Strategic Plan of the West Coast Salmon Genetic Stock Identification Collaboration

March 26, 2010

Vision Statement

A working partnership between fishermen, scientists, and managers in Washington, Oregon, and California that benefits fish and strengthens west coast salmon fisheries by protecting weak stocks, providing sustainable harvest, and improving economic opportunities and fishing practices through better understanding of stock specific ocean distribution and migration patterns of salmon.

Project Goals

Goal 1: Improve understanding of the ocean ecology of salmon by integrating stock-specific distribution patterns over space and time with biological and environmental data.

Goal 2: Integrate multiple disciplines to develop and apply new scientific technology to improve fisheries management strategies across geo-political boundaries.

Goal 3: Improve economic opportunities for fishermen and coastal communities.

Guiding Principles

- Authentic collaboration
- Trust and respect
- Mutual learning
- Integration
- Multiple benefits
- New technology

Overview

The goal of the West Coast Salmon Genetic Stock Identification Collaboration (WC-GSI) is to utilize evolving technologies and research to develop new science and management tools to strengthen west coast salmon fisheries. By improving the quantitative basis of fisheries management we hope to aid managers in rebuilding weak stocks and providing sustainable harvest. Other benefits may include enhanced ecosystem-based science and improved economic opportunities and fishing practices.

Presently, little is known about the behavior and migration patterns of individual natural-origin salmon stocks, and if particular stocks are of concern fishery managers have to, among other actions, implement time/area closures to protect these constraining stocks. When abundance forecasts of key stock s allows for limited fishing, a better understanding of stock-specific distribution patterns may allow for crafting fisheries in more precise way that enables fishing opportunity targeting healthy populations while avoiding weak stocks. By developing and applying digital technologies, such as electronic data-logging systems coupled with Global Positioning Systems, and capitalizing on newly developed genetic stock identification (GSI) techniques, we believe that high-resolution stock distribution patterns can be determined in near real time and made available for fisheries management.

In 2006 and 2007 the states of California, Oregon, and Washington implemented pilot projects to explore the application of GSI to fishery management (see Appendix 1 for overviews of state-based projects). Based substantially on the promising results of these individual West Coast state projects, meetings were held in 2006 and 2007 by West Coast industry representatives, fisheries managers and scientists to discuss developing a West Coast Collaborative Project. These meetings included over forty participants from federal and state agencies for salmon science and management, native American tribes, and representatives from the Washington, Oregon, and California salmon troll industries. West Coast Salmon Genetic Stock Identification Collaboration participants agreed to work together by supporting efforts to: 1) pursue the appropriate federal permit from NMFS to authorize research (i.e., sampling) on ocean salmon for the purpose of exploring the potential use of GSI for science and management applications; 2) coordinate research between National Marine Fisheries Service (NMFS) laboratories, state agencies, universities, and fishing industries from the three West Coast states; and, 3) use developing protocols to direct and facilitate cooperative fishery GSI-based science to benefit salmon populations, provide sustainable harvest, and improve economic opportunities for the fishing industries.

Recent advances in GSI of Chinook salmon now make it possible to fulfill a vision that fishermen have had for decades – to map the ocean distributions of salmon stocks by combining the stock of origin of a fish with its catch location. Many technologies, in addition to GSI, have been developed that can now be applied to help achieve this simple goal and extend it to produce a variety of benefits.

Ocean distribution

It is now possible to outfit small fishing boats with electronics that allow recording of catch and effort with high resolution in space and time. This information can be transmitted via satellite or cellular phone network to shore-side systems that can track the activities of the entire fleet. This information can be summarized and transmitted back to the fishermen to help them improve the efficiency of their fishing operation. Genetic stock identification results can be generated within a week and applied to catch and effort data to help fishermen and managers determine the distribution of stocks and plan their activities to maximize catch while protecting weaker stocks. Improved, fine-scale information on stock distributions and migration patterns will enable fishery managers to improve catch forecasting models and design fisheries that can better achieve the multiple goals of fishery management; maximize catch while producing sustainable fisheries that benefit coastal fishing communities.

Ocean ecology
Fine-scale, stock-specific fish distribution data can be combined with other biological data and measures of the ocean environment from instruments on the boats, regional oceanographic sampling, and satellites, to improve knowledge of the ocean ecology of adult Chinook salmon. Distributions in relation to ocean temperature, salinity, and chlorophyll can yield insights into ocean habitat preferences and help to predict fish distributions based on features of the ocean environment.

Fishery management
The regulatory system governing the harvest of Chinook salmon has primarily used CWTs to estimate exploitation and harvest rates. Several factors affect the utility of the CWT system, such as the difficulties (costs and logistics) of tagging most of the existing stocks and the low tag recovery rates in narrowly defined time and area fishery stratum. GSI data provides a more detailed measure of stock composition from a smaller sample than is needed for CWTs, since all or most fish sampled provide data. Data from fish sampled dockside and at sea can be used in fishery allocation models to calibrate base periods and to track year-to-year changes in distribution. In-season measures of stock composition are likely to lead to new tools for controlling fishery impacts.

Ecosystem based fishery management
Ecosystem based fishery management will require improved spatial representation of stocks, better knowledge of climate-ocean interactions, and refined definitions of habitat (Marasco et al., 2007). The WC-GSI Collaboration provides a mechanism for collecting vast amounts of ecological data directly from the fishing fleet, and at temporal and spatial scales that greatly improve resolution over existing data collection systems. This information is anticipated to improve our understanding of the ocean ecology of adult Chinook salmon, and to assist in learning about factors that drive stock-specific oceanic distribution patterns, key information needs as we move to EBFM.

In a broad sense, ecosystem based fishery management includes both human and biological communities (Marasco et al., 2007). The WC-GSI Collaboration, by its nature, helps to connect fishermen and their communities with the resources they depend on. Because the WC-GSI Collaboration enables understanding of many social, biological, and environmental elements of fisheries in an ecosystem context, it has the potential to connect human and biological communities and thus embodies the most inclusive vision of ecosystem based fishery management.

While GSI can improve the information available on fishery stock contribution rates and distribution it does not provide all the information currently used for fishery management. The principal limitation is lack of age data. Ages can be read from scales collected along with tissue samples, but there is error and, more importantly, potential bias in these ages. Also, stock identifications are not absolute, but statistical. Work is needed to understand uncertainty and bias in GSI-derived stock and age structures in relation to the current system based on coded-wire tags (CWT). There are sampling limitations using CWTs, but these are better understood than for GSI. In the future, a novel intergenerational genetic tagging method, termed parentage based tagging,

will be able to provide this age information, and it is in the early stages of implementation in California and elsewhere. A second difficulty with applying GSI to current management is that not all stocks currently managed can be discriminated using GSI. Notably, fall and spring runs in several systems are not always separable using the current GSI data base. The management system has evolved over the past three decades based largely on data from CWT recoveries. Incorporation of genetic data into the system and, potentially, moving to more fine-scale management will be an on-going process that is driven by new initiatives and the availability of these genetic data. It is expensive to implement at-sea data collection with quick turn-around GSI analyses, and to support data analysis and the development of new models. It will be a challenge to learn how to obtain suitable samples from fisheries to support modeling objectives. Spatial and temporal aggregations under GSI will need to balance statistical power with sampling costs. While these expenses are expected to decrease over time, funding support needs to be identified to enable the development of genetic methods and their integration into fisheries management.

Marasco, R.J., D Goodman, C.B. Grimes, P.W. Lawson, A.E. Punt, and T.J Quinn. 2007. Ecosystem-based fisheries management: some practical suggestions. Canadian Journal of Fisheries and Aquatic Sciences 64: 928-939.

Project Objectives

Objective 1 Consistent with guiding principles, develop an organizational and operational framework to collaboratively improve status of West Coast salmon populations and fisheries and meet mutual goals and objectives.

Action Strategies:

- Develop and finalize a framework for establishing a working relationship (December 2007)
- Hire a coordinator to facilitate the group meeting their goals, objectives and responsibilities (April 2008)
- Establish a system of management and committee structure to implement project goals (Section 1, operational aspects)

Objective 2 Develop a plan to communicate among internal partners and with external stakeholders.

Action Strategies:

- Establish a committee that will develop and implement a communications plan for the WC-GSI Collaboration (Section 2, December 2007). The plan will include strategies for:
    - communicating among internal partners
    - communicating with external audiences
    - developing engagement with extended stakeholders, including fishermen, processors, resource managers, scientists, and the broader public

Objective 3 Develop a model system that can be broadly applied to fish harvest management and that will return value to the fleet by applying electronic technologies to collect high-resolution at-sea fishery, biological, and oceanographic information and make it available rapidly to multiple audiences.

Action Strategies:

- Establish a committee to develop and implement a system to effectively collect, share and manage data (Section 3, December 2007). The plan will include strategies for:
    - developing digital technologies to efficiently collect and transfer data (ongoing)
    - developing a shared database freely accessible to internal partners and external audiences (Fall 2009)
    - developing a web-based method to access the shared database, disseminate results and products, and to engage multiple external audiences (Fall 2010)
    - developing tracking systems that increases economic opportunities (ongoing)
- Establish what ecosystem based fishery management means to the WC-GSI Collaboration and develop strategies to implement principles for improving resource management.

- Develop definition of ecosystem based fishery management as it is relevant to the collaboration (Oversight committee, TBD)
- Develop strategies to implement ecosystem based fishery management (Oversight committee, TBD)

Objective 4 Develop approaches for integrating genetic stock identification information into fisheries management models

Action Strategies:

- Establish a committee to develop/implement strategies that integrate genetic stock identification information into fisheries management models (Section 4, December 2007). The plan will include:
  - Enhancing the existing system based on CWT by providing genetic estimates of stock-specific distribution and abundance. (ongoing)
  - Developing pre-season and in-season management models that incorporate genetic stock identification data (TBD)
  - Incorporating genetic and other WC-GSI data into the Pacific Fishery Management Council's salmon management process (TBD)

Objective 5 Develop strategies to maximize accuracy and precision of genetic stock identification results

Action Strategies:

- Establish a committee to identify methods of genetic analysis that maximize accuracy and precision (Section to be developed[1], 6/2007). The plan will include:
  - Evaluating existing analytical methodologies and recommending analytical procedures (ongoing)
  - Identifying the error structure of GSI estimates taken from operating fisheries (ongoing)
- Ensure that genetic variation present in natural populations is reflected in the Genetic Analysis of Pacific Salmonids (GAPS) databases (ongoing)

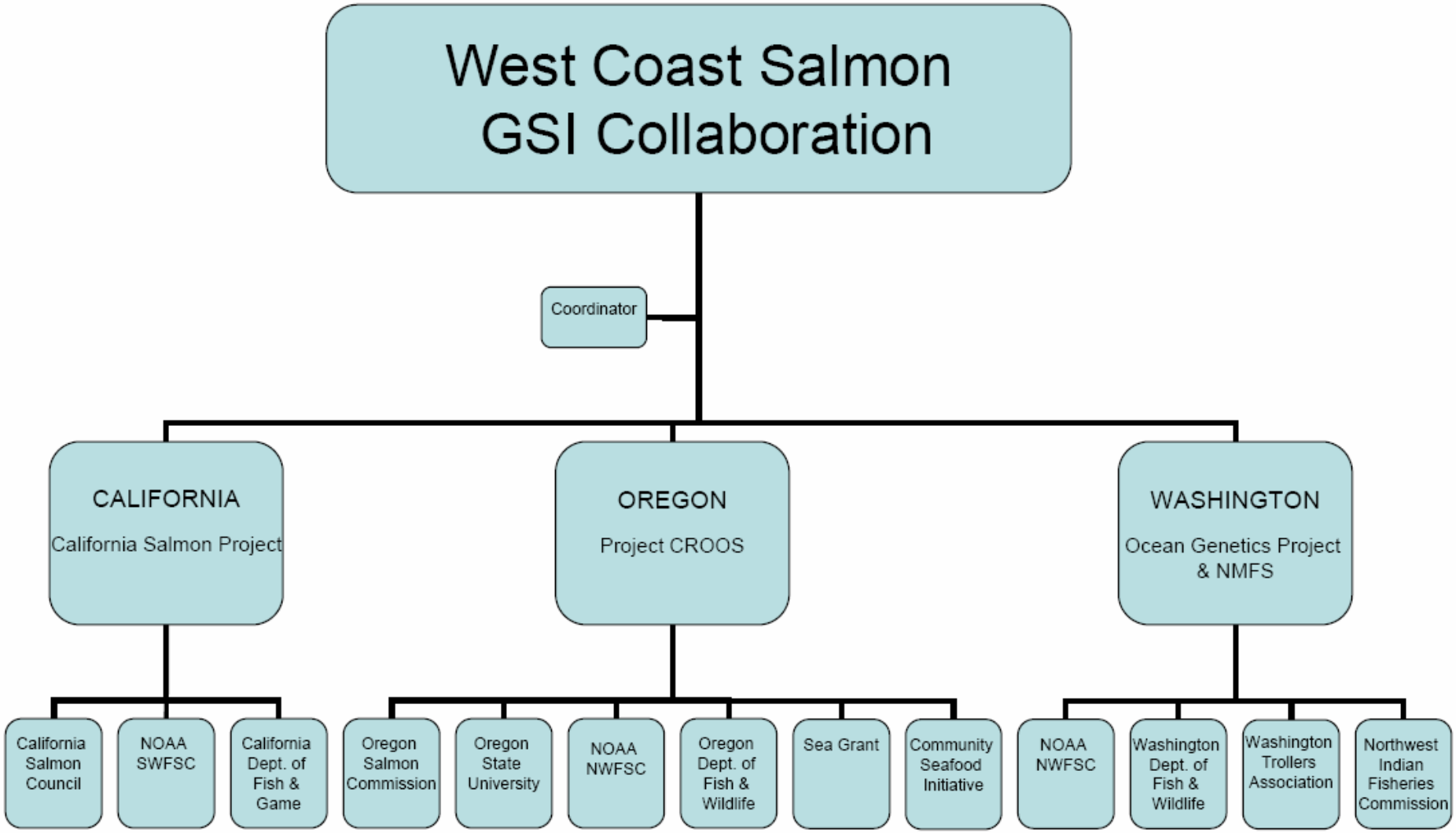
Section I. Operational Aspects: partnership, oversight, working groups (subcommittees) and coordination

In 2007, workshop participants agreed to form a working partnership for a West Coast Salmon GSI Collaboration (WC-GSI). Oversight of the collaboration would be provided by all present at the meeting (Central Oversight Committee, Table 1) and additional interested parties can join by request. See the accompanying flow-chart for visual representation of the coordinating group (Figure 1).

Four working groups (sub-committees) were charged with developing strategies to achieve goals and providing these as recommendations to the central WC-GSI oversight group for approval. The four committees are: Data Standards and Sampling Methodology (Table 2); Genetics (Table 3); Applications to Fishery Management (Table 4); and Communications (Table 5).

[1] This committee originated from informal discussions prior to WC-GSI meeting in December 2007. The committee needs to develop Section 5 and the list of action strategies; it has not held a meeting yet.

Figure 1. West Coast Salmon Genetic Stock Identification Collaboration organizational chart.



Section 1, continued

Table 1. List of members and email addresses for all members of the West Coast Salmon Genetic Stock Identification Collaboration Oversight Committee and Interested Parties.

Shanae	Allen	NOAA Southwest Fishery Science Center	shanae.allen at noaa.gov
Michael	Banks	Oregon State University	michael.banks at oregonstate.edu
Renee	Bellinger	Oregon State University	renee.bellinger at oregonstate.edu
Scott	Blankenship	Washington Department of Fish and Wildlife	blanksmb at dfw.wa.gov
Lisa	Borgerson	Oregon Department of Fish and Wildlife	lisa.borgerson at oregonstate.edu
Rick	Brown	NOAA Northwest Fisheries Science Center	rick.brown at noaa.gov
Peggy	Busby	NOAA Northwest Regional Office	peggy.busby at noaa.gov
Ethan	Clemons	Oregon Department of Fish and Wildlife	ethan.r.clemons at state.or.us
Scott	Davidson	NOAA Southwest Fishery Science Center	r.scott.davidson at noaa.gov
Joe	Dazey	Washington Trollers Association	jdazey at centurytel.net
Peter	Dygert	NOAA Northwest Regional Office	peter.dygert at noaa.gov
Barbara	Emley	California Salmon Council	barbaraemley at sbcglobal.net
Jeff	Feldner	SeaGrant/Oregon Salmon Commission	jeff.feldner at oregonstate.edu
Nancy	Fitzpatrick*	Oregon Salmon Commission	njf at class.oregonvos.net
Mike	Ford	NOAA Northwest Fisheries Science Center	mike.ford at noaa.gov
Matt	Forve	California Salmon Council	mforve at gmail.com
Kathy	Fosmark	Pacific Fishery Management Council	kfosmark at aol.com
Douglas	Fricke	Washington Trollers Association	dfricke at techline.com
Carlos	Garza	NOAA Southwest Fisheries Science Center	carlos.garza at noaa.gov
David	Goldenberg*	California Salmon Council	golden59 at pacbell.net
Churchill	Grimes	NOAA Southwest Fisheries Science Center	churchill.grimes at noaa.gov
Jon	Hess	Columbia River Inter-Tribal Fish Commission	hesj at critfc.org
Jennifer	Hogan	NOAA Southwest Regional Office	Jennifer.hogan at noaa.gov
Bobby	Ireland	Oregon State University	rireland at coas.oregonstate.edu
Robert	Kope	NOAA Northwest Fisheries Science Center	robert.kope at noaa.gov
Brett	Kormos	California Department of Fish and Game	bkormos at dfg.ca.gov
Larrie	LaVoy	Washington Department of Fish and Wildlife	lavoylwl at dfw.wa.gov
Pete	Lawson	NOAA Northwest Fisheries Science Center	peter.w.lawson at noaa.gov
Heather	Mann	Seafood Consumer Center	hmann at seafoodschool.org
Doug	Milward	Washington Department of Fish and Wildlife	douglas.milward at dfw.wa.gov
Michael	Mohr	NOAA Southwest Fisheries Science Center	michael.mohr at noaa.gov
Paul	Moran	NOAA Northwest Fisheries Science Center	paul.moran at noaa.gov
Barbara	Morris	Washington Trollers Association	barbwire1253 at hotmail.com
Mike	O'Farrell	NOAA Southwest Fisheries Science Center	michael.ofarrell at noaa.gov
Jim	Olson	Washington Trollers Association	jaocto at juno.com
James	Packer	Washington Department of Fish and Wildlife	packejfp at dfw.wa.gov
Melodie	Palmer-Zwahlen	California Department of Fish and Game	mpalmer at dfg.ca.gov
Kim	Reisbick	Washington Trollers Association	khreisbick at comcast.net
Eric	Schindler	Oregon Department of Fish and Wildlife	eric.d.schindler at state.or.us
Jim	Seeb	University of Washington	jseeb at u.washington.edu
Lisa	Seeb	University of Washington	lseeb at u.washington.edu
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Mike	Stiller	California Salmon Council	emstiller at aol.com
Gil	Sylvia	Oregon State University	gil.sylvia at oregonstate.edu
Barry	Thom	NOAA Southwest Fisheries Science Center	barry.thom at noaa.gov
Kenneth	Warheit	Washington Department of Fish and Wildlife	warhekiw at dfw.wa.gov

Table 2. Data Standards and Sampling Methodology Committee members and email addresses (*chair):

Michael	Banks	Oregon State University	michael.banks at oregonstate.edu
Renee	Bellinger	Oregon State University	renee.bellinger at oregonstate.edu
Scott	Blankenship	Washington Department of Fish and Wildlife	blanksmb at DFW.WA.GOV
Barbara	Emley	California Salmon Council	barbaraemley at sbcglobal.net
Jeff	Feldner	SeaGrant/Oregon Salmon Commission	jeff.feldner at oregonstate.edu
Nancy	Fitzpatrick	Oregon Salmon Commission	njf at class.oregonvos.net
Carlos	Garza	NOAA Southwest Fisheries Science Center	carlos.garza at noaa.gov
David	Goldenberg	California Salmon Council	golden59 at pacbell.net
Pete	Lawson	NOAA Northwest Fisheries Science Center	peter.w.lawson at noaa.gov
Michael	Mohr	NOAA Southwest Fisheries Science Center	michael.mohr at noaa.gov
Paul	Moran	NOAA Northwest Fisheries Science Center	paul.moran at noaa.gov
Mike	Stiller	California Salmon Council	emstiller at aol.com
Gil	Sylvia*	Oregon State University	gil.sylvia at oregonstate.edu

Table 3. Genetics Committee members and email addresses (*chair):

Eric	Anderson	NOAA Southwest Fisheries Science Center	eric.anderson at noaa.gov
Michael	Banks	Oregon State University	michael.banks at oregonstate.edu
Renee	Bellinger	Oregon State University	renee.bellinger at oregonstate.edu
Scott	Blankenship	Washington Department of Fish and Wildlife	blanksmb at dfw.wa.gov
Mike	Ford	NOAA Northwest Fisheries Science Center	mike.Ford at noaa.gov
Carlos	Garza*	NOAA Southwest Fisheries Science Center	carlos.garza at noaa.gov
Paul	Moran	NOAA Northwest Fisheries Science Center	paul.moran at noaa.gov
Linda	Park	NOAA Northwest Fisheries Science Center	linda.park at noaa.gov
Lisa	Seeb	University of Washington	
Robin	Waples	NOAA Northwest Fisheries Science Center	robin.waples at noaa.gov
Kenneth	Warheit	Washington Department of Fish and Wildlife	warjekiw at dfw.wa.gov

Table 4. Applications to Fishery Management Committee members and email addresses (*chair):

Ethan	Clemons	Oregon Department of Fish and Wildlife	Ethan.R.Clemons at state.or.us
Robert	Kope	NOAA Northwest Fisheries Science Center	Robert.Kope at noaa.gov
Jennifer	Ise	NMFS Southwest Regional Office	Jennifer.Ise at noaa.gov
Larrie	LaVoy	Washington Department of Fish and Wildlife	lavoylwl at dfw.wa.gov
Pete	Lawson	NOAA Northwest Fisheries Science Center	peter.w.lawson at noaa.gov
Michael	Mohr	NOAA Southwest Fisheries Science Center	michael.mohr at noaa.gov
Michael	O'Farrell*	NOAA Southwest Fisheries Science Center	michael.ofarrell at noaa.gov
Jim	Packer	Washington Department of Fish and Wildlife	packejfp at dfw.wa.gov

Table 5. Communications Committee members and email addresses (*chair):

Nancy	Fitzpatrick*	Oregon Salmon Commission	njf at class.oregonvos.net
Carlos	Garza	NOAA Southwest Fisheries Science Center	carlos.garza at noaa.gov
David	Goldenberg*	California Salmon Council	golden59 at pacbell.net
Pete	Lawson	NOAA Northwest Fisheries Science Center	peter.w.lawson at noaa.gov
Eric	Schindler	Oregon Department of Fish and Wildlife	eric.d.schindler at state.or.us

Section 2: Communications plan - *Communications Committee*

The goal of the Communication Committee is to provide a clear line of communication between project collaborators, user groups and interested parties. The committee will utilize a variety of communication systems to convey a two-way flow of information. There will be three forms of communication: Internal, External and Data Management. The day to day focal point of the communications committee will be managed by the West Coast Collaborative GSI (WC-GSI) Coordinator in consultation with the committee co-chairs.

A. Internal communication

Internal communications will be harmonized through the WC-GSI Coordinator by the following systems:

- **Email** to collaborators will contain a detailed header in the subject line to allow participants to self filter their email (the coordinator will maintain a current email list of participants)
    - State based project coordinators (CA, OR, & WA) will keep the WC-GSI participants updated on state projects as necessary.
    - Release of information to the inclusive WC-GSI email list will be initiated through the state coordinators, who in turn will screen the request and forward to the WC-GSI Coordinator.
    - Participants may select to "receive only" major announcements, summaries/updates and release of major documents. They can be removed from these lists by contacting the WC-GSI Coordinator.
    - Coordination of meetings will be conducted by the WC-GSI Coordinator who will establish and distribute an "on-line" (Doodle Poll) scheduling calendar to all participants.
    - Sharing of documents will be coordinated by means of an on-line system such as "go-to-meeting" or an Oracle collaboration suite will be developed as time and expense permits. Currently the Project CROOS utilizes a tab on their website http://www.ProjectCROOS.com, West Coast Collaborative, meeting notes, grant proposals, Experimental Fishing Permit and where other relevant documents are posted.
    - Web based sharing through a dedicated WC-GSI website is not yet complete and will be evaluated as necessary.

- **Conference Calls** will be conducted on an "as needed" basis and will be harmonized through the WC-GSI Coordinator.

- **Published Reports/documents** will be distributed on an "as needed" basis and will be disseminated through the WC-GSI Coordinator.

- Web-based Data Sharing - building a shared database is essential to this project. Data standards and data fields are being developed by the Sampling and Methodology Committee. Methods to access shared data have been tasked to the Communication Committee and a web-based method needs to be developed.

    - Email notices will accompany web-postings to inform participants of additions/changes to website

B. External communication

External communications is an important link to apprise user groups and maintain information sharing with other interested parties. (Eight different audience groups have been identified and strategies to target those groups will be developed as part of the "Communication Plan" scheduled for the fall meeting.)

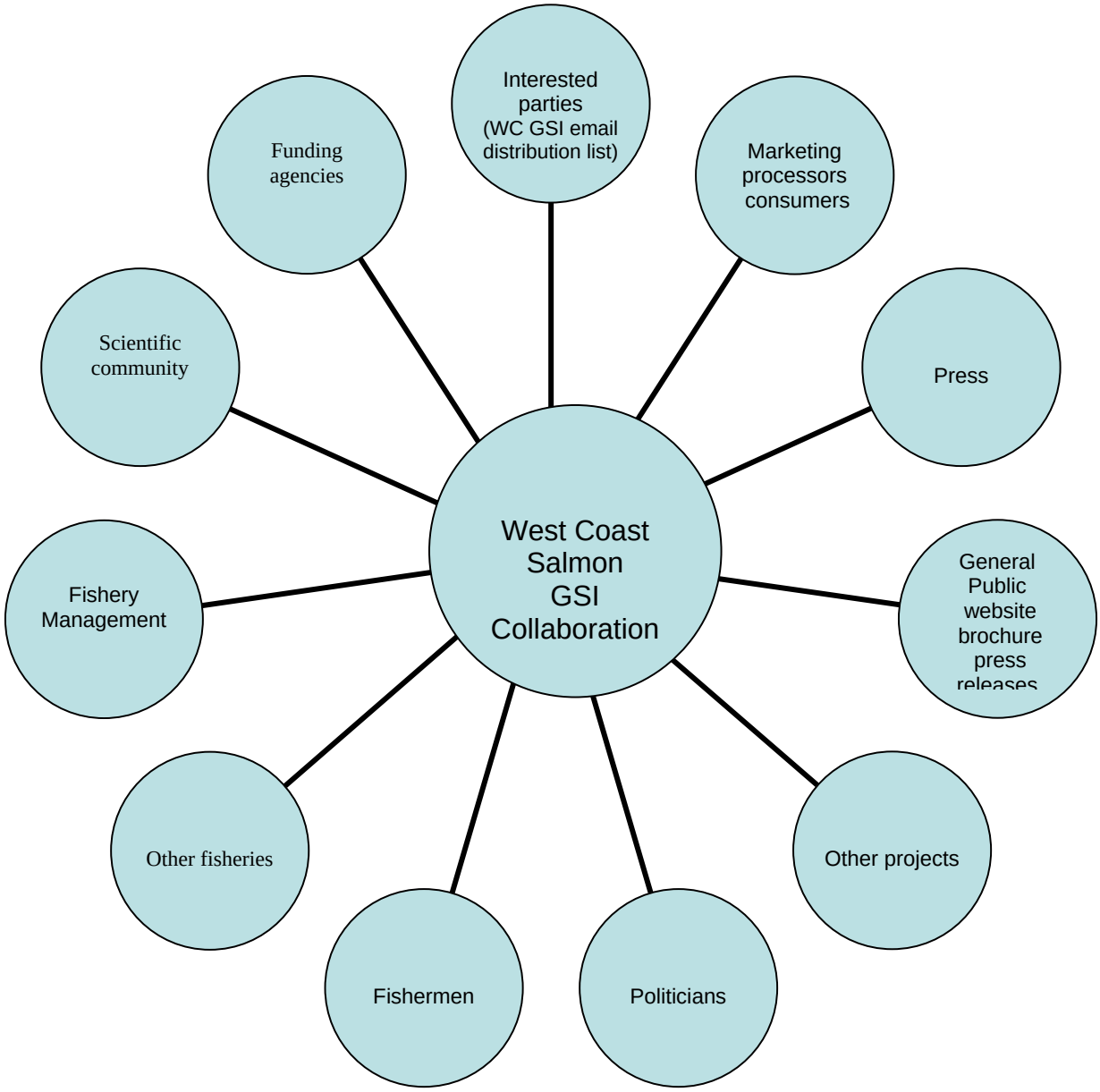
- **Targeted Audience Groups** – see Figure 1: External communication flow
    1. Fishermen
    2. Marketing, Processors, Consumers
    3. Press
    4. Politicians
    5. Fishery management
    6. Scientific community
    7. Funding agencies
    8. General public

• External Projects – sharing relevant data from external projects not directly linked to collaborators (i.e. Coded-wire program) was identified as an important linkage to the WC-GSI project. (This portion of the Communication Committee plan will be further reviewed at the fall meeting.)

C. Field coordination and data management are essential to a successful project

- **Field-coordination and data collection**
    - **Status -** current field communication relies on telephones and radios which can be problematic due to poor signal transmission.
    - **Data-loggers** – will be tested in a pilot project to determine the feasibility of better managing sampling data and exchange of information with fleet managers and labs.

Figure 1. External communication flow



Section 3 – In Development by Data Standards and Sampling Methodology Plan (Gil & Committee)
Section 4 – In Development by Applications to Fishery Management Plan (Fish Management Committee)
Section 5 – Genetic Analysis Plan (standardized data reporting - Genetics Committee TBD)

Appendix 1. State-based geographical overviews of GSI projects related to WC-GSI Collaboration.

Washington

Washington Department of Fish & Wildlife established a laboratory in 1985 for GSI work, which has provided a foundation for incorporating genetic information into harvest management in Washington. While genetic information has been used to investigate fishery harvest and monitor allocation for more than two decades, the increasing capabilities of genetic technology and improving information content provided by molecular genetic tools have recently driven an increasing trend of GSI activity investigating Washington State fisheries. From 2003 through the present, tissue samples have been collected from virtually all the ocean fisheries that have occurred in Washington State. Much of this tissue archive has been analyzed for various fishery-related purposes, from assessment of fishery impacts on specific fish stocks to enhancement of the current fishery management regime.

Oregon

A 2006 Oregon pilot study (Project CROOS) coupled electronic logbooks, global positioning systems, genetic stock identification, oceanography and traceability (tracking systems) to study the at-sea distribution of Chinook salmon. This collaboration of fishermen and scientists included the Oregon Salmon Commission, Oregon State University, Oregon Sea Grant, National Marine Fisheries Services Northwest Fisheries Science Center, Community Seafood Initiative, and the Oregon Department of Fish and Wildlife. Sampling protocols developed in 2006 have produced two years of fine-scale fish distribution data and fishing effort to support long term ecosystem-based fisheries science and management.

California

In 2006 the National Marine Fisheries Service (NMFS) Southwest Fisheries Science Center (SWFSC) in Santa Cruz sampled the recreational harvest of Chinook salmon in Monterey Bay and demonstrated the utility of GSI techniques to determine the stock composition of the harvest on a rapid basis. In 2007, the SWFSC, California Department of Fish and Game, University of California Santa Cruz (UCSC) and the commercial salmon fishing fleet, with the California Salmon Council acting as liaison, commenced a collaborative pilot research project to evaluate the use of genetic stock identification (GSI) technology to estimate stock composition and provide preliminary information about the spatial and temporal distribution of stock composition in the landed catch. The pilot project was largely successful at demonstrating the utility of GSI to provide high resolution data on catch stock composition for a given time and area, and of the ability of the commercial fishing fleet and agency/university scientists to undertake collaborative research. The data from this pilot project suggest great promise for the use of GSI methodology to better understand the stock composition of California's Chinook salmon fisheries and the ocean distribution of the species.