IDENTIFYING FISH SUBPOPULATIONS

PROCEEDINGS OF A
CALIFORNIA SEA GRANT
WORKSHOP

EDITOR, DENNIS HEDGECOCK

A CALIFORNIA SEA GRANT
COLLEGE PROGRAM PUBLICATION

CALIFORNIA
SEA GRANT

Published by the California Sea Grant College Program, Institute of Marine Resources, University of California, La Jolla, 1986. Copies are available from the California Sea Grant College Program, University of California, A-032, La Jolla, California 92093.

This work is the result of research sponsored in part by National Sea Grant College Program, NOAA, Department of Commerce, under Grant #NA80AA-D-00120, Project #A/P-1, through the California Sea Grant College Program, and in part by the California State Resources Agency. The U.S. Government is authorized to produce and distribute reprints for governmental purposes.

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Rosemary Amidei
Communications Coordinator

On the cover: Chinook salmon print. From *The Printer's Catch: An Artist's Guide to Pacific Coast Edible Marine Life* by Christopher M. Dewees (Sea Challengers, Los Osos, California). Mr. Dewees is Marine Fisheries Specialist for the Marine Advisory Program of the California Sea Grant College Program

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JANUARY 27, 1984

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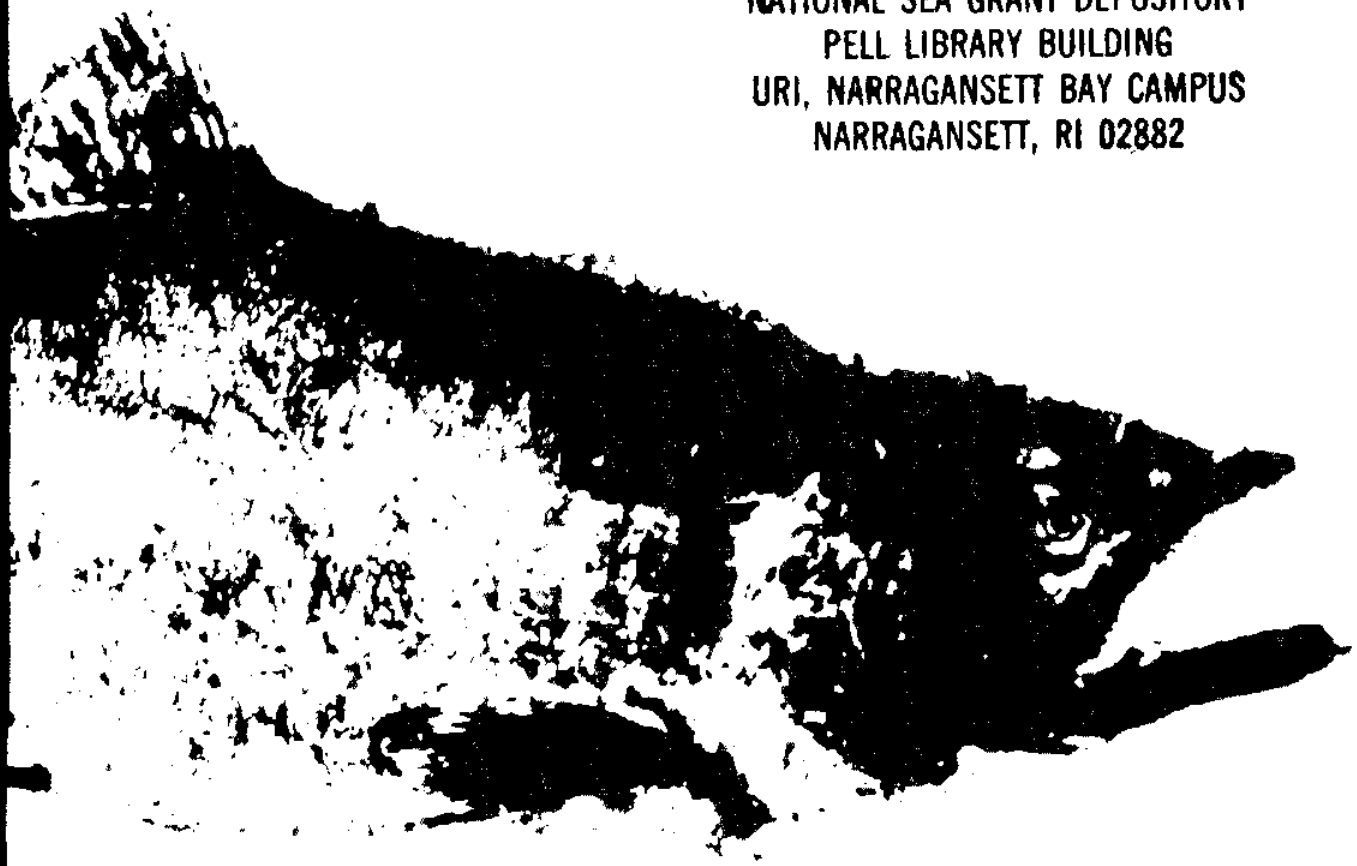

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REPORT NO. T-CSGCP-013

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WELCOME

JAMES J. SULLIVAN, Program Manager, California Sea Grant College Program

It is my very great pleasure to welcome all of you to this workshop on identifying fish subpopulations. The California Sea Grant College Program is sponsoring the meeting (1) to determine why and how techniques such as electrophoresis are being applied to problems of fisheries research, (2) to assess how data on fish subpopulations are presently applied to management policy, and (3) to identify future applications of subpopulation identification to fisheries management.

I am delighted to see so many people here. In particular I would like to introduce the members of the organizing committee: Fred Utter of the Northwest Alaska Fisheries Center, Herbert Frey of the California Department of Fish and Game, and Dennis Hedgecock of Bodega Marine Laboratory, UC Davis, who chaired the committee. I would also like to introduce my assistant, Lindy Nagata, who brought the workshop together.

INTRODUCTION

DENNIS HEDGECOCK, Bodega Marine Laboratory, University of California, Davis

I would like to echo Jim's welcome and extend my appreciation for your attendance. I am gratified by the interest that this subject has generated.

This workshop originated in response to a concern expressed by the National Sea Grant College Program about "the validity of the stock concept and its usefulness in fisheries management." That concern was engendered by a recent proliferation of proposals for utilizing techniques of gel electrophoresis for identifying fish subpopulations. We have therefore attempted to provide a forum for researchers, fisheries managers, and Sea Grant representatives to discuss this methodology, its application to real management problems, and criteria that might be used by Sea Grant to decide among the proposals competing for limited funds for fisheries research.

In its initial stages of organization this meeting was informally called the Electrophoresis Workshop. Because we are addressing a problem that has quite a long history in fishery science, however, the title has been changed to Workshop on Identifying Fish Subpopulations. For reasons that will become clear in the presentations to follow, electrophoresis has simply become the method of choice for examining a general question that dates back to Heinke's 1898 morphological analysis of herring stocks. This and other work during the descriptive phase of fishery science in the early part of the twentieth century was motivated mainly by taxonomic interest. Necessity for taxonomical description eventually gave way with the development of the modern theory of fishing in the 1950s to a biological necessity for identifying subpopulations. Work by Ricker, Beverton, Holt, and others showed that it was possible to fish a population down to a point at which it could not replace itself, a process Cushing later termed "recruitment overfishing." As soon as this problem was recognized, fishery science began to emphasize the process of reproduction and the need to identify the population units responsible for that reproduction.

The next point of biological interest in the subpopulation question is something that has been termed the "fishing up" process. In this process, sympatric species that differ in life history traits are differentially susceptible to overfishing.

Generally positive correlations among adult body size, age, sexual maturity, and fecundity of fishes render the largest, and usually the most highly-prized, species the most susceptible to recruitment overfishing. Once adult stocks are depleted and subsequent recruitment fails, fishing effort is focussed on the next largest species in a multispecies assemblage. In several fisheries, species have been sequentially eliminated on the basis of size selective fishing and the correlation of size with important life history traits. There is no reason to doubt that the "fishing up" process does not also operate among the genetically differentiated subpopulations of a single species.

These two phenomena, "recruitment overfishing" and the "fishing up" process, give identification of species and subpopulations a practical urgency. We are not simply engaged in a taxonomic exercise to find out how many different subpopulations or races exist. Because subpopulations play a crucial role in the reproduction of fishes and in their response to fishing pressures, their identification is necessary for sound fisheries management.[1]

The last point I want to make concerns semantic problems in talking about stocks and subpopulations. In his contribution to a symposium on the identification of fish subpopulations, published in 1957 by the U.S. Fish and Wildlife Service, John Marr pointed out that people do not always agree on the meaning of the word "stock." I concur with Marr's definition of a stock as a population that is actually fished and managed. Thus defined only in relation to human activity, the word "stock" does not pretend to describe a natural unit of biological organization. On the other hand, a subpopulation is a group of fish that interbreeds more or less randomly with itself and less often with other such subpopulations. Subpopulations are natural units of biological organization defined by bonds of mating. Because a stock of fish, as recognized by the fishery and its managers, may comprise more than one subpopulation, a biological basis for management of such a mixed stock demands identification of the underlying subpopulations. For this reason I believe we should speak of a "subpopulation concept" rather than a "stock concept."

I have asked Alec MacCall, who is not a geneticist but a fish population biologist and a manager, to begin the workshop by discussing the biological rationale for identifying populations.

Then we will have a series of papers discussing the techniques and applications of electrophoresis, since this is the primary tool used today. Fred Utter, a pioneer in this field, is going to review the methodology and explain why it has become the primary tool. Graham Gall will then discuss his work on rainbow trout. Irving Kornfield will talk about his work on Atlantic herring and describe another molecular technique with potential for identifying fish subpopulations: restriction enzyme digestion of mitochondrial DNA. Finally, I will speak about my Sea Grant-supported research on the population structure of the northern anchovy.

This afternoon's program is intended to stimulate exchange among managers, researchers, and representatives of agencies responsible for funding fisheries research. A panel discussion to be moderated by Rich Lincoln will address both the concerns raised by Sea Grant and any questions raised by participants.

[1]A comprehensive review of the topic is given in the proceedings of the STOCS Symposium published in the *Canadian Journal of Fisheries and Aquatic Sciences*, Vol. 38, 1981.

PART I

APPLYING ELECTROPHORESIS TO FISHERIES RESEARCH AND MANAGEMENT

REVIEW OF THE BIOLOGICAL RATIONALE FOR IDENTIFYING SUBPOPULATIONS IN FISHERIES

ALEC MAC CALL
Southwest Fisheries Center, National Marine Fisheries Service

In looking through the literature for definitions of "stock," I felt that what I read did not address the subject very well. There are two important questions we have to answer in defining a stock. First, what do we want to use the definition for? I call this the operational consideration. The second question is, what do we know about the presumed stock? This is the informational consideration.

Often the first, or operational, consideration is the main one. If we consider the operational question exclusively, we can wind up with some biologically inappropriate, but nonetheless functional, stock definitions. For example, consider Ecuador's management of tuna in its territorial sea. Although the fish come and go from that area, the Ecuadoran government believes that this tuna is its stock, to manage however it wants. So Ecuador's definition of "stock" is purely operational and has very little biological basis. Similarly, an operational definition sometimes is necessary simply because of lack of knowledge. A good example comes from the multispecies trawl fishery in the Gulf of Thailand where a single trawl may bring up several dozen different species simultaneously, making it difficult to manage any single species. Several years ago during his work on this trawl fishery, John Gulland calculated the catch per effort and determined a production curve for all the species lumped together. Although people said, "You can't do that," his solution was, as a matter of fact, probably the best that could be achieved, and it did give an answer. His technique did relate the abundance and the productivity of the stock (in this case, made up of many species) to the rate of fishing.

These are extreme cases; we hope that most often there will be a balance between the operational and the informational components in the definition of a stock. I think some of the uncertainty about the utility of the stock concept has been the result of overlooking the first question. If we only look at biological considerations in an abstract case, we might formulate definitions of stock that have no use in the real world of management. My definition of stock is a modified version of Peter Larkin's definition[1] in which the operational and informational considerations are well-balanced. Stock is a population of organisms, [ideally] sharing a common gene pool, that is *sufficiently* discrete [and nominally identifiable] to warrant

consideration as a self-perpetuating system that can be managed. (Emphasis and inserts are mine.)

I believe that all fishery management is based implicitly on the concept of a stock. The stock simply is that entity from which the catches are taken, and the problems of definition often reduce to a question of appropriate geographic scale. In many fisheries, the stock is simply defined by the method used to assess it. For example, virtual population analysis, sometimes called cohort analysis, defines the historical abundance of a stock simply by adding up the catches that were taken from it, with correction for mortality and other variables. There is a problem in deciding which catches to include, but, nonetheless, the method defines the stock. Similarly, in production modeling we plot the abundance in the form of a catch per unit effort against the effort. Presumably, the abundance declines as the rate of removal increases. In doing a production model, the question again is whether to put geographically dispersed populations together or to keep them separate. Perhaps the key is whether reproduction by one segment contributes to recruitment to the other segment. One way to answer that kind of question is to do a tagging study and see if the fishes actually move. Again, we wind up with a concept of a *de facto* stock, because the stock is simply defined by where the tags go. This leads to a fairly typical problem though: we have fuzzy edges.

I can demonstrate the nature of fuzzy edges from a tagging study of Pacific mackerel conducted from 1939 to 1941. There were five regions: Monterey Bay, southern California, northern Baja California, Sebastian Vizcaino Bay, and southern Baja. Quite a few tags were released in all of those locations—32,000 in southern California. We plotted the per thousand tags returned from various areas by the two major areas of release, southern California and central California.[2] In southern California we got 28 per thousand tags back, so that was designated unity, to which all the other areas' results were scaled. In northern Baja California, we got only 72% of unity back; in Sebastian Vizcaino Bay, 47%; and in southern Baja California, only 25%. As distance increased, the fraction of tags we got back decreased, but there isn't any place where the tagged fish just disappeared. This points up a continuing problem in stock definition; stocks slowly trail off with distance.

Although such tagging studies provide useful information about fisheries, they are very expensive because the researcher has to go to where the fish are. What we really prefer is some sort of simple, natural tag—an obvious morphological characteristic—so that we can bring the fish to us and figure out which ones they are. Such "tags" do exist, but are often concealed by natural variability among stocks or subpopulations. For example, off New Zealand, some scientists thought there might be two species of *Trachurus*, while others believed there was only one. The taxonomy was completely confused until about ten years ago when R. W. Gauldie used electrophoresis to demonstrate that there were two distinct electrophoretic patterns. This pattern was used to separate these fish into two groups, which then were seen clearly to differ morphologically. The position of the termination of the accessory lateral line differed considerably between the two species, although up to that time this was seen simply as a variable characteristic.[3]

To use a natural tag we must know enough about a species to identify an appropriate, variable characteristic. Often we have little knowledge about subpopulations or species, and about all we can do is to look at different geographic areas—let geography do the separating in a sense. For example, a study of the northern anchovy revealed that its length at a specified age is really quite variable in different areas along the Pacific coast, with variations of about one standard error. This difference is fairly direct evidence that mixing is limited. We do not know whether this is a genetic or an environmental characteristic, but once the fish are past a very small stage, their growth apparently is determined and they are not mixing.

In another study of anchovies, Jerry Spratt of the California Department of Fish and Game noticed that the size of anchovy otoliths relative to the size of the fish seemed to vary up and down the coast.[4] He compared otolith weight to fish length for various areas and found that, although for the very smallest fish there was no difference, as the fish got larger, the difference in otolith weight to fish length between the two groups was 1.5 standard errors apart, which is quite a solid difference. He projected that, based on that characteristic alone, there is about an 80% chance of categorizing a fish into the right group. Again, this strongly suggests that mixing is limited.

Based on tagging studies that showed that some fish actually do travel long distances along the coast, we originally had assumed that the population of anchovies was fairly thoroughly mixed. However, more recent evidence from the studies on length at age and other specific characteristics indicates that the fish in one geographic area are not mixing into other areas. Perhaps the whole population moves up and down to some extent, but there is limited mixing as far as we can tell.

In the case of major coastal pelagic fisheries, such as anchovies, sardines, and Pacific mackerel, the operational considerations are quite important, and for that reason we define our stock by fixed geographic boundaries. These boundaries are well defined operationally, and are particularly suited to fishery independent surveys, such as acoustic surveys, or egg and larvae surveys. The location of those geographic boundaries is based on genetic work done 10 to 20 years ago that indicated that there was a fairly sudden shift in the genetic composition in those areas. The work was limited, however, and we need to know more. One of the most difficult problems with a fixed geographic boundary is that the fish do move north and south seasonally; during oceanic anomalies such as El Niño, the movements are even stronger. Certainly the fish are not respecting our boundary. We do not know how much they move because we do not have good morphological characteristics by which to identify these stocks. In addition, even if the stocks are genetically distinct, they still may mix physically, so that in the vicinity of our boundary we may be able to catch either stock. We might know that two stocks are separate, but we cannot say where the separation occurs.

The boundaries, or clines, can be very strongly affected by fishing pressure, causing general shifts simply as a result of differential removals on one side of the boundary. A good example is the sardine fishery in which there was continuous northward migration of sardines all during the 1950s; as fishing removed sardines from southern California, they seemed to be steadily replaced by fish moving up the Baja California coastline.[5] We had reason to believe from blood serological research that there was a northern and a southern stock of sardines.[6] However, because fishing steadily removed the northern stock and there was a continual influx of southern stock, we may have totally annihilated the northern stock. Now there is a possibility of a

resurgence of the sardine; we have evidence that the population is increasing. For a person like me who is going to have to write a management plan for this fish, it is rather important to determine whether the northern stock still exists. Is the new sardine stock going to be the same as the old or is it going to be something different? If the genetic composition is different, can we expect the productivity to be the same as for the old stock? If it looks as if it is the same stock as it used to be, we would feel more confident that the productivity would be the same. On the other hand, we might want to be more conservative if we see that the genetic composition is actually different than it used to be. Presumably, fish from the south are not as well adapted to reproducing in the colder waters to the north.

In the case of the sardine fishery, as in many cases in the United States, the answer to the first question I posed, "What do we want to use it for?" is clear. The Fishery Conservation and Management Act tells us that we are to manage these fisheries for optimum yield. The major problem is question number two, "What do we know about it?" Our ability to answer that question is limited by politics, money, and all of the usual constraints of scientific research.

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[1]Larkin, P. A. 1972. The stock concept and management of Pacific salmon. *In* R. C. Simon and P. A. Larkin, eds., *The Stock Concept in Pacific Salmon.* H. R. MacMillan lectures in fisheries. Univ. of British Columbia, Vancouver, B.C. Pp. 11–15.

[2]Parrish, R. H. and A. D. MacCall. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dept. Fish and Game, *Fish Bull.* 167.

[3]Stephenson, A. B. and D. A. Robertson. 1977. The New Zealand species of *Trachurus* (Pisces: Carangidae). *J. Royal Soc. New Zealand* 7:243-253.

[4]Spratt, J. D. 1972. The use of otoliths to separate groups of northern anchovies. Calif. Dept. Fish and Game, *Mar. Res. Tech. Rep.* 1.

[5]Felin, F. E. 1954. Population heterogeneity in the Pacific pilchard. U.S. Fish Wildl. Serv., *Fish. Bull.* 86: 201–255.

[6]Sprague, L. M. and A. M. Vrooman. 1962. A racial analysis of the Pacific sardine (*Sardinops caerulea*) based on studies of erythrocyte antigens. *Ann. New York Acad. Sci.* 97:131–138.

VALIDITY OF ELECTROPHORESIS IN IDENTIFYING FISH POPULATION STRUCTURES

FRED UTTER
Northwest Alaska Fisheries Center, National Marine Fisheries Service

There has been a saying for as long as I can remember (and I came to work for the old Bureau of Commercial Fisheries in 1959) that the techniques used to identify genetic variations are useful for "ivory tower" investigations, but that no real management decisions have ever been based on these kinds of data. I am confident that by the end of today's workshop all those in attendance will realize that this statement is no longer true.

I will describe the general techniques of electrophoresis and then I will give more specific detail about using electrophoresis in the study of fish. We start by taking the tissues from an organism, such as a fish. We usually use liver, heart, muscle, and eyes. We make a crude extract from an individual fish by grinding a small piece of a particular tissue. We then apply extracts from a number of fish (usually 50) side by side in a starch gel. When a direct electric current is applied, the extracted proteins move out in the gel itself based on the different charges of particular proteins. This process of electrophoresis is a highly repeatable and quite simple operation.

Following electrophoresis, the gels are sliced and each slice is stained differentially so that we can look for characteristic patterns that might reflect genetic variation. The situation is analogous to a latent photographic image where the same negative can be developed in many different ways. One of the great powers of electrophoresis is the ability to identify specific proteins on the gel by actually using the activity of enzymatic proteins themselves. In this way, from a mixture of hundreds of proteins, you get direct genetic information about a single type of protein.

When analyzing electrophoretic patterns, we must be certain that the variations in the proteins are of genetic origin. The definitive test is to obtain inheritance data involving crosses between individuals with known electrophoretic types (i.e., phenotypes). The types and frequencies of electrophoretic patterns you would expect to see in the progeny can be predicted on the basis of a Mendelian genetic model. Such crosses, of course, can be done rather easily with salmonids.

With some species it is impossible to make breeding crosses, but there are a number of tests that can be made in the absence of breeding data that, in their sum, have equivalent power to breeding tests themselves. For instance, if a particular protein is expressed in more than one tissue, and electrophoresis of both tissues results in a genetically consistent interpretation, you

probably are dealing with a genetic variant. Conversely, the absence of consistency might be the result of some environmental effect that would alter the electrophoretic expression of that particular protein in one of the tissues. Fortunately, most proteins are stable throughout the life of the individual so that electrophoretic analysis yields approximately the same patterns regardless of the individual's point in the life cycle.

We look for patterns reflecting genetic variation at a particular locus (plural, *loci*). Genotype and allele frequencies accumulated over many loci (20 to 100 or more) are the basic units of genetic information that we use. In surveying a population of fish, 50 to 100 individuals are examined electrophoretically to estimate genotype and allele frequencies at a number of loci involved in the synthesis of different types of proteins. Usually fewer than half of the loci will have detectable genetic variation. These polymorphic protein loci provide the informative data for studying genetic variation within and among populations.

The work of Lisa Wishard with the genus *Sebastes*, a group of marine fish represented by many species, demonstrates the power of electrophoretic data for identifying previously undetected species. One part of her project examined a sample of *Sebastes reedii* that had been identified morphologically as the same species. The electrophoretic gels indicated that the sample contained two distinct genetic groups that were apparently not interbreeding although they were taken at the same time and place. These findings are part of an extensive set of electrophoretic data that are currently giving new understandings to the numbers of species and their relationships within this genus.

Genotype and allele frequencies that characterize a population are usually stable, providing that overlapping age groups contribute to a particular year class. For instance, in a study of steelhead trout in Puget Sound, data were collected for different year classes and different generations, and there was substantial agreement of allelic frequencies from one year-class to another, from one period of life history to another.

Such stability is not the case, however, when only a single age class contributes to a year class. Aspinwall, in the early 1970s, studied pink salmon in a rather limited geographic range. Since pink salmon (*Oncorhnychus gorbuscha*) in their native habitat of

the north Pacific have a very rigid two-year life cycle, there are two distinct year-classes: even and odd. Aspinwall found that for at least two polymorphic loci there was less genetic distance among geographically divergent populations of a common year-class than there was among different year-classes spawning in the same streams. The subsequent work of Ken Johnson extended these observations geographically and over a broader number of loci and confirmed that genetic distance was greater between rather than within year-classes.

Populations within a species can be readily projected into clusters based on relative differences of genetic distance measures that are directly obtained from electrophoretic data. Not surprisingly, distinct clusters often coincide with distinct ancestral groupings. Such clusters for chinook salmon (*O. tshawytscha*) and rainbow trout (*Salmo gairdneri*) (including steelhead) taken from a fairly extensive number of locations reflect a geographic basis. Upstream and downstream populations of major drainages such as the Columbia and Fraser rivers form distinct clusters. A common ancestry of rainbow trout populations of the upper Fraser and Columbia rivers has been indicated by electrophoretic data.

Presumed close relationships among populations have also been falsified with electrophoretic data. For example, it has been proposed that sockeye salmon (*O. necka*) on the Columbia River that return to the Wenatchee and Okanagan rivers on the Columbia River are descended from periodic Quinault River (a coastal stream) seedings that have been made ostensibly over the last thirty years. This possibility is strongly refuted by the electrophoretic data. The Quinault and Columbia River populations differ sufficiently at a number of electrophoretically detected loci to exclude recent common ancestries.

The example of the Quinault River sockeye salmon population demonstrates the power of electrophoresis to answer questions by using the actual genetic information of a species or subspecies. There are often many advantages in using genetic identification methods as compared with other methods of identification, such as coded-wire tagging, fin clipping, and scale analyses. A population characterized by a distinct set of electrophoretic information reflecting genetic differences is genetically tagged. You do not have to handle individual fish to impose this tag, as you do for coded-wire tagging and clipping,

and thus the potential for disability or deformity is zero (versus a rather high probability in the case of fin clipping and some degree of risk with coded-wire tagging). And, of course, the genetic tag is 100% permanent throughout the ontogeny of a particular species. There is some genetic component in scale characters, but usually scale marks are based on environmental rather than genetic factors. Genetic tags exist from the moment of fertilization, whereas there is a size requirement for a coded-wire tag to be applied.

Populations characterized by electrophoresis have provided valuable information for policy decisions. The genetic characterizations (i.e., tags) of chinook salmon populations are currently being used as baseline data for estimating contributions of these populations to oceanic fisheries. Maximum likelihood estimates of contributions are more detailed and timely than estimates obtained using other kinds of information. An increasing use of such estimates for managing these and other oceanic salmon fisheries is being made by agencies including Washington Department of Fisheries, Canadian Department of Fisheries and Ocean, and U.S. National Marine Fisheries Service because of the kind of information that can be obtained, its timeliness, and its cost effectiveness.

Within the last few years there have been great advances in electrophoretic techniques that give us confidence in the genetic bases of characters that are used. I want to emphasize that "electrophoresis is the most useful procedure yet devised for revealing genetic variation" [1] because of the ease with which a substantial number (up to 100 or more) of purely genetic characters (reflections from proteins of allelic variation at individual loci) can be examined in a very short time from many individuals. Sets of electrophoretic data are valuable for characterizing both species and discrete breeding populations within species. Proper application of electrophoresis has almost invariably brought new and often unexpected understanding about population structures. Previously unrecognized species have emerged in some instances while, in other cases, previously separated taxa have been joined. The power of electrophoretic data to measure genetic variation, identify origins, and clarify relationships has resulted in their accelerated application in fishery management and research.

[1] Hartl, D. L., 1980. *Principles of Population Genetics*, Sinauer Associates.

APPLICATION OF ELECTROPHORESIS TO RAINBOW TROUT

GRAHAM GALL
University of California, Davis

In reviewing the application of electrophoresis to the identification and management of resident varieties of rainbow trout (*Salmo gairdneri*) in the western United States and especially California, I want to emphasize the generality of this methodology, that is, its applicability to salmon, sardines, tuna, or whatever species you want to think about. Moreover, I hope to generate discussion by suggesting that genetic studies of fish populations render the word "stock" meaningless.

Although very few species have visible morphological characters that are both genetic in origin *and* unaffected by the environment, all species have a variety of genetic markers that can be identified by electrophoresis. I am going to use a study of rainbow trout to illustrate that electrophoresis can be a powerful tool for the study of genetic variation, population structure, and mating systems. I am using rainbow trout because they are *not* anadromous and, in fact, migrate very little if at all. Therefore, there is little population mixing in most of my samples; they were taken from isolated basins, or headwaters of tributaries to larger systems.

After examining electrophoretic gels and recording and analyzing the data, it is useful to produce a *phenogram*, that is, a tree diagram connecting populations by branches that are proportional to their observed genetic similarity. Phenograms are fantastic, if you interpret them properly, because they tell you when there are groups of populations that are more similar to one another than they are to all populations in general. By counting the number of alleles of each kind in the electrophoretic data, we find that some populations have the same frequencies of alleles, from which we can infer that they probably had the same genetic origin—that is, ancestral commonality.

In intense sampling studies in the Kern Basin in California we found five different populations of trout. We now know, because of the tremendous effort of personnel from California Fish and Game in collecting samples for us, that one group is a standard rainbow trout. These rainbow trout, non-native to this basin, were planted there, probably in the 1930s. It must have been barren water, and they survived, establishing populations all by themselves.

We have also been able to trace other populations that are the result of transfers of fish many years ago. While looking at the electrophoretic information in this study, we were surprised to find

identical populations of trout in two creeks that were far apart and in different drainage systems. We think we understand the reason. About 80 years ago a tunnel was dug from Golden Trout Creek down into the South Fork Kern River in an attempt to get more water into the meadow to pasture sheep and cattle. It has been closed for a long, long time. We think that when the tunnel was open, the fish migrated upstream and went into the next drainage.

I have given you an example of the power of electrophoresis to provide information about closely related groups of populations within the same species. We are now challenging the whole taxonomic definitions of the golden and rainbow trout by hypothesizing that they all belong to the rainbow series, but have evolved into very different groups of populations which show extensive diversity.

Cutthroat trout provide a good example of the use of electrophoresis with a species in which traditionally a number of subspecies has been identified. We see about the same level (or greater) of variability between subspecies here as we observe among these groups of rainbow trout. Cutthroats have very low genetic variability within populations. But there is enough variability between geographically dispersed populations to use electrophoresis successfully. The Lahantan cutthroat are very different from the Utah, Colorado, Yellowstone, and West Slope subspecies. The cutthroats have many allele frequency differences, so we can say with certainty that they are not interbreeding and have not for a long time. This study succeeded because of the tremendous enthusiasm of a small group in the Nevada Department of Wildlife that collected trout (whether they seemed like rainbows, cutthroats, or hybrids) from every stream that might have fish in it. The project was undertaken because people believed that the natural populations were endangered by the artificial introduction of rainbows. The records in the department files are unclear, but it is estimated that from 1920 to 1960 3,000 to 4,000 rainbow trout were planted in most of the streams sampled. Using electrophoretic analysis, we were able to establish that most of the populations consisted of extant groups of native cutthroat trout. The Nevada department is now managing the populations to protect their integrity. It is an example of genetic resource conservation at its best, made

possible by unbiased sampling of populations and the intensive application of electrophoretic analysis.

The Nevada cutthroat study demonstrates the power of the technique of electrophoresis. It also demonstrates that management agencies can utilize the concept of populations or subpopulations without resorting to any preconceived notions of a stock. I believe the stock concept is almost useless because it has been misused so badly over the last fifty years. Larkin's definition as modified by Alec MacCall is an improvement, but it still does not tell us much. Setting *a priori* conditions in defining a stock based on location and time of breeding is as ridiculous as the notion that there is such a thing as a pure stock! There has been a desire in fisheries to try to make the stock concept something, because it is felt the term is useful in describing genetic uniqueness. If you want to use the stock concept as a management tool, that's fine, but don't give it a genetic interpretation. Define a stock by whatever parameters are useful in management—geographic location, contribution to fisheries, time of spawning, etc.—but the so-called "stocks" may be artificial subdivisions of a genetic population.

Once stocks are defined, the challenge is to determine what kind of genetic makeup and population structure the stocks have! This is where electrophoresis has a role; but remember that identifying populations of fish with starch gel electrophoresis is only one aspect needed to understand the structure of the population. Careful qualitative as well as quantitative evaluation of results can lead to the identification of the micro-population structure of resident populations because migration is excluded. Although the study of anadromous species, such as salmon, is difficult because of the complexity of the mating system, the use of information on life history and behavior, together with appropriate unbiased sampling for electrophoretic analysis, can lead to an understanding of the reproductive structure and population dynamics of the freshwater phase of anadromous species. Probably the most limiting element in the study of anadromous and pelagic fish species is a lack of knowledge of physical and behavior constraints on random mating. Electrophoretic data can be partitioned and interpreted appropriately only to the extent of one's knowledge of the populations (stocks) being studied.

APPLICATION OF ELECTROPHORESIS AND MITOCHONDRIAL DNA STUDIES TO HERRING STOCKS

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Herring (*Clupea harangus*) is probably the most economically important species of fish in the world, not because it is directly exploited as a source of protein for people, but because it is the foodstuff for a large number of other fish. The species has a worldwide distribution, but I will concentrate on Atlantic herring, found along the New England coast and up to the Maritimes. One interesting thing about the herring is the discreteness of breeding aggregations. There are two kinds of herring in this particular area of the world: fall spawners and spring spawners. Because spawning areas are discrete and breeding is seasonal, one might expect to be able to identify distinct populations of the fish, both in terms of stocks, from the management perspective, and subpopulations, from a genetic perspective.

It is important to investigate the population structure of these fish because they can be exploited differentially, causing a collapse of a portion of the fishery. For example, with the rise of fishing in the Georges Bank by foreign fleets, particularly those of the Soviet Union, the herring in that area almost disappeared. If there is a mixture of distinct subpopulations, that is, discrete breeding units, that are exploited in the same place, then it is possible that the exploitation pressure could eliminate one or more subpopulations differentially. So, it is necessary to know how many genetically distinct subpopulations exist.

From a management perspective, there are two steps involved in identifying herring subpopulations. First we must establish that there are, in fact, discrete subpopulations, that is, interbreeding populations that don't have gene flow between them. Second, we must find some kind of discriminating function that allows us to identify individuals that spawn in those areas even when they are in nonspawning conditions. We thought electrophoresis might be the way to look at the characteristics of both spring- and fall-spawning herring. Herring have a large battery of enzymes that can be screened individually to see whether variance occurs. In this particular study, we examined 42 loci that are reasonably clear on gels. Of those 42 potential genetic markers, 13 are variable. Of those 13, only 5 are sufficiently variable to allow one to discriminate populations on a statistical basis.

There are at least two problems in interpreting population structure from statistical analyses of gene frequencies. Since we

are interested in discriminating *among* geographically separated spawning aggregates, we must be sure that gene frequencies are constant *within* spawning populations over time. We collected herring from three different spawning localities for fall spawners and two for spring spawners and examined the five variable loci to see whether they were constant over time. It turns out, in fact, that two of the loci vary significantly over time so that we are down to three loci that are temporally stable enough to examine geographic variation. The other problem in interpreting genetic data is that (typically in studies of fish and other organisms) there are instances of gradual differences in gene frequency over space. If you look simply at the extreme points of the geographic distribution, you will note a significant difference in frequency, which you might interpret as supporting the idea that the populations are discrete. But if there is a gradual distribution of frequencies between these extremes, as was the case for one of our loci, that locus is non-informative in terms of information for discrimination. So out of 42 potential loci, we wind up with only two loci that might be useful in discriminating separate populations.

There have been a large number of electrophoretic studies conducted both on Atlantic and Pacific herring. One of Fred Utter's students, Dr. Stu Grant, characterized genetic variation within and between the Pacific and the Atlantic subspecies of herring. His results provide some perspective on our ability to use electrophoretic markers. Comparing Atlantic and Pacific herring between which there is now no possibility for gene flow, we would expect substantial differentiation to exist, and, in fact, it does exist. The genetic similarity between the two species is about 0.75 on a scale of zero to one. Grant also characterized regional partitioning of genetic variation within the Pacific subspecies. He was able to discern a highly significant difference in gene frequencies between herring that occur north of the Aleutian peninsula and those that occur south of the peninsula. The geographic barrier of the Aleutian chain is sufficient to prevent the mixing of populations that occur on either side of the barrier.

In the Atlantic we can make comparisons between the herring in the northwestern Atlantic along the Gulf of Maine, with populations that occur in Scandinavia and in Europe. If we lump European populations to include those that spawn both in the

spring and the fall, and compare them to Gulf of Maine samples, we find significant frequency differences, indicating that there is differentiation in these somewhat isolated gene pools. However, if we look only at those fish that spawn at the same time of year, e.g., fall spawners, we cannot detect any differences in gene frequency between samples from the Gulf of Maine and samples from the Baltic Sea. In this case, electrophoresis is incapable of discriminating between populations that are isolated by vast geographic distances and therefore should show some degree of differentiation.

We find a similar situation when using electrophoresis to look at differentiation that occurs in the Gulf of Maine area. We are able to demonstrate a statistically significant difference in gene frequencies between spring and fall herring populations. For example, populations that spawn in the spring in the Gulf of St. Lawrence appear to be different from those that spawn in the fall along the coast of Maine and off Georges Bank. However, when we look at those discrete populations that magically appear at Georges Bank in the fall to spawn *en masse*, we are not able to detect any differences at all. Electrophoresis fails to provide the ability to discriminate among these different populations. If we are correct in assuming that there is very little movement between these different spawning areas, we should see some kind of electrophoretic differentiation.

There are at least three reasons why we are unable to discriminate among these populations. One alternative is that there is in fact a single genetic population that is represented by multiple stocks. A second possibility is that discrete breeding populations do represent separate gene pools, but that there has been insufficient time for those discrete breeding populations to acquire different electrophoretic alleles or to have different frequencies. The third alternative is a mixture of the other two. There may be incomplete isolation of populations with some gene flow occurring through occasional strays or migrants. This would tend to homogenize any differences that might occur, and thus not allow us to detect a concordance between discrete breeding areas and separate gene pools.

Electrophoresis failed to differentiate these populations, but there is a new technique, mitochondrial DNA analysis, which has the potential of affording a different glimpse into what is happening in these natural populations. Mitochondrial DNA

(mtDNA) is very different from nuclear DNA. It is a very small, circular (not linear) piece of DNA. It has a different genetic code from nuclear DNA, and it does not possess any introns (noncoding regions that are found within genes). MtDNA is unique in one other respect as well. It is strictly maternally inherited: that is, it is passed to progeny via the egg. Presumably, the contribution of mitochondria through sperm is extremely small. We can, therefore, use information from mtDNA to erect phenograms that are potentially very different from those that we get when we use nuclear genes.

The techniques for isolating and characterizing mitochondrial DNA for fishes are well established and not far removed from standard starch gel electrophoresis. After the DNA is isolated, it is cleaved by enzymes called restriction endonucleases that recognize specific sequences of either four or six nucleotide bases that occur along the DNA molecule. When the appropriate sequence of bases is found by a particular nuclease, a cut is made in the molecule. If we make two such cuts in the circular mtDNA molecule, we produce two fragments whose mobilities in a gel are correlated with their length. We can calibrate the sizes of fragments by putting standards into the gels.

By using a large number of restriction enzymes independently, we can establish a cleavage profile that is characteristic of the population under consideration. One important feature of mtDNA is that its rate of evolution is significantly faster than that of nuclear DNA; it can potentially allow us to examine differentiation among populations that have not been isolated for very long and may give us a greater sensitivity to detect differences within populations.

Although studies of vertebrates, principally small mammals, have demonstrated the taxonomic utility of mtDNA analysis, studies of fishes have been extremely limited. William Hurst has analyzed both mitochondrial and nuclear DNA for four evolutionarily well separated species of salmonid fishes and demonstrated that the phenograms derived from both analyses were exactly the same. It may be more difficult to determine how much variability exists within populations or species, and there have been extremely few studies on fishes that try to do this. One study by John Graves and coworkers made comparisons of Atlantic and Pacific skipjack tuna, using a number of restriction nucleases on mitochondrial DNA. One would expect to see

significant differences in the cleavage profiles of these two population samples, but there did not appear to be any geographic differentiation between those two oceanic stocks. On the other hand, a study in progress by Bob Chapman on striped bass suggests that mitochondrial DNA analysis will be successful in discriminating populations of these fishes.

It is important to apply mitochondrial DNA analysis techniques to gain the understanding of population structure that is essential for realistic management and long-term exploitation of herring. The electrophoretic studies discussed earlier, which have attempted to characterize population structure, have yielded three classes of results. In the first class, major complexes of herring associated with geographic or temporal barriers to gene exchange could be statistically identified in Pacific and Atlantic subspecies. In the second class, weak differentiation associated with distance was noted within two major groups of Pacific herring. In the third class, differentiation among discrete breeding populations or stocks could not be recognized. The inability to discriminate electrophoretically among breeding stocks of Atlantic herring is probably a function of their recent origin and perhaps limited gene flow. With a more sensitive probe for genetic differentiation, specifically restriction analysis of mitochondrial DNA, stock discrimination might be possible. Although the results of restriction analysis of mitochondrial DNA studies are not uniform, appropriate tests of the power of mitochondrial analysis for herring stocks could provide important new information for management.

RECOGNIZING SUBPOPULATIONS IN CALIFORNIA'S MIXED PELAGIC FISH STOCKS

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After the collapse of the sardine population in the 1950s, the northern anchovy (*Engraulis mordax*) became the basis of two kinds of pelagic fisheries in California, a reduction fishery, which turns these wonderful little creatures into meal and oil commodities, and a live-bait industry, which supports a large, economically important recreational fishery. At present the species is thought to comprise three geographic subpopulations: (1) a northern population found off the coasts of Oregon, Washington, and British Columbia, which breeds near the plume of the Columbia River in summer; (2) a central population ranging from northern Baja California to northern California, which breeds primarily in the Southern California Bight during winter; and (3) a southern Baja California population concentrated below Punta Falsa, B.C.S. Mexico, which also breeds primarily in winter.

The current Fisheries Management Plan for the northern anchovy adopts the concept of three geographic subpopulations, defines the central subpopulation as the unit of management, *i.e.* the stock, and explicitly raises two questions regarding the population structure of this species. The first concerns the ratio of central to southern subpopulation fish caught in the Mexican fishery; fishing mortality in the U.S. anchovy stock is difficult to estimate in the absence of this information. The second question concerns the assumption that the central stock is a homogeneous, randomly mating subpopulation. This assumption underlies the efforts of the National Marine Fisheries Service (NMFS) and the California State Department of Fish and Game (CDFG) to manage a stock that undergoes drastic fluctuations in abundance and recruitment. The egg survey method used to estimate spawning biomass and to set yearly catch quotas, for example, assumes that egg production per unit area may be averaged over the range of the stock and that spawning females responsible for observed egg production are representatives of a single breeding population.

Because of the significance of population structure for management of the northern anchovy fisheries, we may reasonably ask how the concept of three geographic subpopulations arose and what evidence supports it. The chief source of this concept was a study by Vrooman, Paloma, and Zweifel published in *California Fish and Game* in 1981 and entitled, "Electrophoretic, morphometric, and meristic studies of subpopulations of northern anchovy, *Engraulis mordax*." In this

study 26 populations of anchovies ranging from Oregon to southern Baja California were examined. An electrophoretically detectable polymorphism in the serum protein transferrin was found to be determined by four different alleles, one of which was rare but appeared to be more common in northern population samples. From a cluster analysis of allele frequency data for the transferrin locus, the authors concluded that three populations existed as described above. After assigning samples to subpopulations, the authors then showed significant differences among the subpopulations for various morphometric and meristic traits.

However, if one discards data for the rare allele, on the basis of its rarity and statistical unreliability, and tests the independence of remaining allelic frequencies and locality using the *G* statistic of Sokal and Rohlf, one finds the 26 population samples of Vrooman et al. to be statistically homogenous. Moreover, morphometric differences among the three putative subpopulations might well be artifacts of Vrooman et al.'s procedure of clustering samples prior to analysis. In reality the observed morphometric traits may show continuous, latitudinal gradients as have been observed in many species of fish and in earlier studies of anchovies. Thus, the concept of three distinct subpopulations is without sound genetic evidence. While there is good reason to suspect that fish in the northern part of the range are a distinct subpopulation because they breed in summer in a discrete locality, a clear separation of central and southern subpopulations is not supported by the available data.

We began work in 1982 under California Sea Grant Program funding to examine the population structure of northern anchovy with modern techniques, including electrophoresis of a broad spectrum of enzymes and proteins. Our goals were to find out whether southern and central subpopulations could be identified and whether the central stock was a homogeneous breeding population.

Through the NMFS and CDFG sampling programs we obtained fish from three separate cruises, February 1982, December 1982, and February 1983. A total of 25 population samples of at least 50 anchovies each were collected in localities ranging from the Russian River in northern California to Punta Baja, Baja California. Thus, to date we have only had access to samples from the central stock of northern anchovies. We initially screened 41

allozyme loci, then narrowed our study down in much the same way as others have described today to 12 enzymes that were clearly polymorphic. For each specimen we also recorded standard length, sex, and age as determined from counts of annual growth rings in otoliths.

In contrast to the geographic homogeneity revealed by our re-analysis of Vrooman et al.'s transferrin data, allelic frequencies at eight of the twelve loci were statistically heterogeneous among population samples. Two loci showed significant latitudinal trends in gene frequencies. Trawl samples taken very close together in space and time were often quite different in genetic composition, and even more astounding, sexes or year classes caught in single net hauls were sometimes significantly different. These results clearly falsify the hypothesis that the central stock of the northern anchovy is a single, randomly mating population. Yet, how can we account for genetic heterogeneity on a geographic scale much smaller than the dispersal range of the adult northern anchovy?

On the basis of completely independent evidence, Dr. Richard Parrish of NMFS's Pacific Environmental Group (PEG) in Monterey, California, has recently hypothesized that the central stock of northern anchovy may comprise separate populations adapted to different spawning seasons. Part of the evidence for this exciting hypothesis are the clinal variations, reviewed by Alec MacCall this morning, in size-at-age relationships along both latitudinal and inshore-offshore dimensions of the stock's range. But greater support for the notion of seasonal spawning races comes from NMFS-PEG studies relating climatographic and oceanographic factors to fish reproduction and recruitment in eastern boundary current systems such as our California Current. Two environmental factors that appear crucial in determining where and when fish such as anchovies will spawn are: (1) the amount of upwelling with its accompanying offshore transport of surface waters and (2) the amount of wind- or storm-driven turbulence in the water column. The latter factor was recognized earlier by Dr. Reuben Lasker who showed that disruption of phytoplankton layers can reduce algal cell density below a critical level necessary for feeding and metabolism of larval anchovy. What the PEG scientists have done is to map wind speed and Ekman transport data, thus demonstrating a remarkable

correspondence between anchovy reproduction and the predictability of reduced turbulence and offshore transport on both temporal and spatial scales.

Thus, the Southern California Bight is a good place in almost all months for anchovy to breed because upwelling and wind-driven turbulence are much reduced compared to the more exposed central California coast. At Cape Mendocino, for example, persistence of both upwelling and high winds in all seasons precludes anchovy reproduction. For Monterey Bay, on the other hand, Parrish has shown that oceanographic factors are favorable for spawning in the fall, and indeed fall spawning is observed. Do these fall-spawning fish represent a discrete subpopulation? Were they largely sympatric with the winter-spawning subpopulation but genetically distinct from it by virtue of seasonal reproductive isolation, our observations of genetic heterogeneity in the central stock might be explained. Some electrophoretic results support this hypothesis.

Samples taken in December, 1982, near Morro Bay in central California contained sexually mature fish as well as substantial numbers of adult-sized individuals having completely dedifferentiated gonads. These fish, which may have spawned out in the previous fall, had allelic frequencies at one allozyme locus that were strikingly different from those of sexually ripe fish. Later, in a sample taken from the same area in February 1983, juvenile fish about 5 cm in standard length were collected with adults in spawning condition. Again these immature fish, which were small enough to have hatched only in the previous fall, were genetically distinct from winter-spawning adults and similar to the sexually dedifferentiated, presumably fall-spawning, adults taken two months earlier. This slim bit of evidence for Parrish's hypothesis has encouraged us to test more rigorously for the existence of distinct fall- and winter-spawning subpopulations. We are now studying fish collected in both seasons, using an extensive morphometric, electrophoretic, age, sex, and sexual condition data profile for each individual sampled.

In closing I would like to emphasize an inference that might be drawn from the PEG's studies and our results to date. Oceanographic and climatic conditions conducive to fish reproduction occur somewhat predictably in space and time; such localized "spawning windows" have been charted in all four major

eastern boundary current systems. If reproduction of pelagic fish in these current systems has evolved to exploit "spawning windows," then coexistence of genetically-distinct, seasonal spawning races may be a widespread phenomenon in these fish stocks. The danger of not recognizing mixed population structures in pelagic fish stocks is well illustrated by the role that subpopulations apparently played in the demise of the California sardine fishery. (See "The collapse of the California sardine fishery. What have we learned?" in *CalCOFI Report* 23:56–78 by the late J. Radovich.) Our results are thus relevant not only to management of California's pelagic fisheries but also to an understanding of pelagic fisheries in similar current systems whose yields have substantial impact on domestic fish meal markets.

PART II

PANEL DISCUSSION

THE USEFULNESS OF THE "STOCK CONCEPT" IN FISHERIES MANAGEMENT (PANEL DISCUSSION)

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HERBERT FREY, California Department of Fish and Game
EUGENE FRITZ, National Sea Grant College Program, National Oceanic and Atmospheric Administration
JOHN GRAVES, Southwest Fisheries Center, National Marine Fisheries Service
REUBEN LASKER, Scripps Institution of Oceanography, University of California, San Diego and Southwest Fisheries Center, National Marine Fisheries Service
ALEC MAC CALL, Southwest Fisheries Center, National Marine Fisheries Service
CONRAD MAHNKEN, Northwest Alaska Fisheries Center, National Marine Fisheries Service

Lincoln: The first question that we would like to address is whether electrophoretic data have been successfully applied in fisheries management. Many of the capabilities that were previously discussed are fairly recent. It is only within the last year or two that management applications have been envisioned using electrophoresis to satisfy general stock identification needs. Here is another tool to supply the type of information that we have been trying to get from other methods—tagging, for instance.

In this first round we will concentrate on harvest management. How can genetic stock identification be used to optimize yield in mixed stock fisheries? To maximize the sustainable harvest of salmon stocks? To meet allocation obligations between various user groups of mixed stock fisheries?

I will start with some applications to salmon management initiated in Washington, and indicate what we intend to do if we can find the fiscal support. I am sure everyone has heard horror stories about the complex management schemes that we must develop to establish and manage for escapement goals for various specific stocks of salmon. We have management plans for the ocean as well as for the inside commercial and recreational fisheries in order to meet fixed escapement goals for various units, species, and geographic areas. One of the problems we have in mixed-stock salmon fisheries (both inside Puget Sound and in the ocean) is that to satisfy individual escapement goals for geographic areas where the stocks are mixed, you must follow the philosophy of managing the mixed-stock harvest for the needs of the weakest viable natural unit.

To develop management plans to achieve specific escapement goals, we presently use simulation models that take juvenile tagging information and predict what the impact of certain regulatory strategies will be. This is a preseason process to develop run size forecasts for each of the regions; we then develop an aggregate harvest quota in the ocean that meets the escapement allocation needs for the weakest viable natural stock. This preseason planning represents the limit of our management capabilities right now. During the season, we do not have the capability to monitor the impacts on those stocks. We are monitoring an aggregate catch of perhaps 23 coho stocks, for example, toward achieving an allowable harvest. What we want to know is that we are keeping the harvest of the weakest viable component of that aggregate to a level that will meet conservation and allocation goals.

In 1982 we began to apply genetic stock identification to ocean salmon fisheries, to test it as an operational tool, since the other tools we have, such as juvenile tagging, cannot address the needs of in-season monitoring of specific stock impacts. For two years, we have used the baseline data that Fred Utter's staff developed at the National Marine Fisheries Service and actually sampled the mixed-stock catches to make estimates of the stock composition of individual management units (or stocks). This is the first time this has been done in any of the ocean chinook and coho fisheries, and we intend to continue using this operational tool to achieve conservation and allocation goals for individual management units within the mixed-stock fisheries.

We also have strict allocation requirements for these same individual management units. For every stock originating from the treaty area in Washington, there is a court mandate that up to 50% of the harvestable surplus of each management unit must be allocated to treaty[1] Indian tribes. We must estimate what the catch of specific components of mixed-stock harvests will be so that appropriate allocations can be made. Again, we are at present using simulation models that rely on recent historic information derived from tagging data. What we need is a way to measure what the stock composition is, not to simulate what it might be under conditions experienced in the past. Genetic stock identification is a new capability that we hope will provide more immediate and valuable information to help us meet our management objectives.

The final allocation consideration that we have is the pending treaty[2] between the United States and Canada, one component of which will be to establish an equitable sharing of salmon resources between the two countries. The same problem arises: we have no way to measure how many U.S. fish of various species and stocks are being caught by Canadians or vice-versa—other than theoretical approaches like run-size reconstruction or juvenile tagging and simulation modeling. Here, too, genetic stock identification could be used to answer the question: Is it a Canadian or U.S. fish?

These then are some of the critical management areas related to salmon fishing in the Washington region for which we hope to use genetic stock identification. Let's go on now to talk about other management needs and other species applications.

Fritz: At a 1981 symposium in the Great Lakes area dealing with the stock concept, Pete Larkin pointed out that at present there is no explicit working hypothesis of population genetics in salmon management. The implied working hypothesis is that genetic variability should be retained and all meddling with genetics should be minimized. This view needs to be challenged, in Larkin's judgement. He suggests that it may not be the objective of management to preserve *variability*, but rather to foster those characteristics that increase *yield*, which is essentially what fisheries are established for. That idea flies in the face of the traditional value placed by biologists on variability. As Graham Gall has suggested, genetic identification and marking of the organism do not tell you much more than if the populations are in fact distinct. A manager wants to know how much you can allocate to the fisherman, what he is going to use, and how that is going to be translated into his catch. If you see that the catch is exceeding the limits that you set, you cannot close the harvest at that point. You've already had the harvest. The genetics technique exists, and better techniques may be developed, but what do you use them for? Larkin questions whether genetic identification techniques are being used effectively in fishery management. I have looked through the literature, and I have not been able to find any instances of genetic information actually being used.

Lincoln: I think we are talking about two different issues here.

The first is just the basic concept of using this stock identification tool to meet current fisheries management objectives, such as escapement goals, regardless of whether our plans incorporate the desirability of maintaining genetic diversity.

The other question you raised and that Graham Gall alluded to earlier is what use genetic stock identification has in terms of developing genetic policies, stock transfers, hatchery programs and hatchery planning. I think that is something that Connie Mahnken can discuss in relation to hatchery reprogramming plans in the Columbia River.

Mahnken: First of all, I do not think that we can generalize Larkin's statement and apply it to all marine and freshwater fisheries. Larkin himself has commented on the need to identify stocks in mixed fisheries so that we can manage them on a stock basis.

The Pacific salmonids are in a unique situation that goes beyond the need to manage for stocks in a mixed fishery. For example, the Columbia River fishery is influenced by several pieces of legislation. The Northwest Power Act, for example, has a Fish and Wildlife plan component that was heavily influenced by user groups who desired the restoration of upper Columbia River fish stocks that exist there only as remnant populations. Whether this very costly plan is good or bad, it is a portion of the Fish and Wildlife plan. To get those stocks back to pre-McNary dam size, we will have to use hatcheries or control the ocean fishery. In the ocean, tremendous numbers of lower river hatchery stocks are being fished side by side with the upper Columbia River wild stocks. In order to protect these weaker wild stocks, we have to be able to identify differences in their distribution in time and space in the ocean fishery in order to allow them to pass. This transcends basic biological or scientific questions about the mixed-stock fishery. We are charged with enhancing these wild stocks whether it is economical or not; it is decreed by law.

I have one other comment before we go on. If you don't believe in the stock management concept, then there is no reason for us to be doing any electrophoretic work. But my feeling is that the majority of the community, biologists and managers alike, have specific need for information on stock composition of the fisheries they work with.

Fritz: As was mentioned earlier, we do not even have a definition *per se* of "stock." Perhaps we have institutionalized a concept that is intrinsically very appealing, but that may not be valid. Lawmakers grab onto institutionalized scientific concepts and fuse them into law. "Stock depletion" is such a concept; it has been set in concrete, but it may not exist. Does anyone know of some real experimental evidence showing that a stock has been fished down and has never recovered? If such an instance of stock depletion does exist, how do we know that it resulted from the fishing of a stock rather than an environmental perturbation?

MacCall: I firmly believe that we need further genetic work to better define the nature of fisheries so that we can develop viable alternatives to the simplified stock concept that we have been dealing with. The stock concept actually does exist! Whether it is a scientific concept, a political parameter, or a management tool, it is there. For example, legislation regulates the stocks off California. What does that mean? Well, it is defined. From a management standpoint the stock is that portion of a population or resource with which you are dealing. Once a management stock exists, the question is: Is there a biological parameter that is similar? The closer the political parameter is to the biological parameter, the more meaningful management will be. The electrophoretic technique will provide additional information for defining the biological stock.

Lasker: The anchovy fishery being studied by Dennis Hedgecock provides an example of a management problem that requires the kind of information that electrophoresis can supply. As Dennis explained, the population of anchovies that was spawning was very clearly delineated, but we still do not know whether we are fishing from one pot or from two pots. If we do not have that information, then it is very easy to wipe out both pots. From a management point of view, I would like to know if there are two pots; then perhaps I would change my strategy and fish only from the larger one. From my perspective this is just a semantic problem we are facing here, discussing stocks, or populations, or subpopulations; what we really want is a management concept of how to fish. I think that without that information we are really in the dark; we have no defensible means of choosing one management scheme over another.

Allendorf: I would like to respond to Eugene Fritz's question of whether there are any practical examples of the use of electrophoresis and the stock concept. The State of Montana has in the last 20 years been making an extensive effort to preserve the west slope cutthroat trout, a native trout, but they were having trouble raising them in hatcheries. An electrophoretic examination compared the brood stock in the hatchery to the native populations from which they derived and determined that the hatchery population had greatly reduced genetic variability.

The State of Montana is now in the process of replacing that brood stock with a native population brood stock. To assist them, we are doing a survey of all the native populations of cutthroat trout in the state, first to identify electrophoretically which ones are native west slope cutthroat trout and which ones are hybridized (and you cannot do that except with electrophoresis). The second thing we are doing is trying to determine the genetic variability of the natural populations, so that the new brood stock will contain most of the variations present in the wild.

The State of Montana in the last eight years has essentially based its management plan for preserving west slope cutthroat trout on electrophoretic data. First, electrophoretic data identified the breeding problem as a loss of genetic variation, and second, these data will be used to determine how many populations we have to bring into the hatchery to create a new hatchery brood stock.

Gall: You cannot find examples of the application of electrophoresis research in fisheries because it is a very new thing; we have only been trying it for a few years. Fred Utter, myself, and others have been trying to sell this idea to marine fisheries for years. The examples we are giving you are for freshwater fish, because freshwater biologists have been willing to give it a try. I gave you two examples this morning, and Fred Allendorf has just given you another. Our research started in the Kern system in 1973, and it has taken us 10 years of work with California Fish and Game and the U.S. Forest Service to be confident that we have identified the population structure that should be managed. The reason that you are having this problem is that the technique has not been accepted in marine fisheries—plain and simple. Now it looks as though there may be a change of heart.

I think I can clarify Pete Larkin's statement at the Great Lakes symposium to which Gene Fritz referred earlier. Larkin said there is no existing hypothesis of population genetics for salmon, and that is absolutely true. He was saying that there is no genetic basis for the stock concept, and the symposium proceedings reinforce that conclusion. This does not mean there is no validity in the use of the stock concept; it just means you cannot equate physical stocks to genetic population structure. For management purposes you are going to use some concept of a stock; you have to.

It is possible that all pelagic species populations are just as complex as the freshwater species. The difficulty is that pelagic species do not sit in one place where you can collect them. The improvement of productivity through hatcheries or through controlling exploitation of natural populations is not going to occur until you know how many populations (genetic) there are, where those populations are, and until you have information on biological and genetic characteristics of those stocks.

Today we need to talk about the best way to use electrophoresis to do what you want to do, so that we can understand the managers and the managers can understand us. There is no doubt in my mind that electrophoresis has limitations, but it provides better information than we have had in the past.

Woodruff: I am a biologist, but I do not work on fish. I have been doing gel genetics of snails, which are sometimes moved around the world with tropical fish and aquarium plants. I use electrophoresis routinely to trace movements of populations, hybridization, speciation, and the like. I think if you look at other groups of organisms, you will find electrophoresis has more to offer than we have discussed today. For example, in small mammals, which go through dramatic population cycles of periodic increases and decreases, you can tell where a population is in the cycle by examining the genetics of sample individuals. You can learn a great deal about a population's vitality, fitness, and growth rate from its genetics; there are relationships between levels of genetic variability in an individual and the rate at which that individual will grow, the age at which it will first reproduce, and its overall longevity.

Electrophoresis has two things to offer marine fisheries. One

is defining the real entities that you are trying to manage. And the other, which is untouched as yet, is learning how to manage those entities in a more productive manner by selecting animals that are going to grow faster, reproduce earlier, survive bad winters, etc. This technique has been available for nearly 20 years. It is being applied routinely by managers of mammal populations. I believe it could be applied to marine fisheries biology.

Frey: Actually marine scientists have not been asleep. In 1963 when I began working with the California Department of Fish and Game, Al Smith was using electrophoretic techniques in one of our studies. About ten years ago, Ray Ally was working for the Department using electrophoretic techniques to determine the stock structure of the market squid off our coast here. The process was very time consuming, but as I found out today, the techniques of electrophoresis have made a lot of headway in the last seven or eight years.

Gall: But there was no interest in trying to expand that. You were trying to use it in a very elementary way.

Frey: I agree; we were in a primitive stage.

Graves: It is true that the freshwater scientists have led in using electrophoresis, but you must realize that when the technique was being developed, only a few loci were sampled. In cases where there is isolation, you are more likely to find genetic differences. Researchers found differentiation in streams and rivers, but not in the pelagic environment of the ocean where gene flow is greater.

Gall: Differentiation was not found in fresh water either 10 years ago, but we had a few indications that the technique might work. We started in the Kern in 1973 and did not really identify differentiation until 1980 when we went from 8 or 9 identifiable loci to 50.

Mahnken: What you are saying is that the likelihood of finding differentiation in reproductively isolated populations in fresh water is much greater than in marine populations.

Gall: It is much more likely that we could document or prove the nature of the genetic differentiation because we had extensive knowledge of the physical conditions of the populations. However, we still had to contend with artificial transfers, many not documented, which initially confused data interpretation.

MacCall: The problem everybody has been talking about—applied electrophoresis—has important implications for funding.

It seems that one-shot, one-year funding is not likely to produce much of value. If temporal variability is important, then multi-year funding is necessary.

Barrett: Speaking as a representative of an agency that is obliged to put up the money for these multi-year projects, I have to say that we have not been shown much evidence that electrophoresis is an effective management tool. The problem is to convince us that genetic stock identification tools are reliable and produce useful management information.

Dizon: I think that Dr. Barrett is absolutely correct, but there is value simply in knowing that there is differentiation.

Fritz: As a major funder of this type of research, one of the problems that I run into is how to distinguish one proposal from another. When research is proposed and the title is essentially "The Starch Gel Electrophoresis of Species X, Y, Z," *ad infinitum*, what is one to do? When does the proposal represent research, and when is it application of an existing technique? Is processing new samples or trying new staining techniques really research? It is very difficult to tell what the difference is between an electrophoretic study of striped bass in Chesapeake Bay and a study of yellow perch in Lake Erie. How many species do you have to do?

The third largest component of individual fisheries projects funded by the National Sea Grant College Program is electrophoretic or stock differentiation studies. We use several criteria in our office to evaluate projects. We ask, How good is the science? How important is the problem and how does it relate to other problems in the same area? And then for most projects we also ask what the relationship is with the user community. In the case of electrophoresis, which is seen ultimately as a management tool, we look at the research proposal to see whether mechanisms are built in to get information to an agency, such as California Department of Fish and Game or the National Marine Fisheries Service. Are there ties that link the study to a management plan?

For example, Dennis Hedgecock's research on anchovies provides significant information that may point to the necessity for revising the anchovy management plan. How is he going to get that information out? Typically, it would be published in the

scientific literature, but that does not ensure that the information will get to the user community. If the scientist has not made contact with management agencies, then the project might become a nice academic exercise. It may be a very worthy exercise and be very good science, but it will have very little effect.

Mahnken: Doesn't Sea Grant ask managers in the beginning about the potential applicability of their work?

Fritz: No, that is the responsibility of the principal investigator. The person who is going to do the research has to make those links. I am not in a position to tell the researcher how to apply the science.

Utter: Rich Lincoln made a very clear and strong association between science and management. It seems to me you are saying that managers do not read science.

Fritz: In a sense, that is the case. There is clearly a lag time, often as long as five or more years, between the report of new information by a scientist and its application at the management level. The linkages between scientists and managers can be stronger. I am not saying that every project has to have that kind of linkage, but it is one criterion used in evaluation.

Spiess: I would like to offer my experience as a member of an applied research team in a completely different field: underwater acoustics with the Navy. There the users have made very good application of scientific information without requiring that scientists who submit proposals to the Office of Naval Research be solely responsible for the linkage over the ten years or so it will take to develop a new sonar system, or whatever it may be. It is the job of intermediate level administrative people to make these links as well. Often the scientific research is undertaken by people who cannot be expected to know all the management implications of their work. There has to be a middle group of people who are reading the academic literature and are also in contact with the users to make those linkages. I think that it is a bad philosophy to rely on the scientist to see that this information will be used. The reason it takes so long is that there are a lot of people in that chain who are going to have to be convinced, all of whom will have to come up with some money—not in this year's budget, because that has already been committed, and probably not in next year's budget.

Lincoln: What do people feel the responsibilities of researchers and managers are to communicate the needs in one direction and the tools in the other direction?

Spiess: Sea Grant could facilitate the dialogue between scientists and the management people by sending a proposal out not only to peer reviewers to assess the scientific aspects, but also to managers to assess the potential use of the project's results.

Fritz: We do that with some proposals. What I gave was simply a set of general criteria. In certain projects, links with users are not necessary. However, if a proposal justifies research by identifying management needs, I would expect there to have been some contact between the scientist and the appropriate manager and state entity to which that information would be going.

Kornfield: I think the situation is a bit more complicated. One can easily say in a proposal that the scientists have made contact with specific people in management. That does not necessarily mean that there will be effective information transfer. The West Coast is exceptional because there are good linkages in place between the scientific community and management. On the East Coast, that is not always the case. It is difficult for the investigator to establish those linkages.

Fritz: And that sometimes is a weakness of projects submitted to Sea Grant. We have a limited budget and must fund the best proposals that meet established criteria.

Dizon: Are the best projects necessarily the ones with clearly identifiable management goals? In many cases such projects result in very superficial analyses and "quick and dirty" kinds of approaches to problems.

Fritz: We recognize that there are some projects with scientific merit that will not be applicable immediately to fish management—for example, sophisticated refinements of sampling techniques or promising innovations in stock improvement. Other kinds of studies are more directly related to the manager.

MacCall: I think for the most part the managers are not capable of understanding what the scientists are talking about. I think communication must be between scientists and an intermediate level in government agencies. There are people like

myself, Herb Frey, and Reuben Lasker who are in a position to translate basic research into options that will later be acted on by managers. This intermediate level actually creates the possible uses of these new techniques.

Helle: I have been involved in salmon fisheries workshops for 20 years, and every other year researchers get together with managers to learn the others' needs. Managers always say they need to know three basic things: (1) prediction of abundance, (2) optimum escapement, i.e., the precise number of fish we must have in a stream to get back optimum returns, and (3) what stocks are in the fishery. From the researchers point of view, mixed-stock fisheries seem unmanageable—why have them? Given that we will have to live with mixed-stock fisheries, we need to learn how to identify major stocks in these fisheries in order for them to be managed.

A good example of this problem is the U.S./Canada Salmon Interception Treaty we have been trying to settle for about 20 years. The basic premise of the treaty will be that the country which produces the salmon should get the benefits. Several major U.S. and Canadian fisheries near the border of Alaska and British Columbia intercept each other's fish. We have to be able to identify the various stocks so that each country can get credit for what it produces.

For the past two years, we have had a stock identification study of sockeye salmon in this area using several methods: tagging, electrophoresis, scale pattern analysis, and parasite analysis. All of these methods work to differing degrees. Interestingly enough, electrophoresis was the first method to identify that in our outside fishery (Noyes Island) we were catching some sockeye that were probably destined for the Fraser River area this past year; they were not there in 1982. The tagging data verified that some sockeye tagged at Noyes Island were captured in the Johnstone Straits area. The scale analysis is not available yet.

In our efforts to know what stocks are going to each country, we have to be able to identify individual units with tools such as electrophoresis, scale analysis, parasite analysis, and tagging data. Fisheries management must be based on the stock concept, even though catches are from mixed-stock fisheries.

Fritz: I think that is true of almost every fishery in the world, and the same three questions are asked by everyone. But if a manager cannot get an answer to all the questions, management is difficult. If you know that you are fishing Canadian fish, but Canadians are fishing American fish, you still cannot predict how many fish there are or what the escapement has to be. Until you can do all of those things, you will have the same frustration.

Lincoln: I read in Gene Fritz's comments a perception that sometimes electrophoresis is simply a genetic technique—something done in a void. I have also heard it commented that this is a tool that is used along with other tools for stock assessment and measuring standard productivity.

Fritz: Historically the biggest problem that my office has been confronted with is determining whether a genetic research project is pure science or whether it has immediate implications for practical management problems. Correct me if I am wrong, but my understanding is that the techniques of electrophoresis are well understood. You do not need a new set of techniques to run starch gel electrophoresis for every species.

Gall: That is not altogether true. How likely existing techniques will work depends on the species. We are now working on sturgeon, and it has taken us a year to find systems that look promising. Two things are missing in the discussion. First, electrophoresis is a tool, and projects should be judged on the basis of the objectives. Secondly, if this tool, electrophoresis, is not available for a species, the project should be judged on the basis of the potential benefits if the tool is refined for that species, and the capability of the project to accomplish that refinement.

Hankin: I would like to ask if anyone is researching the problem of jointly harvested wild and hatchery fish. In the case of Pacific salmon in California, hatchery fish are straying into natural spawning areas, and we customarily count them for escapement figures for natural production. Electrophoresis is the only tool I have been able to think of that could conceivably be used to study the effect of hatchery fish straying into the wild population.

Gall: There is one reason that electrophoresis has not been used to study this problem, and that is because for the most part salmon fishery biologists will not allow us into the hatcheries or to breed adequate markers into hatchery populations.

Helle: It has been done to some extent in Alaska.

Gall: Fred Allendorf mentioned earlier that in Montana the hatchery process had created a distinguishable individual. But natural differentiation between the hatchery population and the wild population is usually relatively small. If you want to follow the reproductive cycle effectively, you need to introduce a genetic marker into the hatchery stock. The research could be done with a tremendous degree of accuracy and in a much shorter time if you had that marker. Some argue that if you bring a marker into a hatchery population, you will disrupt the population as a result of low fitness caused by the marker or inbreeding resulting from breeding for the marker. I must ask the question, Do you really expect a genetic marker to be more disruptive than the routine management we see in hatcheries? I am not saying hatcheries are bad; I support them completely. But there have been some things done at hatcheries that should not have been done—for example, hatcheries can change the spawning time and alter growth rates. I do not think that putting a marker in for the short term is going to have any particularly adverse effect on the fishery.

Fritz: The object of many electrophoresis studies is simply to differentiate species X, Y, and Z. Sea Grant would like to see more work that is trying to get at a multi-disciplinary question, that includes not only genetics problems but population problems, and management realities. Then electrophoresis becomes a tool rather than an end in itself. I seldom look at a proposal—a research approach—that is comprehensive in scope.

Gall: But would agencies fund a comprehensive project that might take 10 years to complete?

Fritz: We have been funding Thorpe in Washington for 10 years. We have projects that have been going on in Delaware for 12 years.

Gall: Did you put them on the books initially for 10 years? California won't. We fund a project initially for a maximum of three years and come back to review it. But in some cases, such as Chinooks, you have no data at the end of three years—no data. Must you gamble, as a researcher, that you might be able to continue? Should you spend three years on a project that you might not get funding to finish?

Fritz: All the Sea Grant office asks is that a certain amount of progress is being made. I think that Jim Sullivan too would

consider a proposal that said this research probably will take 15 years to complete, but in the first three-year increment, we intend to do this. At the end of three years, an evaluation would determine whether reasonable progress had been made. If so, funding could be continued for another three years.

Lincoln: Does anybody on the panel have any final comments to make?

Frey: I think that it is important to consider the future needs of managers. I am sorry this workshop was called "Identifying Fish Subpopulations." I would have preferred "Identifying Living Marine Resources Populations," because I think that, in California particularly, in another 10 or 20 years, we will have to have a different type of management than the present species-by-species approach. We probably are going to have to set aside certain parts of the state's coastal waters for the establishment of gene pools—breeding places where no fishing will be allowed.

In 1980 about 12.5 million user-days were expended in California in near-shore waters by people with hook and line, i.e., recreationalists. On top of that there has been a huge increase in gill-net and other commercial fisheries. When we begin zonal marine resource management, we will need to know what stocks we are dealing with so that we will not protect one particular gene pool and inadvertently affect another.

One point I want to make, as a manager who must use scientific information, is that it is difficult to apply the results of experiments if the experts are arguing over their validity. We have to ask scientists to come up with techniques that are acceptable to at least a majority of the scientific community involved in that type of work.

Lincoln: Let me close the discussion by thanking all the people who have done research in this area for the past 10 or 20 years. I think the time has come when your work is starting to pay off and to be used in management. Because of your efforts, electrophoresis is being recognized as a valuable tool.

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[1]Medicine Creek treaty signed between various Puget Sound/Washington coastal tribes and the United States federal government.

[2]A U.S.–Canada salmon interception treaty was signed and ratified in March 1985.

SUMMARY OF THE PANEL DISCUSSION

RICHARD LINCOLN
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The panel session included a discussion of the usefulness of the stock concept in fisheries management and an exchange of experience using genetic stock identification as a practical and strategic management tool. Important needs for resource management and research funding were identified for the continued use and development of genetic stock identification techniques. The discussion of current and future applications generated useful criteria for evaluating research proposals.

The validity of the stock concept in fisheries management was one of the primary questions discussed by the panel and workshop participants. The representative from the National Sea Grant College Program questioned whether the concept of identifying and managing separate fish stocks is necessary for perpetuating the resource and suggested that the concept was instead a theoretically pleasing, yet invalid approach that has been institutionalized. Many argued that genetic diversity and integrity is an important goal of management. Resource managers develop goals in most cases to optimize or maximize yield, not merely to prevent the extinction of fish populations. Fisheries managers might ignore population or subpopulation differences within a species without threatening the existence of the species, but this approach would not likely maximize the long-term harvestable surplus from the species groups of subpopulations. And this is the central goal of current fisheries resource management.

Many current studies are aimed at isolating marine stocks and evaluating their productive relationships relative to harvest/yield goals. We do manage fish populations on a stock concept, both from a production and harvest allocation standpoint. The genetic stock identification techniques and applications discussed in the panel session provide the ability to test and continually evaluate management plans.

The active use of genetic stock identification techniques in applied fisheries management has evolved relatively recently. Group discussion attributed this recent surge in usage to refinements and expansion of the technique as well as to a lag in resource managers' recognition of the potential of this technique to help solve complex production and allocation problems. Current applications and projected needs strongly suggest that genetic stock identification techniques should be viewed as increasingly important resource management tools.

The future application of genetic stock identification tools in practical fisheries management appears to be limited by the availability and stability of funds to support this work. A discussion of criteria used by Sea Grant to evaluate proposals provided insight into what this program looks for in a successful proposal. Three criteria were identified: (1) How good is the science? (2) How important is the problem being addressed? Is it a real problem and how does it relate to similar problems? and (3) What is the user relationship? Have scientists made appropriate links with management agencies?

An extended discussion of item 3 indicated that the most attractive proposals are those with clear links to management agencies, that is, where the application need and potential are clearly defined. Whereas this may place an additional burden on the scientist, the extra effort to establish these relationships is likely both to reduce the lag time in incorporation of research results in applied fisheries management and to increase the benefits of the overall work effort. The resource manager obviously shares the burden of effective cooperation by being innovative and progressive, constantly looking for new ideas to improve management approaches. From this perspective, the most effective linkage between science and management is likely to occur between researchers and mid-level technical management staff. The session illustrated the recent development of effective communication and working relationships between researchers and managers as genetic stock identification becomes an important component of applied management programs.

The panel concluded that the stock concept is a useful and valid approach in fisheries management. Most state, federal, and judicial fishery management plans incorporate production goals to maximize or optimize the harvest of fish populations and define specific conservation and allocation goals for individual stocks. Genetic stock identification is a potentially valuable tool in that management process. The evolution of this tool has resulted from the dedication of researchers who had the vision and expertise to develop the capability. Resource managers are now incorporating genetic stock identification into operational programs, but the availability and stability of funds are critical problems that hinder realization of the full potential of these techniques.

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