Modeling Intraspecific Genetic Effects for Management of Aquaculture Programs

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Abstract: Rapid worldwide development of marine finfish cage farming has raised awareness over the possible genetic and ecological effects of escaped fish on wild populations. With increased interest in implementation of marine aquaculture in the United States, NOAA Fisheries and other regulators charged with stewardship of marine ecosystems need tools to understand and mitigate risks presented by aquaculture escapees. To develop an understanding of genetic and ecological effects of escapes and design management strategies to address potential risks to marine resources, NOAA Fisheries has developed a numerical decision-support tool: the Off-shore Mariculture Escapes Genetics/Ecological Assessment (OMEGA) model. The OMEGA model is an extension of concepts from another model, the All-H Analyzer (AHA) that is used successfully in the U.S. Pacific Northwest to evaluate genetic and ecological interactions between hatchery and wild salmon and trout.

OMEGA model input parameters include size and growth characteristics of cultured fish, frequency and magnitude of escape events, survival of escapees in the wild, probability of escapees encountering a conspecific natural population and interbreeding, and population dynamics of the natural population. Model results describe the influence of aquaculture escapees on spawning biomass, juvenile production, and genetic fitness of the composite population. Effects of interactions on fitness and abundance are based on the frequency and relative abundance of cultured fish that escape and survive to encounter a natural population, the difference in survival characteristics between the artificial and the natural environments, and the genetic legacy of the cultured and natural populations.

NOAA Fisheries is using the OMEGA model to identify and evaluate risks of marine aquaculture operations, design sustainable aquaculture programs, explore the effects of regulation, and identify research priorities for areas of uncertainty.

This talk will describe the model and present results for a hypothetical sablefish (*Anoplopoma fimbria*) culture program along the U.S. West Coast. We are interested in speaking with any and all individuals interested in collaborating on the further development of the model, applying the model to other species of interest such as rockfish (*Sebastes* spp.), yellowtail (*Seriola quinqueradiata*), salmon (*Oncorhynchus spp.*), or any other aquaculture candidate species, and to identify opportunities to validate model results.

Key words: escapes, survival, introgression, simulation, fitness, selection, OMEGA.

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The development of world cage farming of marine fishes has raised concerns over the possible genetic and ecological impact of escaped fish on wild populations. Marine fish can escape from farms for a variety of reasons including: when improper mesh size is used or when holes in webbing develop from normal wear and tear, during transfer from cage to cage or while grading or harvesting fish, from high wind and high sea conditions during severe storms, or when net cages are breached by large predators. Potential effects include the introduction of maladaptive genes and reduced fitness, competition for food and space, and predation on native stocks.

Several factors merit consideration when evaluating the likely ecological and genetic impacts cultured fish may have should they escape. Among them are: the wild population genetic structure and phenotypic variability of a species or among stocks within a species, the size of the local (or affected) population relative to the estimated number and frequency of escapement, the type of breeding program to be used, including selection of the founding stock, and the likelihood that unintentional genetic drift (domestication) related to hatchery practices will occur.

In reality, there is little evidence-based information available that can reliably assign risk to escapes of finfish from aquaculture facilities, therefore, escape standards are, out of necessity, more preventative than prescriptive. Because of uncertainty, locally adapted indigenous species will probably be encouraged over the use of nonnative and genetically modified species unless a compelling argument can be made that the genetic and ecological risks are demonstrably low.

The Offshore Mariculture Escapes Genetic Assessment (OMEGA) Model was developed by ICF International (ICF) and NOAA as a tool for use by scientists and resource managers to help with understanding the potential negative impact of farmed escapees on their wild counterparts.

The purpose of OMEGA is to identify and weigh environmental risks of escapes of marine aquaculture fish to their wild conspecifics. OMEGA is intended to: 1) provide insights about factors affecting risks associated with escapes from aquaculture operations, 2) help identify research priorities, 3) explore options for the design of sustainable aquaculture programs, and 4) inform policy and management decisions related to the genetic and ecological risks of aquaculture.

OMEGA characterizes the aquaculture program by brood source, size and growth of cultured fish, and frequency and magnitude of escape events. Genetic and ecological interactions are calculated from assumptions regarding survival of escapees in nature, their likelihood of encountering conspecifics, breeding success, and the consequence of interbreeding on the fitness and abundance of wild conspecifics. The 100-year model simulation describes the influence of aquaculture escapees on survival and genetic fitness of the natural population. By evaluating different aquaculture operation scenarios and wild stock population dynamics, OMEGA allows the user to compare differences in total abundance trends of escapees and wild fish, as well as the effects of aquaculture program on survival and long-term sustainability of wild fish (ICF 2014).

The modeling concepts of OMEGA have been successfully applied over the past decade using a similar model, the All-H Analyzer (AHA). AHA has been successfully used by the Hatchery Scientific Review Group (HSRG) to evaluate 178 salmon and trout hatchery programs in the Columbia River Basin (Paquet *et al*., 2011). Using model simulation results, the HSRG formulated a working hypothesis for baseline conditions from which they evaluated strategies to better achieve stated goals for hatcheries and wild populations. The HSRG concluded that through following recommended management and harvest practices, such as broodstock selection and selective harvest, hatcheries can serve dual goals of contributing to harvest while remaining compatible with or contributing to conservation goals. The guiding principles of the HSRG are core to the purpose of the OMEGA model.

OMEGA Model Structure

As shown in Fig. 1, the OMEGA input data structure is organized around three components:

- the biology and operations of the cultured population, including number of fish by size classification, broodstock source (domesticated or wild), maturation and growth factors;
- the wild conspecific population, including assumptions of abundance, distribution, survival, age and size at maturity, age composition, and age specific harvest rates; and
- factors affecting the potential for interaction between farmed fish escapees and their wild conspecifics, assumptions of frequency and magnitude of fish escaping from the pens, survival of escapees in nature, location of the mariculture pens relative to the wild population, potential movement patterns of escapees and breeding success of escapees in nature.

OMEGA accounts for the different factors by which fish can escape from cages, such as:

- *Chronic leaks* from cages, which can be considered a baseline level of escape from year to year, assuming there are a certain amount of fish lost due to routine factors such as small tears in nets, transfer between cages, or veterinary maintenance;
- *cage failures* due to a mechanical failure or defect in a cage containing one size class of fish (this can also occur because cage farms attract predators);
- *catastrophic events* due to failure of multiple cages in the farm structure, resulting in a massive loss of fish, such as from a major storm event; and
- spawning in cages, leading to release of *gametes*.

Once cultured fish escape into nature, their survival is described by a number of factors, such as size at time of escape, level of domestication and their ability to survive in nature, and environmental factors. An attrition of the escapes occurs in the model simulation based on these factors, resulting in a fraction of escapees surviving to encounter wild-origin fish. If escapees successfully reproduce in the wild, there are spawners in nature persisting with potentially maladapted traits. There leads to an effect on genetic fitness of wild fish, which

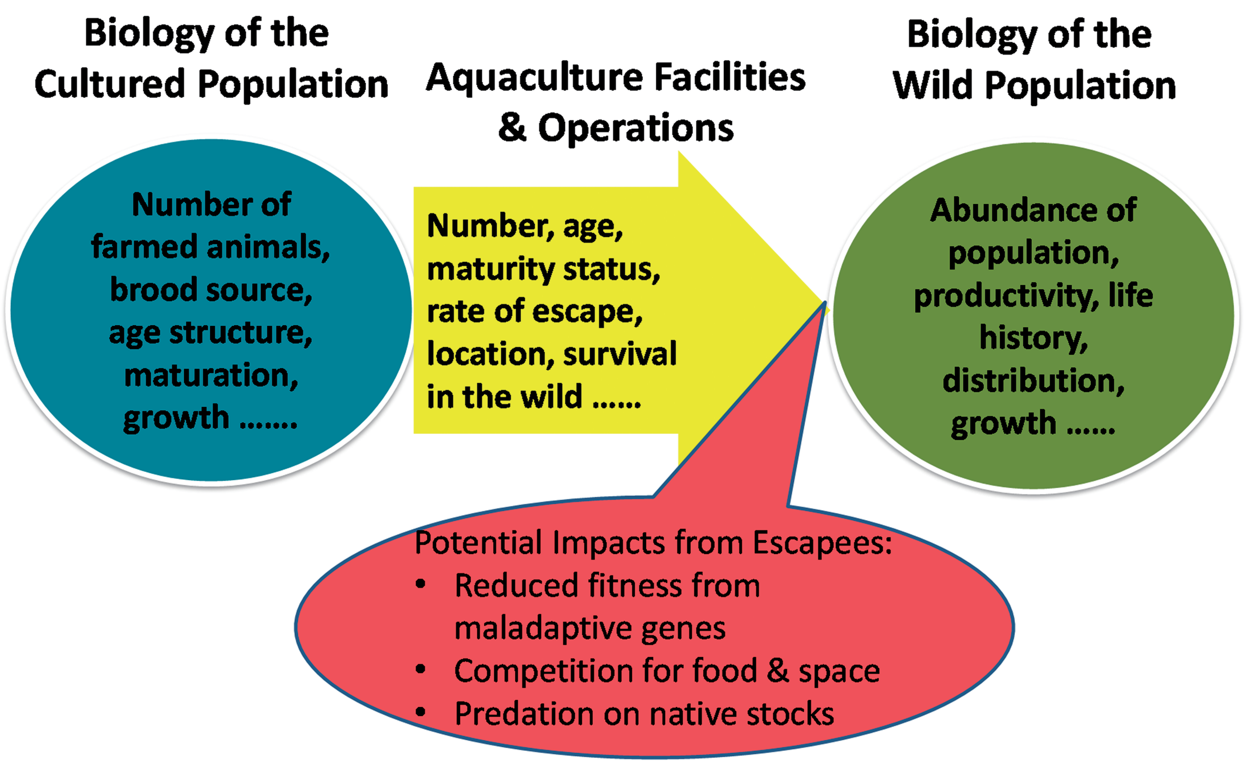

Fig. 1. OMEGA Model Components

consequently affects wild recruitment and harvest.

Included in this module are parameter inputs for the phenotypic fitness model in OMEGA. The equations are those described by Ford (2002) and described in additional detail by Campton (2009) for evaluating relative fitness effects of hatchery salmonids interbreeding with wild populations. The phenotypic trait model is described by two environmental optimum values, an aquaculture optimum and a natural optimum, with selection forcing the respective populations towards their environmental optimum (Fig. 2). The model calculates the shift in phenotype trait value of the wild population based on assumed gene flow between escapees and wild fish. The consequence is a loss in fitness and survival of the wild population as a result of this mixed wild population (the progeny of escapees and wild parents) phenotype.

OMEGA Model Simulation Example

This example uses a hypothetical commercial aquaculture operation for sablefish (*Anoplopoma fimbria*) along the coast of Washington, Oregon and California. The purpose of this example is to show how escapes can affect population abundance and long-term viability, and how limiting escapes can greatly reduce impacts to fitness and abundance of the wild population. These scenarios were developed to demonstrate model capabilities and to test model sensitivity to changes in parameter values, and are not intended to describe the operations of an actual sablefish aquaculture industry, or to suggest standards that should be used to regulate operations; they are provided only to describe the functions of the model.

In nature, sablefish reach maturity at 6 years of age and can live up to 80 years. Fish are fully selected to the fishery at 4 to 5 years of age. In culture, sablefish can grow to a harvestable size of 1 kilogram in approximately 52 weeks. In this example, the culture program is assumed to consist of 50 separate offshore pen operations, each containing multiple pens with different size classifications as fish grow to harvestable size. Total culture production is assumed to be 10,000 metric tons per year. For the two scenarios described below, natural production, harvest, culture production, encounter rate, and fitness and interactions including genetic effects are the same. Only escape rates were changed between scenarios (chronic losses, cage failures, and catastrophic events).

In the "low escape scenario", catastrophic events could occur with a probability of 5% in a given year for the first 25 years. After year 25, it is assumed technology improvements would reduce the probability of catastrophic events (1%) resulting in a loss of up to 20% of cultured stock. The scenario assumes that chronic losses are the same across all fish sizes (0.1% leakage). Cage failure rate is assumed to be the same across all size categories (0.1%). Chronic losses and moderate events together average about 200,000 fish escaping per year.

In the "high escape" scenario, catastrophic events are assumed to occur with a probability of 5–10% on a given year and each event results in up to a 60% loss of cultured stock. Chronic losses depend on fish size classification (3% for the smallest size class, 0.5%

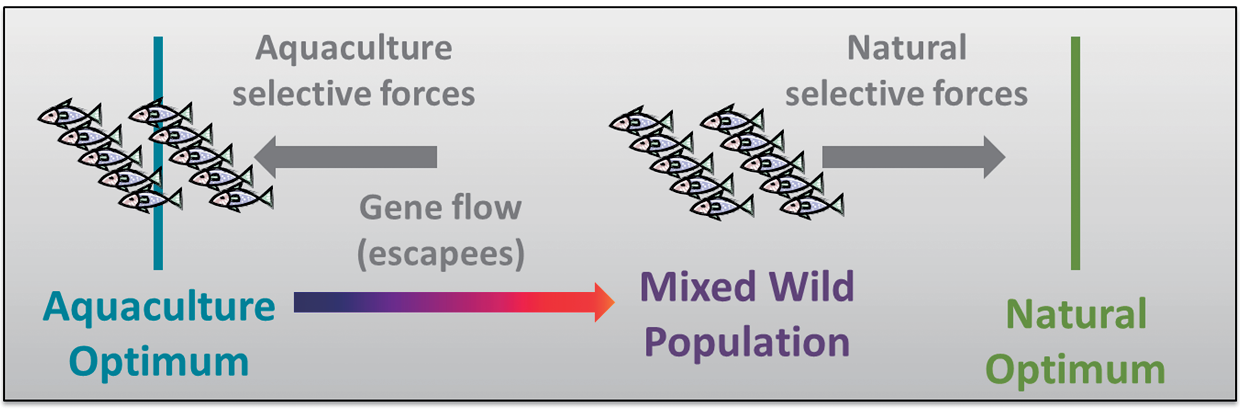

Fig. 2. The Ford Model: Two Environments, Two Selective Forces

for harvest size fish). Cage failure rate is assumed to be 0.5% for smallest size class and 1.0% for harvest size fish. Chronic losses and moderate events together average about 1.0 million fish escaping per year. This is an extremely high percent of total production (10.0 million fish at harvest size) and would represent an extreme example of escapes due to chronic and moderate events. In the 100-year simulation, five random catastrophic events occurred resulting in even larger losses.

The model response in terms of natural population fitness under both scenarios is shown in Figure 3. Escape rates in "low escapes" resulted in a slight shift in the phenotypic trait value of the wild population toward the aquaculture optimum value over the 100-year simulation.

Consistent with the slight shift in trait value, relative fitness also declined slightly, indicating effects of introgression. However, natural fitness reaches an equilibrium value fairly quickly (~year 25). In contrast, under the "high escapes" scenario, natural fitness responded quickly to the effect of escapes on the wild population and it appears fitness does not approach a lower equilibrium value until year 75.

The response of the wild population in terms of mixed population natural recruits under both scenarios is shown in Figure 4. The dark line represents no-escape scenario (i.e. 0% change) as reference. Under the "low escapes" scenario, there is an initial increase in recruitment (progeny of escapee and wild parents) due to increases spawning biomass relative to no escapes, with the value approaching an equilibrium value of about +0.5% at year 100 of

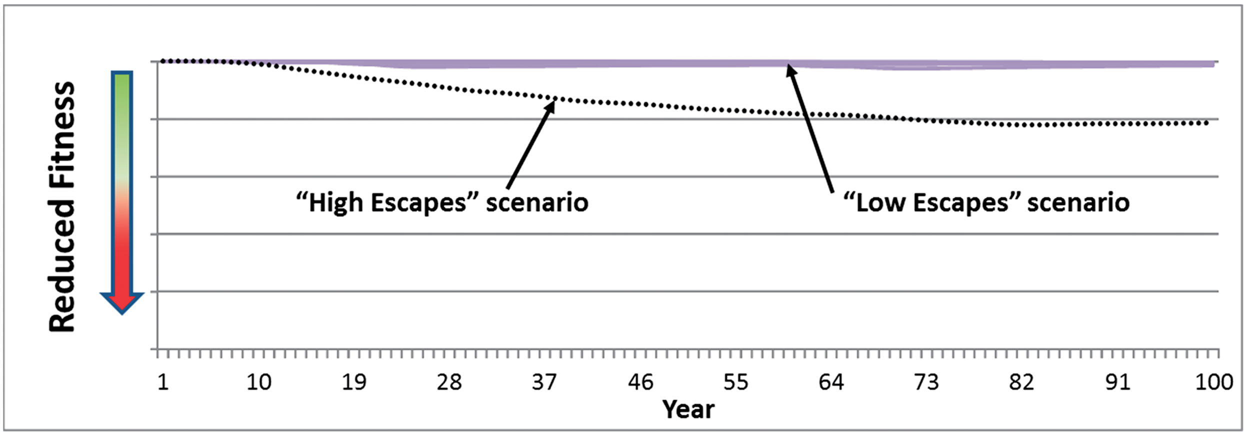

Fig. 3. Natural Population Fitness, 100-year simulation

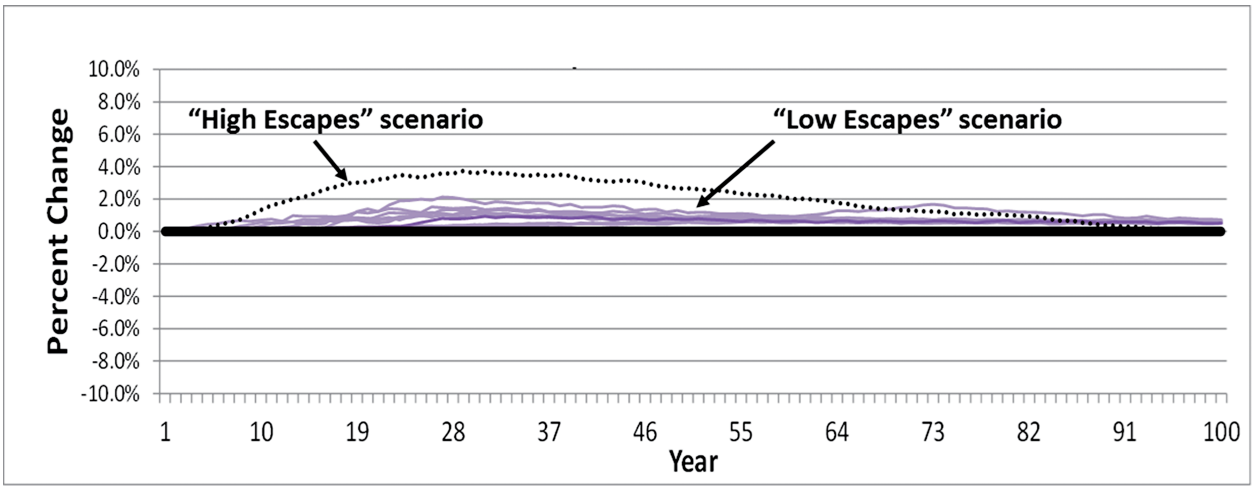

Fig. 4. Mixed Population Natural Recruits, 100-year simulation

the simulation.

The "high escapes" scenario describes the model response if there was greater selective pressure on the population due to a high level of escapes in nature. As in the previous scenario, there is an initial increase in recruitment; more than in the previous scenario but the decline is steep and nearly constant after year 30, approaching negative values in year 100. This trend would likely continue for some years due to a long-term loss in natural fitness.

The results suggest a lag between natural recruitment (Fig. 4) and fitness (Fig. 3). Initially the trend is increasing recruitment while fitness was declining. This lag is likely due to the retention of older, larger and fit adults in the spawning biomass. As more fit fish die out over time the population is shifting to less fit adults and the consequence is a decline in wild production. The results of the "high escape" scenario indicate year-over-year declining fitness and reduced survival of wild fish. The long-lived nature of sablefish is a factor in the delayed effect on wild fish biomass.

OMEGA includes many other parameter inputs that allow for exploration of different scenarios and evaluate model sensitivity due to combinations of parameter value changes (culture and wild population).

Balancing aquaculture goals with conservation goals will require careful evaluation of the risks and benefits. The challenge of decision makers is to find solutions that serve both goals. The purpose of OMEGA is to help identify possible solutions, or if a range of solutions exists, how programs can be managed for the best outcomes.

Next Steps

OMEGA is ready for general use. The model is available from NOAA along with a user guide that includes model background and instructions for using the model. The model also includes the scenarios for sablefish discussed in this presentation. We are interested in your feedback and comments. At this time we seek collaborators to develop case studies for currently farmed or considered aquaculture finfish species. Items for future development include completing a sensitivity analysis of scenarios for sablefish or other species, and developing an economic cost/benefit analysis module.

OMEGA is available at:
http://www.nmfs.noaa.gov/aquaculture/science/26_omega_model_homepage.html

References

Campton D. E., (Hatchery Scientific Review Group), 2009: Columbia River hatchery reform system-wide report. February 2009 Appendix A. 278 p. Available: <http://www.hatcheryreform.us/hrp_downloads/reports/columbia_river/system-wide_full/columbia_river_hatchery_reform_system-wide_report.zip>.

Ford M. J., 2002: Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology*, **16**, 815–825.

ICF International., 2014: Offshore Mariculture Escapes Genetic/Ecological Assessment (OMEGA) Model Version 1.0 Model Overview and User Guide. August. Prepared for NOAA Fisheries, Seattle, WA.

Paquet P. J., Flagg T., Appleby A., Barr J., Blankenship L., Campton D., Delarm M., Evelyn T., Fast D., Gislason J., Kline P., Maynard D., Mobrand L., Nandor G., Seidel P., and Smith S., 2011: Hatcheries, Conservation, and Sustainable Fisheries—Achieving Multiple Goals: Results of the Hatchery Scientific Review Group's Columbia River Basin Review, Fisheries, **36:11**, 547–561.

Annotated Bibliography

Jensen Ø., Dempster T., Thorstad E. B., Uglem I., and Fredheim A., 2010: Escapes of fishes from Norwegian sea-cage aquaculture: causes, consequences and prevention. *Aquaculture Environment Interactions*, **1**, 71–83.

The authors broadly discuss the magnitude of the problem of escapes from salmon and cod cage-farming aquaculture operations in Norway and provide specific recommendations to prevent escapes. Current knowledge about the extent of threats presented by escapes in terms of economic and ecological impacts are discussed in the context of experiences in the Norwegian aquaculture industry. While escapes occur due to several internal and external factors, reports from fish farming companies indicated that cage failure was by far the most common cause of large-scale escape in Atlantic salmon farming operations. They report studies that show the mechanisms of escape are not the same across species. Atlantic cod may cause more wear to nets and be more likely to escape through tears in the net. Consequences of escape, such as disease transfer, interbreeding, competition, and predation are generally discussed as areas for further research. The main message of this paper is that prevention is the best tool to reduce the risk of escapes. The authors report evidence that the level of escapes from cages was greatly reduced in Norway following legislation that has specific requirements for design of farms and the handling and use of equipment. They recommend countries develop similar measures to reduce escapes such as mandatory reporting of escapes, a process to use these reports to develop better standards, mandatory technical assessments following reported "large" escape events, technical standards for equipment, and finally, identification of key operational components that have a higher potential to cause an escape event, including training of staff to reduce human errors. This paper was used to identify mechanisms of escape through cage failure and operational scenarios, which are central to development of the escapes component of the OMEGA simulation model.

Meager J. J., Sklæraasen J. E., Fernö A., and Løkkeborg S., 2010: Reproductive interactions between fugitive farmed and wild Atlantic cod (*Gadus morhua*) in the field. *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 1221–1231.

The authors present a study of spawning interactions between cultured and wild Atlantic cod and tested the potential for hybridization between farm escapes and wild conspecifics. Using a spatial and temporal analysis of wild and farmed cod tracked through biotelemetry, positioning of fish based on sex and origin indicated that farmed fish behave differently from wild fish relative to spawning ground location. However, despite these differences, hybridization is likely, especially between farmed females and wild males. The results illustrate that behavioral differences between cultured and wild fish may not preclude spawning interactions. The authors conclude there is a high potential for farmed cod to hybridize with wild fish. They recommend further research should be a priority to further understand the consequences of interbreeding and to identify methods for escape prevention.

Ford M. J., 2002: Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology*, **16**, 815–825.

Much of the concern surrounding effects of escaped cultured fish involves interbreeding with wild conspecifics and potential loss of genetic fitness of the wild population. Ford presents a single trait phenotypic model that assumes different optimum trait values for the culture and natural environments. The Ford model describes how mean phenotype values of captive and wild fish shift relative to optimum values for the environments based on gene flow between escapees (or captive breeding) and wild fish. The results suggest that cultured fish can have a strong influence on the fitness and sustainability of wild populations depending on the amount of interbreeding. The level of effect depends on the details of the model such as differences in optimum trait value, selection pressure, and trait heritability. Controlling gene flow between wild and cultured fish can potentially reduce the domestication effect in wild populations. Overall outcomes of fitness in the wild also depend heavily on habitat capacity and population dynamics. This model has been used in several other studies to explore the potential consequences to wild population fitness from captive breeding to increase the size of wild populations, and from the unintended straying of cultured fish to wild populations.

Paquet P. J., Flagg T., Appleby A., Barr J., Blankenship L., Campton D., Delarm M., Evelyn T., Fast D., Gislason J., Kline P., Maynard D., Mobrand L., Nandor G., Seidel P., and Smith S., 2011: Hatcheries, Conservation, and Sustainable Fisheries—Achieving Multiple Goals: Results of the Hatchery Scientific Review Group's Columbia River Basin Review. *Fisheries*, **36**: 11, 547-561.

The Hatchery Scientific Review Group (HSRG) was established by the U.S. Congress to review salmon and trout hatchery programs in the Pacific Northwest with the goal of recommending hatchery reform guidelines while still retaining the goal of providing fish for harvest and conservation goals for natural populations. This paper presents the approach used and recommendations that included an assessment of 178 hatchery programs and 351 salmonid populations within the Columbia River Basin. This approach included a scientific framework and three principles to guide their assessment: 1) "clear and specific quantifiable goals for harvest and conservation," 2) "be scientifically defensible," and 3) "include monitoring and evaluation of benefits and risks." HSRG used the All-H Analyzer (AHA) model to evaluate dynamics of populations in the Columbia River system through an integrative analysis of several factors related to hatchery operations, and productivity and capacity of wild populations. Using model simulation results, HSRG formulated a working hypothesis for baseline conditions and to evaluate strategies to better achieve stated goals for hatcheries and wild populations. The HSRG concluded that through following recommended management and harvest practices, such as broodstock selection and selective harvest, hatcheries can serve dual goals of contributing to harvest while remaining compatible with or contributing to conservation goals. The guiding principles stated by the HSRG are the core purpose of the OMEGA model.