two most similar units, taking the group mean, and then joining this mean to the next most similar unit, and so on. Distortion can result from incorrect pairings early on, and from rate variation over evolutionary time. Neighbor Joining allows for variable branch lengths, accounting to some extent for rate variation. A third method applied ('Boundary Rank') is very similar to UPGMA, but constrained

with respect to which population units are compared (described in an unpublished document by Martien, Sellas, Rosel, Taylor and Wells).

The clustering methods are based on a number of assumptions. The initial units are defined on the basis of inference from population and life history data generating hypotheses about dispersal range, breeding behavior, etc. If the units so defined are too large, then information on stock structure could be lost. The constrained clustering method links these units in a matrix of connections, which limit the possible pairs produced while generating the tree. Again, these connections are based on inference about the behavior of the seals, and any errors will distort the tree. In this case the assumption is that the distribution follows a 'stepping stone' model, whereby seals only disperse to neighboring populations. One objective of these methods is to define units that are smaller than the true population size, and thereby allow the clustering method to define true populations as clusters of units. This leads to the inclusion of only individuals from a small geographic region in the initial units, which can lead to two problems. First, especially in social species, local sampling may bias unit samples with the inclusion of close kin. This would tend to exaggerate the difference between units. Second, small samples risk large errors in the estimation of allele frequencies, and when frequency based methods of distance assessment are used, this could lead to erroneous patterns of clustering. In this case, simulation performance tests (Martien & Taylor, in press) suggested that a method based strictly on allele frequency (χ^2 /d.o.f.) gave the highest power, and therefore this method was chosen for the assessments of harbor seal stock structure. Therefore, the method will be sensitive to unit sample size. Arguing that type 2 errors (accepting the null hypothesis of no difference when it should be rejected) are more likely than type 1 errors (rejecting the null hypothesis when it should be accepted), they set alpha to 0.1, instead of the conventional 0.05. This will decrease the chance of a type 2 error, but inevitably increase the risk of a type 1 error.

Another consideration is the fact that any errors introduced by sampling effects will be compounded in the subsequent construction of the tree. The authors also make the case that mtDNA will likely be more informative with respect to the identification of unit structure, and therefore focus on the analysis of this marker. This can be the case, depending on the dispersal behavior of males and females, and the effective size of populations, but it also means that the structure defined relates only to the movement of females.

As elsewhere in the world, the distribution of harbor seals in Alaska shows some discontinuities, but they are also found in continuous distributions across large geographic ranges (e.g. over approximately 900 km in Southeast Alaska). In the latter case, there may be genetic differentiation across a contiguous range, but the precise boundary between populations may be difficult to discern, or non-existent. Instead, there may be a diffusion gradient of genotypes along an extended range. In this case there are methods, such as spatial autocorrelation, that can facilitate the assessment of the relationship between geographic distance and individual genotype, and it may be useful to include these analyses to help define population structure in these contiguous distributions (see below).

The dispersal rate of females among putative populations was estimated for three putative population pairs (those thought to be most similar) using a maximum likelihood estimation based on a coalescent approach, implemented in the program MIGRATE (Beerli & Felsenstein 2001). Interpretation of these data depends in part on the model assumption of constant population size over time.

Review of results and interpretation

The comparison of five population centers showed clear evidence of structure at this level, and the Mantel test showed a correlation with geographic distance that was similar to analyses presented in earlier studies (Stanley et al. 1996, Goodman 1998), though this assessment was over a larger geographic scale. Pairwise comparisons between these centers explained up to 8.5% of the variance (depending on the method applied), although the comparison between Prince William Sound and Kodiak showed comparatively weak structure, with only one of two statistics showing a significant difference (F_{ST} was significant, while the measure that incorporates genetic distance as well as haplotype frequency, Φ_{ST} , was not). The same was true of the comparison between the Pribilof Islands and Bristol Bay. The evidence for geographic structure was stronger for the mtDNA data (Westlake & O'Corry-Crowe 2002) than for the preliminary microsatellite DNA data (Campbell & O'Corry-Crowe 2003), but both supported structure at the level of the three designated stocks at a minimum. In some cases, a lack of clear structure could be due to substructure within the designated 'centers'. Further assessment using sexually recombining markers, such as microsatellite DNA, would help resolve this, permitting an assessment of the possible inclusion of multiple populations in a sample (see below). It should also be noted that the interpretation of F_{ST} is based in theory on the island model proposed by Wright (1951). Calculation of F_{ST} incorporating all putative populations in the comparison is likely to be more consistent with this model than pairwise comparisons between individual putative populations. These data were not presented in this study, but showed strong evidence of structure ($\Phi_{ST} = 0.72$) for the combination of putative populations from Japan to California in Stanley et al. (1996).

The assessments of finer-scale population structure using clustering methods provided some evidence for structuring within some of these initial population centers. The units used in the analyses were defined on the basis of where samples had been acquired, and on the telemetry data suggesting a 50km radius for harbor seal foraging excursions. Sample size and the likely proportion of diversity accounted for by the sample (estimated as a measure they term ' n_a ' with an arbitrary cutoff of 4), were taken into account in the definition of units, and this led to the omission of 226 samples for the final designation of 16 units. The sample sizes represented by these units ranged from 16 to 87. As indicated above, samples as small as 16 are likely to be affected by problems associated with sampling error and the distortion of allele frequencies. This in turn could lead to errors in the construction of the dendograms (since this is dependent on the relative magnitude of χ^2 /d.o.f. values, which are highly dependent on allele frequency). A trial to test this was undertaken during the site visit, whereby units defined by larger sample sizes ($N > 50$) were re-sampled for 20 individuals at random. This changed the structure of the resulting dendogram. The omission of poorly sampled regions resulted in the omission of samples from the Aleutians and from the Yakutat, Icy Bay region. Some preliminary analyses undertaken during the site visit suggested the possible inclusion of Aleutian samples together in a stock with the Pribilof Islands, though the resolution of this will require further sampling and analysis.

The constrained clustering method (Boundary Rank) identified substructure within the Kodiak Archipelago and Southeast Alaska, partially supported by the other clustering methods. No substructure was supported within the Prince William Sound sample. Putative populations defined by the clustering methods were compared using

F_{ST} and Φ_{ST} during the site visit. Some of the comparisons within the Kodiak and Southeast Alaska regions were significant, explaining up to 3% (F_{ST}) or 11% (Φ_{ST}) of the variance (for the comparison between Ketchikan and Glacier Bay in Southeast Alaska). These data provided some support for a southern and a western stock within the Kodiak system, and up to four stocks in Southeast Alaska (an inland region from Ketchikan to Frederick Sound, Grand Island, Sitka and Glacier Bay). Not all of these were supported by both statistics. Among all comparisons, the strongest support was for the differentiation of Bristol Bay and the Pribilof Islands from each other, and from the rest of the regions.

Migration rate was estimated using MIGRATE (Beerli & Felsenstein 2001) for three selected putative population pairs. The highest rate was found between Frederick Sound and Ketchikan (up to 34 migrants per generation, or 4.25 per year, assuming a generation time of 8 years). The 95% confidence limits bring this estimate up to as high as 49.6 migrants per generation. Note that these numbers cannot be taken too literally, due to error associated with violation of model assumptions and unknown stochastic effects associated with the evolution of the specific genetic marker. The large number of apparent migrants between Frederick Sound and Ketchikan is consistent with the lack of support for this putative population division based on F_{ST} and Φ_{ST} . Beyond a certain level of gene flow, populations become panmictic. The expectation for equilibrium populations is that panmixia can be maintained with one genetic migrant per generation, while the number is likely to be higher in non-equilibrium systems. However, beyond this point (and the exact number is difficult to determine), any apparent differentiation is likely to be due to sampling effects. Two other comparisons showed migration levels closer to 8 females per generation (1 per year). These were West Kodiak & Kamishak Bay, and Prince William Sound & the Kenai Peninsula. From the initial study comparing population centers, both the minimum spanning network phylogeny and the mismatch distribution (see introduction) suggested the possibility of population expansion (over a timeframe relevant to expansion since the last ice age). This means that the coalescent model's assumption of constant population size is likely violated for this analysis, but it may not greatly affect the outcome.

Review of conclusions

Four main conclusions are presented in the main review document (Administrative report LJ-03-08). The first two state that the current stocks of harbor seals in Alaska are too broadly defined to meet the management objectives of the MMPA, and that further re-appraisal is required. Based on the population genetic markers, I would agree that there are more than three populations that should be managed as separate stocks in this region. This is consistent with data from North Atlantic where a similar geographic range would include at least nine management units for this species. A third conclusion is that the genetic study is limited by sample coverage, and that further samples are needed from the Aleutians, the Alaska Peninsula, the northeastern Gulf of Alaska, parts of Southeast Alaska and the Kodiak Archipelago. This seems to be especially true of the Aleutians, but some further subsampling may help refine population assessment in other regions as well. The final conclusion is that there are multiple small units that should be managed as separate stocks, and that further sampling is unlikely to alter this conclusion. While there are apparently more than the currently designated three stocks, the exact number

and size of stocks is not yet clear. Further sampling should help refine this, but further analyses of the existing samples could also facilitate stock definition (see below).

Recommendations

This study is very focussed on an analysis of fine-scale population structure based on one mtDNA marker and clustering methods for the identification of population structure. In particular, a clustering method is employed that depends on the effective classification of the initial sample-sets to serve as units in the cluster analysis, and on the accuracy of assumptions about the dispersal behavior of harbor seals - specifically that they disperse only among neighboring units. While other populations of harbor seals seem to show dispersal ranges of 300 km or less (Goodman 1998), the possibility of dispersal to more distant populations, as seen in other species, remains. There are other methods, based on the comparison of individuals rather than units, that could facilitate the identification of population boundaries, and help clarify this point. One such method is spatial autocorrelation (e.g. see Cassens et al. 2000). This would be especially useful for assessing suspected structure in contiguous distributions, as suggested above. The Mantel test already undertaken by Westlake and O'Corry-Crowe (2002) is an example of this method, but if applied on a smaller geographic scale and based on the comparison of the genotypes of individuals, it may be possible to more clearly define population boundaries. This can be done using either mtDNA or microsatellite DNA data (and should be done using both).

Likelihood assignment methods are another useful method for the determination of population structure and the identification of migrants using individual genotypes. These methods need to use bi-parentally inherited, independently segregating, co-dominant markers (such as microsatellite DNA), but a large sample-set from relevant geographic regions (especially Southeast Alaska and Kodiak) has already been genotyped for 11 loci. These methods can either help assign individual samples to established populations to help refine the identification of boundaries, or determine population boundaries without any a priori designation. The latter method is based on a Bayesian likelihood approach that tests assignments against equilibrium expectations with respect to linkage and the Hardy-Weinberg rule (STRUCTURE; Pritchard et al. 2000). A high rate of male-mediated dispersal or low resolution (too few markers or too little diversity) can lead to the failure to detect structure by this method. However, data from the North Atlantic suggests that males and females show similar dispersal range, and 11 loci should be sufficient to provide good resolution.

I would, therefore recommend that each of these methods (spatial autocorrelation, assignment tests and STRUCTURE) be employed on existing data to help assess putative stocks, especially within the Kodiak and Southeast Alaska systems. The inclusion of more genetic markers is also important to avoid biases that may result from the analysis of a single gene, due to stochastic factors affecting the evolution of that gene. In general, given the potential for error in the assumptions on which the constrained clustering method is based, independent corroboration using different methods will help support the case for new stock designations.

In some regions samples were collected over time. The comparison of samples from different time periods could help determine that differences were due to

underlying structure, and not just sampling effects. Therefore, the comparison of sample-sets from different time periods should be undertaken, where possible.

I would also concur with the already expressed conclusion that further sampling is required for some regions. This should especially include the Aleutians, where existing sample sizes are small and geographically dispersed. Having said this, some methods require relatively few samples to adequately define a population (such as the coalescent method used in MIGRATE), and in most cases the inclusion of more loci is more important to the effective definition of populations than the inclusion of more samples. Further analysis using MIGRATE with existing samples could therefore help, both to assess migration patterns and to test the consistency of the program as applied to these populations (especially given possible violations of model assumptions). However, one simple way to increase statistical power for comparisons based on allele frequency is to increase sample size, so from this perspective, larger samples sizes will also be useful in regions where substructure is suspected, such as Kodiak and Southeast Alaska.

Final interpretation of results should incorporate a comparative analysis in the context of previous population genetic studies for this species. While most of the relevant studies are cited in the report, they are mentioned only briefly, and none of the details of the findings are comparatively assessed to facilitate interpretation of the Alaskan study. A comparative assessment would help support the proposal of finer stock division, as this proposal is consistent with findings for harbor seals in other parts of the world.

Implications

This study suggests that a re-appraisal of harbor seal stock structure in Alaska is needed, and it provides some of the data that should form an essential part of that re-appraisal. It is expected that new stock subdivisions will be recognised on a finer geographic scale than the current stock divisions, and that further analysis of existing data, together with the inclusion of some further samples from poorly sampled regions, will be required to define these new stock boundaries. It is also expected that an integration of genetic and non-genetic indicators of population structure will facilitate the definition of these new stocks. The final number is likely to include at least the Pribilof Islands, Bristol Bay, the Kodiak region, Prince William Sound, and Southeast Alaska as separate stocks, with further subdivision within the Kodiak and Southeast Alaska regions possible, as well as the possible addition of more stocks following further analysis from regions such as the Aleutians and Yakutat Bay. The location of boundaries will require further refinement, especially in regions such as Yakutat and the Kenai Peninsula.

References

- Beerli, P. & Felsenstein, J. 2001. Maximum likelihood estimation of a migration matrix and effective population sizes in n subpopulations by using a coalescent approach. *PNAS* 98:4563-4568.
- Burg, T.M., Trites, A.W. & Smith, M.J. 1999. Mitochondrial and microsatellite DNA analysis of harbor seal population structure in the northeast Pacific Ocean. *Can. J. Zool.* 77:930-943.
- Cassens, I., Tiedemann, R., Suchentrunk, F. & Hartl, G.B. 2000. Mitochondrial DNA variation in the European otter (*Lutra lutra*) and the use of spatial autocorrelation analysis in conservation. *J. Hered.* 91:31-41.
- Frost, K.J., Lowery, L.F. & Ver Hoef, J.M. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Valdez oil spill. *Mar. Mamm. Sci.* 15:494-506.
- Goodman, S.J. 1998. Patterns of extensive genetic differentiation and variation among European harbor seals (*Phoca vitulina*) revealed using microsatellite DNA polymorphisms. *Mol. Biol. Evol.* 15:104-118.
- Lowry, L.F., Frost, K.F., Ver Hoef, J.M. & DeLong, R.A. 2001. Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. *Mar. Mamm. Sci.* 17:835-861.
- Martien, K. K. & Taylor, B. L. in press. Limitations of hypothesis-testing in defining management units for continuously distributed species. *Journal of Cetacean Research and Management*.
- Pritchard, J.K., Stephens, M. & Donnelly, P. 2000. Inference of population structure using multilocus genotype data. *Genetics* 155:945-959.
- Rogers, A.R. & Harpending, H. 1992. Population growth makes waves in the distribution of pairwise genetic differences. *Mol. Biol. Evol.* 9:552-569.
- Small, R.J. & DeMaster, D.P. 1995. Alaskan mammal stock assessment, 1995. US Dept. Commer., NOAA Tech. Memo. NMFS-AFSC-57, 93pp.
- Small, R.J., Pendleton, G.W. & Pitcher, K.W. 2003. Trends in abundance of Alaska harbor seals, 1983-2001. *Mar. Mamm. Sci.* 19:344-362
- Stanley, H.F., Casey, S., Carnahan, J.M., Goodman, S. J., Harwood, J. & Wayne, R.K. 1996. Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (*Phoca vitulina*). *Mol. Biol. Evol.* 13:369-382.
- Westlake, R. L., & O'Corry-Crowe, G.M. 2002. Macrogeographic structure and patterns of genetic diversity in harbor seals (*Phoca vitulina*) from Alaska to Japan. *J. Mamm.* 83: 1111-1126.

Wright, S. 1951. The genetical structure of populations. *Ann. Eugen.* 15:323-353.

Appendix 1: Statement of Work

Consulting Agreement between the University of Miami and Dr. A. Rus Hoelzel

Background

In the 1995 Alaska Marine Mammal Stock Assessment Reports, the National Marine Fisheries Service (NMFS) defined three stocks of harbor seal in Alaska, based primarily on broad-scale geographic differences in trends in abundance. NMFS, however, recognized that considerable uncertainty about Alaskan harbor seal stock structure remained and in the fall of 1994 initiated genetic studies of harbor seal stock structure in Alaska. The report resulting from these studies, “The Analysis of Population Genetic Structure in Alaskan Harbor Seals, *Phoca vitulina*, as a Framework for the Identification of Management Stocks,” is the subject of this review.

The format of this review will include an interactive panel to ensure a thorough presentation of the science as well as the management context. Further, the best way to obtain review and scientific recommendations from the panel is to establish a process that allows reviewers with different expertise both to interact with one another and to interact with the scientists responsible for the research being reviewed. These interactive presentations and discussions may require up to two full days of the panel’s time. A third day should be planned for the review panel to provide feedback to the authors and to begin to draft the review. Although this review is for scientific research, the motivation for the research was to provide guidance for resource management. The management context is summarized in the report to be reviewed.

Reviewer Responsibilities

Expertise needed to review this analysis will include the following expertise: (1) knowledge of harbor seal biology, especially expertise in behavior and movements; (2) knowledge of population genetics, including statistical analysis of genetic data to detect/delineate population structure; (3) knowledge of conservation genetics including the different uses of mitochondrial and nuclear DNA in a conservation context; and (4) general knowledge of marine-mammal biology, bearing on population structure including basic population dynamics and an understanding of metapopulation dynamics.

Documents supplied to the consultant shall consist of draft manuscripts and a number of background papers (relevant publications and reports). The consultant shall become familiar with the ten references (see Appendix I), focusing on references 1, 3, and 10. Reference 10 provides the details needed to address the novel method referred to in Task 3B, described below. The consultant’s duties shall not exceed a maximum total of three weeks, including one week to read all relevant documents, three days to attend a meeting with scientists at the NMFS La Jolla Laboratory, in San Diego, California, and several days to produce individual written reports comprised of the consultant’s comments and recommendations. It is expected that the consultant’s report shall reflect that his/her area(s) of expertise; therefore, no consensus opinion (or report) will be required.

Specific Reviewer Tasks and Schedule

1. Read and become familiar with the relevant documents provided in advance of the panel meeting.

2. Discuss relevant documents with scientists at the NMFS La Jolla Laboratory, in San Diego, CA, for three days, March 16-18, 2004.

3. Specifically address the following points (at a minimum):

A) Genetic samples and data:

Were the methods of selecting, collecting, and handling samples adequate relative to the conclusions drawn?

Were limitations of the sampling scheme and data adequately acknowledged and considered?

B) Analytical methods:

Were the laboratory analyses appropriate and applied correctly?

Were the statistical analyses appropriate and applied correctly?

Were the novel methods used in the study developed and tested in a scientifically sound manner?

C) Discussion and interpretation of other studies:

Was the interpretation of other, non-genetic evidence relevant to harbor seal population structure logical and appropriate?

D) Conclusions:

Were the conclusions sound and derived logically from the results? Specifically, are the twelve population units described in the report consistent with the definition of stocks, as provided in the Marine Mammal Protection Act (MMPA) and as implemented by NMFS (see reference 4, Wade and Angliss, 1997)?

4. Address the primary conclusions as stated in the executive summary of reference 1. Specifically, state whether each of the following conclusions is scientifically sound, and provide justifications for each of their assessments.

A) These findings indicate that current stocks of harbor seals in Alaska are too broadly defined to meet the management objectives of the MMPA of maintaining population stocks as functioning elements of their ecosystem.

B) These findings also provide a framework for the identification of more meaningful management stocks and highlight the need for a re-appraisal of other information of relevance to stock structure including the interpretation of information on distribution, movement patterns, trends in abundance and foraging ecology as well as the incorporation of traditional ecological knowledge.

C) The genetic study is still limited by sample coverage. Substantial gaps exist in areas of high conservation concern (see the non-circled areas in Figure ES-3), including the Aleutian Islands, the Alaska Peninsula, the northeastern Gulf of Alaska

and parts of Southeast Alaska and the Kodiak Archipelago. Active collaboration with Alaska Native subsistence hunters and directed sampling is necessary if these important areas are to be sampled.

D) Although further sampling is needed to refine stock boundaries, the conclusion that there are multiple small units that need to be managed as separate stocks is not likely to change.

5. No later than April 1, 2004, submit a written report of findings, analysis, and conclusions (see Annex 1). The report should be addressed to the University of Miami Independent System for Peer Reviews, and sent to David Die, UM/RSMAS, 4600 via email to ddie@rsmas.miami.edu, and to Mr. Manoj Shivlani via email to mshivlani@rsmas.miami.edu.

Appendix 2: Reference Material

1. O'Corry-Crowe, G. M., K. K. Martien, and B. L. Taylor. 2003. The analysis of population genetic structure in Alaskan harbor seals, *Phoca vitulina*, as a framework for the identification of management stocks. Administrative Report LJ-03-08. Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA, 92037.
2. The Marine Mammal Protection Act (MMPA; specifically Sections 2 [findings and declaration of policy], 3(11) [definition of population stock], and 117 [stock assessments]).
3. Taylor, B.L. 1997. Defining populations to meet management objectives for marine mammals. pp. 49-65 in Molecular Genetics of Marine Mammals (A.E. Dizon, S.J. Chivers, and W.F. Perrin, eds.) Special Publication 3. Society of Marine Mammalogy, Lawrence, Kansas.
4. NMFS' guidelines for identifying population stocks (Wade, P.R., and R.A. Angliss. 1997. Report of the GAMMS Workshop, April 3-5, Seattle, Washington. NOAA Technical Memorandum NMFS-OPR-12. National Marine Fisheries Service, Office of Protected Resources, Silver Spring, MD. 69 pp.).
5. ANHSC and NMFS. 1999. Agreement between the Alaska Native Harbor Seal Commission and the National Marine Fisheries Service, for conservation and management of harbor seals. 12 pp.
6. Westlake, R. L., and G.M. O'Corry-Crowe. 2002. Macrogeographic structure and patterns of genetic diversity in harbor seals (*Phoca vitulina*) from Alaska to Japan. *Journal of Mammalogy* 83(4): 1111-1126.
7. Federal Register notice 67[165]:54792-54794.
8. Martien, K. K., and B. L. Taylor. 2003. Limitations of hypothesis-testing in defining management units for continuously distributed species. *Journal of Cetacean Research and Management*.
9. Taylor, B. L. 2003. Determining Units to Conserve. Unpublished manuscript presented at the Marine Mammal Commission Workshop on Future Directions in Marine Mammal Research, August, 2003, Portland, OR.
10. Martien, K. K., A. B. Sellas, P. E. Rosel, B. L. Taylor, and R. S. Wells. Submitted. Defining management units in Gulf of Mexico bottlenose dolphins in the absence of long-term observational data.