Guidelines for determination of spatial management units for exploited populations in Alaskan groundfish fishery management plans

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EXECUTIVE SUMMARY

The process of defining a "stock" can be considered the first step of a stock assessment. However, there is not a consistent set of criteria for the definition of what represents a fish stock, nor what management goals should be achieved by our definitions of fish stocks. Additionally, the Scientific and Statistical Committee and Groundfish Plan Teams of the North Pacific Fishery Management Council (NPFMC)and National Marine Fisheries Service -Alaska Fisheries Science Center stock assessment scientists typically have limited expertise in interpreting genetic data that is often used to infer stock structure. These two factors have the potential to lead to inconsistencies between species in data interpretation and definitions of stock structure. The objectives of this report are to consider the management goals to be achieved when defining spatial management units, develop some guidelines for interpreting genetic and non-genetic data, propose a framework for synthesizing and evaluating scientific information and apply it some Alaskan examples, and propose a process for determining spatial management units for populations managed by the NPFMC.

Management objectives

The definition of a stock is dependent upon management goals, and thus stock definitions under the Endangered Species Act (ESA), with its emphasis on conserving genetic variability, differ from stock definitions under the Magnuson-Stevens Fishery Management and Conservation Act (MSA), which emphasize maximizing sustainable yield and prevention of overfishing. Given the primary emphasis on sustainable yield in the MSA, a stock definition that focuses on demographically independent units on time scales relevant to fisheries management seems most appropriate. However, spatial structure may exist within a demographically independent stock, and recent studies have recommended the conservation of genetic diversity as a fishery management goal. Although no objectives have been established by the NPFMC or the MSA for conserving genetic diversity, such objectives could potentially lead to implementation of management measures that are designed to avoid local depletion and also, by maintaining the spatial pattern of the stock recruitment and production, meet the MSA objectives of achieving maximum sustained yield and avoiding overfishing.

Given the primary emphasis on sustainable yield in the MSA, a stock definition that reflects the ecological paradigm and focuses on the demographic independence on time scales relevant to fisheries management seems most appropriate. This view is emphasized by the requirement to rebuild overfished stocks within an ecological time scale (e.g. either ten years or one generation plus ten years). In most cases, stocks defined as demographically independent populations will occupy non-overlapping spatial areas, though annually-migrating stocks that mix on feeding grounds are important exceptions, and some overlap may be expected for adjacent stocks. Stocks that are demographically independent do not have significant exchange of either recruits or adults. Mature individuals within a demographically independent population are equally likely to produce offspring that recruit to the same population. Similarity in life history characteristics, such as growth and maturation, is another characteristic of a demographically independent population.

Several measures have been taken both at the national and regional levels to implement precautionary catch limits, including establishing maximum sustainable yield (MSY) as an upper bound to harvest and a reduction in harvest rates for stocks with increased uncertainty. Because of the essential link between identification of management units and determination of harvest quotas, a precautionary approach for managing harvest could be undermined by incorrect stock structure assumptions if the realized harvest rate for a fished stock is larger than would be recommended based upon its stock size. Thus, a precautionary approach to identifying stock structure should not be seen as a layer of precaution "additional" to that developed for harvest control rules, but rather a necessary component to ensure an effective and consistent application of the precautionary approach.

Guidelines for interpreting genetic and non-genetic data

Genetic data can provide a window to demographic processes that may not be readily measurable in other ways, although it is often not well integrated into fishery management plans or the process of determining stocks. One reason for this is that large populations become homogenized at very low levels of gene flow so that demographically independent stocks may not be detectable by genetic methods even if they exist. For scientists without specialized training in genetics, it can be difficult to understand such data and its implications for stock structure. Despite these limitations and challenges, the consensus emerging from a mounting body of evidence is that many marine species exhibit detectable genetic population structure, which indicates that breeding populations are localized and dispersal is limited at all life history stages. Some important considerations for obtaining and interpreting genetic data are: 1) inclusion of temporal replication at sample locations; 2) consistency of results from several loci and/or types of genetic markers (i.e., mitochondrial DNA, allozymes, and microsatellites); 3) recognition that an isolation by distance (IBD; genetic similarity decreases as geographic distance increases) pattern is clear evidence for restricted gene flow in continuously distributed species; and 4) genetic information for high-latitude species are likely to reflect ice-age effects and isolation.

In cases with an IBD pattern where obvious geographic breakpoints at which to define management boundaries do not occur, it is important to note that the lack of an obvious breakpoint is not synonymous with a lack of stock structure. In these cases, the nature of the structure of continuously distributed species requires only that management areas be of the same spatial scale as the genetic structure. This provides some flexibility in locating management units – the boundaries could coincide with geographical features, but could also reflect boundaries that are convenient for a given assessment and management system.

The limitations of genetic information have led to calls for integrating the analysis of genetic information with other lines of evidence. The types of non-genetic data that pertains to stock structure includes physical barriers or transition zones, life-history characteristics (growth, maturity, etc.), age and size compositions, trends in population abundance, morphometric and meristic data, mark-recapture data, and "natural" tags such as otolith microchemistry and parasites.

Three Case Studies - Example Applications

In this report, three species or species complexes (BSAI blackspotted/rougheye rockfish, Atka mackerel, and Pacific cod) were considered because they illustrate the issues and challenges associated with defining stock boundaries in large marine ecosystems. They illustrate the importance of using multiple sources of data to make inferences on stock boundaries.

Prior to 2004, the BSAI blackspotted/rougheye rockfish complex was managed as part of larger multi-species rockfish complexes, with separate harvest quotas for the AI and BS subareas. The movement from management with multi-species complexes to single-species management coincided with combining the BS and AI areas into a single management unit, in part due to small rockfish populations and small harvest quotas which would occur in the BS subarea (the genetic data did not exist at the time of this decision) (NPFMC 2000). Distribution patterns showed marked differences by species and genetic data provided evidence for partitioning the species and further partitioning stocks. Genetic data for BSAI blackspotted rockfish revealed an IBD pattern that indicates that the movement of fish from birth to reproduction occurs at a much smaller scale than the geographic scale of the BSAI management area. Interpretation of non-genetic data by species is complicated by the difficultly of parsing the historical data for the two-species blackspotted/rougheye complex into the component species.

The NPFMC currently manages Pacific cod as a single stock. Size at age differs between the EBS and AI, and a genetic study using 11 microsatellite loci found significant differentiation among sample pairs, including a comparison between the eastern Bering Sea and Aleutian Islands, and a clear IBD pattern in the northeast Pacific Ocean. In lieu of this new evidence the Plan Team and SSC have recommended separate ABCs for the BS and AI areas. The NPFMC has not acted upon the PT and SSC advice because of issues related to distributing harvest allocation across gear groups that have not been resolved.

For Atka mackerel, separate ABCs by areas were enacted in the mid-1990s in response to disproportionate harvesting within the AI subareas. BSAI Atka mackerel provide an example where the phenotypic data and genotypic data provide contrasting views on stock structure. Length at age increases from west to east along the Aleutian Islands archipelago. However, both microsatellite and mitochondrial DNA (mtDNA) do not reflect genetic differences between areas, although the genetic diversity for the microsatellite data was larger than that observed for mtDNA. The strong contrast between microsatellite and mtDNA diversities may be due to stronger effects of population bottlenecks, post-glacial colonization patterns, or natural selection on mtDNA than for nuclear genes. Given the potentially large effective sizes of contemporary populations, the number of generations since post-Pleistocene colonization of the Aleutian Islands archipelago is likely insufficient for significant divergence to arise through genetic drift. Thus, neutral genetic markers may be of little value for resolving putative stocks of Atka mackerel.

A process for determining spatial management units

We recommend allocating the Acceptable Biological Catch (ABC) across sets of INPFC areas within the BSAI and GOA management areas as a precautionary measure even in the absence of specific scientific information. This approach is consistent with the Council's objective of applying a precautionary approach to fisheries management, and most species in the North Pacific are currently managed in this way. Within the BSAI management region, these areas have typically been the western, central, and eastern Aleutian Islands, and the Bering Sea subarea. Within the GOA management region, these areas have typically been sub-GOA combinations of the INPFC areas 610-650.

More intensive management measures (separate OFLs by area, or defining separate stocks with separate assessments and status determination criteria, etc.) could be evaluated with the following steps:

1) *Identification of priorities for stock structure evaluation.* This would occur at the September Plan Team meeting either by having the Plan Team identify species of high concern, or by developing a schedule by which stock structure is evaluated for all stocks.

2) *Production of a stand-alone stock structure evaluation report.* This report would be generated by the lead assessment author in collaboration with those with expertise in genetics, population connectivity, fishery economics, etc. The report will consist of two components:

   a) a review of available scientific information using the template provided in this report;

   b) a qualitative or quantitative evaluation of the risks (biological and fishery) under alternative hypotheses regarding stock structure.

3) *Review of the recommendations from the stock structure evaluation report.* This would be performed by the Plan Teams (or a separate review body, perhaps as a formal NPFMC committee) and SSC.

A variety of spatial management tools are currently used to address stock structure issues. Partitioning ABC by area is especially effective for target stocks as it limits retention once the ABC level is reached and would reduce the probability of local depletion. For nontarget species, additional steps such as lowering the maximum retention allowance (MRA) and placing the stock on bycatch status could be employed. Finally, even if fishing needs to be restricted to limit harvest of bycatch stocks, the NMFS In-Season Management Program routinely restricts fishing in only areas of high bycatch instead of the entire fishing grounds, thus reducing the burden on the fishing fleet.

It is important to recognize that management can be split by area even if the assessment and data are not split by area. In cases where doing area-specific assessments would lead to limited and poor quality data, an area-wide assessment can be conducted with harvest quotas apportioned across areas. As mentioned above, ABCs and harvest quotas are typically apportioned across areas, and OFL could be apportioned if

there is a higher risk to stock sustainability. The ultimate goal is to craft management measures that reflect both the level of risk and uncertainty of the information.

1.0 INTRODUCTION

The North Pacific Fishery Management Council's (Council) Groundfish Plan Teams and Scientific and Statistical Committee (SSC) recently considered the appropriate spatial management units for several groundfish species, including blackspotted/rougheye rockfishes and Pacific cod in the Bering Sea/Aleutian Islands. These discussions pertain to defining the "stocks" for which stock assessment models are applied and status determination criteria are developed. Despite the clear importance of this task, there has not been a consistent set of criteria for the definition of what represents a fish stock, nor what management goals should be achieved by our definitions of a fish stock.

The stock concept in fisheries dates back to the 19th century, when Heincke (1898) demonstrated that Atlantic herring were composed of self-sustaining populations; this concept was later generalized to other species by Hjort (1914) (see Sinclair 1988 for a review). A variety of definitions for a stock have been proposed since the work of Heinke and Hjort. For example, Booke (1981) defined a stock as "a species group, or population, of fish that maintains and sustains itself over time in a definable area", and Ihssen et al. (1981) proposed that a stock is " . . . an intraspecific group of randomly mating individuals with temporal or spatial integrity". However, these (and other) definitions have not provided unambiguous management advice; for example, terms such as "maintains and sustains", "randomly mating", or "temporal and spatial integrity" are not defined and their meanings likely differ between scientists.

The definition of a stock differs between three major conservation acts in the U.S., the Magnuson-Stevens Fishery Management and Conservation Act (MSA), the Endangered Species Act (ESA), and the Marine Mammal Protection Act (MMPA), and reflects the dependence of a stock definition upon management goals. A NMFS workshop was convened in 2006 to examine the consistency of stock definitions between populations managed under these conservation acts (Eagle et al. 2008). Although guidance on managing stocks is provided in National Standard 3 (NS3) of the MSA, Eagle et al. (2008) found this guidance did not provide sufficient clarity to meet other portions of the MSA due, in part, to a lack of definition of a "stock" and its potential confusion with a "fishery" and "management unit" (which is not referred to in the MSA, but is in the NS3 guidelines).

Apart from the management goals to be considered in defining fishery stocks, the interpretation of data is often problematic for the typical stock assessment scientist or fisheries manager (Waples et al. 2008). Genetic data are often used to infer stock structure, and new types of data are becoming available in this rapidly developing field. For scientists without specialized training in genetics, it can be difficult to understand such data and its implications for stock structure. Even commonly used genetic measures, such as F_{ST} (the proportion of total genetic variation that is attributable to differences between populations), may not be fully appreciated by non-geneticists. For example, non-geneticists may not recognize the factors that can affect F_{ST} for marine fish, including population connectivity, population size, and population history (Hauser and Carvalho 2008), and their implications for inferring stock structure. Despite the existence of textbooks (e.g. Cadrin et al. 2005) and special issues in peer-reviewed journals (e.g. Hauser et al. 2008) on stock identification and incorporation of genetic data in fisheries management, consistent and clear guidance for identifying stocks has not been developed within the Alaska region or nationally.

This report develops basic guidelines for defining stock structure. The role of stock structure in meeting national and regional management objectives is discussed in Section 2.0, and in particular we address how the precautionary approach could be applied when limited data are available to identify stocks. In Section 3, we consider how some common types of genetic measurements, such as F_{ST}, are influenced by marine environments for large fish populations, and how to reasonably interpret these measures with

respect to inferring stock structure. In Section 4, we discuss how several other types of data, such as meristics, morphometrics, life-history parameters, migration studies, ecological discontinuities can be used in combination with genetics to infer stock structure. A proposed format for evaluating numerous types of data on stock structure is presented in Section 5. We apply this format to stocks of interest in Section 6, and propose a process for determination of spatial management units in Section 7. Some final conclusions are presented in Section 8.

2.0 MANAGEMENT OBJECTIVESS

Objectives for managing North Pacific fisheries resources are derived from the MSA. National Standard 1 states that *"Conservation and management measures shall prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery for the United States fishing industry."* National Standard 3 pertains specifically to the issue of stock structure: *"To the extent practicable, an individual stock of fish shall be managed as a unit throughout its range, and interrelated stocks of fish shall be managed as a unit or in close coordination."* National Standard 3 supports National Standard 1, because unless management measures are applied on a stock-by-stock basis, National Standard 1 would not necessarily be achieved. For example, if two stocks with differing productivities are assessed and managed together over a period of time, the stock with lower productivity would more likely become overfished. Additionally, if disproportionate harvesting of one stock occurred because the two stocks are managed as a single unit, it is less likely that the fish depleted in one area would be replenished from nearby areas. Identifying stock structure in managed resources therefore should be regarded as an important initial step in stock assessment and development of fishery management measures.

As noted above, the definition of a stock may vary with respect to management goals and views on populations. Two contrasting paradigms with which to view populations are 1) evolutionary and 2) ecological (Andrewartha and Birch 1954, Waples and Gaggiotti 2006). The evolutionary paradigm views populations as groups of interbreeding individuals within a species that transfer genetic material between generations. In contrast, the ecological paradigm defines populations with respect to the demographic interactions between co-occurring individuals (Waples et al. 2008). Because the ESA aims to conserve genetic variability, the evolutionary paradigm and a focus on reproductive isolation is a major consideration in stock definition. In contrast, because the MMPA and the MSA aim to, respectively, maintain stocks at an optimal level or ensure maximum sustainable yields, the definition of stocks have commonly focused the ecological paradigm and the demographic linkages between areas (Eagle et al. 2008).

Given the primary emphasis on sustainable yield in the MSA, a stock definition that reflects the ecological paradigm and focuses on the demographic independence on time scales relevant to fisheries management seems most appropriate. This view is emphasized by the requirement to rebuild overfished stocks within an ecological time scale (either ten years or one generation plus ten years). In most cases, stocks defined as demographically independent populations will be assessed and managed as occupying non-overlapping spatial areas, although annually-migrating stocks that mix on feeding grounds are important exceptions, and some overlap may be expected for adjacent stocks. Stocks that are demographically independent do not have significant exchange of either recruits or adults. Mature individuals within a demographically independent population are equally likely to produce offspring that recruit to the same population.   Similarity in life history characteristics, such as growth and maturation, is another characteristic of a demographically independent population.

This view of stocks as demographically independent forms the basis for MSA conservation and management objectives, although spatial structure can exist within a demographic stock. First, adaptive divergence can occur within demographically independent populations despite gene flow. Hauser and Carvalho (2008) demonstrate that local adaptation of Atlantic cod can occur at much smaller spatial scales than previously imagined, and argue that conservation of genetic resources is a worthwhile fisheries management goal. This view is also echoed by Conover et al. (2006), who summarize research

indicating that selection pressure may be a force that maintains adaptive variation in marine environments despite gene flow, and argue that the spatial scale of selection gradients should be considered. Second, the productivity of the stock may depend on maintaining the stock's spatial distribution. Population level stock-recruit relationships are assembled from local spawning aggregations and spatially-patchy recruitment. Some spawning aggregations may be sources that contribute disproportionately to recruitment, while others may be sinks whose reproductive output is lost to the population (Turner et al. 2002).

Although no objectives have been established by the North Pacific Council or the MSA for conserving genetic diversity, such objectives could help to achieve the broad objectives for sustainability of fisheries resources and associated ecosystems. In general, genetic diversity would be expected to allow a species to more readily adapt to varying environmental conditions, although exceptions can exist for loci under strong selection pressure. Several examples exist that document the loss of genetic diversity for commercially harvested stocks, including New Zealand snapper (Hauser et al. 2002) and North Sea cod (Hutchinson et al. 2003). An objective to maintain within-stock genetic diversity could potentially lead to implementation of management measures that are designed to avoid local depletion and also, by maintaining the spatial pattern of the stock recruitment and production, meet the MSA objectives of achieving maximum sustained yield and avoiding overfishing.

2.1 Application of the precautionary approach when determining spatial management units

Modern development of the precautionary principle can be traced to the German "Vorsorgeprinzip" (which translates into "precaution principle") movement in the early 1980s concerning the environmental effects of pollution (Garcia 1994). The precautionary "principle", a hard-line rule that avoids making irreversible mistakes, can be distinguished from the precautionary "approach", which is a more flexible set of practical measures that can achieve precaution (Garcia 1994). The precautionary approach is applicable to marine fisheries management because the effects of management actions are generally thought to be reversible (Mace and Gabriel 1999). Numerous formulations of the precautionary principle have been developed, however a universally accepted comprehensive definition has not emerged. Sandin (1999) identified the following four dimensions of the precautionary principle: 1) recognition of a potential threat (an undesired possible state) that is under anthropogenic control and thus preventable; 2) some uncertainty regarding the threat; 3) a course of action to respond to the threat; and 4) the status of the action (i.e., whether an action is allowed, recommended, or required). In a fisheries context, the FAO Code for Conduct for Responsible Fisheries declared that "*the absence of adequate scientific information should not be used as a reason for postponing or failing to take measures to conserve target species, associated or dependent species and non-target species and their environment*" (FAO 1995). In essence, the precautionary approach requires restraint of human activities when the deleterious effects of such actions upon the resource are uncertain.

In the U.S., fisheries policies at national and regional levels have been developed to implement the precautionary approach. At a national level, the Sustainable Fisheries Act (SFA) requires management actions that are consistent with a precautionary approach, particularly in the establishment of maximum sustainable yield (MSY) as an upper bound to harvest (Darcy and Matlock 1999). The Magnuson-Stevens Reauthorization Act of 2007 requires implementation of annual catch limits and accountability measures (DiCosimo et al., in press). At a regional level, the NPFMC has a strong commitment to the precautionary approach. As a result of the 2004 Programmatic Supplemental Environmental Impact Statement (PSEIS), the Council adopted Amendment 74 of the Gulf of Alaska (GOA) Groundfish Fishery Management Plan (FMP) and Amendment 81 of the Bering Sea and Aleutian Islands (BSAI) Groundfish FMP, which, in part, states: "*The Council's precautionary approach applies judicious and responsible fisheries management practices, based on sound scientific research and analysis, proactively rather than reactively, to ensure the sustainability of fishery resources and associated ecosystems for the*

benefit of future and current generations." Several steps have been taken by the Council to ensure precautionary harvest policies, including separating catch targets from catch limits, reduction in harvest rates for depleted stocks, and reduction of target harvest rates with increased uncertainty (Thompson 1996).

Because of the essential link between identification of management units and determination of harvest quotas, a precautionary approach could be undermined by incorrect stock structure assumptions. For example, consider the case of two demographically independent stocks that are managed with a single harvest quota. A harvest quota that was appropriate for the population size equal to the sum of the two stocks could be too high if applied to only one of the two stocks, as the loss from fishing would not be replenished from movement from the other stock. The realized harvest rate experienced by the fished stock could be higher than would be recommended based upon its stock size, and may result in a reduction in biomass. In this manner, application of precaution to harvest control rules but not to decisions regarding stock structure could potentially result in unsustainable and non-precautionary harvest rates upon the fished stock due to a spatial allocation of harvest that is not proportionate to biomass. Thus, a precautionary approach to identifying stock structure should not be seen as layer of precaution "additional" to that developed for harvest control rules, but rather a necessary component to ensure an effective and consistent application of the precautionary approach.

The precautionary principle pertains to risk analysis, or the process of making decisions under uncertainty (Sandin 1999). Thus, it is useful to examine the types of outcomes that can occur under various management actions, as shown in Fig. 1. A simple categorization of potential states of nature is that the stock either is panmictic or is not panmictic. A simple set of management actions would be to manage the population in question as either a single stock or as multiple stocks. Two types of incorrect decisions that can occur are the "lumping" of multiple stocks into single management unit (spatial scale too large), or the "splitting" of a single stock into separate management units (spatial scale too small). The errors associated with incorrect "lumping" are described above, and could result in unsustainable harvest rates and the potential for overfishing. However, errors also are associated with incorrectly splitting a stock. Incorrectly splitting a stock could result in unnecessarily small quotas that reduce benefits from the fishery. The stock assessment models are likely to be inaccurate because movement (immigration and emigration) is generally assumed to be negligible but in fact could play a major role in the dynamics of population units smaller than a demographically independent stock. A recent example is Pacific halibut, which for many years was managed with separate area assessments but are now considered to be a single stock across the North Pacific. Additionally, data may become more limited on a finer spatial scale, decreasing the amount and precision of data available for assessments and potentially leading to errors in estimated harvest quotas. A simple example for Gulf of Alaska pollock can help illustrate this effect. The coefficient of variation (CV) for pollock biomass on a Gulf-wide basis ranges between 11% and 38%, and average 18%. For pollock biomass by regulatory area, the CVs range between 14% and 68%, and average 27%. The impact of incorrectly splitting a stock would be heightened if the extent of precautionary reductions to harvest quotas is a function of the estimated uncertainty.

A precautionary approach applied to decisions regarding stock structure requires careful consideration of the level of conservation that results from the types of outcomes shown Fig. 1. As with the harvest control rules, when information on stock structure is uncertain it is expected that a precautionary approach would apply a greater level of conservation. Note that because the errors would not be expected to be similar in magnitude, some weighting of the type of errors is necessary. For example, as described above, incorrectly lumping of separate stocks could lead to overfishing of stocks if the spatial allocation of harvest is not proportional to biomass. In contrast, incorrectly splitting of a single stock could lead to incorrect harvest allocations at management units smaller than a stock, which may be characterized as the potential for localized depletion rather than overfishing. Additionally, the issue of reduced precaution with lower precision and quality of data could be addressed with a management system that increases the level of precaution for data-poor stocks.

The weighting of the relative risks will require careful evaluation for each individual case. However, on balance, it appears that the risk to the resource of incorrectly lumping of multiple stocks is greater than that of incorrectly splitting a single stock. In practice, in many cases the evaluation of stock structure considers a null hypothesis of a single panmictic stock, and the task is to ascertain if enough evidence exists to reject this null hypothesis (Taylor and Dizon 1999, Waples et al. 2008). In an hypothesis testing framework, the off-diagonal elements in Figure 1 can be considered as the risk of rejecting structure when it exists (a type II error) and recognizing structure when it does not exist (a false positive or type I error). Although most scientists are trained to minimize false positives by specifying a low type I error rate, Taylor and Dizon (1999) point out that such an approach can potentially lead to a high type II risk of incorrectly lumping stocks, thus revealing an implicit policy choice inherent in the analysis. Taylor and Dizon (1999) recommend formulating specific, biologically meaningful null and alternative hypotheses that would allow evaluation of the two types of risks. Simulation modeling can potentially be used to evaluate the potential risks associated with designation of spatial management units (Fu and Fanning 2004).

Finally, it is important to note that application of the precautionary approach occurs when making management and policy decisions regarding spatial management units, not in the evaluation of scientific information regarding stock structure. Just as the role of a stock assessment is to provide the most accurate assessment of stock size and productivity, a review of information on stock structure should begin with an interpretation of stock structure that is most consistent with the available data. Evaluation of the risks associated with lumping vs splitting, and the uncertainty of the information available, should be considered after evaluation of the scientific information. The separation between evaluation of the scientific information and evaluation of potential management responses are further considered in Section 8.

3.0 GUIDELINES FOR INTERPRETATION OF GENETIC DATA

Fishery genetics has become increasingly important for identifying the biologically relevant scales for stock conservation and management. Although genetic methods for stock identification have been available for over 60 years (Waples et al. 2008a), much of the effort historically has been directed towards assessment of freshwater-resident and anadromous salmonid species. Marine fishery genetics is a discipline still very much in its infancy and relatively little is known regarding the genetic structure of exploited marine species that can be used in a management context. Similarly, management policies to conserve important genetic diversity in exploited fish populations are just beginning to be developed (Kenchington et al. 2003).

The lack of integration of genetic data into fishery management stems, in part, from the goals of fisheries management largely pertaining to the ecological paradigm whereas population genetics pertains to the evolutionary paradigm (Waples et al. 2008). A fundamental difficulty with reconciling these two approaches is that genetic measures of population differentiation among large populations become homogenized at very low levels of gene flow (number of migrants exchanged). Consequently, demographically independent stocks may not be detectable by genetic methods even if they exist. The result is a strong asymmetry in the power of genetic techniques to identify stocks of interest to management: genetic differentiation may strongly infer separate stocks but a lack of differentiation does not preclude their existence. This unsatisfying reality often is exacerbated further by characteristics of marine populations and environments (e.g., large population sizes and lack of physical barriers to dispersal) that limit spatial resolution of discrete stocks.

Despite these limitations and challenges, the consensus emerging from a mounting body of evidence is that many marine species exhibit detectable genetic population structure, which indicates that breeding populations are localized and dispersal is limited at all life history stages. For those species, recruitment is more localized than previously recognized. Molecular genetics data can now be collected and analyzed faster, easier, and more cheaply than ever before and the results from these studies will be increasingly

utilized to help identify appropriate biological entities to manage as 'stocks'. The purpose of this section is to acquaint those conducting stock assessments with the basic theory, practice, and interpretation of population genetics results as they apply to marine species.

3.1 Evolutionary processes

There are four evolutionary forces largely responsible for the spatial patterns of genetic variation observed within (and between) species: mutation, migration, genetic drift and natural selection. Mutation creates heritable genetic variation in germ line (gamete producing) cells of sexually reproducing species. If the mutation confers no fitness advantage or disadvantage to the individual (in terms of reproductive success), that particular genetic variant (allele) is neutral with respect to natural selection and its frequency (including all descendants) is determined by migration and genetic drift. Collectively, these three forces determine neutral population structure, the spatial distribution of neutral genetic variation among populations.

Mutations that affect the fitness of an organism (e.g., gene function) may be either beneficial or deleterious, and thus influenced by natural selection at some point in the life history. Dominant deleterious alleles usually are eliminated rapidly from populations, since individuals possessing them either fail to reproduce or leave fewer offspring. However, mutations conferring an advantage to the individual in a particular environment may ultimately rise to high frequencies depending upon the strength of selection (mediated by gene interactions such as dominance and epistasis) relative to the effects of migration and genetic drift. All four forces thus come into play, resulting in adaptive genetic divergence among populations. These two processes (neutral versus adaptive divergence) are discussed separately below but should be recognized as occurring simultaneously in natural populations.

3.2 Neutral genetic processes and descriptive statistics

In the absence of gene flow, divergence of neutral gene frequencies among populations will occur by the stochastic process known as genetic drift. Drift results from the random survival of gene copies in finite populations and is inversely related to population size (i.e., small populations drift quickly while large ones do not). Genetic drift is thus a very weak force in large marine populations and its effects are readily overwhelmed by demographically trivial amounts of gene flow via migration (Fig. 2). Neutral genetic theory provides an indirect means to infer the levels of connectivity among populations (via migration and gene flow). Perhaps the most common statistic used to describe the spatial distribution of genetic variation in terms of gene frequencies is the fixation index, or F_{ST} (Wright 1921)), which is calculated for a two allele loci as:

$$F_{ST} = \frac{\sigma_p^2}{p(1-p)} \qquad\qquad (1)$$

where σ_p^2 is the variance in allele frequencies among populations and p is the mean allele frequency at that locus (marker). This ratio estimate, ranging from 0 to 1, may also be described in terms of the migration rate (m) and effective population size (N_e; approximately the numbers of spawners that succeed in producing the subsequent generations):

$$F_{ST} = \frac{1}{4mN_e + 1} \qquad\qquad (2)$$

In an analysis of variance (ANOVA) framework, F_{ST} may be interpreted as the proportion of the variance of allele frequencies among subpopulations (e.g., putative stocks) relative to the total (all stocks combined). In theory, $F_{ST} = 0$ indicates a panmictic population (random mating) whereas $F_{ST} = 1$ indicates two different clonal populations for which all of the genetic variation is among groups and there is no within group variation.

A number of factors contribute to the levels of F_{ST} observed in natural populations, including their size, demographic histories, and levels of connectivity through migration (Fig. 3). An implicit assumption when estimating other population parameters (such as mN_e in equation 2) is that equilibrium between migration and drift has been reached, producing a maximum estimate of F_{ST}. This is unlikely to be the case in many large marine populations, and particularly so for those at high latitudes. The approach to migration-drift equilibrium is inversely related to population size and thus may be very slow in abundant marine species, perhaps several thousand generations (Fig. 4). Most (if not all) commercially exploited marine species in the North Pacific Ocean and Bering Sea have recolonized or expanded in those areas since the end of Pleistocene glaciation (16,000 – 18,000 years BP) and are unlikely to have achieved full equilibrium conditions between migration and drift during that period, especially if their numbers are large and generation times are long. An approximation of the time (t, in generations) to approach halfway to this equilibrium value is

$$t = \frac{\ln 2}{2m + \dfrac{1}{2N_e}} \tag{3}$$

where m is the migration rate (Crow & Akoi 1984). Thus, a population of 1000 fish receiving 5 migrants from another population will be halfway to migration-drift equilibrium in ~ 67 generations. Contemporary estimates of F_{ST} are likely to be biased downward, inflating estimates of migration rates connecting populations. Since managers are likely more interested in identifying isolated populations rather than estimating migration rates, it may be more interesting to consider how long it would take for two populations to become significantly differentiated. In the example presented in Fig. 4, F_{ST} would reach 0.002 (significant with a reasonably powerful approach) after only 5 generations. Therefore genetic approaches may be more powerful than generally assumed for the identification of significant differentiation, but not for the estimation of migration rates.

3.3   *Interpreting temporal and spatial patterns in F_{ST} and other genetic distances*

Temporal variation in genetic data has not been the main focus in most surveys of marine species, but may represent an important component of metapopulation structure and connectivity. Changes in gene frequencies among adults at the same location, or between adults and recruits, have been documented (Planes & Lenfant 2002; Burford & Larson 2007; Vigiola et al. 2007), but the dynamic processes responsible for them are not easily inferred from genetic data alone. Temporal differences can also arise from nonrandom sampling effects. If only a portion of the population is sampled, for example by size-selective gear, some cohorts may be over/under represented relative to the whole population. Similarly, sampling only larvae could introduce sampling bias. The high fecundity and mortality for most marine species creates the potential for 'sweepstakes' recruitment success, where chance matching of favorable environmental conditions with reproduction and larval development enables a small number of spawners to be disproportionately successful in producing the sampled cohort (i.e., a very small N_e). While sweepstakes recruitment has been documented in oysters (Hedgecock 1994; Li and Hedgecock 1998) and in marine fish (Planes and Lenfant 2002), the frequency and severity of this effect on temporal variation in most marine fishes has been examined in only a few fish species (see review in Hauser et al. 2008). One of the most powerful approaches for estimating N_e is the temporal method (Waples 1989), where the observed rate of genetic change (random genetic drift) over time is transformed into an estimate of the effective population size per generation. The most effective and pragmatic approach in many cases is to compare temporal samples over multiple years, especially when historical samples are available (Hauser et al. 2002, Hutchinson et al. 2003, Nielsen and Hansen 2008). If annual differences at the site are not observed, and the magnitude of spatial differentiation with other samples is consistent, one may be more

confident that the genetic signal does have a biological basis and is not sampling artifact. Additional strategies may include sampling discrete cohorts (e.g., young of year) and tests for temporal stability.

Spatial patterns of genetic and geographic distances can be used to infer the relative influences of gene flow (*m*) and genetic drift over various scales (Fig. 5) as well as indications of the influence of sweepstakes effects. When drift and migration exert relatively uniform influences over the sampled range, some degree of regional equilibrium may develop to form a clear isolation-by-distance pattern (Fig. 5A). If migration predominates (Fig. 5B), F_{ST} values will be low throughout the region and show little variance. The resultant genetic panmixia perhaps would infer a single stock throughout, but consideration should be given to where the population may lie on the continuum to migration-drift equilibrium (Fig. 4). If drift is the dominant genetic force (Fig. 5C), then a chaotic pattern of F_{ST} values will result with a higher mean value and variance. This pattern, if temporally stable, suggests that these stocks are largely independent of one another. Finally, migration and drift may affect regional population structure differently, depending upon geographic scale (Fig. 5D).

An important consideration when examining the genetic structure of marine fish species is the signature of historical isolation. A recurrent pattern observed in some widely-distributed species in the North Pacific Ocean is genetically discrete subpopulations occupying eastern and western portions of the range, but relatively broad-scale homogeneity or limited isolation by distance within each region (walleye pollock, Grant & Utter 1980, O'Reilly et al. 2004; Pacific herring, Grant & Utter, 1984; yellowfin sole, Grant et al. 1983; Pacific halibut, Grant et al. 1984; Pacific cod, Grant et al. 1987). A sharp genetic discontinuity was observed between NW Pacific and NE Pacific groups of Pacific cod (Fig. 6A) that likely is due to long periods of isolation during glacial maxima followed by a return of contact during warmer interglacial periods. Another ice-age signal evident in Pacific cod is the isolation of fjord stocks in the Georgia Basin (Fig. 6B); this region was most recently colonized 10,500 – 6,000 years BP, following the last Pleistocene glaciation (~ 18,000 years BP). Clear departures from the isolation-by-distance (IBD) pattern of coastal cod seen in microsatellite results and a distinct regional clade of mitochondrial DNA haplotypes (Canino et al. in press a) clearly inferred demographically independent populations.

In many cases, no clear genetic 'break' will be observed in the monotonic increase of F_{ST} with geographic distance (e.g., Pacific cod from the NE Pacific coast, Cunningham et al. 2009). A definable boundary for management purposes may thus not exist, yet a population with limited dispersal of individuals is clearly not panmictic and subject to local overexploitation. A simple and potentially useful exercise may be to calculate the slope of the least-squares regression of $F_{ST}/1-F_{ST}$ on geographic distance to approximate the variance of the parental position relative to its offspring (σ^2) over a realistic range of population sizes

$$\sigma^2 = \frac{1}{4 D_e b} \qquad (4)$$

where D_e is the effective density (the effective number of individuals (N_e) per linear kilometer), and *b* is the regression slope. This one-dimensional model is a reasonable choice for estimating dispersal when differentiation occurs over spatial scales greater than the habitat width (Rousset 1997), and seems generally appropriate for broadly-distributed species confined to continental margins, particularly for species with sedentary adults. Estimates for three rockfish species (Buonaccorsi et al. 2005) were on the order of 1-40 km per generation for effective adult densities ranging from 10- 10,000 per km. Assuming a normal distribution for (σ^2) and symmetrical dispersal, a crude genetic 'neighborhood' (inclusive of 95% of potential parents) could be approximated as a distance spanning 4σ. An example of this calculation applied to blackspotted rockfish is presented in Section 6.1.

3.4   Genetic marker types, characteristics, power and limits

Nearly all genetic studies of marine fishes to date relied upon at least one of three types of neutral genetic markers: nuclear allozymes, microsatellite loci, and mitochondrial DNA (mtDNA). An important consideration for any genetic marker is that its statistical power is largely determined by the number and diversity of the loci examined. In finite populations, each locus represents an independent realization of the evolutionary forces of migration and genetic drift. Sampling more loci (and individuals) reduces the interlocus variance asymptotically, improving the precision of F_{ST} estimates (Waples 1998).

Allozymes were the initial workhorse of population genetics beginning in the late 1960s (Utter 1969). Enzymatic variation could be readily and cheaply screened, providing the first evidence for population structure in (apparently) homogeneous marine environments. However, the limited number of available loci and their low levels of variability (polymorphism) constrained their power to detect the low levels of differentiation (F_{ST}) characteristic of marine species (e.g., Grant et al. 1987).

Mitochondrial DNA was the first nucleic acid marker used for examining population structure, either by direct DNA sequencing of gene fragments or variation in their length after digestion with specific enzymes. This haploid organellar genome is inherited strictly down maternal lines, resulting in a four-fold reduction in N_e, and thus higher rates of genetic drift. While mtDNA can provide powerful insights into the phylogeography of many marine species (Grant and Bowen 2006), its use as a marker for resolving population structure is limited, primarily because it is inherited as a single locus, leaving no opportunity to sample multiple independent loci.

Microsatellites are the contemporary workhorse of genetic markers for marine fish species. These noncoding nuclear loci consist of tandem arrays of short nucleotide repeats (e.g., $GCTC_{12}$) that are highly polymorphic due to high mutation rates. For example, locus *Gma100* isolated from Pacific cod (Canino et al. 2005) was found to have 101 length variants (alleles) in 818 individuals from across the NE Pacific Ocean (Cunningham et al. 2009). Such high levels of polymorphism provide much greater statistical power (higher number of independent alleles) for microsatellites compared with mtDNA and allozymes for resolving weak population structure and unparalleled precision for conducting studies of parentage or assignment of individuals to populations (Hauser et al. 2006). Empirical results from multiple studies indicate that screening 10 – 15 moderately to highly polymorphic microsatellite loci in 50 – 100 individuals generally gives sufficient precision to detect F_{ST} values at or below the median value (0.02) reported for marine fish (Ward et al. 1994).

The high mutation rates of microsatellites provide abundant genetic variation but may also present challenges to their application and interpretation. Mutations most often involve the addition or deletion of a single repeat unit (stepwise mutational model) but other mutation patterns may be more complex. The first and perhaps more serious is size homoplasy, where mutations to the microsatellite array may create new alleles of identical size (i.e., fragment length) but are not descended from the same lineage. This process reduces the signal to noise ratio in highly polymorphic loci, potentially limiting their power to resolve small frequency differences (O'Reilly et al. 2004). In addition, the potential for null (non-amplifying by PCR) alleles and genotyping scoring error in the laboratory can be higher with microsatellites than with mtDNA or other nuclear markers, which may introduce unknown bias into the results or become technically problematic when comparing data generated in different laboratories or with existing literature values.

A final issue with microsatellite data is largely interpretive. Wright's (1921) initial formulation of F_{ST} (equation 1) was for a single locus marker with only two alleles. A multilocus F_{ST} analog (G_{ST}, Nei 1973) can be calculated for microsatellite data

$$G_{ST} = 1 - \frac{H_S}{H_T} < 1 - H_S \qquad\qquad (5)$$

where H_S is the expected heterozygosity in a random mating subpopulation and H_T is the mean expected heterozygosity in the total population. The maximum value that G_{ST} can attain is that of the subpopulation homozygosity (1- H_S), and so this F_{ST} analog statistic cannot range from 0 – 1. For example, if the expected subpopulation heterozygosity is 0.873 (a common value for microsatellites in marine species), the maximum possible G_{ST} value is 0.127. In this case, one may standardize the estimated value by the maximum it can obtain given the genetic variation (G_{ST}) for direct comparison with results from other loci (Hedrick 2005). Because of these limitations, F_{ST} values are often calculated for microsatellite loci using the analysis of variance (ANOVA) approach described previously (Weir and Cockerham 1984). Additionally, more recent statistical approaches, i.e., Jost's (2008) *D*, have been developed to reduce the bias introduced by heterozygosity on *F*-statistics and their analogues.

The next generation of molecular markers that will be routinely utilized in marine fisheries genetics are single nucleotide polymorphisms (SNPs), single base DNA substitutions in neutral or adaptive genetic markers (see below). SNPs occur in the genome on the average of one in several hundred base pairs of sequence data, so a large number of loci may ultimately be screened. Assays for SNPs are more easily automated and show less genotyping error rates than microsatellites (Middleton et al. 2004). While SNP discovery for non-model organisms (i.e., all marine fishes) is currently expensive and beyond the budgets for most small laboratories, 'next generation' sequencing techniques (Mardis 2008) and unbiased, inexpensive discovery methods that do not rely on mass sequencing (Garvin and Gharrett 2007) have lowered the costs by several orders of magnitude. Combined with data from public databases (e.g., GenBank, FishBOL, etc.) the discovery of thousands of new SNPs and development of automated, high-throughput assay platforms will allow an unprecedented amount of genetic variation to be routinely surveyed in marine species, with limits more likely determined by sample collection constraints than molecular screening efforts.

3.5   *Adaptive genetic variation*

Adaptive genetic variation has become a topic of recent interest (Conover et al. 2006), although studies for marine fishes are rare due in large part to the lack of suitable genetic markers. Selection counteracts the effect of gene flow and analysis of loci under selection may permit detection of essentially self-recruiting populations which have sufficiently high exchange with other populations to homogenize allele frequencies at neutral loci, and may in some cases, be potentially informative for marine species. While disentangling the relative strengths of gene flow and selection may be problematic (e.g., differences may be due to strong selection with high gene flow or weak selection coupled with low levels of migration), results from selected markers can significantly improve the power of population assignment tests and mixed stock analysis.

The few empirical studies of selected genes in marine species to date have shown greater amounts of population structure than neutral markers. Reported estimates of F_{ST} from the pantophysin (*Pan* I) locus were an order of magnitude (or more) larger than microsatellites in Atlantic cod (Pampoulie et al. 2006; Skarstein et al. 2007) and walleye pollock (Canino et al. 2005). Similarly, differentiation at a heat shock protein gene was also much greater than for microsatellites in the European flounder *Platichys flesus* (Hemmer-Hansen et al. 2007). A recent genome-wide survey of nuclear genes in Atlantic cod in Norway revealed 29 loci that showed clear evidence for directional selection (F_{ST} range 0.08 – 0.83; Moen et al. 2008). Advances in genomic sequencing techniques virtually guarantee that more genes influenced by natural selection will be detected and applied in studies of marine species. Interpretation of those results, in terms of demographic independence of populations, may not be resolved without some estimates of differentiation from neutral markers (e.g., microsatellites). However, results from selected loci may provide valuable insights into the biology (e.g., in what life history stage does selection occur?) and spatial scales of localized adaptation.

3.6 Important considerations for interpreting genetic data in stock assessments

1. **Temporal stability in genetic differentiation.** A well-designed study should include temporal replication at some sites. If estimated F_{ST} values between geographic locations are significant (and of comparable magnitude) in different years or year classes, and not significant for temporal replicates at the same site, then one can be reasonably confident that the signal of genetic divergence has a biological basis and is not the result of inadequate/incomplete sampling, or an effect of sweepstakes recruitment.

2. **Concordance of results from different marker classes and loci.** Results from each locus constitute an independent evolutionary history, the end result of random genetic drift and migration. Differentiation may not be significant for each individual locus. However, if ten microsatellite loci are screened and six single-locus F_{ST} values are significant, one can be more confident that genetic substructure exists. If migration rates were high, frequency differences (whether large or small) at all of the loci would be homogenized and no single-locus estimates would be significant. Similarly, general agreement among results from mtDNA, allozymes, and/or microsatellites provides independent verification of genetic differentiation or panmixia.

3. **Interpretation of spatial patterns in genetic variation.** An isolation-by-distance (IBD) pattern is clear evidence for restricted gene flow in continuously distributed species. It is desirable to have the scale of spatial management units correspond to the spatial scale of genetic population structure. Departures from the IBD pattern associated with geographic and hydrographic features (e.g., fjord populations of Pacific cod, Fig. 6B) and depth zones (e.g., the beaked redfish *Sebastes mentella* have been observed to segregate by depth zone; Cadrin et al. 2009) indicate more isolated (and often smaller) populations that are likely to be demographically independent stocks. In marine environments, these clear breaks associated with physical features are likely less widespread than the IBD pattern, so interpreting how the IBD pattern relates to management units is an essential issue.

   Spatial structuring regarding movement of fish stocks exists along a continuum ranging between highly viscous stocks showing little movement and low viscosity stocks with high rates of movement. Such structure can occur if individual movements between birth and reproduction are short distances relative to the range of the species. Genes serve as natural markers that reveal this structure in that they can disperse only as fast as the individuals that carry them. Consequently, detection of genetic structure within a species' range, even a continuously distributed species, is evidence of limited dispersal and a signal that the demographic units are smaller than the species' range. The degree of genetic divergence that is observed from one location to the other depends on the density of fish and the lifetime dispersal rate (Eq. 4). Note that "lifetime" is the average generation time, which can be several decades for long-lived species with high ages at maturity such as rockfish. This spatial scale of genetic structure provides guidance for management, and can be estimated from information on F_{ST} and distance (see Section 6.1 for an example calculation).

   For species that are continuously distributed without obvious geographic points at which to define boundaries between management units, it is important to note that the lack of an obvious breakpoint is not synonymous with a lack of stock structure. In these cases, the nature of the structure of continuously distributed species requires only that management areas be of the same spatial scale as the genetic structure. For continuously distributed species, the boundaries on spatial management units do not necessarily imply strong differences between fish immediately on either side of the boundary; rather, the boundaries exist to ensure that the spatial scale of management units is consistent with the spatial scale of population structure. This provides some flexibility in locating management units – the boundaries could coincide with geographical features, but could also reflect boundaries that are convenient for a given assessment and management system.

Sometimes scales of structure may be smaller than can be managed using traditional tools such as setting ABCs by management area, and this could occur for either discretely or continuously distributed species. In such situations, an important element of the stock assessment will be to evaluate whether the concentration of harvest on one or a few sites (or stocks) has the potential to cause depletion of stock(s) at important scales of genetic structure. If this analysis indicates that there is concern, alternative management approaches should be considered by managers, such platooning effort, rotational closures, or other novel management approaches.

4. **Evolutionary history of the species.** High-latitude species are likely to show effects of ice-age displacements and isolation in their genetic structures. This may result in a strong genetic discontinuity between samples at either end of the geographic range (e.g., Pacific cod in the NW and NE Pacific Ocean, Fig. 6A) and clinal variation across a postglacial zone of secondary contact. The spatial extent of this 'hybrid' zone of contact can provide significant inference on the limits to contemporary effective gene flow in other parts of the range.

3.7   Statistical analyses of genetic information.

Even after recognizing these considerations, the incorporation of genetic information in the management process will be hindered, as mentioned above, by the need to reconcile the evolutionary and ecological paradigms (i.e., a stock based on the concept of reproductive isolation may not be the most relevant for fishery management purposes), the extent to which F_{ST} values are influenced by large population sizes and complex evolutionary histories, and the inability of genetic information to "prove" the existence of a panmictic stock. This latter issue stems, in part, from the interpretation of genetic information in a hypothesis testing framework in which a null hypothesis of a single panmictic stock is evaluated against a non-specific alternative hypothesis of "not panmictic". As Waples et al. (2008) note, a simple test of panmixia is not particularly helpful in determining the extent to which individuals from local areas are more connected to each other than individuals from distant areas. The situation could be improved by developing more refined statistical tests that allow evaluation of the trade-off in the probability of type I errors (i.e., recognizing population structure when it does not exist) vs. type II errors (i.e., failing to recognize population structure when it does exist) (Taylor and Dizon 1999). More generally, the limitations of genetic information have led to calls for integrating the analysis of genetic information with other lines of evidence in order to evaluate the "best available science" (Waples at al. 2008) in a more integrated manner. In Section 4.0, we consider other types of data that may be helpful in inferring stock structure.

4.0   GUIDELINES FOR INTERPRETATION OF NON-GENETIC DATA

Putative populations have been delineated throughout history by identifying differences in phenotypic characters rather than direct measures of genetic differentiation (Swain and Foote 1999). In many cases, data on these characteristics often exist prior to any genetic analyses and are thus often the starting point for consideration of spatial management units. In this section, we will briefly review the use of non-genetic information such as physical barriers, age and size compositions, phenotypic information (traits that are influenced by genotype and the environment, such as morphology, meristics, rates of growth and maturity), environmental information (otolith chemistry, parasites), and movement information (tagging, seasonal distributions).

4.1   Physical barriers or transition zones

Establishing physical mechanisms for demographic or reproductive isolation should be an essential first step in creating a stock hypothesis. In marine environments physical barriers are much less prevalent than in freshwater or terrestrial systems. One type of strong physical barrier that exists in many marine coastal environments are series of islands, fjords, and channels that can result in local entrainment of spawning populations and their respective larvae (e.g. Cunningham et al. 2009). Alternatively, more subtle barriers

have been referred to as "biophysical transition zones" (Logerwell et al. 2005) which can be used to infer potential separation between areas. For example, Logerwell et al. (2005) found distinct step changes in species occurrence, diversity, population distributions, and food habits at Samalga Pass in the eastern Aleutian Islands, and this transition zone corresponds to changes in ocean circulation (Ladd et al. 2005). Other features that have been linked with limiting larval dispersal are temperature and salinity discontinuities (Nielsen et al. 2004) and oceanographic gyres that retain larvae close to spawning sites (Iles and Sinclair 1982). Several recent studies have used larval transport models to help explain genetic differentiation. White et al. (2010) showed a significant improvement in explaining genetic variability by calculating an oceanographic distance through transport models, where no IBD pattern was evident under typical Euclidian distance. Selkoe et al. (2008) describe the multidisciplinary approach of using oceanographic and ecological data to improve interpretation of genetic data when detecting patterns is tenuous.

4.2   *Life history characteristics*

Differences in vital rates have long been used as a basis of stock identification because of the relative ease of assessing life history parameters (Begg et al. 1999). However their extreme plasticity in response to short-term environmental variation often reduces their value (Pawson and Jennings 1996). Begg et al. (1999) examined differences in vital rate parameters to assess their utility for stock identification of Atlantic cod, haddock and yellowtail flounder. Differences between vital rate parameters were found between putative stocks which were supported by other evidence such as spawning locations and tagging. In one case, the general lack of differences between two putative stocks provided evidence for their continuity as a single stock. Evidence for stock mixing during the early life-history stages indicates that some of these phenotypic differences do not reflect reproductively isolated genotypic differences but rather segregation into differing environments after the larval stage (Begg et al 1999). This distinction pertains to whether the definition of stocks is strictly based upon reproductive isolation or rather units that are largely demographically independent. From a stock assessment perspective, temporally stable differences in growth and maturity can be considered as important as genetic differences because they require separate population modeling.

We suggest that life history parameters such as vital rates can be used as a way to begin when population structure is suspected. If spawning timing is available, these should be compared between stocks. Significantly different spawning times would be strong evidence of reproductively isolated populations. When segments of a population have consistently differing maturation rates, this can be an indication of selection pressure from fishing or from local adaptation to the environment. Growth parameters from putative stocks should be analyzed for significant differences that are consistent over time. Finally, although the generation time of an organism is not an indicator of stock separation, extremely long generation times should alert managers of the potential risks in defining management units due to the extremely long recovery times once an overfishing event occurs.

4.3   *Age and size composition*

Differences in age and size composition could potentially be an indicator of differences in recruitment and thus reflect the demographic independence and reproductive isolation between areas. In evaluating this type of information it is necessary to discern if any difference is due to some areas serving as nursery grounds that eventually supply fish to other areas.

4.4   *Morphometrics and meristics*

Meristics and morphometrics also have been used to distinguish fish from different origins and, as one component of a multidisciplinary study of stock identity, can provide useful results (Pawson and Jennings 1996). Although these two concepts both relate to morphology, they can reveal different information on stock structure. Meristics refers to counts of features that occurs in series (vertebrae, fin rays, scales, etc),

with the pattern typically established during the early life-history stages. Morphometrics pertains to the variation in size and shape and typically reflect growth and maturity patterns for juvenile and adults. Waldman et al. (1997) concluded that morphometric approaches performed best among phenotypic methods. Multivariate morphometric analysis can easily delineate phenotypically different groups, but interpretation of these group differences is difficult (Cadrin 2005). Two challenges to meristic and morphometric analysis are that intra-stock variation in individual meristic counts can be almost as large as inter-stock variation and very large sample sizes may be required to elucidate morphometrics differences between fish stocks (Pawson and Jennings 1996).

Putative populations should be examined for differing physical attributes through these techniques. When stocks have obvious morphometric or meristic distinctions, this could be evidence that there has been some underlying genotypic divergence or adaptation to local environmental conditions. As mentioned above, it is important to determine at what life stage these local phenotypic differences are established. For example, if phenotypic modifications occur at early life stages (e.g. mersitic traits such as the number of gillrakers), this would indicate low intermingling of adult fish (Turan 2004). Alternately, the adaptations could happen somewhere during the adult life stage (e.g. change of jaw morphology during an ontogenetic shift toward deeper water and larger prey), which would indicate potential for adult mixing (Swain and Foote 1999).

4.5   *Mark recapture studies*

Mark-recapture studies are a direct way to evaluate stock hypotheses. Sablefish were shown to be separated into two large stocks in the Northeast Pacific ocean despite extensive long-range movement (Kimura et al. 1998). Begg et al. 1997 showed results from tagging studies for two species of mackerel where that showed one species exhibited very little movement, and the other species showed large coastal migrations. They used this evidence in concert with commercial fishery catch data to infer that one species was composed of multiple stocks, and the highly migratory species was one stock. Dunn and Pawson (2002) used life history data and tagging experiments to propose one discrete population of plaice, where previously several had been proposed.

Inferring population structure from tagging must consider the life-history and reproductive processes of the organism. For example, a tagging study of salmon during its ocean feeding phase may lead one to conclude that a single well-mixed stock was present, potentially missing that individual stocks would later home to their spawning grounds. Conversely, for stocks with the potential for larval dispersal and limited adult movement (e.g., rockfish), a tagging study of adults would not recognize any connections between areas resulting from larval dispersal. These issues can be addressed by conducting the tagging study on the individuals most relevant for inferring stock structure (i.e., spawning grounds for salmon).

4.6   *"Natural" tags*

Otolith microchemistry (Gao et al. 2005, 2010) and the abundance and species composition of parasites (Westerheim 1987, Adveev and Adveeve 1989; Pallson 1990), can be considered "natural" tags that could reflect the level of intermixing between areas. Otolith microchemistry has the potential to distinguish particular water bodies occupied by fish, although the microchemistry may be influenced by physiology, ontogeny, and environmental influences. Miller and Shanks (2004) used otolith microchemistry to propose limited movement of larval and juvenile black rockfish. A recent study (Bradbury et al. 2008) was one of the first to attempt to integrate otolith microchemistry and molecular genetics. The study was focused on estuarine fish that already exhibited fairly high genetic differentiation. Selkoe et al.(2008) suggested that the utility of such an approach may be limited to few species that have high enough migration to show different microchemistry, but low enough migration to exhibit sufficient genetic differentiation.

The use of parasites as natural tags is based in the idea that fish only become infected with certain parasites when they move into an area where that parasite resides (MacKenzie and Abaunza 1998). Differences in the type and levels of parasites can be caused by differences in the life-history of either the fish or parasites. Separation between areas could be indicated by consistent differences in these natural tags, as a well-mixed stock might be expected to have homogeneous levels of these quantities. McKenzie (2002) reported that a number of recent studies that have used parasitic tags to infer stock structure (e.g. Sewell and Lester 1995), but few in the North Pacific Ocean. However, Moles et al. (1998) found three parasites that could work as potential markers for shortraker and rougheye rockfish in the Gulf of Alaska.

5.0 PROPOSED FRAMEWORK FOR EVALUATING SCIENTIFIC INFORMATION ON STOCK STRUCTURE

A holistic approach to determining management units relies upon evaluation of many different types of information available that could infer stock structure (Cadrin and Secor 2009). Most of the types of data outlined above have limitations that can result in differences being attributed to factors other than demographic independence. Thus, increased confidence in data interpretation would occur if a consistent picture emerges from several types of data. A framework for an interdisciplinary approach is proposed in Table 1.

A first step in the process is to determine whether there is a potential management concern. For example, if the fishing mortality rates are much less than the rate associated with MSY and catches are not spatially concentrated, and this situation is not expected to change in the future, then identification of spatial structure may not be required. A key element of this step is identification of a *potential* concern. For example, the NPFMC has expressed the goal of addressing management issues in a proactive rather than reactive manner, which is consistent with the concept that the lack of management concerns in the past does not imply that potential concerns do not exist for the future.

If a potential concern regarding spatial management has been identified from the harvest data, then the various types of information shown in Table 1 can be evaluated. The table is organized into four major categories: 1) harvest and trends; 2) barriers and phenotypic characters; 3) behavior and movement; 4) genetics. The organization of the table is meant to reflect that information on harvest and trends, and barriers and phenotypic characters, may be more readily available for some stocks than behavioral or genetic information and thus may be among of the first types of data analyzed. However, it is important to note that in an interdisciplinary framework each of these types of information can provide a point of view on stock structure, and the information and limitations of each data type would be recognized. For example, Cope and Punt (2009) propose a method of inferring stock identification based solely upon similarities in abundance trends (either from fishery-dependent or fishery-independent data) between areas, and could be applied in data-limited situations. In particular, the value of genetics studies is that they provide a window to demographic processes that may not be readily measurable in other ways. Demographic and geographic structure determines the genetic structure of species. The patterns and extent of dispersal interact with local abundances and the recruitment successes of individual families to produce the genetic patterns observed. Even though many of the demographic attributes that contribute to the genetic structure of a species are difficult or impossible to estimate, the genetic structure is often apparent. Geneticists are rapidly learning how to interpret genetic structure to obtain information about the demographic information, which is often necessary for understanding and predicting the dynamics of populations.

It is clear that formulating a quantitative and inclusive system to determine whether a population should be divided into smaller management units is improbable; thus, the criteria for evaluating these types of data are expressed in qualitative rather than quantitative terms. For any given stock, information will only be available for a portion of data types in Table 1, and those data may reveal uncertainty regarding stock structure.

A framework such as that proposed in Table 1 has utility in comparing information available across species. The proposed framework does define a methodology for evaluating consistency across species and ensuring a more defensible system for changing the resolution or structure of harvest recommendations. In Section 6.0, we provide example applications of this framework to three cases of interest to the NPFMC.

Finally, it is important to recall that changes in spatial management units can, of course, affect a number of aspects of how stocks are assessed by scientists, regulated by managers, and harvested by the fishing industry. In order to provide information on how various factors have been considered with regard to existing spatial management units, the three examples in Section 6.0 each contain a brief description of the management and regulatory framework that has influenced decisions on spatial management units. In Section 7, we consider decision-making processes that aim to more clearly delineate the various factors involved in determinations of spatial management units.

6.0 EXAMPLE APPLICATIONS TO ALASKAN STOCKS

6.1   Bering Sea/Aleutian Islands Blackspotted/Rougheye rockfish

6.1.1   Genetic information

Prior to 2009, broad-scale tests for homogeneity and isolation by distance (IBD) were conducted on microsatellite data for blackspotted rockfish and rougheye rockfish sampled in collections along the continental shelf break from Queen Charlotte Islands to the western Aleutians and along the Bering Sea slope. Although allele frequency distributions of those collections were not homogeneous, there was no signal for isolation-by-distance (IBD) for the collections as a whole. Homogeneity tests are used to compare allele frequency distributions from two or more collections. Rousset (1997) developed an IBD analysis that describes the relationship between increase of genetic divergence and distance that is based on the work of Sawyer (1977) and others. More recently, however, Rousset (2000 and 2004) emphasized that the geographic scale at which the analysis is conducted is critical to its proper interpretation because the IBD signal can erode and become chaotic over long distances, and there may be geographic/oceanographic/ecological barriers that disrupt the signal. For Pacific ocean perch (Palof 2008) as well as blackspotted, rougheye, and shortraker (Matala et al. 2004) rockfish, there appears to be a boundary that separates eastern and western populations in the north central Gulf of Alaska. Consequently, we reanalyzed the blackspotted rockfish microsatellite data in 2009 and focused on collections made along the Aleutian Islands and the Bering Sea Slope west of 165° W (n = 173). Both tests of homogeneity and IBD were conducted. The samples were pooled into four groups, two relatively discrete sets of collections along the Aleutian Islands and two pools of collections along the Bering Sea slope for which a break point was chosen to produce groups that were similar in numerical and geographic size. Pairs of collections that differed significantly are separated with red lines (Figure 7); usually, more than a single locus exhibited the divergence in these tests. However, the homogeneity tests were conducted to demonstrate that there were geographically-based genetic differences, but were not intended to provide geographic boundaries or estimates of spatial scale of genetic structure.

Recently, more sensitive analyses have been developed for IBD by extending the IBD analysis to the divergence *between individuals* relative to the geographic distance that separates them (Rousset 2000). The result can be expressed in a linear relationship for species that are distributed in one dimension, which is interpreted as a habitat width that is small relative to its length, such as along the continental shelf break. Prior to development of the individual-based approach to IBD (Rousset 2000), geneticists generally made efforts to obtain large samples from each location that was sampled, which is conceptually what was done to conduct the homogeneity tests. This approach is still appropriate in many instances in which we are evaluating little-studied species and need to verify the tools (loci) for which we obtain data. However, that has not always been possible, hence the pooling of samples over a geographic range to assemble a sufficiently large sample for analysis. In applying the individual-based approach, it

was fortuitous that multiple samples were spread along the continental shelf edge from the central to the eastern Bering Sea and again from the mid to the western Aleutian Islands (Figure 8).

Rousset's (2000) expression for low mutation rates, which are appropriate at short time scales such as for fisheries conservation issues, is

$$\frac{F_{ST}}{1 - F_{ST}} \approx \frac{A_1}{4\sigma D_e} + \frac{1}{4\sigma^2 D_e} * \text{distance} \tag{6}$$

where A_1 is a constant, σ^2 is the variance of the distance of parents from offspring (axial displacement). Its square root is roughly the average distance between parents and offspring, or roughly the dispersal distance and D_e is the effective density, which is the effective number of individuals (N_e) per unit distance. The effective number is an index of population size that scales the efficiency with which genes are passed between generations relative to an idealized population that follows a Poisson distribution of family size. N_e has been estimated for very few populations, but we can use a plausible set of ratios of the effective population size to the census size (N_e/N_{census}) to estimate a range of D_e from empirically densities observed during abundance surveys ($D_e = D* N_e/N_{census}$). Reasonable ratios of effective to census numbers could be any place between 10% and 0.01%. From those values we can conduct a sensitivity analysis to estimate a range of values for value 4σ or for N_e. In this instance, the spatial dimension (σ) is our target, which can be determined from a significant slope of the regression of $F_{ST}/(1-F_{ST})$ on distance. The value 4σ is approximately the span that includes 95% of parents of an offspring, and 2σ in each direction is the distance an individual might move between birth and reproduction with a 95% likelihood (if dispersal is distributed as one of the exponential families of distributions).

Our analysis showed a significant IBD relationship for the BSAI blackspotted data, which demonstrates a gradient of genetic divergence along the shelf edge of the Bering Sea and Aleutian islands ($P = 0.0049$). A simple example shows how Eq. 6 can be used to estimate spatial scale of genetic divergence. The linear distance from the Bering Sea slope to the western end of the Aleutian Islands is approximately 2500 km, and the AI blackspotted/rougheye population size (from the 2008 stock assessment) is estimated as 25,575,055 fish. Increasing this value by 10% to account for the Bering Sea fish yields an estimate of 28,132,561 fish, and a resulting linear density of ~ 28,132,561 million/2500 km = 11,253 fish per km. The width of rockfish habitat along the Aleutian Islands is probably 1/3 degree latitude (37.04 km), much smaller than the length and meeting the criteria for a linear distribution.

Ranges of effective population to census size routinely are less than 0.1 for wild populations. For fecund, long-lived marine species, the ratio may even be below 0.01. A sensitivity analysis was conducted based upon five values of D_e/D_{census} ranging from 0.1 to 0.001, and three values for the slope of the IBD relationship (the mean estimate, and the upper and lower estimates associated with 95th percent confidence interval) (Table 2). From our calculations of the mean estimated for the slope of the relationship between genetic divergence and distance, and assuming a low D_e/D_{census} ratio, we get a likely scale (4σ) of roughly 58 to 185 kilometers (Table 2). By using the upper estimate of a 95% confidence interval for the slope, the largest distance is only 547 km. Clearly, the spatial scale of genetic divergence for any of the estimates in sensitivity analysis is much smaller than the distance along the continental shelf break that extends around the eastern Bering Sea to the western Aleutian Islands. The demographic implication is that movement of fish from birth to reproduction is at a much smaller scale than the geographic scale of the BSAI area. Consequently, whatever movement of fish occurs would be measured over a multigenerational time scale. We have also seen a similar IBD relationship for Bering Sea/Aleutian Island northern rockfish (Riley, Spencer, and Gharrett in prep.).

There are caveats to this analysis. The first is that it was based on data from only 173 individuals. For these analyses and for such a large geographic range, this is a very small sample. Second, the homogeneity tests were conducted on pools of samples collected over relatively large ranges (the ellipses

in Figure 8). For the homogeneity tests, it is likely that some of the geographic signal is eroded by this "averaging" process.

By the same token, the samples may be too concentrated to provide a good estimate of the slope (*b*) of the relationship. Also, the analyses were conducted with data from only seven microsatellite loci. However, the IBD analysis clearly resolves a strong signal and provides preliminary estimates of dispersal distances. Most important, this analysis demonstrates the potential of this approach for estimating the spatial scale of genetic structure, and a research priority is to collect more extensive data for application of this method. Although this analysis was conducted from a small sample, the results are the best current estimate of genetic spatial scale and consistent with those of other rockfish (i.e., northern rockfish). The preliminary nature of this analysis should be considered in the context of the precautionary principles discussed in Section 2.1.

6.1.2 Non-genetic information

Fish historically referred to as "rougheye" rockfish are now recognized as consisting of two separate species (Orr and Hawkins 2008), with rougheye rockfish retaining the name *Sebastes aleutianus* and resurrection of a new species, blackspotted rockfish (*S. melanostictus*). Because the stock structure template is intended to evaluate stock structure within a single species, concerns regarding area differences in species composition within multispecies complexes are not specifically addressed. In general, if the productivity differs between species and separate areas have different proportions of the high or low productivity species, then the productivity would be expected to differ across areas.

Several types of genetic and morphometric data have been used to document the scarcity of rougheye rockfish west of the eastern Aleutian Islands and the occurrence of blackspotted rockfish throughout the BSAI area, thus establishing differences in species composition between areas in the BSAI, including allozymes (Hawkins et al. 2005), mitochondrial and microsatellites (Gharrett et al. 2005), and meristics and morphometics (Orr and Hawkins 2008). A similar pattern of species distribution is seen in the 2006 AI trawl survey, although some error likely exists in the species identification. Little information is known regarding most aspects of the biology of blackspotted and rougheye rockfish.

Some information exists for size at age, age compositions, and length compositions for the blackspotted/rougheye complex. These data indicate generally younger and smaller fish in the EBS relative to the AI. Statistical differences in growth curves do exist between the areas and reflect generally larger size at age in the EBS than in the AI for ages between approximately 10 and 30; however, differences in size at age did not occur for fish older than approximately 30 years. Although interpretation of these observations is confounded at the species level, it does not appear to be consistent with the concept of a well-mixed stock complex across the BSAI.

One of the metrics in Table 1 for evaluating stock structure of BSAI species is "physical barriers". Although physical barriers are rare in the open marine environment, the general ecological differences between the EBS slope and the Aleutian Islands was a motivating factor in the creation of management subareas. In the Aleutian Islands, "biophysical transition zones" have been identified by Logerwell et al. (2007), as step changes in food habits and species diversity and abundance were found between Samaga Pass (near the boundary between the BS and AI sub-management areas) and points farther west. In addition, research on oceanographic currents within the BSAI area reveals some connection between the EBS and the eastern AI (via the Aleutian North Slope Current), but limited connection with the western and central AI. The connection between the Bering Sea slope and the north side of the AI west of 180° W is limited due to the break associated with Petral Bank and Bowers Ridge, which results in water flowing away from the Aleutian Islands archipelago (Stabeno et al 2005).

6.1.3 History of spatial management units for BSAI blackspotted/rougheye rockfish
Rougheye rockfish (*Sebastes aleutianus*) have historically been managed within various stock complexes within the BSAI region. From 1991 to 2000, rougheye rockfish in the EBS were managed under the "other red rockfish" species complex, which consisted of shortraker (*Sebastes borealis*), rougheye (*S. aleutianus*), sharpchin (*S. zacentrus*), and northern rockfish (*S. polyspinis*), whereas in the AI area during this time rougheye rockfish were managed within the rougheye/shortraker complex. In 2001, the other red rockfish complex in the eastern Bering Sea was split into two groups, rougheye/shortraker and sharpchin/northern, matching the complexes used in the Aleutian Islands. Additionally, separate TACs were established for the EBS and AI management areas, but the overfishing level (OFL) and ABC level pertained to the entire BSAI area. Beginning in 2000, the BSAI Plan Team recommended separate management by species with harvest quotas applied across the BSAI area. This recommendation reflected the desire to avoid disproportionate harvesting across species within the complex, and also recognition that low abundance of rockfish in the EBS could be constraining to other fisheries (NPFMC 2000). The Plan Team also recognized that a risk of establishment of area-wide ABCs was disproportionate harvest across areas if separate stocks existed, and for this reason recommended apportionment of TACs across the BS and AI areas. From 2001-2003, the rougheye/shortraker complex was managed with separate TACs for the BS and AI subareas. Species –specific catch data was available beginning in 2004, at which point rougheye rockfish was managed as single species with BSAI-wide OFL, ABC, and TAC.

The desire to have single species management has been hindered by the recognition from genetic and morphological data that fish historically referred to as "rougheye" rockfish comprise two distinct species. The current information is not sufficient to support species-specific assessments for "true" rougheye rockfish and blackspotted rockfish because historical catch and survey cannot be parsed into the component species, Field identification between these two species is difficult, and accuracy of field IDs is a current research topic. This is especially an issue in the GOA, where both species are common; in the BSAI, the distribution of *S. aleutianus* does not extend west of the eastern AI. Expanded training on species identification for the trawl survey group and observer program will be critical to improve the accuracy of the catch and survey biomass estimates.

Stakeholders have historically encouraged area-specific rockfish specifications as a mechanism for avoiding harvest levels disproportionate with estimated biomass. Given this concern, and the history of separate management quotas for the BS and AI areas, a comparison of catches to potential area-specific harvest levels have typically been presented in the stock assessment. Care should be taken not to interpret the results as evidence of overfishing, as this definition depends upon the definition of the stock or stock complex, and at no point has the catch of a stock or stock complex exceeded its OFL level. In the Aleutian Islands, the catch exceeded the estimated area-specific ABC in four of the ten years from 2001-2010, by small amounts in 2002, 2004, and 2008 (8%, 6%, and 3%, respectively) and a large amount in 2001 (154%; catch of 585 t, potential area-specific ABC of 230 t). In the eastern Bering Sea, the catch exceeded the estimated area-specific ABC in two of the ten years from 2001-2010, by 3 t in 2004 and 6 t in 2008. The EBS-specific ABCs from 2001-2007 ranged from 21 t to 32 t; an increased in the biomass estimate of blackspotted/rougheye rockfish in the 2008 EBS slope survey increased the area-specific ABC in 2009 to 40 t. A reduction in the maximum retainable bycatch limit has been enacted since 1998, and separate management for rougheye rockfish and shortraker rockfish, appears to have helped regulate the catch in most years.

6.1.4 Summary for blackspotted/rougheye rockfish.
A summary of the information available for blackspotted/rougheye complex is shown in Table 3. Information that is supportive of area-specific management of the complex are the different species composition of the complex between the BS and AI areas, and several genetic results for blackspotted rockfish including homogeneity tests indicating differences among sample locations, a general IBD

pattern, and estimation of a spatial scale that is much smaller that current management areas. Differences also occur in the age and size distributions and size at age (for ages between 10 and 30) between the AI and EBS for the blackspotted/rougheye complex. Although interpretation of these observations is confounded at the species level, it does not appear to be consistent with the concept of a well-mixed stock complex across the BSAI.

6.2   *Bering Sea/Aleutian Islands Pacific cod*

The application of the proposed template to Pacific cod is shown in Table 4. During the past 30 years, the total allowable catch (TAC) in the Bering Sea/Aleutian Islands (BSAI) management area has averaged about 82% of the acceptable biological catch (ABC), with the aggregate commercial catch averaging about 89% of the TAC (Thompson et al. 2008a). Harvests are generally concentrated along the shelf edge and near Unimak Island. Relative harvests between BS and AI have been similar to relative survey biomasses between the areas. Population trends in the eastern Bering Sea, based upon assessment, have declined recently, while those in the AI region, based upon survey, have been variable.

In the Gulf of Alaska (GOA) management area, much of the fishing effort is concentrated in the Kodiak region, although trawling occurs at multiple locations along the shelf both north and south of Kodiak. Trawling accounted for the largest share of the catch in every year but one from 1991 – 2002, and pot gear has taken the largest share since 2003 (Thompson et al. 2008b). TAC in the GOA area averaged about 83% of ABC and landings averaged approximately 81% of TAC from 1986 through 1996. Since 1997, the Federal TAC has been set well below the ABC to accommodate an increasing fishery within State of Alaska waters. Contemporary levels of abundance in the GOA region estimated from survey from 1999 to present are generally lower than pre-1996 levels (Thompson et al. 2008a; Table 2.11) but show no discernable population trends.

Pacific cod populations have a transoceanic distribution across continental shelves and slopes to depths of 500 m from approximately 34 – 63º N latitude (Allen & Smith 1988). Cod appear to spawn at predictable times and locations in the BSAI and GOA management areas. The time of peak spawning varies with latitude, with southern populations spawning earlier than northern ones (see review by Gustafson et al. 2000). Stocks south of Alaska grow and mature more quickly than northern stocks, achieve lower maximum size, and have shorter lifespans (see review by Gustafson et al. 2000; Ormseth and Norcross 2008). Within the Alaska management regions, length at age is significantly greater for both male and female cod in the AI compared with the Bering Sea. Age at 50% maturity was significantly less for female cod (4.6 vs. 4.9 years) in Gulf of Alaska compared with Eastern Bering Sea, as was length at 50% maturity (Stark 2007).

Morphometric and meristic characters have been of equivocal value for identifying discrete stocks of Pacific cod. Wilimovsky et al. (1967) reported four geographic subdivisions of cod (British Columbia, Southeast Alaska, eastern Aleutian Islands/Bering Sea, and western Aleutian Islands) but differences among areas were insufficient to delineate stock structure over smaller spatial scales. Tagging studies have indicated that Pacific cod are not highly migratory, although some individual adult movements exceeding 1,000 km have been documented (Shimada and Kimura 1994; see review by Gustafson et al. 2000). Cod tagged in the eastern Bering Sea exhibited high site fidelity, with 70% of recaptures occurring within 80 km (Shi et al. 2008). Studies in the Gulf of Alaska have shown that while some fish traveled in excess of 600 km, about 75% stayed within 25 km over considerable time periods (D. Urban, NMFS, pers. comm. 2006). Fish captured during summer months and recaptured during the next spawning period had some of the longest recovery distances, and some tagged and recaptured over two successive spawning seasons the shortest, suggesting that cod may make extensive annual feeding migrations prior to returning to prior spawning locations or that some stock components are non-migratory. Natural acquired tags also infer limited movement of cod stocks. Otolith chemistry (Gao et al. 2005) and protistan parasite incidence (Westrheim (1987; Palsson 1990) distinguish Puget Sound cod from coastal cod off Vancouver Island.

Population genetics studies have provided some of the most rigorous evidence for population substructure in Pacific cod. The earliest study (Grant et al. 1987) found significant differentiation at allozyme loci between the northeast Pacific Ocean/Bering Sea and Asian populations, but did not detect population subdivision within or between the BSAI and GOA management areas. A more comprehensive survey using 11 microsatellite loci (Cunningham et al. 2009) found significant differentiation among sample pairs, including a comparison between the eastern Bering Sea and Aleutian Islands, and a clear isolation-by-distance (IBD) pattern in the northeast Pacific Ocean. Notable outliers to this pattern were cod populations in the Georgia Basin (Strait of Georgia and Puget Sound). Estimates of mean dispersal distances derived from the IBD relationship were less than 100 km per generation over a range of effective adult densities of 10 – 10,000 per km (Cunningham et al. 2009). Subsequent analyses of mitochondrial DNA (mtDNA) sequences (Canino et al. in press a) confirmed the results from microsatellites and showed two distinct evolutionary lineages in coastal and Georgia Basin populations of cod.

6.2.1 History of spatial management units for BSAI Pacific cod

The sequence of actions for managing BSAI Pacific cod resulted in the allocation of fishing privileges to commercial fishing sectors (i.e., gear groups) for the entire BSAI FMP area prior to the SSC's recommendation to manage the P. cod ABC/TAC by management area (BS/AI) based on stock structure and other biological characteristics. In 2008 Amendment 85 revised nine sector allocations of the (combined) BSAI Pacific cod TAC (shown in the box at right). The Council deferred a decision to apportion the TAC for the separate BS and AI management areas because the Council's scientific advisors had not yet recommended separate benchmarks.

Pacific cod sector allocations.	
Sector	**Allocation**
AFA trawl CP	2.3%
Non-AFA trawl CP	13.4%
Hook & line CP	48.7%
Pot CP	1.5%
Trawl CV	22.1%
Hook & line CV>60'	0.2%
Pot CV>60'	8.4%
<60' fixed gear	2.0%
Jig CV	1.4%

In October 2008 the SSC reported that there is sufficient justification for a split in Pacific cod between the BS and AI areas and recommended that a precautionary approach be taken by specifying separate ABCs, while setting a combined BSAI OFL. This finding was based on a review of the biological information and Plan Team comments, but came too late to influence the Council's selection of a preferred alternative under Amendment 85. The SSC has not implemented area-specific ABCs and TACs for BS and AI Pacific cod stocks because it recognizes the potential economic consequences of redefining the management units on stakeholders, which likely would occur if the BSAI Pacific cod TAC is apportioned between subareas in the future. Since reauthorization of the Magnuson-Stevens Act in 2007, the SSC has sole authority for setting the OFLs and ABCs and can adopt separate BS and AI specifications.

The current problem statement for the proposed action to revise Pacific cod sector splits references the need to recognize differences in dependence among gear groups and sectors that harvest Pacific cod in the BS and AI management areas:

In the event that the BSAI Pacific cod ABC/TAC is apportioned between the BS and the AI management areas, a protocol needs to be established that would continue to maintain the benefits of sector allocations and minimize competition among gear groups; recognize differences in dependence among gear groups and sectors that fish for Pacific cod in the BS and AI; and ensure that the distribution of harvest remains consistent with biomass distribution and associated harvest strategy.

Absent any further action by the Council on revising BSAI Pacific cod sector allocations to account for proposed separate benchmarks, NMFS has identified that it only would be authorized to implement allocations for the subareas equal to that of the combined area (e.g., if a sector receives a 40% BSAI TAC allocation, then it would receive 40% of the BS TAC and 40% of the AI TAC) upon implementation of a TAC split. The Council and fishing fleet, however, have expressed concern that the default reallocation does not reflect recent historical catch by sector in the AI and would disenfranchise stakeholders. In effect, sectors that have very little recent history in the AI would be forced to fish in the AI if they wanted to harvest their entire allocation. This approach would serve to limit flexibility for all sectors, but would likely be most onerous on the sectors comprised of smaller vessels, as they would be required to travel greater distances to fish in conditions that may not be well-suited for their vessels. In addition, many vessels do not currently hold an AI endorsement, which would be necessary to prosecute an AI Pacific cod TAC. Thus, some participants would not be eligible to harvest the entire sector allocation. The Council has been concerned with the potential disruption to the fishing sectors and establishing an allocation scheme between the two areas that does not reflect current harvest patterns by sector.

In December 2008 the SSC encouraged the Council to revise the sector allocations so that the SSC could implement ABCs and TACs at what it determined to be the appropriate management unit. A December 2008 discussion paper noted that the Council recognizes that 1) the cod fishing sectors have different catch history and dependency on the two areas; 2) none of the proposed management alternatives (including status quo) provides a satisfactory solution to the problem; and 3) a reasonable solution is not readily identifiable. The concerns with establishing sector allocations for the subareas equal to that of the combined area are discussed above. Other solutions include retaining sector allocations at the BSAI level, and a sector's allocation could be harvested anywhere in the BSAI as long as TAC was available in that area. While creating operational flexibility and a relatively simple management system, the concern is that it could cause sectors (both within and among sectors) to race for Pacific cod in the area they expect to close first. This could affect a sector's ability to rationalize their harvest, especially if some members of the sector wish to fish the area that is expected to close later in the year. Another complication with this approach is the current absence of gear-specific seasonal apportionments by area, which is a Steller sea lion (SSL) concern. The existing Steller sea lion protection measures include an overall seasonal split of the BSAI Pacific cod TAC, as well as more refined seasonal apportionments by gear type. No guidelines currently exist for establishing AI seasonal apportionments by gear type or overall, and lack of such guidelines in the AI risks harvesting all of the AI cod TAC in the first half of the year. Thus, NMFS is concerned that this alternative deviates from the consultation in the 2001 BiOp and what is currently being consulted on in the forthcoming BiOp.

The Council also considered establishing AI allocations to the individual sectors based on recent harvest activity, while maintaining the sector's overall allocation established under Amendment 85. Concerns with this approach include the relatively small AI allocation that results for several sectors, especially when further apportioned by season, which may prevent the opening and management of a directed fishery. In addition, depending upon TAC fluctuations, a sector's annual subarea allocation could exceed its overall BSAI allocation, resulting in a negative or zero allocation in one subarea. This could severely affect the ability of vessels to continue participating in their sector for Pacific cod if they do not have a license endorsement for the open subarea, and could affect the ability of the entire sector to harvest its allocation.

In addition to a lack of a reasonable management solution, the Council has tabled further action on identifying a solution to the problem while awaiting the release of the Biological Opinion (BiOp) on Steller sea lions, which may indicate that additional or different management actions affecting the Pacific cod fisheries may be needed to facilitate SSL recovery. The latest BiOp was released in summer 2010 and consideration of the management conundrum related to redefining the management units for BSAI Pacific cod is scheduled tentatively for December 2010.

6.3   *Bering Sea/Aleutian Islands Atka mackerel*

The application of the proposed template to Atka mackerel, *Pleurogrammus monopterygius*, is shown in Table 5. Atka mackerel are members of the family Hexagrammidae and are widely distributed along continental shelves from Asia to North America (Allen and Smith 1988; Lauth et al. 2006). It has supported a commercial fishery with annual total allowable catch (TAC) averaging 51,507 metric tons (1996–2006) along the Aleutian Island Archipelago, the region of greatest abundance (Lowe et al. 2008) with an average ratio of catch to ABC of 0.75. The trawl fishery occurs in areas of highest abundance, excluding Stellar Sea Lion Exclusion Zones, usually at depths less than 200 m. Atka mackerel populations are characterized by highly variable recruitment but have exhibited no clear demographic trends over time (Lowe et al. 2008).

Atka mackerel are obligate demersal spawners; females spawn egg masses on rocky substrates in areas of moderate to strong currents that are cared for and defended by males (Lauth et al. 2006). Nesting begins in June at known locations (site fidelity), and the overlapping mating and brooding seasons may last up to 7 months (Lauth et al. 2007). Newly-hatched larvae are neustonic (Kendall and Dunn 1985) and develop in epipelagic waters for up to a year before juveniles recruit into demersal populations. Tagging results indicated that adults form local aggregations and generally do not move in excess of 70 km (McDermott et al. 2005).

Contrasting patterns of geographic variability are evident in previous studies of growth and life-history characteristics. Phenotypic differences among areas indicated the possibility of discrete Atka mackerel populations (Lee 1985; Lowe et al. 1998). In particular, length and weight at age differ significantly among locations along the Aleutian Islands (Kimura and Ronholt 1988), and length at age varied clinally, increasing from west to east along the Aleutian Islands archipelago (Lowe et al. 1998). These differences are consistent with limited adult migration, but may not necessarily reflect genetic differences that have accumulated among populations. Indeed, a pattern of geographical heterogeneity did not appear in the frequencies of allozymes (Lowe et al. 1998). A survey of 22 polymorphic allozyme loci in four samples ($n = 329$) along the Aleutian Islands archipelago failed to show significant frequency differences ($F_{ST} = 0.004$). The level of nuclear genetic diversity ($H = 0.137$) was exceedingly large, more than double the average reported by Ward et al. (1994) for 57 marine fish species.

More recently, samples from Japan to the western Gulf of Alaska were collected between 2004 and 2006 from six locations and screened for variation at nine microsatellite markers and mitochondrial DNA (mtDNA) sequences (Canino et al. in press b). Microsatellite allele-frequency homogeneity across the North Pacific indicated an apparent lack of genetic population substructure. While levels of polymorphism at microsatellite loci were typical for marine fishes, ($h = 0.34–0.96$), mtDNA control region diversity was extremely low ($\pi = 0.00007$, $h = 0.033$). Only three mtDNA haplotypes, two occurring as singletons, were detected among 119 individuals from across the sampled range. The strong contrast between microsatellite and mtDNA diversities may be due to stronger effects of population bottlenecks, post-glacial colonization patterns, or natural selection on mtDNA rather than for the nuclear genome. Given the potentially large effective sizes of contemporary populations, the number of generations since post-Pleistocene colonization of the Aleutian Islands archipelago is likely insufficient for significant divergence to arise through genetic drift. Thus, neutral genetic markers may be of little value for resolving putative stocks of Atka mackerel.

6.3.1 History of spatial management units for BSAI Atka mackerel

Atka mackerel OFL is set for the entire BSAI, while separate ABCs are set for EAI/EBS, CAI, and WAI. Prior to 1994, Atka mackerel was managed with a single BSAI ABC and TAC, and the TAC was set lower than the ABC due to concern over the harvest occurring in a small area of the Aleutian Islands. Beginning in 1994, the ABC was allocated among the three management subareas within the Aleutian Islands.

There are few management implications for stock separation for Atka mackerel compared to those identified above for P. cod. There may be additional management recommendations for the Atka mackerel fishery in the SSL BiOp. There are very few vessel participants fishing for two or three companies in the directed Atka mackerel fishery. Most if not all participants are eligible under Amendment 80 and could choose each year whether to operate in a cooperative. The current Atka mackerel allocation between Area 541 and EBS is 94% to the Amendment 80 fleet and 6% to the trawl limited access fleet (which is all other trawlers). In 2012 the allocation will be 90% to the Amendment 80 fleet and 10% to the trawl limited access fleet.

7.0 A PROCESS FOR DETERMINATION OF SPATIAL MANAGEMENT UNITS

In considering steps to improve the process to determine spatial management units, it is useful to consider how this topic is currently evaluated within our management system. At present, stock structure issues are usually brought before the NPFMC groundfish Plan Teams and SSC by assessment authors, who may be responding to new research, or a perception of an inconsistency between in the current management structure and biological reality. The scientific information is then reviewed by the Plan Teams, and recommendations are developed concerning stock structure. The SSC considers the Plan Team recommendations and makes a recommendation to the Council. In developing Plan Team recommendations, management and regulatory considerations may be evaluated simultaneously with scientific information on stock structure, and this melding of issues has the potential to lead to inconsistent determinations of spatial management units. For example, the potential exists to evaluate stock structure differently for cases in which the proposed area-specific harvest quotas are relatively small and are perceived as imposing costs to the regulatory system and fishing industry as compared to cases where the regulatory and industry costs are perceived to be minimal. In addition, Plan Team and SSC members, and stock assessment scientists, typically have limited expertise in interpreting the genetic data that is often used to infer stock structure, and this may also result in inconsistencies when clear guidance regarding interpretation does not exist.

There is room for improvement in current practices in several areas. First, the current approach is not explicitly precautionary or risk averse for small stocks, because scientific uncertainty regarding demographic independence does not necessarily lead to management action that results in increased conservation to the resource. Second, some inconsistencies exist in currently used spatial management units. Given the uncertainties in stock structure the ABCs are often, but not always, allocated by management area. For example, ABCs for rockfish in the GOA are allocated by area, but only POP are managed this way in the BSAI. Northern rockfish, shortraker rockfish, and the blackspotted/rougheye complex each have a single BSAI-wide ABC and OFL.

The working group that produced this report was formed to address these issues, and the purpose of this report is to provide guidelines on the interpretation of scientific information and identify a consistent procedure by which this information would be evaluated. The above description also highlights that decisions on stock structure incorporate some consideration of management concerns regarding industry and regulatory costs, as it is understandable that the imposition of these costs should not be taken lightly. Thus, an additional component to the process involves evaluation of the industry and regulatory risks/costs as well as risks to stock sustainability.

First, the inconsistency regarding area allocation of ABCs can be addressed in a straightforward manner. We recommend allocating the ABCs across sets of INPFC areas within the BSAI and GOA management areas as a precautionary measure even in the absence of specific scientific information. This approach is consistent with the Council's objective of applying a precautionary approach to fisheries management, and most species in the north Pacific are currently managed in this way. Within the BSAI management region, these areas have typically been the western, central, and eastern Aleutian Islands, and the Bering

Sea subarea. Within the GOA management region, these areas have typically been sub-GOA combinations of the INPFC areas 610-650. More intensive management measures (separate OFLs by area, or defining separate stocks with separate assessments and status determination criteria, etc.) would be evaluated with our proposed process discussed below.

A central feature of our proposed decision-making process is an attempt to separate the consideration of the scientific information regarding stock structure from the consideration of the management implications. This separation is consistent with the decision-making framework in other well-established natural resource management systems. For example, in applying the Endangered Species Act, an early step is the formation of Biological Review Teams (BRTs) that determine Evolutionary Significant Units (ESUs) based upon the scientific information pertaining to reproductive isolation and evolutionary importance (Waples 1995). The management implications of such determinations are not considered by the BRTs, but are considered by managers. Another example is within the ICES system, where review panels with expertise on stock structure have been created to evaluate hypotheses regarding population connectivity, and these panels have conducted their work outside of the ICES assessment framework (WKREDS 2009).

The first step of our proposed process should be should be identification of priorities for stock structure evaluation, which could occur in several ways. One option is for the Plan Team to propose species of highest concern at the September meeting, which the SSC would review and make recommendations. This has the advantage of efficiently allocating our efforts to the stock of highest concern, but has the disadvantage of potentially not applying a consistent process for all stocks. A second approach is to develop a schedule by which spatial management units and stock structure is evaluated for all managed stocks. The evaluations for some stocks would likely be relatively clear and straightforward whereas others may require more effort, but the advantage of this approach is that a consistent and clearly documented procedure is applied. The SSC, in the minutes of their October 2009 meeting, recommended establishing either a three- or five-year schedule.

Once a stock is identified for stock structure evaluation, the lead assessment author or other designated individual will, in collaboration with others, develop a stand-alone stock structure evaluation report. This report will include: 1) a review of available scientific information using the template provided in this report; 2) qualitative or quantitative evaluation the risks (biological and fishery) under alternative hypotheses concerning stock structure (for example, long-lived and relatively sedentary species such as rockfish may be subject to local depletion and require long rebuilding times should they become depleted, whereas species capable of rapid colonization, may not have the same level of concern). A risk assessment typically involves considering alternative management approaches for dealing with stock structure, such as setting separate ABCs and OFLs by area, or separate stock assessments and status determination criteria by area.   The risk assessment may be qualitative, or more formal approaches such as Management Strategy Evaluation (MSE) may be applicable. Evaluation of management implications, such as impacts on target fisheries and other fisheries, operational costs of changes to the management system, is also part of the risk assessment.

Because much of the material for the stock structure evaluation report (genetics, population connectivity, fishery economics, regulatory impacts, etc.) is outside the range of expertise of a typical stock assessment scientist, it is essential that the lead assessment author collaborate with the appropriate experts. Finally, it must be recognized that the data available for this report will likely be limited; a fully quantitative evaluation of risk for all alternative hypotheses regarding stock structure is not necessarily expected. For each category of information in the template in this table it is important to characterize its strength of evidence for the alternative hypotheses concerning stock structure.   It is unreasonable to expect definitive information, and decision-making will have to take place when available data are uncertain. Delaying action until definitive information is available (particularly if it is unlikely to be available soon) is neither proactive nor precautionary.

The stock structure evaluation report could be reviewed in several ways. One option is for review by the Plan Team and SSC in the fall of the year following the request to produce the report. While the Plan Team and the SSC have familiarity with the biology and population dynamics of North Pacific stocks, the expertise on these panels regarding population genetics and connectivity may be limited. An alternative review process may be to create a separate review body, perhaps as a formal NPFMC committee, with the appropriate expertise that would evaluate the stock structure report, potentially at time outside of the fall assessment cycle. In either case, the results of this review would be presented to the SSC and would determine the extent of revisions necessary before the SSC develops its recommendations to the Council. Thus, it is essential that the review committee have members who are familiar with the NPFMC management process.

8.0 CONCLUSIONS

Unfortunately, there are no simple scientific "rules" that can be invoked to determine stock structure. Recommendations should consider evidence of competing hypotheses in a comprehensive way, and apply considerations such as whether the evidence is strong, weak, or ambiguous. Both the definition of what is a "population" and the level of conservation required depends upon the management goals desired, which is largely in the policy arena. A rough analogy is the use of a harvest control rule that defines the buffer between target and limit reference points. The size of buffer came about as a result of policy deliberation; there was no "rule" to indicate what that buffer should be.

For the goal of preventing overfishing upon demographically independent population units, a primary consideration is to ensure that harvest is proportional to biomass. A variety of spatial management tools are currently used to achieve this goal. Partitioning ABC by area is especially effective for target stocks as it limits retention once the ABC level is reached and would reduce the probability of local depletion. For nontarget species, additional steps such as lowering the maximum retention allowance (MRA) and placing the stock on bycatch status could be employed. Finally, even if fishing needs to be restricted to limit harvest of bycatch stocks, the NMFS In-Season Management Program routinely restricts fishing in only areas of high bycatch instead of the entire fishing grounds, thus reducing the burden on the fishing fleet.

It is important to recognize that management can be split by area even if the assessment and data are not split by area. In cases where doing area-specific assessments would lead to limited and poor quality data, an area-wide assessment can be conducted with harvest quotas apportioned across areas. As mentioned above, ABCs and harvest quotas are typically apportioned across areas, and OFL could be apportioned if there is a higher risk to stock sustainability. The ultimate goal is to craft management measures that reflect both the level of risk and uncertainty of the information.

9.0 ACKNOWLEDGEMENTS

10.0 REFERENCES

Allen, M.J. and G.B. Smith. 1988. Atlas and zoogeography of the common fishes in the Bering Sea and northeastern Pacific. NOAA Technical Report NMFS 66, 151p.

Andrewartha, H.G. and L.C. Birch. 1984. The Ecological Web. University of Chicago Press, Chicago, IL.

Avdeev, V. V., and G.V. Avdeev. 1989. A study of walleye pollock population structure and migration routes using parasitological indicators. In Proceedings of the International Symposium Biological Management of Walleye Pollock, pp. 569–590. Alaska Sea Grant Report No. 89-1, University of Alaska, Anchorage, AK, USA.

Begg, G.A. 2005. Life history parameters. *In* Cadrin S.X., K.D. Friedland , and J.R. Waldmann [eds]. Stock identification methods applications in fishery science. Elsevier Academic Press, London, pp. 119–150.

Begg, G.A. and S.X. Cadrin. 2009. Stock identification. *In* Jakobsen, T, M.J. Fogarty, B.A. Megrey, and E. Mokness, E. [eds.]. Fish reproductive biology: implcations for assessment and management. Wiley, 429 pp.

Begg, G.A., D.S Cameron, and W. Sawynok. 1997. Movements and stock structure of school mackerel (Scomberomorus queensladicus) and spotted mackerel (S. munroi) in Australian east-coast waters. Mar. Freshwater Res. 48: 295-301.

Begg, G.A., J.A Hare, and D.D. Sheehan. 1999. The role of life history parameters as indicators of stock structure. Fish. Res. 43:141–163.

Bradbury I.R., S.E .Campana, and P. Bentzen. 2008. Otolith elemental composition and adult tagging reveal spawning site fidelity and estuarine dependency in rainbow smelt. Mar. Ecol.-Prog. Ser. 368: 255-268.

Booke, H.E. 1981. The conundrum of the stock concept – are nature and nuture definable in fisheries science? Can J. Fish. Aquat. Sci. 38:1479-1480.

Buonaccorsi, V.P., C.A. Kimbrell, E.A. Lynn, and R.D. Vetter. 2005. Limited realized dispersal and introgressive hybridization influence genetic structure and conservation strategies for brown rockfish, Sebastes auriculatus. Conservation Genetics 6:697-713.

Burford, M.O. and R.J Larson. 2007. Genetic heterogeneity in a single year-class from a panmictic population of adult blue rockfish (Sebastes mystinus). Marine Biology 151:451-465.

Cadrin, S.X. 2000. Advances in morphometric identification of fishery stocks. Reviews in Fish Biology and Fisheries 10:91-112.

Cadrin, S.X. and D.H. Secor. 2009. Accounting for spatial population structure in stock assessment: Past, present, and future. In Beamish, R.J. and B.J. Rothschild.[eds]. The future of fisheries science in North America. Springer Science. pp. 405-426.

Cadrin, S.X., K.D. Friedland, and J.R. Waldman. 2005. Stock identification methods: applications in fishery science. Academic Press, 719 pp.

Cadrin, S, M.Bernreuther, A.K. Danielsdottir, E. Hjorleifsson, T. Johansen, L. Kerr, K. Kristinsson, S. Mariani, C. Pampoulie, J. Reinert, F. Saborido-rey, T. Sigurdsson, and C. Stransky. 2009. Mechanisms and consequences of life-cycle diversity of beaked redfish, *Sebastes mentella*. ICES CM 2009/H:01.

Canino, M.F., P.T. O'Reilly, L. Hauser, and P. Bentzen. 2005. Genetic differentiation in walleye pollock (Theragra chalcogramma) in response to selection at the pantophysin (Pan I) locus. Can. J. Fish. Aquat. Sci. 62:2519-2529.

Canino, M.F., I.B. Spies, and L. Hauser. 2005. Development and characterization of novel di- and tetra-nucleotide microsatellite markers in Pacific cod (Gadus macrocephalus). Mol. Ecol. Notes 5:469-471.

Canino M.F., I.B.Spies, K.M. Cunningham, L. Hauser, W.S. Grant. (in press a). Multiple ice-age refugia in Pacific cod, Gadus macrocephalus. Molecular Ecology.

Canino, M.F., I.B. Spies, S.A. Lowe, and W.S. Grant (in press b). Discordant patterns of genomic diversity in Atka mackerel, Pleurogrammus monopterygius. Marine and Coastal Fisheries.

Conover, D.O., L.M. Clarke, S.B. Munch,. G.N. Wagner. 2006. Spatial and temporal scales of adaptive divergence in marine fishes and the implications for conservation. Journal of Fish Biology 69:21–47.

Cope, J.M. and A.E. Punt. 2009. Drawing the lines: resolving fishery management units with simple fisheries data. Can J. Fish. Aquat. Sci. 66:1256-1273.

Crow, J.F. and K. Aoki. 1984. Group selection for a polygenic behavioral trait: estimating the degree of population subdivision. Proc. Nat. Acad. Sci. USA 81:6073-6077.

Cunningham, K.M., M.F. Canino, I.B. Spies, and L. Hauser. 2009. Genetic isolation by distance and localized fjord population structure in Pacific cod (Gadus macrocephalus): limited effective dispersal in the northeastern Pacific Ocean. Can. J. Fish. Aquat. Sci. 66:153-166.

Darcy, G.H. and G. C. Matlock. 1999. Application of the precautionary approach in the national standard guidelines for conservation and management of fisheries in the United States ICES Journal of Marine Science, 56:853–859.

DiCosimo, J., Methot, R. D., and Ormseth, O. A. In press. Use of annual catch limits to avoid stock depletion in the Bering Sea and Aleutian Islands management area (Northeast Pacific). ICES Journal of Marine Science

Dunn M. R., and M.G. Pawson. 2002. The stock structure and migrations of plaice populations on the west coast of England and Wales. Journal of Fish Biology 61:360–393

Eagle, T.C., S.X. Cadrin, M.E. Caldwell, R.D. Methot, and M.F. Nammack. 2008. Conservation Units of Managed Fish, Threatened or Endangered Species, and

Marine Mammals. NOAA Technical Memorandum NMFS-OPR-37. 100 pp.

FAO, 1995. Code of conduct for responsible fisheries. Food and Agriculture Organization of the United Nations. Rome. 41p.

Fu, C. H., and L. P. Fanning. 2004. Spatial considerations in the management of Atlantic cod off Nova Scotia, Canada. North American Journal of Fisheries Management 24(3):775.

Gao, Y.W., G.G. Bargmann, U. Brand, ande D.L.G. Noakes. 2005. Stable isotopic and trace elemental composition of otoliths and the stock structure of Pacific cod, Gadus macrocephalus. Env. Biol. Fish. 74:335-348.

Gao Y.W., D.L.Dettman, K.R.Piner, and F.R.Wallace. 2010. Isotopic Correlation (delta O-18 versus delta C-13) of otoliths in identification of groundfish stocks. Trans. Am. Fish. Soc. 139:491-501.

Garcia, S.M. 1994. The precautionary principle: its implications in capture fisheries management. Ocean & Coastal Management 22:99-125.

Garvin, M.R. and A.J. Gharrett . 2007. DEco-TILLING: an inexpensive method for single nucleotide polymorphism discovery that reduces ascertainment bias. Molecular Ecology Notes 7:735-746.

Gharrett, A.J., A.P. Matala, E.L. Peterson, A.K. Gray, Z. Li, and J. Heifetz. 2005. Two genetically distinct forms of rougheye rockfish are different species. Trans. Am. Fish. Soc. 134:242-260.

Gharrett, A.J., A.P. Matala, E.L. Peterson, A.K. Gray, Z. Li, and J. Heifetz. 2007. Distribution and population genetic structure of sibling rougheye rockfish species. Pages 121-140 *In* J. Heifetz, J. DiCosimo, A.J. Gharrett, M.S. Love, V.M. O'Connell, and R.D. Stanley (eds.) 2007. Biology, assessment, and management of North Pacific rockfishes. Alaska Sea Grant College Publication AK-SG-07-01, University of Alaska Fairbanks.

Grant, W.S., and F.M. Utter. 1980. Biochemical genetic variation in walleye pollock,Theragra chalcogramma: population structure in the southeastern Bering Sea and the Gulf of Alaska. Can. J. Fish. Aquat. Sci. 37:1093-1100.

Grant, W.S., and F.M. Utter. 1984. Biochemical population genetics of Pacific herring (Clupea pallasi). Can. J. Fish. Aquat. Sci 41:856-864.

Grant, W.S., C.I Zhang, T. Kobayashi, and G. Ståhl. 1987. Lack of genetic stock discretion in Pacific cod (Gadus macrocephalus). Can. J. Fish. Aquat. Sci. 44:490-498.

Grant, W.S., R. Bakkala, F.M. Utter, D.J. Teel, and T. Kobayashi T. 1983. Biochemical genetic population structure of yellowfin sole, Limanda aspera, of the North Pacific Ocean and Bering Sea. Fish. Bull. 81:667-677.

Grant, W.S. and B.W. Bowen. 2006. Living in a tilted world: climate change and geography limit speciation in Old World anchovies (Engraulis; Engraulidae). Biological Journal of the Linnean Society 88:673-689.

Grant, W.S., C.I. Zhang, T. Kobayashi, and G. Ståhl G. 1987. Lack of genetic stock discretion in Pacific cod (Gadus macrocephalus). Can. J. Fish. Aquat. Sci. 44: 490-498.

Gustafson, RG, W.H. Lenarz, B.B McCain, C.C. Schmitt, W.S Grant, T.L. Builder, and R.D. Methot. 2000. Status review of Pacific Hake, Pacific cod, and walleye pollock from Puget Sound, Washington. NOAA Technical Memorandum NMFS-NWFSC-44, 275p.

Hauser, L. and G. R. Carvalho. 2008. Paradigm shifts in marine fisheries genetics: ugly hypotheses slain by beautiful facts. Fish and Fisheries 9:333–362

Hauser, L, G.J. Adcock, P.J. Smith, J.H.B. Ramirez, and G.R. Carvalho. 2003. Loss of microsatellite diversity and low effective population size in an overexploited population of New Zealand snapper (Pagrus auratus). Proceeding of the National Academy of Sciences 99:11742-11747.

Hawkins, S.L., J. Heifetz, C.M. Kondzela, J.E. Pohl, R. L. Wilmot, O. N. Katugin, and V.N. Tuponogov. 2005. Genetic variation of rougheye rockfish (Sebates aleutianus) and shortraker rockfish inferred from allozymes. Fish. Bull. 103:524-535.

Hedgecock, D. 1994. Does variance in reproductive success limit effective population sizes of marine organisms? *In* Beaumont AR [ed.]. Genetics and Evolution of Aquatic Organisms (ed. Beaumont AR), pp. 122-134. Chapman & Hall, London.

Hedrick, P.W. 2005. A standardized genetic differentiation measure. Evolution 59:1633-1638.

Heincke, F. 1898. Naturgeschichte des Herings I. Die Lokaformen und die Wanderungen des Herings in den europäischen Meeren. Abhandlungen der deutschen Seefischereivereins 2. 136 pp.

Hemmer-Hansen J, E.E. Nielsen, J. Frydenberg, and V. Loeschcke. 2007. Adaptive divergence in a high gene flow environment: Hsc70 variation in the European flounder (Platichthys flesus L.). Heredity 99:592-600.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapports et Proces-verbaux des Reunions. Conseil international pour l'Exploration de la Mer 20:1-228.

Hutchinson, W.F., C. van Oosterhout, S.I. Rogers, and G.R. Carvalho. 2003. Temporal analysis of archived samples indicates marked genetic changes in declining North Sea cod (Gadus morhua). Proceedings of the Royal Society of London B 270:2125-2132.

Ihssen, P.E., H.E. Booke, J.M. Casselman, J.M. McGlade, N.R. Payne, and F.M. Utter. 1981. Stock identification: methods and materials. Can J. Fish. Aquat. Sci. 38:1838-1855.

Iles, T. D. and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science. Vol. 215, No. 4533 pp. 627-633 .

Jost, L. 2008. Gst and its relatives do not measure differentiation. Molecular Ecology 17:4015-4026.

Kenchington, E., M. Heino, and E.E. Nielsen EE. 2003. Managing marine genetic diversity: time for action? ICES J. Mar. Sci. 60:1172-1176.

Kendall, A.W. and J.R. Dunn. 1985. Ichthyoplankton of the continental shelf near Kodiak Island, Alaska. U.S. Department of Commerce, NOAA Tech. Memo. NMFS 20.

Kimura, D.K., A.M. Shimada, and F.R. Shaw. 1998. Stock structure and movement of taggled sablefish, Anoplopoma fimbria, in offshore northeast Pacific waters and the effects of El Nino-Southern Oscillation on migration and growth. Fish Bull. 96:462-481.

Ladd, C., G.L. Hunt Jr., C. Mordy, S Salo, and P. Stabeno. 2005. Marine environment of the eastern and central Aleutian Islands. 14 (Suppl. 1):22-38.

Lauth, R.R., S.W. McEntire, and H.H. Zenger Jr.. 2006. Geographic distribution, depth range, and description of Atka mackerel, Pleurogrammus monopterygius, nesting habitat in Alaska. Alaska Fishery Research Bulletin 12:164-185.

Lauth, R.R., J. Guthridge, D. Nichol,S.W. McEntire, and N. Hillgruber. 2007. Timing and duration of mating and brooding periods of Atka mackerel (Pleurogrammus monopterygius) in the North Pacific Ocean. Fish. Bull. 105:560-570.

Lee, J.U. 1985. Studies on the fishery biology of the Atka mackerel Pleurogrammus monopterygius (Pallas) in the north Pacific Ocean. Bulletin of Fisheries Research and Development Agency 34:65-125.

Li, G. and D.Hedgecock. 1998. Genetic heterogeneity, detected by PCR-SSCP, among samples of larval Pacific oysters (Crassostrea gigas) supports the hypothesis of large variance in reproductive success. Can. J. Fish. Aquat. Sci. 55:1025-1033.

Logerwell, E.A., K. Aydin, S. Barbeaux, E. Brown, M.E. Conners,

S. Lowe, J.W. Orr, I. Ortiz, R. Reuter, and P. Spencer. 2005. Geographic patterns in the demersal ichthyofauna of the Aleutian Islands. Fish. Oceanogr. 14 (Suppl. 1):93–112.

Lowe, S.A., D.M. Van Doornik and G.A. Winans. 1998. Geographic variation in genetic and growth patterns of Atka mackerel, Pleurogrammus monopterygius (Hexagrammidae), in the Aleutian archipelago. Fish. Bull. 96:502-515.

Mace, P.M. and W. Gabriel. 1999. Evolution, scope and current applications of the precautionary approach in fisheries. Proceedings of the 5th National Stock Assessment Workshop, V. Restrepo (editor). National Marine Fisheries Service, Office of Science and Technology, 1315 East- West Highway, Silver Spring, MD 20910.

MacKenzie, K. and P. Abaunza, 1998. Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods, Fish. Res. 38, pp. 45–56

MacKenzie, K. 2002. Parasites as biological tags in population studies of marine organisms: an update. Parasitology 124:7:153-163.

Mardis, E.R. 2008. Next-generation DNA sequencing methods. Annual Review of Genomics and Human Genetics 9:387-402.

Matala, A.P, A.K. Gray, J. Heifetz, A.J. Gharrett. 2004. Population structure of Alaskan shortraker rockfish, Sebastes borealis, inferred from microsatellite variation. Environmental Biology of Fishes 69:201-210.

Middleton F.A., and 22 co-authors. 2004. Genomewide linkage analysis of bipolar disorder by use of a high-density single-nucleotide-polymorphism (SNP) genotyping assay: A comparison with

microsatellite marker assays and finding of significant linkage to chromosome 6q22. The American Journal of Human Genetics 74:886-897.

Miller, J.A. and A.L. Shanks. 2004. Evidence for limited larval dispersal in black rockfish (Sebastes melanops): implications for population structure and marine reserve design. Can. J. Fish. Aquat. Sci. 61: 1723–1735.

Moen, T, B. Hayes, F. Nilsen, M. Delghandi, K.T. Fjalestad, S.-E. Fevolden, P.R. Berg, and S. Lien. 2008. Identification and characterisation of novel SNP markers in Atlantic cod: Evidence for directional selection. BMC Genetics 9:18.

Moles. A., J. Heifetz, and D.C. Love. 1998. Metazoan parasites as potential markers for selected Gulf of Alaska rockfishes. Fish. Bull 96: 912-916.

NPFMC. 2000. Bering Sea/Aleutian Islands Plan Team summary for Other Red Rockfish. In Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands, pp 22-23. North Pacific Fishery Management Council, , 605 W. 4th Ave, suite 306. Anchorage, AK 99501

NRC. 1998. Improving Fish Stock Assessments, National Academic Press, Washington, DC.

Nei, M. 1973. Analysis of gene diversity in subdivided populations. Proc. Nat. Acad. Sci. 70:3321-3323.

Nielsen E.E., and M.M.Hansen 2008. Waking the dead: the value of population genetic analyses of historical samples. Fish and Fisheries 9:450-461.

Nielsen E.E., P.H. Nielsen, D. Meldrup, and M.M. Hansen. 2004. Genetic population structure of turbot (Scophthalmus maximus L.) supports the presence of multiple hybrid zones for marine fishes in the transition zone between the Baltic Sea and the North Sea. Molecular Ecology, 13, 585–595.

O'Reilly, P.T., M.F. Canino, K.M. Bailey, and P. Bentzen. 2004. Inverse relationship between F_{ST} and microsatellite polymorphism in the marine fish, walleye pollock (Theragra chalcogramma): implications for resolving weak population structure. Molecular Ecology 13:1799-1814.

Ormseth, O.A. and B.L. Norcross. 2009. Causes and consequences of life-history variation in North American stocks of Pacific cod. ICES J. Mar. Sci. 66:349-357.

Palof, K.J. 2008. Population genetic structure of Alaskan Pacific ocean perch (Sebastes alutus). M.S. thesis, University of Alaska-Fairbanks.

Palsson, W.A. 1990. Pacific cod (Gadus macrocephalus) in Puget Sound and adjacent water: biology and stock assessment. Wash. Dep. Fish. Tech. Rep. 112, 137 p.

Pampoulie, C, D.E. Ruzzante, V. Chosson, T.D. Jörundsdóttir, L. Taylor, V. Thorsteinsson, A.K. Daníelsdóttir, and G. Marteinsdóttir. 2006. The genetic structure of Atlantic cod (Gadus morhua) around Iceland: insight from microsatellites, the Pan I locus, and tagging experiments. Canadian Journal of Fisheries and Aquatic Sciences 63:2660-2674.

Pawson, M.G. and S. Jennings. 1996. A critique of methods for stock identification in marine capture fisheries, Fish. Res. 25:203–217.

Planes, S., and P. Lenfant. 2002. Temporal genetic changes between cohorts in a natural population of a marine fish, Diplodus sargus, induced by large variance in individual reproductive success. Molecular Ecology 11:1515-1524.

Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145:1219-1228.

Rousset, F. 2000. Genetic differentiation between individuals. J. Evol. Biol. 13:58-62.

Rousset, F. 2004. Genetic structure and selection in subdivided populations. Princeton University Press, Princeton, NJ.

Sandin, P. 1999. Dimensions of the Precautionary Principle. Human and Ecological Risk Assessment 5:889-907.

Sawyer, S. 1977. Asymptotic properties of the equilibrium probability of identity in a geographically structured population. Adv. Appl. Prob. 9:268-282.

Selkoe K,A,, C.M. Henzler, and S.D. Gaines. 2008. Seascape genetics and the spatial ecology of marine populations. Fish and Fisheries, 9, 363–377.

Sewell, K.B., and , R.J.G. Lester. 1995. Stock discrimination and movement of gemfish, Rexea solandri, as indicated by parasites. Can. J. Fish. Aq. Sci. 52 (Suppl. 1), 225-232.

Shi, Y., D. Gunderson, and P. Munro. 2008. Pacific cod, Gadus macrocephalus, movement between and within eastern Bering Sea, Gulf of Alaska and Aleutian Islands management areas. Final Progress Report, Project # 620. North Pacific Research Board, Anchorage, AK.

Sinclair, M. 1988. Marine populations: an essay on population regulation and speciation. Washington Sea Grant, Seattle. 252 pp.

Skarstein, T.H., J.I. Westgaard, and S.E. Fevolden. 2007. Comparing microsatellite variation in north-east Atlantic cod (Gadus morhua L.) to genetic structuring as revealed by the pantophysin (Pan I) locus. Journal of Fish Biology 70:271-290.

Stabeno,P.J., D.G. Kachel, N. B. Kachel, And M. E. Sullivan. 2005. Observations from moorings in the Aleutian Passes: temperature, salinity and transport. Fish. Oceanogr. 14 (Suppl. 1), 39–54.

Stark, J.W. 2007. Geographic and seasonal variations in maturation and growth of female Pacific cod (Gadus macrocephalus) in the Gulf of Alaska and Bering Sea. Fishery Bulletin 105:396-407.

Swain, D.P., and C.J. Foote. 1999. Stocks and chameleons: the use of phenotypic variation in stock identification. Fish Res 43:113-128.

Swain D.P., J.A. Hutchings, and C.J. Foote. 2005. Environmental and genetic influences on stock identification characters. *In* Cadrin, S.X., K.D. Friedland, and J.R. Waldmann [eds]. Stock identification methods applications in fishery science. Elsevier Academic Press, London, p 45–85.

Taylor, B.L. and A. E. Dizon. 1999. First policy then science: why a management unit based solely on genetic criteria cannot work. Molecular Ecology 8:S11–S16.

Thompson, G.. 1996. The precautionary principle in North Pacific groundfish management. National Marine Fisheries Service, AFSC Quarterly Report, July 1996.

Thompson, G., J. Ianelli , R. Lauth, S. Gaichas,. and K. Aydin. 2008a. Assessment of the Pacific Cod Stock in the Eastern Bering Sea and Aleutian Islands Area. North Pacific Fishery Management Council, 605 W. 4th Ave., suite 306 Anchorage, AK 99501, 182 p.

Thompson, G.G., J.N Ianelli and M. Wilkins. 2008b. Assessment of the Pacific cod stock in the Gulf of Alaska. North Pacific Fishery Management Council, 605 W. 4th Ave., suite 306 Anchorage, AK 99501, 132 p.

Turan. C. 2004. Stock identification of Mediterranean horse mackerel (Trachurus mediterraneus) using morphometric and meristic characters. ICES Journal of Marine Science: 61(5):774-781

Turner, T. F., J. P. Wares, and J. R. Gold. 2002. Genetic effective size is three orders of magnitude smaller than adult census size in an abundant, estuarine-dependent marine fish (*Sciaenops ocellatus*). Genetics 162(3):1329-1339.

Utter, F.M., and H.O. Hodgins. 1969. Lactate Dehydrogenase Isozymes of Pacific Hake (Merluccius productus). Journal of Experimental Zoology 172:59-67..

Vigliola, L., P.J. Doherty, M.G. Meekan, D.M. Drown, M.E. Jones, and P.H. Barber. 2007. Genetic identity determines risk of post-settlement mortality of a marine fish. Ecology 88:1263-1277.

Waldman, J.R., R.A. Richards, W.B. Schill, I. Wirgin, and M.C. Fabrizio. 1997. An empirical comparison of stock identification techniques applied to striped bass. Trans. Am. Fish. Soc. 126: 369-385.

Ward, R.D., M. Woodwark, and D.O.F. Skibinski. 1994. A comparison of genetic diversity levels in marine, freshwater, and anadromous fishes. J. Fish. Biol. 44: 213-232.

Waples R.S. 1989. A generalized approach for estimating effective population size from temporal changes in allele frequency. Genetics 121:379-391.

Waples, R.S. 1995. Evolutionary significant units and the conservation of biological diversity under the endangered species act. American Fisheries Society Symposium 17:8-27.

Waples, R.S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J. Heredity 89:438-450.

Waples, R.S. and Gaggiotti, O. 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their

degree of connectivity. Molecular Ecology 15:1419–1439.

Waples, R.S., W.W. Dickhoff, L. Hauser, and N. Ryman. 2008a. Six decades of fishery genetics: Taking stock. Fisheries 33:76-79.

Waples, R.S., A.E. Punt and J.M. Cope. 2008. Integrating genetic data into management of marine resources: how can we do it better? Fish and Fisheries 9:423–449.

Weir, B.S. and C.C. Cockerham. 1984. Estimating F-statistics for the analysis of population structure. Evolution 38:1358-70.

Westrheim, S.J. 1987. Parabrancial X-cell lesions in trawl-caught Pacific cod (Gadus macrocephalus) off the west coast of Canada -- incidence and effects. Can. Tech. Rep. Fish. Aquat. Sci. 2092, 390 p.

Wilimovsky, N.J., A. Peden, and J. Peppar. 1967. Systematics of six demersal fishes of the north Pacific Ocean. Fish. Res. Board Can. Tech. Rep. 34, 95 p.

WKREDS. 2009. Report of the Workshop on Redfish Stock Structure. ICES CM 2009/ACOM:37.

Table 1. Example framework for defining spatial management units.

HARVEST AND TRENDS	
Factor and criterion	Justification
Fishing mortality (5-year average percent of F_{abc} or F_{ofl})	If this value is low, then conservation concern is low
Spatial concentration of fishery relative to abundance (Fishing is focused in areas << management areas)	If fishing is focused on very small areas due to patchiness or convenience, localized depletion could be a problem.
Population trends (Different areas show different trend directions)	Differing population trends reflect demographic independence that could be caused by different productivities, adaptive selection, differing fishing pressure, or better recruitment conditions
Barriers and phenotypic characters	
Generation time (e.g., >10 years)	If generation time is long, the population recovery from overharvest will be increased.
Physical limitations (Clear physical inhibitors to movement)	Sessile organism; physical barriers to dispersal such as strong oceanographic currents or fjord stocks
Growth differences (Significantly different LAA, WAA, or LW parameters)	Temporally stable differences in growth could be a result of either short term genetic selection from fishing, local environmental influences, or longer-term adaptive genetic change.
Age/size-structure (Significantly different size/age compositions)	Differing recruitment by area could manifest in different age/size compositions. This could be caused by different spawning times, local conditions, or a phenotypic response to genetic adaptation.
Spawning time differences (Significantly different mean time of spawning)	Differences in spawning time could be a result of local environmental conditions, but indicate isolated spawning stocks.
Maturity-at-age/length differences (Significantly different mean maturity-at-age/ length)	Temporally stable differences in maturity-at-age could be a result of fishing mortality, environmental conditions, or adaptive genetic change.
Morphometrics (Field identifiable characters)	Identifiable physical attributes may indicate underlying genotypic variation or adaptive selection. Mixed stocks w/ different reproductive timing would need to be field identified to quantify abundance and catch
Meristics (Minimally overlapping differences in counts)	Differences in counts such as gillrakers suggest different environments during early life stages.
Behavior & movement	
Spawning site fidelity (Spawning individuals occur in same location consistently)	Primary indicator of limited dispersal or homing
Mark-recapture data (Tagging data may show limited movement)	If tag returns indicate large movements and spawning of fish among spawning grounds, this would suggest panmixia
Natural tags (Acquired tags may show movement smaller than management areas)	Otolith microchemistry and parasites can indicate natal origins, showing amount of dispersal
Genetics	
Isolation by distance (Significant regression)	Indicator of limited dispersal within a continuous population
Dispersal distance (<<Management areas)	Genetic data can be used to corroborate or refute movement from tagging data. If conflicting, resolution between sources is needed.
Pairwise genetic differences (Significant differences between geographically distinct collections)	Indicates reproductive isolation.

Table2. The linear density of *S. melanostictus* that was obtained from abundance surveys was used with a set of plausible N_e/N_{census} ratios to evaluate effective densities (D_e) which were in turn used to estimate ranges of distances (4σ) that represent the spatial scale of population structure from the slope (b) of the relationship between genetic divergence and geographic distance.

		mean		Lower 5%		Upper 5%	
		b	$b^{-1}=4D_e\sigma^2$	b	$b^{-1}=4D_e\sigma^2$	b	$b^{-1}=4D_e\sigma^2$
		$1.041*10^{-5}$	$9.602*10^4$	$1.186*10^{-6}$	$8.434*10^5$	$2.009*10^{-5}$	$4.977*10^4$
N_e/N_{census}	De	σ^2	4σ	σ^2	4σ	σ^2	4σ
0.1	1125	21	18	187	55	11	13
0.05	563	43	26	375	77	22	19
0.01	113	213	58	1873	173	111	42
0.005	56	427	83	3746	245	222	60
0.001	11	2134	185	18732	547	1108	133

Table 3. Summary of available data on stock identification for BSAI blackspotted/rougheye rockfish.

HARVEST AND TRENDS	
Factor and criterion	Available information
Fishing mortality (5-year average percent of F_{abc} or F_{ofl})	Recent catch in the BS and AI areas are comparable to potential area-specific ABCs
Spatial concentration of fishery relative to abundance (Fishing is focused in areas << management areas)	Catches are distributed throughout the Aleutian Islands and along the EBS slope north to the Pribilof Islands
Population trends (Different areas show different trend directions)	Population trends appear to be stable in the Aleutian Islands and EBS slope
Barriers and phenotypic characters	
Generation time (e.g., >10 years)	The generation time is approximately 53 years
Physical limitations (Clear physical inhibitors to movement)	The Aleutian North Slope Current does not extend west of the central AI, limiting the connection with the EBS slope for the central and western AI. Also, studies of the AI ecosystem indicate a "biophysical transition zone" at Samalga Pass (Logerwell et al. 2005)
Growth differences (Significantly different LAA, WAA, or LW parameters)	Differences growth curves and length-at-age relationships between the EBS and Aleutian Island subareas. However, differences in size at age are not observed for all ages
Age/size-structure (Significantly different size/age compositions)	Significant differences in both age and size compositions between the EBS and Aleutian Island subareas based upon survey data from 2002 and 2008
Spawning time differences (Significantly different mean time of spawning)	Unknown
Maturity-at-age/length differences (Significantly different mean maturity-at-age/ length)	Unknown
Morphometrics (Field identifiable characters)	Unknown (within either blackspotted or rougheye rockfish)
Meristics (Minimally overlapping differences in counts)	Unknown (within either blackspotted or rougheye rockfish)
Behavior & movement	
Spawning site fidelity (Spawning individuals occur in same location consistently)	Unknown
Mark-recapture data (Tagging data may show limited movement)	Mark-recapture data not available
Natural tags (Acquired tags may show movement smaller than management areas)	Unkown
Genetics (for blackspotted rockfish only)	
Isolation by distance (Significant regression)	Significant pattern of isolation by distance
Dispersal distance (<<Management areas)	Single generation dispersal scale of <= ~ 550 km, which is << the combined BSAI management area
Pairwise genetic differences (Significant differences between geographically distinct collections)	Significant pairwise difference between EBS and Aleutian Island genetic samples

Table 4. Summary of available data on stock identification for Pacific cod.

HARVEST AND TRENDS	
Factor and criterion	Justification
Fishing mortality (5-year average percent of F_{max})	Fishing mortality rates are typically close to F_{ABC}, which is much lower than F_{max}.
Spatial concentration of fishery relative to abundance (Fishing is focused in areas << management areas)	Harvests are concentrated along the shelf edge and near Unimak Island. Relative harvests between BS and AI have been similar to relative survey biomasses between the areas.
Population trends (Different areas show different trend directions)	Trend in BS, based on assessment, has been down recently. Trend in AI, based on survey, has been variable recently.
Barriers and phenotypic characters	
Generation time (e.g., >10 years)	Generation time is < 10 years
Physical limitations (Clear physical inhibitors to movement)	No apparent physical barriers to adult dispersal, except perhaps warm coastal waters in NW Pacific Ocean
Growth differences (Significantly different LAA, WAA, or LW parameters)	Higher initial growth rates at lower latitudes
Age/size-structure (Significantly different size/age compositions)	Significant differences in size structure for male and female cod in commercial catches between Eastern Bering Sea and Aleutian Islands.
Spawning time differences (Significantly different mean time of spawning)	Significantly different mean times of spawning among North American populations.
Maturity-at-age/length differences (Significantly different mean maturity-at-age/ length)	Significantly lower age at 50% maturity for female cod (4.6 vs. 4.9 years) in Gulf of Alaska compared with Eastern Bering Sea. No evidence for differences between the Eastern Bering Sea and Aleutian Islands
Morphometrics (Field identifiable characters)	Morphometric characters did not distinguish among putative stocks from British Columbia to the Bering Sea.
Meristics (Minimally overlapping differences in counts)	Meristic counts of five characters showed an irregular clinal trend and suggested separate stocks in British Columbia, SE Alaska, and Bering Sea
Behavior & movement	
Spawning site fidelity (Spawning individuals occur in same location consistently)	Demographically discrete and temporally stable spawning locations.
Mark-recapture data (Tagging data may show limited movement)	Tagging results indicated limited adult movement and/or some components of the stock are non-migratory.
Natural tags (Acquired tags may show movement smaller than management areas)	Biologically acquired tags (otolith microchemistry and parasite loads) indicate discrete demographic histories for some groups
Genetics	
Isolation by distance (Significant regression)	Highly significant IBD patterns in North American Pcod samples with both microsatellite DNA markers and mtDNA sequence data.
Dispersal distance (<<Management areas)	Dispersal estimates from the IBD relationship over realistic range of effective adult densities were << the size of contemporary management areas, less than 100 km per generation.
Pairwise genetic differences (Significant differences between geographically distinct collections)	Significant differentiation between sample pairs routinely observed at geographic distances exceeding ~ 1500 km with both microsatellite markers and mtDNA sequence data.

Table 5. Summary of available data on stock identification for BSAI and GOA Atka mackerel

HARVEST AND TRENDS	
Factor and criterion	Justification
Fishing mortality (5-year average percent of F_{max})	Fishing mortality rate (F) and catch/biomass rate averaged 0.225 and 0.120, respectively, over the last five years.
Spatial concentration of fishery relative to abundance (Fishing is focused in areas << management areas)	Fishery concentrated in areas of highest abundance with trawlable habitat, excepting Steller Sea Lion Exclusion zones.
Population trends (Different areas show different trend directions)	Stable population size characterized by highly variable recruitment.
Barriers and phenotypic characters	
Generation time (e.g., >10 years)	Generation time is < 10 years
Physical limitations (Clear physical inhibitors to movement)	No apparent barriers to movement throughout life history. Neustonic larvae develop in pelagic habitats for a year before recruitment into demersal populations. Dispersal potential during larval phase is very high.
Growth differences (Significantly different LAA, WAA, or LW parameters)	Apparently higher growth rates in eastern Aleutian Islands and Gulf of Alaska versus western Aleutian Islands.
Age/size-structure (Significantly different size/age compositions)	None observed
Spawning time differences (Significantly different mean time of spawning)	None observed
Maturity-at-age/length differences (Significantly different mean maturity-at-age/ length)	Size at maturity increases from west to east across Aleutian Islands to Gulf of Alaska
Morphometrics (Field identifiable characters)	Unknown
Meristics (Minimally overlapping differences in counts)	Unknown
Behavior & movement	
Spawning site fidelity (Spawning individuals occur in same location consistently)	Yes
Mark-recapture data (Tagging data may show limited movement)	Tagging results indicate that adults apparently not highly migratory.
Natural tags (Acquired tags may show movement smaller than management areas)	Unknown
Genetics	
Isolation by distance (Significant regression)	No apparent IBD or genetic structure throughout most of geographic range using microsatellites.
Dispersal distance (<<Management areas)	No dispersal distances estimated as no prerequisite IBD pattern observed.
Pairwise genetic differences (Significant differences between geographically distinct collections)	No consistent pairwise genetic differences between geographically discrete samples using microsatellite markers. Analysis of mtDNA variation inferred a recent, severe population bottleneck or selective sweep, followed by population expansion. Insufficient time has elapsed for significant genetic divergence to accrue in large effective populations spanning the contemporary geographic range.

Management Action

	One stock	Multiple stocks
One stock	✓	Management spatial scale too small
Multiple stocks	Management spatial scale too large	✓

States of Nature

Figure1. The outcomes of management decisions regarding stock structure applied to two states of nature; the green checks correspond to a management action consistent with the state of nature.
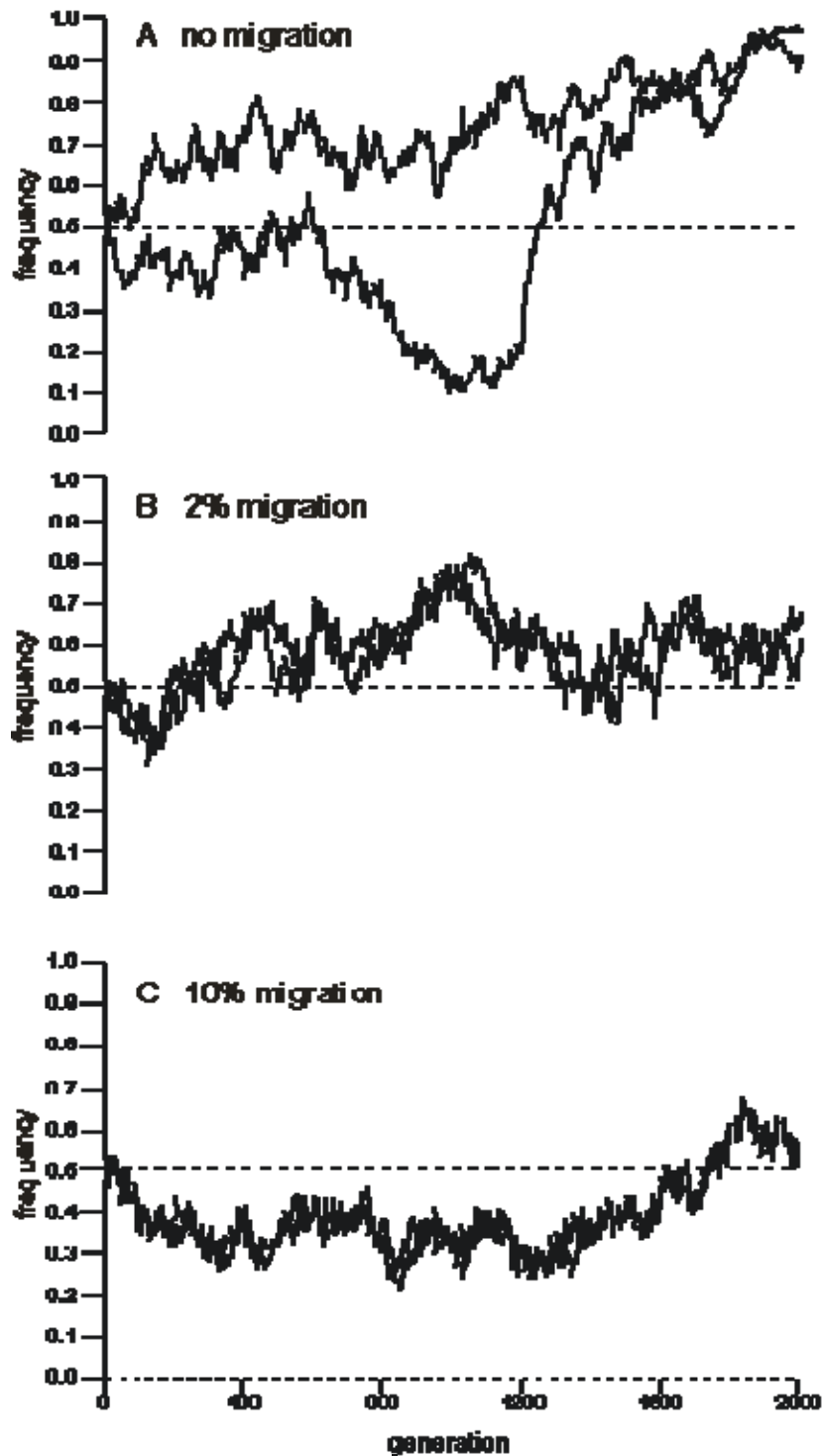
Figure 2. The influence of migration rate on genetic drift in two simulated populations of 1,000 individuals, each starting with an initial allele frequency of 0.5. A, no migration between populations; B, 2% migration (20 individuals per generation); C, 10% migration (100 individuals per generation). Note that allele frequencies drift both towards and away from each other.
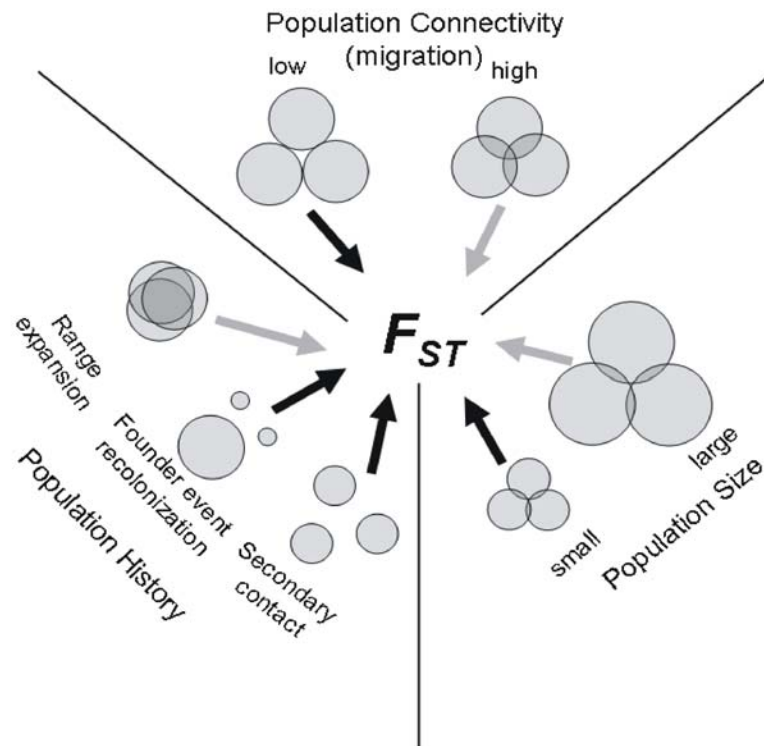
Figure 3. Conceptual diagram showing the influence of population history, size, and connectivity on estimates of F_{ST}. Black arrows show population characteristics that promote differentiation while gray arrows designate characteristics that prevent differentiation. Adapted with permission from Hauser and Carvalho (2008).
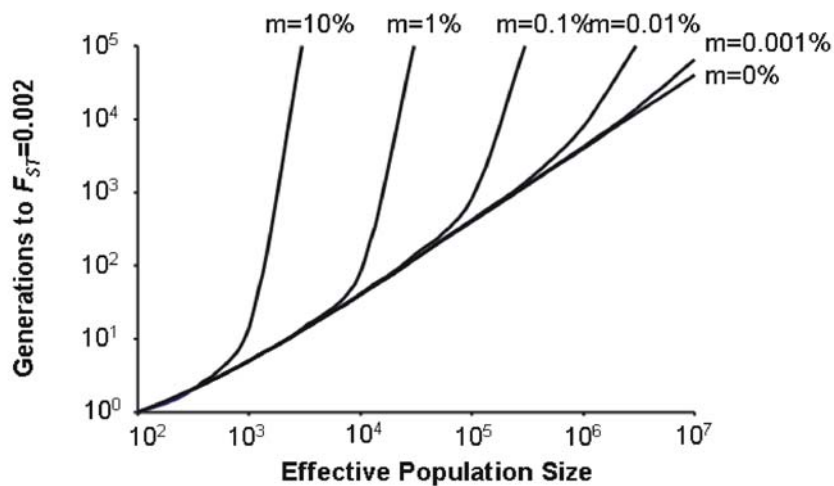
Figure 4. Number of generations required for F_{ST} to reach 0.002, a level statistically significant from zero and commonly reported in marine species in response to different migration rates (m). Note that several thousand generations may be required to reach that level of F_{ST} even under complete isolation (m = 0) Adapted from Hauser and Carvalho (2008).
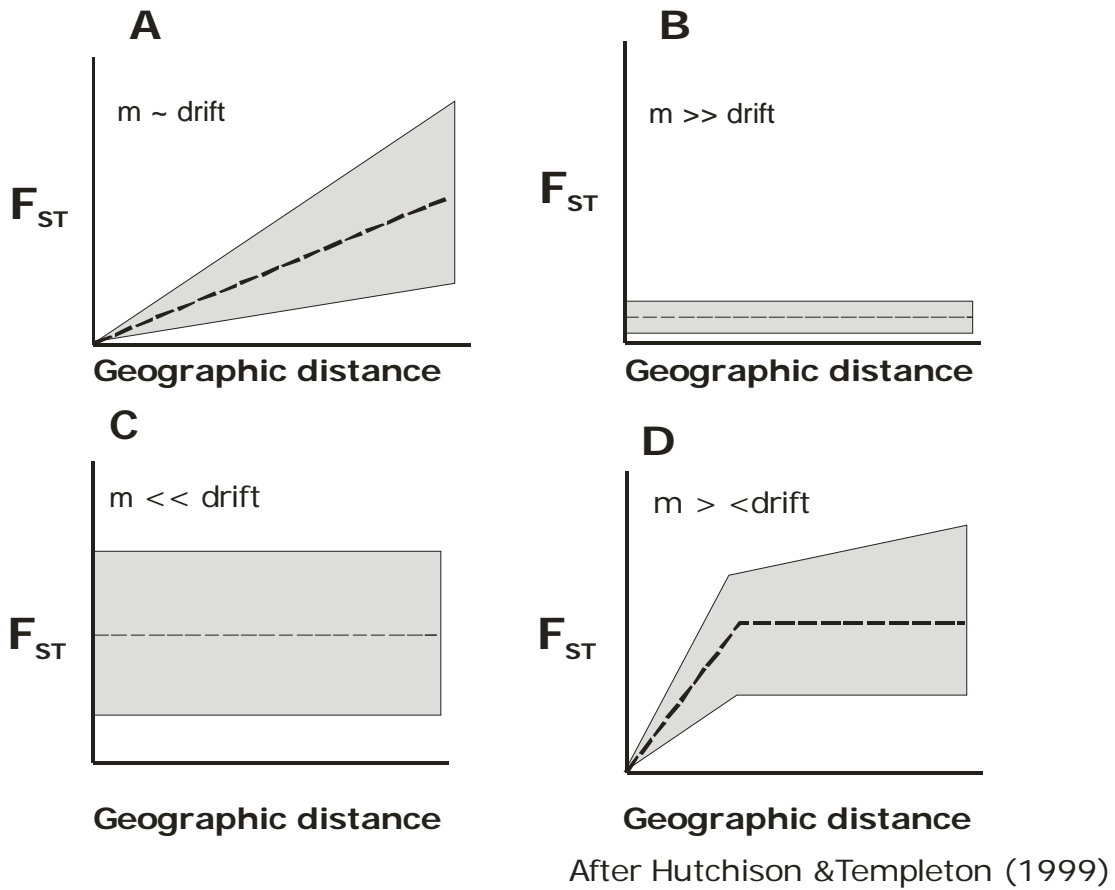
Figure 5. Hypothetical relationships between genetic divergence (F_{ST}) and geographic distance with differing relative influences of genetic drift and migration. A, regional equilibrium where drift is proportional to migration; B, migration predominates; C, drift predominates; D, migration or drift predominates at different spatial scales.
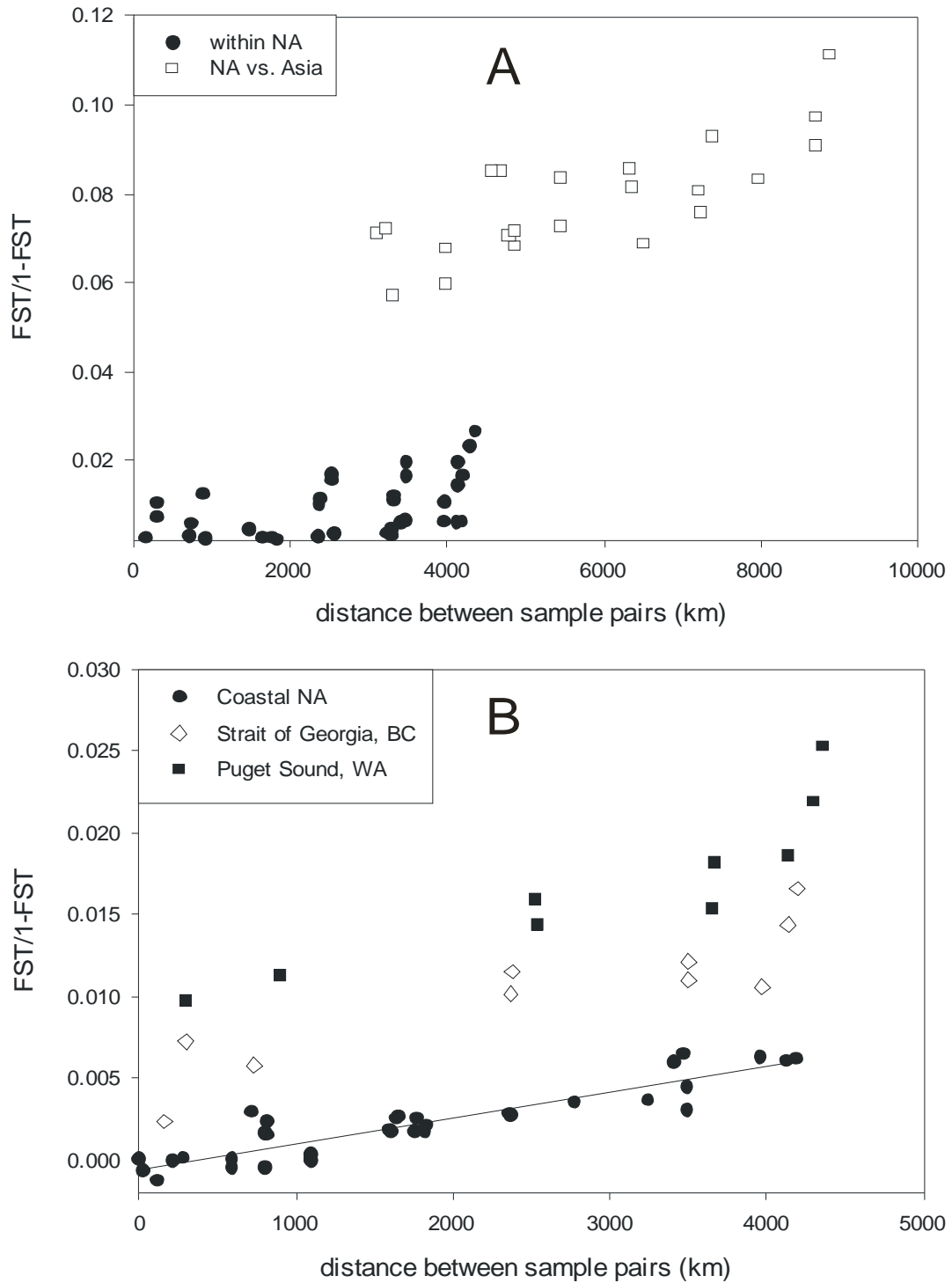
Figure 6. Departures from genetic isolation by distance patterns over various spatial scales in Pacific cod. A, pairwise linearized F_{ST} values from 11 microsatellite loci between locations in North America (NA) and Asia (Canino et al in press a); B, pairwise linearized F_{ST} values for the same loci between locations in North America only (coastal Washington State to Aleutian Is.).Note differences in both axes. Samples from the Georgia Basin (Puget Sound and Strait of Georgia) are clear outliers to the coastal groups (Cunningham et al. 2009).
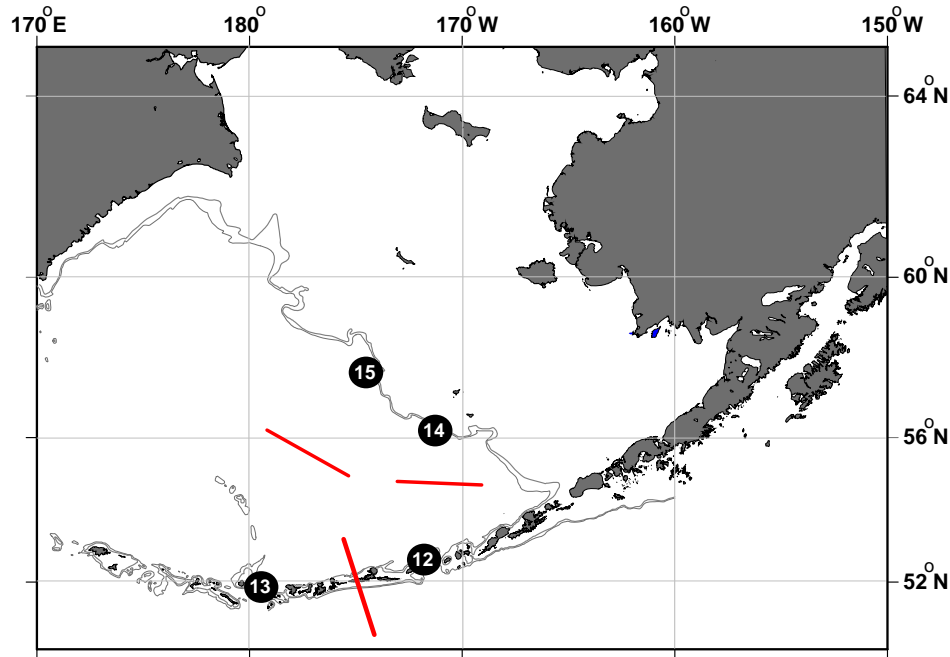
Figure 7. Map of geographic centers of collections of *S. melanostictus* which were subjected to genetic analysis. The set of populations was not genetically homogeneous. Red lines reflect significant pairwise tests (based on *G*-tests for which significance levels were estimated by Monte-Carlo simulations) with a sequential Bonferroni adjustment.
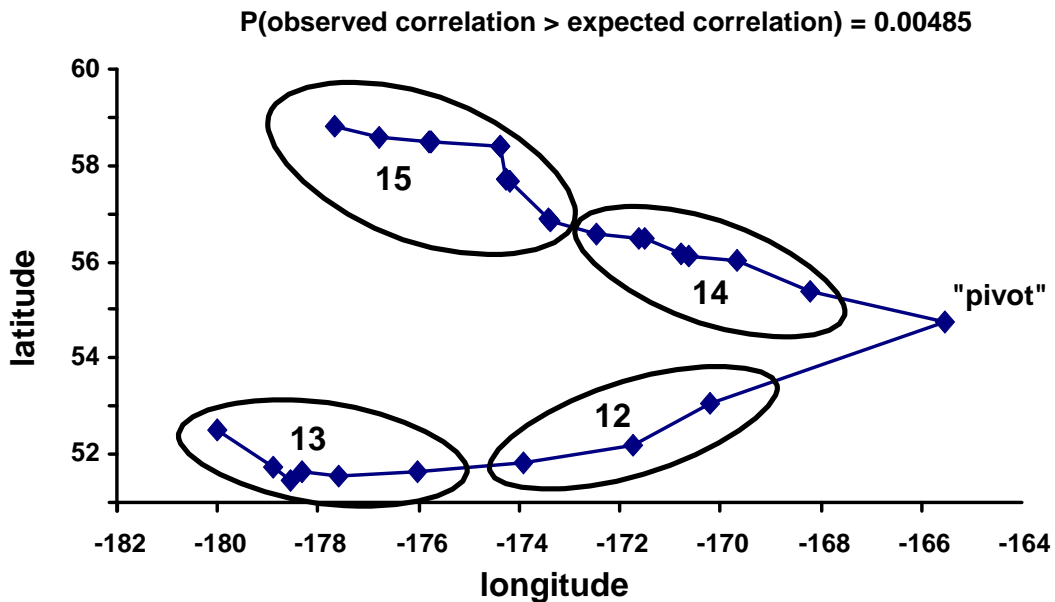

Figure 8. Distribution of all sampling locations along the Bering Sea shelf break. Diamonds demonstrate the geographic spread, but not the numbers of individuals. The ellipses in this figure represent the pools of collections analyzed previously. For example the six collection sites in 15 were combined for previous analyses. The "pivot" in the figure is the easternmost corner of the shelf edge in the Bering Sea (Figure 7).