Fisheries and Oceans Canada | Pêches et Océans Canada
Ecosystems and Oceans Science | Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2018/019

Pacific Region

Genetically Based Targets for Enhanced Contributions to Canadian Pacific Chinook Salmon Populations

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March 2018 (Erratum: October 2023)

Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Withler, R.E., Bradford, M.J., Willis, D.M., and Holt, C. 2018. Genetically Based Targets for Enhanced Contributions to Canadian Pacific Chinook Salmon Populations. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/019. xii + 88 p. (Erratum: October 2023)

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ABSTRACT

The Wild Salmon Policy (WSP) establishes conservation of wild Pacific salmon and their habitat as the highest priority for Pacific salmon resource management decision-making. Hatchery production in the Salmon Enhancement Program of DFO is used as a conservation tool for wild populations and can increase the availability of fish for harvest but is a risk factor to wild genetic diversity that requires management and mitigation to safeguard Pacific salmon biodiversity in Canada. We recommend use of the proportionate natural influence (*PNI*) and associated metrics developed by the U.S. Hatchery Scientific Review Group to evaluate and monitor the adaptive state of integrated hatchery populations, and to identify hatchery-influenced populations for WSP assessments. We develop a classification system for Canadian Pacific salmon populations that reflects the adaptive state of the population based on constituent proportions of natural- and hatchery-origin fish. Among the biological categories, increased genetic risk is associated with increasing hatchery influence and a decreasing proportion of wild fish. We modelled the population dynamics of a Chinook Salmon population including the genetic impacts on fitness from hatcheries to evaluate the use of three management measures - hatchery program size, proportion of hatchery fish marked, and proportion of marked fish selectively removed - in managing to a target *PNI* level. Except for populations at risk of extirpation, limiting hatchery size by scaling the size of the hatchery program to natural production is an effective way to minimize genetic risk of enhancement to wild populations. Limiting hatchery program size also limits the production of fish for harvest, resulting in a trade-off between genetic risk and socioeconomic benefit in enhancement programs implemented for harvest augmentation. Genetic risk associated with higher levels of hatchery production can be minimized by reducing the proportions of hatchery-origin fish included in the hatchery broodstock and/or allowed to spawn in the natural environment. Manipulation of proportions of natural- and hatchery-origin fish is dependent upon some type and level of marking that allows pre-spawning differentiation of fish originating from the two spawning environments. In conservation programs, the risk of domestication occurring at low *PNI* values must be balanced against the genetic and demographic risks of small population size in the absence of high proportions of hatchery-origin fish. We provide recommendations for the classification and management of enhanced populations consistent with the principles of developing explicit biological goals for hatchery-influenced populations, implementing scientifically defensible hatchery programs and using adaptive management of hatchery programs to meet objectives in a risk averse manner.

Génétiquement selon cibles pour Contributions accrues aux Populations canadiennes Saumon Chinook

RÉSUMÉ

La Politique concernant le saumon sauvage (PSS) établit la conservation des stocks de saumons sauvages du Pacifique et de leurs habitats comme la plus haute priorité pour ce qui est de la prise de décisions de gestion du saumon du Pacifique. La production d'écloserie dans le cadre du Programme de mise en valeur des salmonidés du MPO est utilisée en tant qu'outil de conservation des populations sauvages et peut se traduire par une augmentation de la disponibilité des poissons pour la récolte. Cependant, elle constitue un facteur de risque pour la diversité génétique dans la nature, lequel exige des mesures de gestion et d'atténuation pour protéger la biodiversité du saumon du Pacifique au Canada. Nous recommandons d'utiliser l'influence naturelle proportionnelle et des mesures connexes élaborées par le U.S. Hatchery Scientific Review Group (groupe d'examen scientifique des écloseries des États-Unis) pour évaluer et surveiller l'état adaptatif des populations intégrées en écloserie et pour identifier les populations sur lesquelles les écloseries ont une incidence aux fins des évaluations réalisées en vertu de la PSS. Nous élaborons un système de classification des populations de saumons du Pacifique canadien, lequel reflète l'état adaptatif de la population d'après les proportions de poissons d'origine naturelle ou élevés en écloseries. Parmi les catégories biologiques, on associe un risque génétique accru avec une augmentation de l'incidence des écloseries et une diminution de la proportion de poissons sauvages. Nous avons modélisé la dynamique d'une population de saumons quinnat, notamment les impacts génétiques sur l'adaptation au milieu des poissons élevés en écloseries, afin d'évaluer l'utilisation de trois mesures de gestion visant à nous permettre d'atteindre un niveau cible d'influence naturelle proportionnelle : la portée du programme d'écloseries, la proportion de poissons élevés en écloseries marqués et la proportion de poissons marqués enlevés de manière sélective. Sauf pour les populations qui présentent un risque de disparition, la limitation de la taille de l'écloserie en mettant à l'échelle la portée du programme d'écloseries pour une production naturelle constitue un moyen efficace de réduire le plus possible le risque génétique accompagnant la mise en valeur des populations sauvages. La limitation de la portée du programme d'écloseries limite également la production des poissons pour la récolte, ce qui se traduit par un compromis entre le risque génétique et les avantages socio-économiques découlant des programmes de mise en valeur mis en œuvre aux fins d'augmentation de la récolte. Le risque génétique associé à des niveaux de production d'écloserie plus élevés peut être réduit au minimum en diminuant les proportions de poissons provenant d'écloseries qui sont inclus dans le stock de géniteurs des écloseries ou qui sont autorisés à frayer en milieu naturel. La manipulation des proportions de poissons d'origine naturelle et élevés en écloserie dépend du type et du degré de marquage permettant la différenciation entre les poissons provenant des deux milieux de frai, avant le frai. En vertu des programmes de conservation, le risque de domestication à des valeurs faibles d'influence naturelle proportionnelle doit être équilibré en tenant compte des risques génétiques et démographiques qui pèsent sur les populations de petite taille en l'absence de proportions élevées de poissons élevés en écloseries. Nous fournissons des recommandations pour la classification et la gestion de populations mises en valeur, conformément aux principes d'établissement de buts biologiques explicites pour les populations qui subissent l'incidence des écloseries, de mise en œuvre de programmes d'écloseries défendables sur le plan scientifique et d'utilisation de la gestion adaptative au sein des programmes d'écloseries pour atteindre les objectifs selon une démarche d'aversion au risque.

1. INTRODUCTION

1.1. BACKGROUND AND OBJECTIVES

The DFO's Salmonid Enhancement Program (SEP) guidelines for hatchery program management have been in place for many years in the Pacific Region, and are used in an integrated enhancement planning process to address multiple biological and socioeconomic objectives. Whereas over-arching SEP objectives are commonly framed in broad socioeconomic terms, management of risk to natural populations requires a detailed assessment of the nature, degree and duration of enhancement on a species, population and site-specific basis.

One of the most significant differences between the hatchery management system in the US and Canada is the existence of Canada's Wild Salmon Policy (WSP) (DFO 2005). The WSP states that a fish is considered wild if it is born in the natural environment and both its parents were born in the natural environment. As monitoring of the parentage status of salmon at the population level for all populations is not possible, several practical approaches have been applied in the conduct of WSP Status Assessments of Conservation Units (CUs) to "operationalize" the definition of wild salmon. While the WSP does state that "hatcheries will be used to rebuild populations with an unacceptable chance of extirpation…" there is an inherent difficulty in understanding how to properly assess a CU when it is uncertain that a CU (sustained with wild fish) would still exist in the absence of hatchery production for conservation. In the development of a standardized approach to WSP assessment efforts, there is a clear rationale for aligning enhancement guidelines with the current scientific understanding regarding the effect of gene flow between hatchery and wild fish in the context of the WSP. There is a need to relate the level of hatchery influence in a salmon population to the risk level that the hatchery fish pose to the natural adaptive and productive characteristics of the hatchery-influenced and surrounding wild populations in the context of the WSP. Analysis to provide the information on risk levels is required to support effective hatchery planning, as well as to provide clarity to managers and scientists in the assessment of wild CUs that are or have been subjected to varying levels of hatchery supplementation.

Recent advances in scientific understanding of salmon population structure and the effects of gene flow between wild and hatchery salmon populations require incorporation into an updated hatchery planning process as was highlighted in an independent science panel report on southern British Columbia Chinook Salmon (Riddell et al. 2013) that recommended SEP hatchery programs be brought into better alignment with WSP principles. DFO has defined a need for a comprehensive set of biological goals for hatchery production that is clearly aligned with levels of genetic risk to wild populations to more effectively operate a SEP hatchery program on the basis of scientifically supported risk benefit analysis. In order to address this need, the objectives of this paper are to:

1. Review the current scientific understanding of observed and potential genetic risks to wild populations associated with hatchery propagation.
2. Describe categories of biological status for enhanced Chinook Salmon populations measured in terms of proportion of wild fish as defined in the WSP. Describe how to assess hatchery influence on Chinook Salmon populations, using the Proportionate Natural Influence (*PNI*) metric, including its rationale and its applicability to the Canadian context.
3. Provide advice on quantitative benchmarks for the *PNI* and/or other appropriate metrics for the biological categories of status, and management measures to achieve those benchmarks.

4. Summarize the information and analyses needed to implement the *PNI*-based genetic risk management guidelines.
5. Summarize advice and guidance for development of new enhancement guidelines.

With guidelines that more explicitly identify the potential risk to enhanced populations from hatchery production, managers and stakeholders can make decisions that explicitly align with their risk tolerance in achieving the hatchery program's stated objectives.

1.2. WSP CONSERVATION UNITS IN CANADIAN PACIFIC SALMON MANAGEMENT

The WSP states that conservation of wild salmon and their habitat is the highest priority for Pacific salmon resource management decision-making. It stipulates that the goal of restoring and maintaining healthy and diverse salmon populations will be advanced by safeguarding the genetic diversity of wild salmon populations, maintaining habitat and ecosystem integrity, and managing fisheries for sustainable benefits (DFO 2005). The first objective of the WSP is to safeguard the genetic diversity of wild Pacific salmon and it indicates that wild salmon will be maintained in designated CUs that reflect their ecological and genetic diversity. The definition of a CU is a group of wild salmon sufficiently isolated from other groups that, if lost, is very unlikely to recolonize naturally within an acceptable timeframe (e.g., a human lifetime). Based on this WSP guidance, 67 geographically-based CUs were defined for Chinook Salmon within BC reflecting genetic distinctiveness at neutral genetic loci, different ecological zones, and life history variation (Holtby and Ciruna 2007). These were subsequently subjected to minor modification (DFO 2013a).

Under the WSP, Pacific salmon are wild if they and both their parents were born in the wild. This differs from a common practice to consider only hatchery-origin and natural-origin salmon, irrespective of the origin of their parents. Therefore, under the WSP, three types of salmon can be defined; 'wild salmon' originating in the natural environment from parents also born in the wild, 'enhanced salmon' originating from hatchery production and a third 'transition type' consisting of fish born in the natural environment from one or both parents of hatchery birth. In this document, we use the term wild to designate fish that are wild under the WSP definition. The descriptors 'natural origin' and 'naturally-spawned' are used to describe wild and transition fish combined, and distinguish them from fish of 'hatchery origin' or 'hatchery-spawned' fish. The WSP indicates that a full range of habitat, hatchery and fishery management actions should be considered to reverse declines in CUs with low levels of abundance and/or a decreasing distribution of spawning components. The WSP considers a productive natural habitat as integral to a wild salmon population and recognizes fisheries, hatcheries, and habitat alterations as human activities that may place wild populations at risk. Indeed, the WSP states that hatcheries, termed salmon enhancement, "will focus on sustaining wild salmon" (DFO 2005, p. *vi*). Nevertheless salmon enhancement is also mandated by the WSP a means to increase or develop harvest opportunities for economic benefit.

In this document, we focus on the risks to genetic diversity of enhancement, but recognize that the genetic diversity of wild salmon populations is constrained by the amount of natural habitat available to them and impacted by the degree of harvest they sustain. The interplay between high levels of enhancement and harvest, and their effects on wild populations, mean that reducing genetic risk will by necessity involve fishery and habitat, as well as enhancement management.

1.3. DESCRIPTION OF CANADIAN HATCHERY PROGRAM

The Canadian hatchery program is managed by the Salmonid Enhancement Program (SEP) of the Department of Fisheries and Oceans (DFO). The focus of the program is one that supports a range of objectives, including harvest augmentation, conservation & rebuilding of depleted stocks, provision of stock assessment information, and support of local stewardship and education programs. There are currently 17 major DFO hatcheries, 6 spawning channels and 94 smaller community-based hatcheries in operation, with a release target of 44 million Chinook Salmon in 2017. Production of salmon from hatcheries is just one tool that is employed by the SEP to achieve the program's stated final outcome,

- Enhanced salmon and habitat contribute to ecosystem health and economic productivity

The stated final outcome (above) is supported by two intermediate program outcomes:

- Enhanced salmon and improved habitat contribute to sustainable economic, social and cultural harvest opportunities
- Citizens engage in a culture of salmon and ecosystem stewardship

Although production of hatchery salmon is used in conjunction with habitat restoration, community stewardship, provision of stock assessment information, and provision of educational and technical expertise to meet the program's objectives, it is the activity that results in the greatest level of intervention in the salmon life cycle.

Canada's hatchery programs are based on an integrated model, meaning that native broodstock are used, natural-origin fish are included in the hatchery broodstock, and hatchery-origin spawners are allowed to spawn with co-migrating natural-origin spawners within the population. This approach allows for gene flow between the hatchery and the natural population components as a means of mitigating potentially negative effects of genetic divergence (DFO 2013b). However, very high levels of hatchery-origin salmon in some hatchery programs makes them effectively more similar to those operated as segregated hatchery populations, in which natural-origin fish are not included in the hatchery broodstock.

The process by which hatchery production planning occurs is described in *SEP Production Planning: A Framework (*DFO 2012). There are five immediate objectives for which hatchery programs are operated in Canada (Table 1). Hatchery programs have biological and socio-economic objectives, and production planning decisions by hatchery program managers consider the relative risk posed by a hatchery program against the magnitude of the beneficial outcomes. Large scale harvest-focused projects typically allow for the greatest risk tolerance in terms of potential effects on the target and surrounding wild populations, due to the significant economic and social benefits that are conferred. Hatchery programs operated for the other four objectives are planned to minimize risks to the target and non-target populations. For *Conservation* programs minimization of genetic risk is required because the explicit purpose of the program is to rebuild or preserve a salmon population that is deemed to be at unacceptable risk of extirpation in the absence of hatchery production; *Rebuilding* programs are designed to restore a depleted population to a state of greater abundance and natural viability; *Assessment* programs have the objective of creating salmon to be coded wire tagged and released for estimation of survival and exploitation rates; and *Stewardship/Education* programs are designed to utilize low risk and small scale production to foster community engagement and provide educational opportunities for promotion of a wild salmon conservation ethic among the public.

The policy decisions that have been made in allowing high levels of enhancement on certain populations for harvest augmentation have been documented historically in the salmon

Integrated Fisheries Management Plans published annually by DFO, but these plans have not always fully documented details of the risk-benefit trade-offs.

Table 1. The five fish production objectives at DFO hatcheries, their descriptions, and the nearest equivalent hatchery objective used in the United States (HSRG 2014).

SEP Enhancement Objective	**Description**	**Equivalent HSRG Hatchery Purpose/Phase**
Harvest	*Enhancement for fisheries that are reliant on enhanced production, and would disappear or become severely constrained in the absence of enhancement.*	Harvest Augmentation
Rebuilding	*Enhancement of a stock that is below apparent carrying capacity. This includes rebuilding depleted populations and mitigating for habitat loss.*	Conservation -Full Recovery -Local Adaptation
Conservation	*Enhancement of a stock highly at risk of extirpation or extinction, or a vulnerable stock that has been identified as a regional priority (e.g. populations which have an approved conservation/recovery strategy). This includes re-establishing locally extinct populations and rebuilding populations at high risk of extirpation.*	Conservation -Recolonization -Genetic Preservation
Assessment	*Fish produced for marking where stock assessment information contributes to Pacific region assessment priorities, such as the Pacific Salmon Treaty.*	Not applicable
Stewardship/Education	*Small numbers of fish produced to provide a stewardship or educational opportunity.*	Not applicable

1.4. CURRENT POLICY CONTEXT & GUIDELINES

Current policy context for planning of hatchery and harvest activities on the Pacific coast of Canada is provided by the WSP which mandated the development of a biological risk assessment framework to manage risks of hatchery production. The current Biological Risk Management Framework for Enhancing Salmon in the Pacific Region (RMF) outlines biological risks associated with each stage of the enhancement process on a hatchery activity (production line) basis (DFO 2013b). The document identifies general mitigation measures under the control of hatchery management that may be implemented to reduce genetic risk in enhancement operations, but does not provide overarching guidance for wild population maintenance nor the higher level management process of balancing the trade-off between socioeconomic gain and biological risk in enhancement activity. In the RMF, enhancement guidelines been modified to address genetic risk to wild populations on a qualitative basis, but a more quantitative categorization of populations by level of hatchery contribution and associated risk is required to inform the balancing of harvest and conservation objectives for each enhancement activity.

The existing guidelines are summarized in *A Compilation of Operational and Planning Guidelines for the Salmonid Enhancement Program,* which is unpublished and provides significant flexibility to hatchery and program managers. For populations enhanced for harvest objectives, or for those that have significant habitat damage, the guidelines state "*the proportion of the naturally spawning escapement that may be comprised of hatchery fish and collected for brood may be established as part of an endorsed integrated planning process…"* and also *"it is acceptable to obtain all broodstock required from fish that swim into the hatchery…"*. This can result in hatchery programs that are closer to segregated (hatchery brood based entirely on hatchery-origin fish) than integrated, although there is no formal intent to prevent hatchery-origin spawners from remaining in the natural environment. Importantly, there is no guidance on recommended limits of impacts from straying on non-target populations.

For populations that are part of a rebuilding or conservation program, existing guidelines recommend that salmon of hatchery origin do not exceed 50% of the spawning escapement in order to limit the risk of loss of genetic diversity. In addition to the 50% guideline, a secondary recommendation is that no more than 30% of the total return to the river be used for broodstock. Use of simple life stage survival models suggest it is likely that the two guidelines are incompatible with each other (if the hatchery fish have an egg to adult survival rate greater than 2x natural-origin fish, the 50% guideline will be exceeded unless they are harvested selectively). Guidelines to limit the proportion of hatchery-produced fish in the natural and/or hatchery spawning components of the population have not been rigorously developed or followed.

For populations that are part of a formal rebuilding strategy (termed *Conservation* in the current framework), the guidelines are relaxed to allow for the use of up to 50% of the total escapement for broodstock, and enabling program-specific thresholds for the hatchery-origin contribution. Current guidelines support the use of natural-origin fish in broodstock, but indicate that use of hatchery-origin fish may be necessary. Guidance on composition of broodstock recommends that, if possible, the proportion of natural-origin fish in the broodstock be the inverse of the proportion of natural origin fish in the natural spawning escapement. It is noted in the SEP guidelines restricting the proportion of hatchery-origin fish that they "*may be exceeded in years prior to full achievement of target."* This can be especially problematic in that there are few formal targets established for rebuilding and conservation programs in BC.

There is currently no specific guidance on the appropriate duration of enhancement, on biologically-based thresholds to trigger-transition from *Conservation* to *Rebuilding* programs, or for management of risk tolerance in the assessment of the benefits in hatchery production planning.

1.5. POLICY CONTEXT IN OTHER JURISDICTIONS

Salmonid enhancement occurs in countries bordering the north Pacific and Atlantic oceans. Although the regulatory, political and biological conditions vary between other jurisdictions and DFO's Pacific region, review of aspects of the frameworks used to manage the risks of hatchery-wild salmon interactions can be useful. The most proximate and relevant context to examine is that in the Pacific Northwest and California. There are a number of agencies that operate hatcheries in Washington, Oregon, California and Idaho, and the work consists of a mix of projects to meet harvest objectives and wild population conservation objectives. In response to listing of several salmon stocks under the US Endangered Species Act (ESA) in the 1990s, the Hatchery Reform Project was initiated in 2000 with the objective of reducing risks of hatchery programs to salmon stocks that had been listed as Threatened or Endangered under the Endangered Species Act. The Hatchery Scientific Review Group (HSRG) was formed to undertake a thorough and systematic review of hatchery programs, as well as to develop

specific recommendations for hatchery reform. The HSRG approach is based on 3 principles (HSRG 2014):

1. Develop clear, specific, quantifiable harvest and conservation goals for natural and hatchery populations within an “All-H” context
2. Design and operate hatchery programs in a scientifically defensible manner
3. Monitor, evaluate and adaptively manage hatchery programs

A primary outcome was development of quantifiable guidelines for hatchery influence in wild populations to be used in consideration of the biological and the socioeconomic objectives for the population. The development of clear, specific and quantifiable harvest and conservation goals for enhanced populations is central to the HSRG policy approach, and necessitated development of biologically-based benchmarks of population status based on outcomes of gene flow between hatchery- and natural-origin fish. The HSRG application of benchmarks is described in more detail in Section 3.

California conducted a similar hatchery review process (CHSRG 2012) that produced similar outcomes and resulting policy guidance. The CHSRG provided more qualitative standards and guidelines on broodstock composition, as well as distinctive recommendations on program objectives and monitoring. Nevertheless, the policy context in California is very similar to that in the US Pacific Northwest and Canada in that it is based on risk to wild populations from hatchery production, and may prove informative to development of updated Canadian benchmarks and guidance.

Other North American jurisdictions with salmon enhancement programs include Alaska, Eastern Canada and the Eastern US. Salmon enhancement programs in Alaska differ significantly from those in Canada and the lower 48 states in that they were not designed to supplement wild populations, but solely to support and increase fisheries (Heard 2012). Large scale ecological interactions between hatchery and natural salmon have been identified as a concern in Prince William Sound (Amoroso et al. 2017), as has straying of hatchery Chinook Salmon into non-natal streams, but hatchery guidance based on the risks of gene flow between hatchery- and natural-origin fish has not been developed, thus providing little of use in the Canadian context.

The Province of British Columbia manages a steelhead (*Oncorhynchus mykiss)* hatchery program in collaboration with DFO and other partner groups. Hatchery programs are used exclusively as a means to provide harvest opportunities, and are not considered for rebuilding of wild steelhead populations. In those streams designated as “Hatchery Augmented”, the risk of enhancing is deemed to be acceptable if the program is not expected to impact the health of wild populations. One of the mechanisms by which this is achieved is through the use of a wild (unmarked) broodstock only policy (Fish and Wildlife Branch, 2016).

In Atlantic Canada there are several enhancement programs in place to support Atlantic Salmon conservation, including two DFO operated biodiversity facilities, and several other facilities that have been divested to First Nations, private, and not-for-profit organizations. *Canada’s Policy for Conservation of Wild Atlantic Salmon* is very similar to the WSP that guides Pacific salmon management (DFO 2009). The definitions of a wild Atlantic and Pacific salmon are virtually identical, with one significant difference. Atlantic salmon that are the progeny of captive breeding at biodiversity facilities are deemed to be ‘wild’ once they are released into the natural environment (DFO 2009). The focus for hatchery programs in Atlantic Canada is strictly conservation oriented, providing important guidance for implementation and management of captive breeding methodology but little information for balancing harvest and conservation goals.

Japan has been operating salmon hatcheries since 1978 (Morita et al. 2006) that are focused primarily on large scale enhancement of Chum, Pink and Masu Salmon to support commercial harvests. Management of the hatchery program in Japan is more similar to that in Alaska than with the Canadian or southern US jurisdictions; it acknowledges the risk of interactions between natural- and hatchery-origin fish interactions on a broad scale but lacks guidance for direct management of gene flow between the two spawning habitats.

2. GENETIC DIVERSITY IN WILD CHINOOK SALMON POPULATIONS

2.1. CHINOOK SALMON POPULATION STRUCTURE

Genetic diversity in anadromous salmonids is partitioned among breeding aggregates (populations) on a hierarchal basis, with adaptation to the local spawning environment and marine migratory patterns comprising the selective forces promoting differentiation. Strong regional structuring of Chinook Salmon populations reflects current gene flow mediated by distance between populations, dispersion of distinctive refugial populations in recolonization of freshwater habitats over the 12,000 years since the most recent Pleistocene glaciation and, potentially, ancient lineages that predate the last glacial period (Moran et al. 2013). Regional groups consisting of networks of coastal watersheds and broad interior regions of major North American watersheds comprise the most distinctive and easily defined genetic units, with relationships among regional groups increasingly obscured by the influence of multiple, overlaid phylogeographic events as both genetic and geographic distances increase. Canadian Chinook Salmon populations encompass genetic diversity representative of 14 of the 27 distinctive groups of North American Chinook Salmon recognized by Moran et al. (2013).

Deep genetic relationships among many of the Canadian Chinook Salmon genetic groups, and between Canadian groups and those resident entirely within American watersheds, are complex due in part to the poorly understood phylogeography of the central Chinook Salmon range. Moreover, within Canadian watersheds, life history variation in smolt age and adult migration patterns is not well correlated with deep genetic relationships; similar life history patterns do not reflect common ancestry in historical lineages so much as parallel evolution and phenotypic plasticity in the face of environmental heterogeneity (Beacham et al. 2006, Moran et al 2013). Regional Chinook Salmon groups of British Columbia and transboundary Canada-USA watersheds reflect postglacial colonization from multiple and, in many cases, mixed refugial sources. The rich biodiversity of the species in Canada presents both challenge and opportunity for conservation and exploitation, especially in face of climate change and anthropogenic alteration of freshwater and marine migration routes.

2.2. GENETIC RISKS ASSOCIATED WITH INTEGRATED AND SEGREGATED HATCHERY PROGRAMS

Supplementation programs for salmon populations are of two types, developed for different purposes. Integrated hatchery programs, generally based on the local watershed population, are programs intended to produce fish genetically similar to the wild population in which both naturally- and hatchery-spawned fish reproduce in both environments (the hatchery and river system) each generation. The long-term goal is to maintain or create a self-sustaining, naturally-spawning population capable of providing adult fish for broodstock each year (Trushenski et al. 2015). Additionally, fish from an integrated hatchery program may support harvest if such fish can be produced and selectively harvested in a manner that does not disrupt the adaptive process of maintaining the wild populations in the watershed (and elsewhere throughout the CU) that are capable of self-sustainability. In contrast, segregated hatchery programs are those that rear a distinct, hatchery-supported population that is reproductively

isolated from wild populations; such a program creates a new, hatchery-adapted population intended to meet goals for harvest or other purposes, even when founded with the local wild population. In a segregated population, broodstock are selected only from hatchery-produced fish and hatchery fish must be precluded from natural spawning areas within the watershed/CU that are being managed to maintain natural or wild populations (HSRG 2014, Flagg 2015, Trushenski et al. 2015).

In a segregated hatchery population, hatchery broodstock selection is confined to returning adults from hatchery releases, making the hatchery strain susceptible to loss of diversity through founder effects, genetic drift and domestication selection (Mobrand et al. 2005, Paquet et al. 2011). Lack of gene exchange with fish spawning in the natural environmental is expected to increase both the rate of domestication and the ultimate level of differentiation from natural spawners reached in a segregated hatchery strain relative to one which is integrated with the natural spawning population. A recent comparison of genetic change in integrated and segregated lines of spring Chinook Salmon developed from the same wild population confirmed expectations that genetic diversity decreased and genetic divergence from the founding population increased more rapidly in the segregated than in the integrated strain (Waters et al. 2015). The researchers documented directional genetic alteration in some genomic regions over three generations in the segregated but not the integrated hatchery strain, an observation consistent with domestication occurring more rapidly in the absence of hatchery-natural gene exchange.

Recent studies such as this, indicating that hatchery fish of a segregated line may diverge rapidly from the founding natural population and become highly adapted to the hatchery environment, have led to the suggestion that segregated hatchery lines be used with caution and only in situations where complete segregation can be achieved (Lorenzen et al. 2012, CHSRG 2012, HSRG 2014). The HSRG concluded that its current prescribed level for the proportion of segregated hatchery fish strays in natural populations (5%) might lead to a greater fitness loss in the natural population than previously recognized and may therefore be too high.

Canadian Chinook Salmon hatchery programs were developed and have been managed as integrated programs, with hatchery broodstocks founded from local populations and maintained with inclusion of both naturally- and hatchery-spawned fish. Importantly, with only a few exceptions, watersheds containing hatcheries are lacking control devices such as weirs or fences that enable the handling of migrating adults to maintain the exclusion of hatchery fish from the natural environment. Thus, even with complete visual marking (typically adipose fin clips are used) of hatchery fish, there would no means to control numbers of hatchery-origin fish in natural spawning locations within the watershed or in surrounding rivers. Segregated hatchery strains could be developed for locations in which self-sufficient natural reproduction is not possible and gene flow with surrounding populations is naturally highly constrained. Maintenance of a segregated hatchery population in CUs containing the typical interconnected network of wild populations would likely require management by mark selective harvest of hatchery fish. A high level of visual marking of hatchery fish would be required for effective monitoring of straying into surrounding wild populations.

In Canadian integrated hatchery programs, naturally-spawned fish are included in broodstock collection, but many of the hatcheries have ‘swim-in’ facilities that tend to disproportionately attract hatchery-produced fish from which the broodstock are selected. Additionally, a lack of visual marking of hatchery fish in most species precludes the ability to preferentially select the naturally-origin individuals that are present.

2.3. FITNESS OF HATCHERY-ORIGIN FISH SPAWNING IN NATURAL RIVER SYSTEMS

The fitness of salmonids is generally measured as adult-to-adult reproductive success and the terminology applied to hatchery-origin fish is 'relative fitness' or relative reproductive success (RRS), meaning the adult-to-adult reproductive success of a hatchery fish relative to a wild fish spawning in the same habitat (Araki et al 2008). In an integrated salmonid supplementation program, natural- and hatchery-origin fish typically spawn in both the river and hatchery environments, and the RRS of the hatchery fish may differ in the two environments. Of concern is the observation that the RRS of hatchery salmonids is often less than one in the natural environment (Christie et al. 2014a). The reduced reproductive capacity of hatchery fish may be due to a combination of interacting hatchery influences that alter environmentally-mediated, genetic and epigenetic attributes of hatchery fish.

Epigenetic effects are heritable chemical and structural alterations of DNA, often environmentally-induced, that are not reflected in the genotype (i.e. DNA sequence). An epigenetic change in DNA structure can result in heritable patterns of altered gene expression and phenotypes in individuals. Epigenetic mechanisms include DNA methylation, histone modification, microRNA, small interfering RNA, spatial location of DNA, and chromatin matrix or scaffold attachment regions, as well as the DNA three-dimensional templating mechanisms and self-sustaining loops found in microorganisms (Richards et al. 2010).

Genetic and epigenetic alterations of hatchery fish have the potential to reduce their productivity in the natural environment in a heritable manner, resulting in an extended impact on survival of naturally-spawning fish in the population (Araki et al. 2010, Christie et al. 2014a). Genetic differentiation in hatchery-origin fish can be generated by the use of the hatchery brood that are not representative of the natural population in the river system (or transplanted from a different river system), as well as by the hatchery mating design and altered or relaxed selection in the hatchery environment compared with the natural environment. Altered mating patterns combined with differential selection imposed by the hatchery environment are often referred to as 'domestication' and can be expected to increase in an integrated hatchery program with the proportion of fish produced in the hatchery environment and the duration (in generations) of hatchery supplementation (HSRG 2009, Lorenzen et al. 2012).

Little is known of the possible role of epigenetic factors in contributing to the reduced fitness of hatchery salmonids, with research being undertaken only very recently (e.g. Christie et al. 2016, Le Luyer et al. 2017). However interest in these investigations has burgeoned for at least two reasons; an increased understanding of the importance of epigenetic change underlying phenotypic diversity in other organisms, and observations in salmonids that the heritable reduction in the fitness of hatchery fish can occur within in a single generation, more rapidly than expected if based entirely on altered allele frequencies arising through genetic drift or domestication.

Atlantic Salmon in a captive breeding program that had been released to the natural environment for two years as juveniles produced progeny that survived twice as well during a 4-month exposure to the natural environment than did parents that had no wild exposure during rearing (Evans et al. 2014). Genetic selection may have altered allele frequencies in the surviving fish that were re-collected from the natural environment and used as parents in the captive program. However, it is also possible that transgenerational (heritable) epigenetic effects resulting from parental exposure to the natural environment and transmitted to their progeny contributed to the increased survival of their progeny upon exposure to the natural environment (Evans et al. 2014). In salmon of the same captive breeding program, an initial increase in growth of captive versus wild salmon was observed in the first generation of captive

rearing but no incremental increase in growth rate was observed in the second generation of captivity as would be expected if the increased growth rate was due to altered gene frequencies resulting from altered selection pressures in captivity (Wilke et al. 2015). Recently, increased methylation of the genome was detected in muscle tissue of hatchery-spawned Coho Salmon smolts relative to naturally-spawned fish from the same populations (Le Luyer et al. 2017). Duration of the epigenetic alteration, and transgenerational transmission were not investigated.

Epigenetic changes are not detectable by DNA sequencing, nor are they reflected in altered allele frequencies, but can be transmitted from parent to offspring and therefore can alter gene expression in a transgenerational manner, although the duration and reversibility of epigenetic alteration is unknown. Demonstration of differential expression of several hundred genes between the juvenile progeny of wild and first-generation hatchery steelhead provided the first preliminary evidence for a role of heritable epigenetic modification in hatchery-spawned and reared salmonids (Christie et al. 2016). Thus, altered performance of hatchery-produced salmon in the natural environment may be due to epigenetic changes induced by the hatchery environment, as well as environmentally-mediated plasticity and altered allele frequencies. Identification of epigenetic alterations in salmonids, their induction by environmental factors, their association phenotypic and life history diversity and their persistence or loss over generations are being undertaken (e.g. Jonsson et al. 2014, Baerwald et al. 2016, Marandel et al. 2016), but much remains to be understood before their role in the hatchery modification of salmonids can be elucidated.

The production of hatchery fish with RRS<1.0 is most detrimental in ‘conservation’ hatchery programs implemented with the intent to restore or rebuild abundance in the natural environment, but also has ramifications for hatchery programs intended primarily to produce additional fish for harvest without reducing fitness and productivity in the natural environment. This is because an integrated supplementation program with a ‘harvest’ goal typically is implemented on the basis of maintaining a wild population in which adaptation to the natural environment is not lost (Paquet et al. 2011, Flagg 2015, HSRG 2014, Trushenski et al. 2015). High levels of hatchery production combined with a low level of visible marking of hatchery fish can mask the lowered productivity of natural spawning in an integrated hatchery program, with the hatchery contributing an increasing proportion of relatively unfit individuals to the natural spawning component of the population over time. Two control factors available for management to avoid or reduce the loss of fitness, and possibly the capacity for self-sustainability, in an integrated hatchery program consist of

1. the maintenance of a certain proportion of naturally-spawned adult fish in the natural environment and
2. the maintenance of a certain proportion of naturally-spawned fish in hatchery broodstock.

These factors can be used to curtail the level of hatchery supplementation and domestication in the integrated population to levels commensurate with the capacity for the natural environment to support a viable wild population.

The reduced RRS of hatchery fish spawning the natural environment can happen quickly and can be variable among brood years depending on environmental factors (Araki et al. 2007, Christie et al. 2014a). This may reflect an interaction between environmental and genetic influences on fitness. Hatchery fish may have reduced RRS in the natural environment under harsh conditions of low survival but perform similarly to wild fish in a benign natural environment. Another aspect of environment by genotype interactions is the extent of differentiation between the hatchery and natural environments and its influence on hatchery fish phenotype. Hatchery spawning and juvenile rearing results in environmentally-mediated phenotypic differentiation between hatchery- and natural-origin fish of the same genotype – this

may initiate genetic alteration of hatchery fish. Natural selection against the maladaptive hatchery juvenile or adult phenotype can result in the reduced prevalence in the natural environment of genotypes that, had been they produced through natural spawning, would be have been highly fit. This mismatch between the genotype carried and phenotype displayed by a hatchery fish in the natural environment may be a critical element of the rapid reduction in RRS of hatchery fish (Ford et al. 2012, Ford et al. 2015). The phenotypic changes that precede any genetic alteration of hatchery fish are immediate and actually become the drivers of genetic alteration of the integrated population to a state in which natural selection is consistently favouring hatchery-produced phenotypes that will produce suboptimal genotypes (and phenotypes) among their naturally-spawned progeny.

The reduced fitness of the integrated population in the natural environment resulting from this process will be especially acute when the maladaptive hatchery phenotype is expressed only after the reproductive life history phase, enabling hatchery-origin adults to participate fully in spawning in the natural environment. High survival of hatchery juveniles throughout marine migration will produce increased abundance for harvest and escapement. Whereas the increased abundance may provide the appearance of a healthy and productive integrated population, it may actually reflect the high fitness of hatchery fish spawned in the hatchery environment and mask a low and decreasing productivity of the natural environment. Further magnification of the effect can occur when the progeny of hatchery-origin spawners experience a temporary advantage in the natural freshwater environment (e.g. due to early emergence, increased aggression or rapid growth) enabling them to displace progeny of natural-origin spawners, but subsequently perform poorly throughout the marine and reproductive life history stages (Cote et al. 2015).

The process will be obscured when hatchery production is high and the level of marking in hatchery fish is low such that hatchery fish may dominate both the hatchery and natural environments without being apparent. The result can be an entire population becoming increasingly adapted to the productive hatchery environment and increasingly maladapted to the natural environment. Finally, the process can further reduce productivity in the natural environment if abundance of the integrated population becomes very large relative to surrounding wild conspecific spawning populations into which fish from the integrated population typically stray. Even at normal stray rates, and especially at the elevated strays rates sometimes characterizing hatchery production, surrounding spawning locations may receive unusually high numbers of maladapted strays from the enhanced population (Bett et al. 2017). These fish may produce natural-origin but relatively unfit progeny in the recipient populations, whether they spawn with each other or with local mates. If the mismatch in abundance between the enhanced population and those occupying surrounding watersheds is great enough, and/or persists long enough, the hatchery population is likely to cause significant genetic differentiation in (Hess and Matala 2014) or simply replace surrounding populations on a regional scale (McClure et al. 2008, Jasper et al. 2013, Ozerov et al. 2016). As long as hatchery production (source population) continues, there is no need for the fish spawning in the recipient (sink population) locations to be self-sustaining, just as there is no requirement for the fish spawning in the natural environment of the enhanced watershed to be self-sustaining.

An understanding of the above process has led to the overarching conclusion that in situations in which integrated hatchery supplementation is intended to coexist with (rather than replace) the network of genetically connected but diverse natural spawning populations such as those comprising a Canadian CU, a primary requirement is limitation of the number of hatchery-origin fish that spawn in the supplemented and surrounding watersheds (McClure et al. 2008, Paquet et al. 2011, Flagg 2015, HSRG 2014, Trushenski et al. 2015).

2.4. HATCHERY BROODSTOCK MANAGEMENT

The RMF indicates that natural-origin fish should be included in broodstock collection and genetic guidelines are needed for spawning protocols appropriate to the population size and enhancement objectives. In this section, considerations for broodstock management are reviewed that can be used to develop protocols appropriate for enhancement programs with various objectives and of widely differing scale. Metrics and benchmarks developed in subsequent sections will be proposed to enable quantification of genetic risk posed to natural and wild populations by enhancement programs with defined harvest opportunities, conservation objectives, broodstock number and composition (hatchery- and natural-origin fish) targets, brood collection methods and mating designs.

In an integrated hatchery program, in which fish belonging to a single population spawn in two very different freshwater environments, broodstock management activities involve three groups of related but separate tasks comprised of:

1. Broodstock collection: total numbers and brood composition
2. Management of proportions of natural- and hatchery-origin fish in the natural and hatchery spawning environments to meet biological objectives for the integrated population, and
3. Mating design and spawning practices for hatchery broodstock

Broodstock Collection

Fundamental to determination of broodstock composition in an integrated hatchery program is a focus on keeping the hatchery broodstock representative of the genetic and phenotypic diversity in the original wild population, and ensuring that removal of fish from the natural environment for use as hatchery broodstock does not negatively impact abundance and diversity of fish remaining to spawn in the natural environment. For the hatchery program, the need for representative broodstock places an emphasis on the collection of sufficient numbers of hatchery brood over the duration of the adult return migration to ensure that genetic diversity of hatchery-origin fish is representative of the entire population. Of special concern is the production of few families that may encompass very little of the total genetic and phenotypic diversity in the adult population (e.g. Christie et al. 2012). The loss of diversity that can take place in an integrated hatchery population due to the use of limited broodstock in hatchery spawning each year is termed the Ryman-Laikre effect and results from a smaller ‘genetic effective size’ in the integrated population than in the founding wild population (Ryman and Laikre 1991). The reduction in effective size of the population occurs because of an increase in the variability in reproductive contributions to the next generation among individuals in the population. It may occur rapidly after initiation of hatchery production and even as the overall population abundance increases due hatchery production (Ryman and Laikre 1991).

Hatchery production typically reduces freshwater mortality compared to natural production, with the result that hatchery fish may make a disproportionate contribution to the spawners of the next generation (in both the hatchery and natural environment) unless specifically controlled. Therefore, any limitation of the genetic diversity encompassed in the founding generations of an integrated population may be magnified into a highly disproportionate contribution of those few families to the integrated population over the course of relatively few generations of enhancement.

An assumption often made, especially for programs initiated on populations poorly characterized prior to enhancement, is that hatchery origin itself does not alter the phenotypic distribution of the integrated population, especially early in hatchery generations. In fact, alteration of growth and maturity expressed much later in life can result from environmentally-

mediated acceleration of juvenile development that often occurs immediately in hatchery rearing (due to altered temperature, photoperiod and feeding regimes). Ford et al. (2012) showed that hatchery rearing of stream-type Chinook Salmon resulted in an increased proportion of male fish that returned as age 2 'jack' males rather than age 3 'adult' males, and that the jacks were responsible for the decreased RRS of hatchery fish in the natural environment. Naturally-spawned jacks were also less reproductively successful than older males in the natural environment, but were present in lower proportions (Ford et al. 2012). Epigenetic alteration of hatchery fish may also take place after a single generation of hatchery rearing (Christie et al. 2016) and is another mechanism by which immediate alteration of the phenotypic distribution of returning adults might be occur.

The potential for rapid phenotypic alteration, including age structure, of hatchery-origin adult fish needs to be recognized in management of broodstock collection. This may be done by keeping brood collection representative of the original (pre-enhancement) phenotypic distribution of the population, entailing active selection to reduce the contribution of hatchery fish with early maturation (or other altered) phenotypes favoured by hatchery production. This would reduce the inadvertent selection for younger age at maturity otherwise resulting from continued random selection of hatchery-origin fish for broodstock (Hankin et al. 2009). Simulation analysis indicated that discrimination against 'jacks' was effective in counteracting the hatchery selection for reduced age of maturation, but that ensuring that each female was mated with a male of equal or larger size (assortative mating) was even more effective (Hankin et al. 2009).

Meeting Biological Objectives

The current understanding that selective forces imposed by the hatchery and natural stream spawning environments on Chinook Salmon in an integrated enhancement program tend to exert opposing pressures on spawners sets up a trade-off between harvest and conservation goals in program management. Integration of hatchery production into a natural population ensures that fish produced in one environment are likely to spawn in the other, with the selective (adaptive) equilibrium for the integrated population established at an intermediate point between two adaptive (natural and hatchery) extremes (Ford 2002). The overall population will reach or approach an adaptive condition best matched with the more productive environment; i.e. the environment that contributes the higher number of successful spawners to the next generation (Ford 2002, Goodman 2005). The production of more hatchery fish for harvest leads to more hatchery fish spawning in the natural and hatchery environments, resulting in increased hatchery adaptation, or domestication, of the integrated population. Thus, increased production for harvest must be balanced against increased maladaptation and decreased sustainability of the integrated population in the natural environment.

Enhancement conducted to maintain a natural population with the biological objective of minimizing domestication must be conducted in a manner that ensures the natural environment is more productive (i.e. produces the majority of the effective spawners in the next generation) than the hatchery. Gene flow from the natural environment to the hatchery environment should exceed the reverse flow (Mobrand et al. 2005). Gene flow is difficult to monitor directly but can be controlled by management of the proportion natural-origin fish in the hatchery broodstock and of hatchery-origin fish among spawners in the natural environment. A metric designed to estimate the relative strength of the hatchery and natural selective pressures resulting from gene flow between the two environments is the 'proportionate natural influence' (*PNI*) indicator (HSRG 2009, HSRG 2014) that is described in Section 3.

Since successful spawners of the next generation will be present in both environments (natural and hatchery), management of the integrated population will require knowledge of the numbers of hatchery- and natural-origin individuals in both environments each year and, ideally, the RRS

of hatchery salmon. Since the RRS of hatchery fish is usually <1 (though the exact value is uncertain and can vary over time), it may be necessary to set the prescribed levels of natural-origin fish in the integrated population at a sufficiently high level to compensate for an anticipated reduced success of hatchery-origin fish in the natural environment. Values of RRS for hatchery Chinook Salmon used in models have ranged between 0.8 and 1.0 (HSRG 2014), although lower values have been observed. The hatchery environment and release strategies/locations, as well as genetic adaptation to the environment, may contribute to reduced fitness (Williamson et al. 2010).

Mating Design and Spawning Practices

Broodstock spawning practice is of concern in all hatchery programs because the goal of supplementation is to produce additional fish for harvest and/or population restoration while minimizing disruption of the natural spawning process that is critical for maintenance of genetic diversity and natural adaptation in the integrated population. Natural spawning involves complex processes including competition for mates, mate selection and, often, polygamy that cannot be replicated in hatchery spawning (Chargé et al. 2014). Instead, maintenance of genetic diversity in a hatchery environment has been generally focused on maintaining high broodstock numbers, achieving a sex ratio as close to 1:1 as possible, keeping broodstock collection reflective of the phenotypic structure of the original wild population and ensuring the approximately equal contribution of all parents to the next generation (Hard et al. 1992). In large hatchery programs, spawning is often conducted on a random basis with respect to phenotypic diversity of the parental fish and in single pair matings in which milt from one male is applied to an egg lot from that is water-hardened before mixing with other egg lots. This prevents the sperm competition possible among male brood; in which individual males may dominate fertilization of large egg batches to which the milt of several males is applied before completion of egg fertilization and water hardening (Withler and Beacham 1994). Such methods, combined with management of the scale hatchery production to maintain prescribed proportions of the natural-origin fish in both hatchery and natural environments, may be typically considered sufficient to minimize the loss of genetic diversity and/or fitness in the integrated population.

Maintenance of diversity and fitness (in the natural environment) is much more critical in a conservation program in which the provision of additional spawners for rebuilding of a natural population is the enhancement objective. In these programs, the critical requirement is to produce enough highly fit fish for natural population rebuilding without negatively impacting the existing natural spawning component of the population. The low abundance of the natural population introduces several additional considerations for brood management and mating design in conservation programs:

1. Removal of fish for hatchery brood from the natural environment must be limited by the restoration goal of return to a productive state through natural spawning (i.e. ‘broodstock mining’ in which the natural environment is under-supplied with spawners, or provided with a sub-optimal group of adult fish as the result of hatchery removals, must be avoided).
2. Low adult abundance may reflect the return of only a few successful families in each spawning season, increasing the likelihood that highly related individuals dominate the adult return; under these circumstances information from molecular genetic markers can be used to select appropriate mates for inbreeding avoidance (Fisch et al. 2015).
3. Low abundance of the natural population increases risk of strays from nearby populations constituting an atypically large proportion of the adult returns; under these circumstances outbreeding avoidance may also be facilitated by genetic screening prior to breeding.

4. Although management of both broodstock and escapement to the natural spawning grounds in a conservation program will also be facilitated by visual marking of hatchery fish (as in a harvest program), implementation of non-visual marking may be necessary to avoid over-exploitation of the recovering population in mark-selective mixed-stock fisheries. Under these circumstances, brood management and escapement monitoring will require an effective physical or biological tagging method that can be read quickly and non-lethally (i.e. prior to spawning in the hatchery and in spawning ground surveys of live fish).
5. Duration of the hatchery program becomes of greater concern, as domestication of the integrated population is expected to increase with both the proportion of hatchery-produced individuals in the population and duration (in generations) of hatchery supplementation (Araki et al. 2007, Waters et al. 2015, de Mestral and Herbinger 2013).

Various mating options can be adopted in a conservation program to maximize genetic diversity, maintain or increase effective population size and reduce hatchery adaptation (Fisch et al. 2015). Mating strategies to increase the range of juvenile genetic combinations by full or partial factorial adult mating (Busack and Knudsen 2007) can be paired with genetic selection of unrelated mates and equalization of parental contributions to progeny production prior to release to meet several genetic management goals simultaneously (Fisch et al. 2015). Where it can be managed, allowing adult spawning to take place in the natural environment enables natural selection to occur in mate selection and egg incubation. More commonly, juvenile rearing is modified to establish conditions more closely resembling those in the natural environment and minimize domestication selection (Berejikian et al. 2000, Roberts et al. 2011). Some of these activities can be facilitated through hatchery design, in which the traditional structures devoted to production maximization are replaced by facilities devoted to specialized production dependent on temperature and photoperiod control, increased adult holding and sorting, specialized juvenile rearing and improved individual tracking capacity.

In cases of extreme conservation concern, and especially for captive brood programs in which fish are reared in captivity throughout the entire life cycle, genetic management of brood selection and mating can be undertaken to avoid both inbreeding and outbreeding in the hatchery program, and develop detailed mating designs for individual brood parents (Fisch et al. 2015). Rapid, cost effective sets of genetic markers are available for implementation of a fully pedigreed hatchery program, in which genetic relationships among all individuals in the hatchery are established and used to control matings (O'Reilly and Kozfkay 2014). Pedigreed programs are also useful in locations where adult escapement to the natural environment, as well as for brood selection, can be handled, sampled and managed (e.g. at passage through a fence). The RRS of hatchery-produced fish upon their return to spawn in the natural environment can be monitored over time (Hess et al. 2012, Christie et al. 2014b), enabling a cost-benefit analysis of the hatchery production (i.e. does the increased abundance of spawners in the natural environment provided by hatchery production compensate for any reduction in individual reproductive output experienced by hatchery fish and their mates).

Genetic markers can also be employed to monitor and manage hatchery breeding in the absence of a fully pedigreed hatchery program. Loss of genetic diversity or increased inbreeding levels can be monitored through loss of allelic variants or increased homozygosity levels at polymorphic genetic markers. Estimates of effective population size can be made from molecular data sets (Do et al. 2014), enabling monitoring the effectiveness of transmission of genetic variation over generations in the integrated population. Estimates of relatedness among potential brood fish can be based on the pairwise calculation of shared genetic variants, although accuracy in the relationships identified requires a suitably informative set of markers (Csilléry et al. 2006). Brood management options based on molecular markers range from simple avoidance of full/half-sib crosses to sophisticated mean kinship (MK) approaches (Ballou

and Lacy 1995). MK estimation can be especially important for selecting the founding individuals of a captive breeding program, as the opportunity to include maximal diversity within the program likely occurs at this point. The estimation enables incorporation of the least related individuals into the founding broodstock and the design of specific mating options for each brood fish in the founding and subsequent generations. Implementation can be facilitated by cryopreservation of milt for future use in the hatchery program, enabling expansion of available male partners for ripe female brood within and over breeding seasons.

Currently, genetic markers can be used to monitor diversity and relationships at neutral loci and to measure the decreased fitness of hatchery fish in the natural environment, but not to control hatchery reproduction to avoid domestication (i.e. to prevent the accumulation of genetic variants in the population that decrease the fitness of fish in the natural environment). However, the identification of genes associated with domestication is now underway in genomics analyses (Mäkinen et al. 2015, Gutierrez et al. 2016) made possible by the sequencing and annotation of several salmonid genomes. Once the genetic processes underlying domestication become better elucidated, genetic analysis may facilitate brood selection and mating choices to avoid genetic alteration at critical adaptive loci.

2.5. INTERACTIONS OF HATCHERY AND WILD FISH: MANAGEMENT AND MITIGATION

Genetic risks to natural populations resulting from interactions between hatchery and natural origin fish arise both through direct (altered hatchery breeding patterns and interbreeding of hatchery and natural origin fish) and indirect (competitive and predatory ecological interactions) mechanisms. All genetic risk to natural populations will be minimized at low levels of hatchery production relative to natural production, except when natural populations are in danger of extirpation. Higher levels of hatchery production employed to increase harvest opportunities or ensure persistence of threatened wild populations will likely require mitigation based on the identification and management of hatchery-origin fish. Risk may be reduced by management in the hatchery environment alone, or in combination with efforts to reduce interaction in the natural environment.

In conservation programs, high levels of enhancement may be required to counteract the demographic risk of extirpation and genetic risks of inbreeding and/or outbreeding depression. Increasing broodstock collection efforts over time and/or space increases the risk of including strays or fish still migrating to other natal locations in the brood. Genetic screening in brood selection and individualized mating designs can be used to mitigate the risks associated with both outbreeding and inbreeding as well as to maintain maximum genetic diversity in entirely captive or integrated conservation hatchery programs. As population abundance in a conservation program increases, a staged process can be implemented to reduce hatchery influence and restore the dominant selective influence of the natural environment (see section 5.3).

Ecological interactions between hatchery- and natural-origin fish release can also affect the abundance, composition and genetic diversity of returning adult fish and those of ensuing generations. Broodstock collection and holding sites, hatchery rearing environment and juvenile release sites/times may increase the tendency for hatchery fish to stray relative to their natural counterparts (Dittman and Quinn 1996, Candy and Beacham 2000, Keefer and Caudhill 2014, Bett et al. 2017). Hatchery juveniles released to the natural environment in the vicinity of natural spawning habitat may effectively displace their natural counterparts through competition for territories and food, especially if released earlier than natural emergence or at larger size than natural-origin juveniles. Of particular concern is the situation in which hatchery-origin juveniles displace or effectively outcompete natural-origin ones in the freshwater environment but

underperform natural-origin fish in the marine environment and/or when they return as adults to spawn in the natural environment. Thus, whereas releasing hatchery juveniles in proximity to the spawning sites to which their return is intended may improve their homing fidelity and reduce straying, it may also increase counterproductive competitive interactions between hatchery- and natural-origin juveniles.

Increased straying of hatchery fish upon return represents potential losses to integrated populations being enhanced for rebuilding purposes and an increased risk of regional genetic homogenization when the strays originate from large harvest-oriented hatchery programs. The risk may be greatest for fish such as ocean type Chinook Salmon with short freshwater residence times and migration routes (Westley et al. 2013), and be of sufficient geographic scale to affect CU status (Jasper et al. 2013, Hess and Matala 2014, Ford et al. 2015, DFO 2016). Risk mitigation measures for hatchery production include a wide range of options for producing fish more adaptively matched with the natural environment and with less opportunity to impact natural-origin fish (Maynard and Trial 2014, Dittman et al. 2015, Rosengren et al. 2017). Effectiveness of these measures can be evaluated through the adaptive management approach for enhancement outlined in the RMF to determine if the benefit achieved justifies any increased costs incurred.

Visual marking and/or parentage-based genetic tagging of hatchery fish provides the ability to preferentially select natural-origin fish for hatchery broodstock; internal physical marks may not enable broodstock selection but can be used to monitor proportions of hatchery- and natural-origin fish in broodstock and spawning ground carcass sampling. Visual marking also provides increased non-lethal monitoring capability in the natural environment (including wild populations in neighbouring river systems). The effectiveness of various marking levels, management of broodstock composition (hatchery- and natural-origin) and the selective removal of hatchery fish from the natural environment in reducing the direct genetic risks of enhancement in the integrated population are evaluated in Section 4.

3. MEASURES OF GENETIC RISK

3.1. *PNI* AS A MEASURE OF HATCHERY INFLUENCE

The most widely-applied metric to assess the genetic risks of hatchery production on natural populations is an index of gene flow called the 'proportionate natural influence' (*PNI*) developed and applied through the American HSRG process (HSRG 2009, HSRG 2014). The indicator was developed to measure the relative influence of selection by natural and hatchery environments on mean phenotypic values at equilibrium based on rates of gene flow between the two environments. For an integrated hatchery program, and under a series of simplifying assumptions, the adaptive state of both hatchery and wild-origin fish is approximated as:

$$PNI \approx \frac{pNOB}{pNOB+pHOS} \qquad (1)$$

where *pNOB* and *pHOS* are the proportion of natural-origin parents in the hatchery broodstock and the proportion of hatchery-origin fish on the spawning grounds, respectively.

PNI values can range between 0 and 1, with values >0.5 indicating a population in which the adaptive influence of the natural environment is greater and values <0.5 indicating a population in which the adaptive influence of the hatchery environment is dominant.

An important special case occurs when *pNOB* is zero and there is only one-way gene flow from hatchery to wild. This is the situation that arises for segregated hatchery programs and for straying from an out-of-basin hatchery where it is unlikely that natural-origin spawners from the

recipient stream will enter the broodstock. In this case Equation 1 cannot be used and alternative calculations are needed (see section 3.1.3 below).

Both HSRG (white paper 1) and others (RIST 2009) highlight that *PNI* is a useful indicator of hatchery influence but it is not appropriate to use it for making quantitative predictions about trajectories of hatchery-wild interactions for specific populations due to the many simplifications and requirements for parameters that are largely unknown. Flagg (2015) describes *PNI* as a "tool not a rule" noting that it provides general directional guidance for hatchery management and should not be used prescriptively, especially at yearly time scales given large interannual fluctuation in the abundance and composition of spawning populations.

PNI and fitness

PNI is based on the model of Ford (2002) that assumes that fitness can be modelled as a single multi-locus quantitative trait. Phenotypic variation is assumed to be normally distributed around a mean, and a fraction of the phenotypic variation is due to additive genetic variation. That fraction is designated as h^2, the heritability of fitness. Other forms of genetic variation (e.g. epistasis) are ignored, and it is assumed that genetic variability and heritability do not change over time.

The optimal phenotypes for hatchery and natural environments are assumed to be distinctly different (Figure 1). Phenotypes that are different from the optimal for that environment are less fit; their fitness is computed from a normal fitness function that is centered at the optimum. Evolution occurs because the fitness function selects those phenotypes that will be successful in the subsequent generation and that selection causes the mean phenotype to change. The strength of selection is determined by ω^2, the variance parameter for the fitness function, and the rapidity of evolution depends on both the strength of selection and the heritability of fitness.

The Ford model predicts the long-term equilibrium in the phenotypic mean values for hatchery- and natural-origin fish. Equilibrium results from the balance between selection in each environment that will tend to reinforce differences between the two spawning components, and gene flow that will reduce differentiation between them as the result of hatchery-origin fish spawning in the wild and natural-origin fish in the hatchery broodstock. The result of the opposing forces will be a population in which phenotypes converge to an intermediate value.

The phenotypic and genotypic convergence of natural- and hatchery-origin fish in an integrated hatchery program belies the common perception that fish originating from the two spawning environments represent adaptively distinct 'populations' that can be assessed and managed separately. Over time fish originating from both spawning locations will have an intermediate phenotype that is closest to the more productive environment.

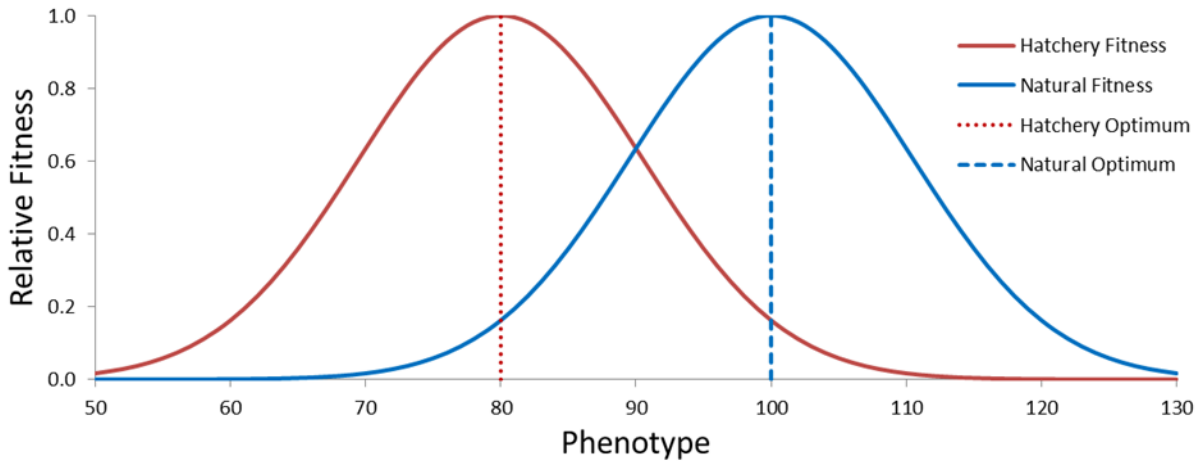

Figure 1. Fitness functions for hypothetical hatchery and wild phenotypes as a function of their phenotypic value relative to the optimal for each environmental. Parameters are those used by the AHA model, in the baseline case (HRSG 2009).

PNI computed using Equation (1) is an approximation of the Ford equilibrium and can be interpreted as the expected phenotypic value of the population on an arbitrary 0-1 scale, where 0 is the phenotypic optimum for hatchery and 1 is the optimum for the natural environment. It is assumed that the strength of selection, phenotypic variability, and heritability are similar in the hatchery and wild environments. Equation (1) is an approximation that applies to both hatchery and natural origin fish when there is exchange between the two; exact values for *PNI* for each environment can be calculated with more detailed formulae but the resultant values are very similar to those generated by Equation (1).

Underlying the Ford approach is a genetic model that describes changes in phenotypic values as a function of natural selection on fitness, and the heritability of fitness. The potential implications of interactions of the selective forces posed by hatchery and natural environments on population abundance and productivity can be made by estimating the change in population fitness associated with the change in phenotype. In the Ford model fitness, *F*, is modelled using the Gaussian formulation:

$$F = e^{-\frac{(P-\theta)^2}{2(\omega^2+\sigma^2)}} \qquad (2)$$

Where *P* is the phenotype, θ is the optimum phenotype for that environment, ω^2 is the variance around the fitness function and σ^2 is the phenotypic variation of the trait. When the fitness is at the optimum, $P-\theta = 0$, and the relative fitness is 1. As *P* differs from θ, fitness declines at a rate defined by ω.

The use of *pHOS* in *PNI* calculations

The preceding equations assume hatchery-origin fish have similar reproductive success in the wild as natural-origin fish and thus contribute to gene flow in proportion to their relative abundance. However, considerable evidence has accumulated that first-generation hatchery spawners have a lower relative reproductive success (*RRS*) compared to natural-origin spawners and their contribution to the next generation is lower than that expected based on census abundance (Christie et al. 2014a). Lower RRS can be caused by changes in gene frequency as a result of selection in the hatchery environment. This is the process modelled by the Ford (2002) model and is indexed by PNI. Lower RRS can also be caused by epigenetic effects and environmentally-driven phenotypic changes that result from the hatchery

environment and fish handling practices. Environmentally induced changes include changes in age at maturity, morphology, and behavior. For example, the location of juvenile releases can change the location of spawning in a watershed, which can result in the utilization of suboptimal habitats that contribute to lower fitness (Hughes and Murdoch 2017, Bowerman et al. 2017). The observed lower reproductive success of hatchery-born males may be due to their failure to gain access to females when competing with natural-origin males; similarly the reduced success of females may be related to sub-optimal redd locations or an inability to compete with natural-origin spawners for good spawning sites.

Recent updates by HSRG (2015) on the computation of *PNI* distinguish between $pHOS_{eff}$ and $pHOS_{census}$, with $pHOS_{eff}$ being the proportion of effective number of hatchery-origin spawners in the wild and $pHOS_{census}$ defined as the census or count-based estimate of the proportion of hatchery-origin spawners (HSRG 2015). The use of $pHOS_{eff}$ is designed to account for the failure of hatchery fish to successfully reproduce in the wild as a result of factors other than genetic selection. Further, it is assumed that these factors are not transmitted across generations as intergenerational effects are assumed to be accounted for in the genetic model.

The two variants of *pHOS* are computed as:

$$pHOS_{census} = \frac{N_H}{N_H+N_N}, \qquad (3)$$

and

$$pHOS_{eff} = \frac{\gamma N_H}{\gamma N_H+N_N} \qquad (4)[1]$$

Where N_H and N_N are census estimates of hatchery- and natural-origin spawners in the stream and γ is a multiplier that accounts for non-additive genetic, phenotypic and behavioural effects that result in hatchery fish being less successful at producing offspring relative to natural-origin fish. Here γ takes values between 0 and 1, and effectively discounts the number of hatchery-origin spawners on the spawning grounds. The two measures can be converted as:

$$pHOS_{eff} = \frac{\gamma}{\gamma+\frac{(1-pHOS_{census})}{pHOS_{census}}} \qquad (5)$$

for *pHOS* > 0.

Uncertainty surrounding the interpretation of $pHOS_{eff}$, and the values to use for γ (called *RRS* or *cf* in HSRG literature) led NOAA (NOAA 2016) to suggest that only $pHOS_{census}$ should be used for genetic risk assessment as it is the most risk-averse assumption with respect to the effects of hatchery production on selection and gene flow. However, for the purposes of understanding how these effects contribute to genetic risk, as well as their impacts on population productivity, we report a range of values of γ, but also include the corresponding $pHOS_{census}$ as this is the parameter that can be readily estimated in the field. Parameter values are discussed in section 4.1.1

One-way gene flow and straying

One-way gene flow (when *pHOS* or *pNOB* = 0) is most likely to take place when hatchery-origin fish spawn in the wild, but wild fish from the recipient population are not used for hatchery broodstock. This will occur for segregated hatchery programs that do not use wild broodstock, and for situations where out-of-basin hatchery or aquaculture spawners ("strays") spawn in the wild. Under the Ford (2002) model, the long-term equilibrium *PNI* under one-way gene flow for

[1] Erratum: RSS corrected to γ in numerator of equation.

the naturally spawning population is calculated using a different formula that requires values for selection intensity and heritability of fitness (HSRG 2009 appendix C, equation 33):

$$PNI_{wild} = \frac{h^2}{h^2+(1-h^2+\omega^2)pHOS_{eff}} \qquad (6)$$

Equation 6 predicts the long term equilibrium for *PNI* for the wild population as result of the balance between the continuous inflow of genes from an outside source and selection against those genes in the wild environment.

To evaluate the effects of straying on *PNI*, baseline parameters for fitness modelling used in Section 4 (h^2 = 0.25, ω = 10 or 100) were used in Equation 2. Computations show low levels of straying will have strong effects on the long-term equilibrium value of *PNI* under the scenario of one-way gene flow (Figure 2). To maintain *PNI* > 0.50, with γ = 0.8, $pHOS_{census}$ has to be less than 0.02-0.03.

To model the change in phenotype, *PNI* and population fitness over time, equations 35 and 36 of HSRG (2009 appendix C) can be used. Results show that even after only 10 simulated generations decreases in *PNI* occur at low rates of straying (indicated by $pHOS_{census}$ in Figure 2). Strong stabilizing selection and high heritability reduce the impact of introgression, as maladapted genes are more efficiently purged from the population than genes adapted to the natural environment. Modelled fitness is also predicted to decline as a result of these relatively low rates of straying into the population although the extent is also dependent on assumptions about ω^2 and h^2. When selection is weak the decrease in fitness is smaller when the phenotype deviates from the optimum (Figure 2).

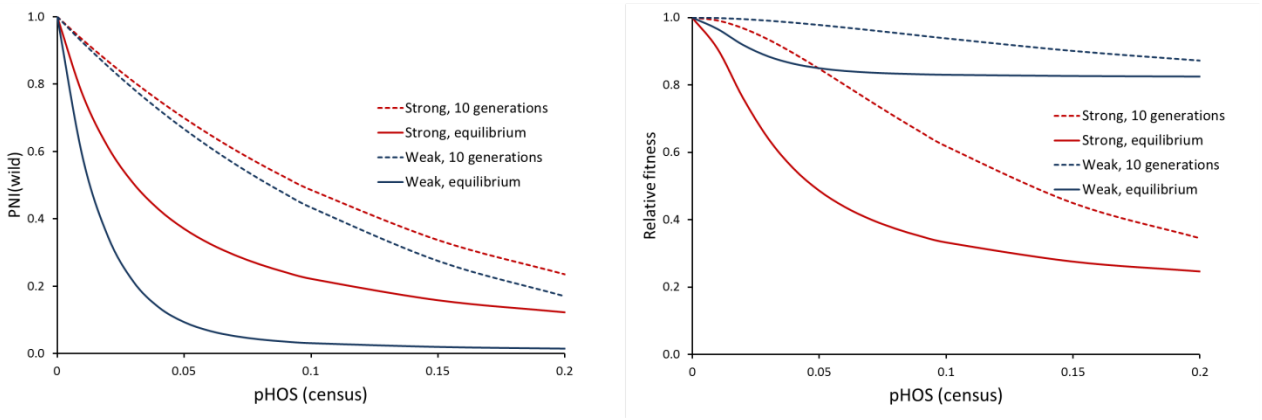

Figure 2. Left: PNI for a wild population that experiences one-way gene flow from a segregated or independent hatchery population. $pHOS_{census}$ is the proportion of spawners that are of hatchery origin; γ = 0.80. Shown is the long-term equilibrium, and results after 10 generations for strong and weak selection, Baseline parameters are used (θ_H = 80, θ_W = 100, σ^2 = 10, h^2 = 0.25); weak selection is $100\sigma^2$, strong selection is $10\sigma^2$. Right: relative fitness declines for cases with strong and weak selection.

No empirical information could be found to compare model results with field observations of the long-term changes in fitness or productivity associated with low levels of out-of-basin straying. Long-term impacts of larger-scale hatchery programs from a segregated (McGinnity et al. 2009) or out-of-basin (Le Cam et al. 2015) population have been detected, but the rates of stocking (straying) in those studies were much larger than the ranges of most interest here.

Theoretical modelling approaches have generated fairly consistent results that are similar to those in Figure 2. Lynch and O'Hely (2001) modelled the effects of the accumulation of deleterious mutations in captive (closed hatchery) populations, and Huisman and Tufto (2012)

explicitly modelled a finite number of alleles and compared those results to an infinitesimal (many allele) model similar to that of Ford (2002). Although the exact results depend on the assumed parameters, the predicted relations between the migration of individuals from a breeding program and changes in phenotype and fitness of the wild population are consistent in finding significant changes in genetic composition and potential impacts on fitness from sustained one-way gene flow, even at low levels of immigration.

3.2. HATCHERY MANAGEMENT MEASURES TO ACHIEVE *PNI* GUIDELINES

From the perspective of *PNI,* genetic risks to wild salmon populations from integrated hatchery programs can be minimized by reducing the number of hatchery-origin fish that spawn in the wild, and increasing the number of natural-origin fish in hatchery broodstock. These outcomes can be achieved by

1. minimizing the size of the hatchery program,
2. manipulating the composition of the broodstock and
3. decreasing the returns of hatchery-origin fish to the river by selective harvest or the use of a weir or similar device.

These factors are considered in combination with long-term fitness impacts in the population modelling in section 4. As an introduction to how these factors affect *PNI*, the effects of broodstock composition, selective removals and marking rates on *PNI* are analyzed independently below.

Broodstock composition

Increasing the use of natural-origin spawners in the broodstock is a management measure that can increase *PNI* in integrated hatchery programs. Figure 3 shows the effects of broodstock composition on *PNI* for different abundances of hatchery spawners in the river (indexed by *pHOS*). The effect of changing broodstock composition on *PNI* is generally modest, unless the incidence of hatchery-origin fish in the broodstock is high. When more than 60-70% of the broodstock are hatchery-origin spawners increasing natural-origin spawners in the broodstock may be a particularly effective measure to increase *PNI*.

In some situations it may be difficult to collect natural-origin broodstock. This can occur when hatchery-origin spawners predominate in river reaches near the hatchery where broodstock collections are made, or if hatchery-origin spawners enter the hatchery directly via a tailrace. In these cases changes to broodstock collection protocols may be needed to increase the number of natural-origin fish to meet *PNI* goals.

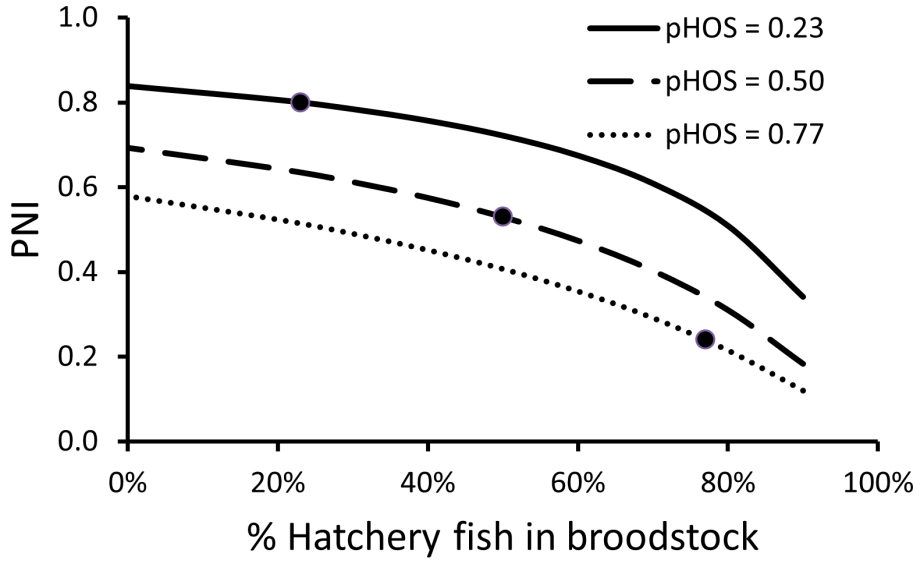

Figure 3.[2] *Relation between PNI and the proportion of hatchery-origin spawners in the broodstock (1-pNOB) for three levels of pHOS, the overall proportion of hatchery-origin fish returning to the river. Symbols on the lines indicate cases where the composition of the broodstock is the same as in the river. Values to the right of the circles are situations where hatchery-origin fish are more frequent in the broodstock than they are in the river. Reduced reproductive success of hatchery origin fish in the wild is modelled with γ = 0.80.*

Selective removal of hatchery fish

PNI can be increased by preventing hatchery-origin fish from spawning thus decreasing *pHOS*. For example, a weir or collection facility (e.g., fishway at a dam) can be used to collect hatchery fish to prevent them from spawning in the wild. Figure 4 shows the relation between *PNI* and selective removal of hatchery fish under the assumption that the composition of the broodstock will be the same as the river after removals. The effects of hatchery removal are greatest when hatchery fish dominate the returns. This example is for illustration only as selective removals will have effects on natural production that will then impact the composition of returning fish the subsequent generation. Interactions among factors are dealt with in the population model in Section 4.

[2] Erratum: Figure revised to reflect changes to benchmarks in Table 3.

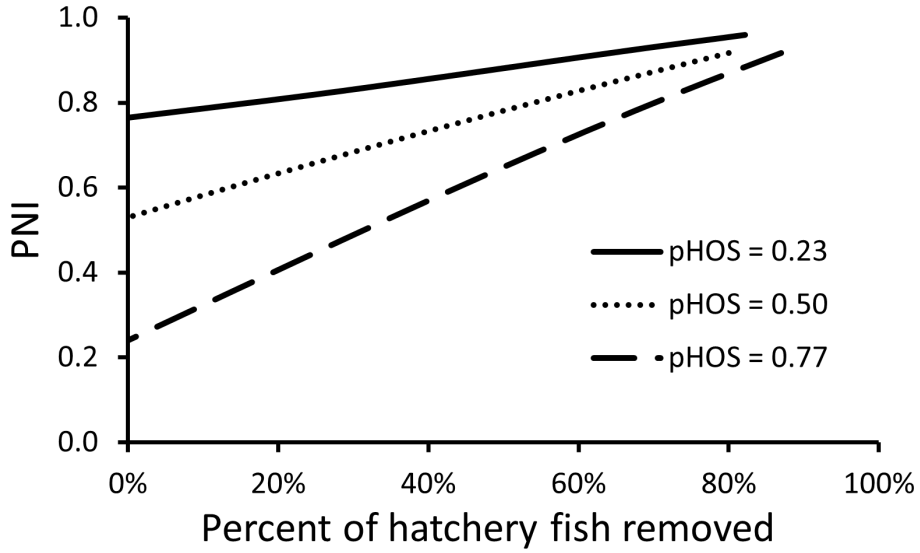

Figure 4.[2] Effects of selective removal of hatchery-origin spawners from the river on PNI for three scenarios of different proportions of hatchery-origin fish returning to the river. Broodstock composition is the same as the river after hatchery fish removal; γ = 0.80.

Marking

Increasing the proportion of natural-origin fish in broodstock or in the river spawning population is usually dependent on the availability of an external mark to separate and screen out hatchery-origin spawners. Externally visible marks can also be used in mark-selective fishing programs to reduce the incidence of hatchery-origin fish returning to the river. The proportion of hatchery-origin fish that are marked will affect the potential of selective harvest as there will be unmarked hatchery fish that are indistinguishable from natural-origin fish if the marking rate is less than 100%.

This analysis considers effects of marking on broodstock only. The proportion of natural-origin fish in the broodstock is:

$$pNOB = \frac{N}{H+N} \qquad (7)$$

Where *H* is the number of hatchery fish (marked and unmarked) and *N* is the number of natural-origin fish among fish taken for broodstock. If marked hatchery fish are then removed from the broodstock sample, the adjusted *pNOB** is now

$$pNOB^* = \frac{N}{(1-mr)H+N} \qquad (8)$$

where *mr* is the marking rate. Noting that Equation 7 can be rearranged to yield $N = \frac{1-pNOB}{pNOB}H$, substitution for N in (8) and simplification yields:

$$pNOB^* = \frac{\frac{pNOB}{1-pNOB}}{(1-mr)+\left(\frac{pNOB}{1-pNOB}\right)} \qquad (9)$$

This expression can be used to evaluate the effects of mark rate and selective removal of marked fish from a broodstock sample that has a total hatchery (marked and unmarked) and natural-origin contribution defined by *pNOB*. Figure 5 shows the effect of removing marked fish from broodstock on *PNI* for three different proportions of hatchery and wild fish under the

assumption that there is no selective removal of hatchery fish from the river spawning group (i.e., *pHOS* remains unaffected). The figure shows that when the population is dominated by hatchery fish increases in *PNI* are possible through the removal of marked fish in the broodstock, but the marking rates must be very high for the effect to be significant. The mark rate and selective removal of marked fish in the broodstock has little effect on *PNI* when the population is mainly natural origin fish (i.e., *pHOS* < 0.5).

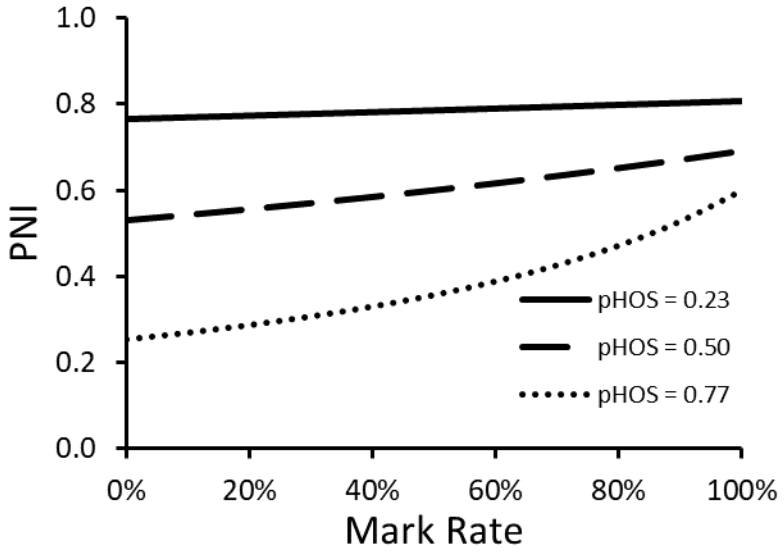

Figure 5.[2] Effects of removing marked fish from broodstock collections on PNI. Shown are results from three levels of pHOS, the proportion of hatchery-origin fish returning to the river. Here it is assumed that the initial composition of the broodstock is the same as the river spawning population (as specified by pHOS). PNI values will be lower if the broodstock sample is biased in favour of hatchery-origin fish; γ = 0.80.

3.3. GUIDELINES FOR THE APPLICATION OF *PNI*

HSRG (2009) developed guidelines or standards for *PNI*, *pHOS* and *pNOB* based on the designation of natural populations in the context of ESA recovery measures. That designation was first developed for the US Lower Columbia River area, and has since been applied elsewhere.

Under the ESA, *Evolutionary Significant Units* (ESUs) are the primary unit for listing decisions at the sub-species level. For Chinook Salmon, ESUs are generally larger and include more spawning sites and populations than Conservation Units (CUs) under Canada's Wild Salmon Policy.

Strata are then identified within each ESU; strata are defined on the basis of life history diversity at the population level and ecological zones (LCFRB 2010). The goal of the Lower Columbia recovery program is to ensure each stratum has a high level of persistence. Stratum persistence is achieved by having 2 or more populations within the stratum being designated as "primary" populations; these are located where habitat and other factors ensure a high likelihood of good productivity and recoverability. "Contributing" populations are considered to have moderate prospects for viability, given the state of habitat and other factors that affect their status whereas "stabilizing" populations are those for which the current viability is low and the prospects for recovery to a better viability status are poor.

HSRG developed standards for *PNI*, *pHOS* and *pNOB* for each population designation for both integrated and segregated hatchery programs (Table 2). Standards are most stringent for primary populations, reflecting a desire to maintain natural characteristics and minimize hatchery influences for those populations that have the greatest potential viability based on natural reproduction. Less stringent standards were established for contributing populations, and no specific criteria were developed for stabilizing populations where existing hatchery programs are considered adequate. These standards were designed to be consistent with recovery objectives, and contribute to increasing viability of the strata as a whole by addressing concerns about how hatchery programs may contribute to reduced viability, particularly for primary populations (Paquet et al. 2011).

Table 2. Hatchery standards for three categories of populations, and two types of hatchery programs developed by HSRG (2009). Note in 2014 HSRG revised these such that pHOS refers to $pHOS_{eff}$.

Designation	Segregated	Integrated	Comments
Primary	*pHOS* < 0.05	*pNOB* > 2·*pHOS* *PNI* > 0.67, *pHOS* < 0.3	Core populations for strata recovery, maintain natural characteristics
Contributing	*pHOS* < 0.1	*pNOB* > *pHOS* *PNI* > 0.5, *pHOS* < 0.3	Populations with moderate viability
Stabilizing	No standards	No standards	Goal is no decrease in viability

Achievement of these goals for primary and contributing populations can require measures to reduce the number of hatchery fish on the spawning grounds. This may be achieved through removal of marked hatchery fish using a weir or selective harvest, or reducing the overall size of the hatchery program relative to natural production.

Standards for segregated hatchery programs are also applicable to out-of-basin hatchery strays. HSRG (2015) notes that the *pHOS* standards for segregated programs in Table 2 are inconsistent with standards for integrated programs because they result in much lower *PNI* and potentially larger losses of fitness. HSRG (2015) acknowledges that the existing standards for segregated programs may be insufficient to protect naturally spawning populations. These findings apparently caused the California hatchery review group (CHSRG 2012) to be unsupportive of segregated hatchery programs due to the difficulty in managing hatchery returns to the required very low *pHOS* values.

HSRG (2014, 2015) also recognized current conservation status of individual populations can also inform genetic guidelines, particularly for broodstock management. In particular they note that captive breeding programs with low *pNOB* values may be required during the initiation of a conservation hatchery program, with the expectation that a transition to the values of Table 2 would occur as population recovery reaches defined mileposts with respect to population viability. These are explained further in section 5.3.

Proposed Canadian Approach

The original HSRG guidelines for hatchery programs are structured by viability-based population designations designed to protect and recover key populations within each ESU strata. In the Canadian context for the management of genetic risks of hatchery-wild interactions it may be

appropriate to designate populations or spawning aggregations within CUs with respect to the extent of these interactions. Designations can range from populations virtually free of hatchery influence, to those that are dominated by hatchery production. Category definitions can be informed by HSRG metrics and the proportion of fish in the population that meet the definition of wild under the WSP. While the process to determine how many and which populations should be designated to various categories is beyond the scope of this review, identifying the biologically-based categories under such a framework does allow the development of hatchery guidelines appropriate to each category.

For example, taking the WSP definition of wild fish and extending that to wild populations, and the WSP objective to safeguard genetic diversity of wild salmon into consideration, a Canadian Chinook Salmon population could be considered wild if, for a minimum of two generations, the wild environment has been sufficiently productive to be self-sustaining and wild fish are estimated to comprise on average the majority[3] of the spawning population.

Under the assumption of random mating of hatchery and natural origin fish, and accounting for the reduced relative reproductive success of a hatchery-origin spawner relative to natural origin spawners, the proportion of wild fish in the spawning population (*pWILD*) in generation *t* can be approximated as:

$$pWILD_t = (1 - pHOS_t)\frac{(1 - pHOS_{t-1})^2}{(1 - pHOS_{t-1})^2 + 2\gamma\, pHOS_{t-1}(1 - pHOS_{t-1}) + \gamma^2 pHOS_{t-1}^2}$$

Here the first term accounts for returns of hatchery fish in the present generation from ongoing enhancement and second term is the proportion of wild fish in the offspring from spawning in the previous generation, accounting for the reduced reproductive success of hatchery spawners (Riddell et al. 2013, p. 219).

Thus to meet the requirement for the majority of spawners to be wild for a population where both natural and hatchery origin spawners are present, *pHOS* must be less than or equal to 0.23, which results in *PNI* ≥ 0.80 (assuming γ = 0.80).[4]

The following 5 biological designations are proposed for populations that vary in their degree of hatchery influence. Guidelines for genetic risk management metrics are then presented for each category (Table 3).

The ***wild*** category is for populations that are designated to not be part of, or be influenced by, hatchery programs. No broodstock collection or hatchery releases will occur in the population's natal habitat. A stringent level of *pHOS* is proposed to protect these populations from genetically distinct strays from hatchery-origin fish from outside of the watershed. Modelling results show rates of migration from non-integrated hatchery fish (e.g. from segregated programs, or strays from different populations) must be very low (*pHOS* < 0.02) to avoid risk of genetic impacts as

[3] Erratum: "at least 51%" corrected to "the majority".

[4] Erratum: Replaced text read "Note that the definition of wild under the WSP requires that both parents of a wild fish also be born in natural environments. Given the assumption of random mating of hatchery- and natural-origin fish, and equal survival and reproductive success for crosses involving both types of parents, in the natural environment, a requirement for 51% wild fish should be met in populations in which at least 72% of the fish are naturally-spawned (i.e., pHOS < 0.28). Fifty-two percent of crosses in the wild will then be between two naturally-spawned fish, as is required for the production of 'wild' progeny (0.72 x 0.72 = 0.52). If, as is often the case, the reproductive success in the natural environment of crosses involving one or both hatchery-origin parents is less than that of crosses involving two naturally-spawned parents, the proportion of wild fish produced may be slightly higher. This approach combines direction from the WSP with the principles of the HSRG for the management of genetic impacts to populations from hatchery programs."

indexed by *PNI* (Section 3.1.3). It is important to note the extent of potential impact on population fitness and productivity from this level of straying is uncertain given current information. Benchmarks for this category are similar to those for HSRG "primary" populations for immigration from segregated hatchery programs (Paquet et al. 2011). However, we propose the standard for *pHOS* be lowered from HSRG's proposed value of 0.05 given concerns raised by HSRG (2015), the California hatchery review, and our analyses.

Wild-stray influenced populations receive strays from out-of-basin hatchery programs at rates greater than the limit specified for the ***wild*** designation. Although the majority of fish may be wild, one-way gene flow modelling suggests that over time *PNI* values will decline to levels inconsistent with a population dominated by natural influences (see Figure 2).

Integrated-wild populations have an integrated hatchery program that is managed to achieve conservation and genetic goals while contributing to production. Benchmarks associated with this category ensure the majority (>50%) of fish spawning in the river meet the criteria for wild under the WSP and 80% or more[5] of the spawning population will be of natural origin. The resultant *PNI* is large enough (> 0.80[6]) that the population will be dominated by natural-origin genetic influences. This can be achieved by limiting hatchery-origin fish spawning in the wild, retaining a high proportion of natural-origin fish in the broodstock and limiting the overall size of the hatchery program (see section 4 below).

Integrated-transition populations retain *PNI* > 0.5, indicating there is net gene flow from the natural-origin component to the hatchery component, but only 13-<50%[7] of spawners in the natural environment are considered wild under WSP. The equilibrium adaptive state for populations in this category will be intermediate between the hatchery and natural optima and such a population may or may not be self-sustaining in the absence of hatchery production. Populations undergoing rebuilding through enhancement may be in this category. If the goal is to improve the WSP status of the CU containing the population, it is expected that the hatchery program will transition to meet the *Integrated-wild* benchmarks once abundance is increased to satisfactory levels

Integrated-hatchery populations are those in which hatchery fish dominate both broodstock and natural spawning components. It is recognized that the magnitude of hatchery production, the small proportion of natural-origin and near absence of wild fish are likely to have impacts on the fitness and productivity of the integrated population. These populations may occupy locations in which habitat conditions or other factors preclude the existence of viable natural populations (similar to stabilizing populations in Table 2) or may be justified by the social or economic benefits of extensive hatchery production.

[5] Erratum: "nearly three fourths" corrected to "80% or more" to reflect corrected calculation of pWILD.

[6] Erratum: 0.72 corrected to 0.80 to reflect corrected calculation of pWILD.

[7] Erratum: 25-50% corrected to 13-<50% to reflect corrected calculation of pWILD.

Table 3. Proposed designations for individual salmon populations that vary in the degree of influence of integrated hatchery programs and the proposed genetic guidelines for hatchery management. PNI is computed using $pHOS_{eff}$. The pWILD column shows the expected proportions of wild fish in the spawning population. The remainder of the spawning population is made up of offspring of matings with one or two hatchery parents in the wild, and returns from ongoing hatchery production at a rate defined by $pHOS_{census}$. Matings are assumed to be random and γ, the proximal reproductive success of a hatchery fish spawning in the wild, was set to 0.8.[8]

Designation		***$pHOS_{eff}$*** ***$pHOS_{census}$***[9]	***pNOB***[9]	***PNI***[9]	***pWILD***[9]	**Comments**[9]
A	Wild	≤ 0.02 ≤ 0.03	n/a	n/a*	≥ 0.92	Designated wild populations that do not have hatchery programs (for at least two generations); strays from out-of-basin hatchery production are limited to <3% per year.
B	Wild-stray influenced	>0.02 >0.03	n/a	n/a*	*< 0.92*	Population receives strays from an out-of-basin hatchery. A very large fraction of fish may be wild but gene flow modelling suggests a long-term decline in *PNI* as *pHOS* increases.
C	Integrated wild	≤ 0.19 ≤ 0.23	≥ 0.77	≥ 0.80	≥ 0.50	Hatchery production is managed to keep wild fish ≥ 50% of the spawning population.
D	Integrated-transition	≤ 0.47 ≤ 0.53	≥0.47- <0.77	≥0.50- <0.80	≥0.13- <0.50	*PNI* ≥ 0.5 ensures natural-origin influence predominates but wild fish are in the minority.
E	Integrated-hatchery	> 0.47 > 0.53	< 0.47	< 0.50	< 0.13	Net gene flow from hatchery environment; most fish are hatchery origin. Few fish are wild.

*When *pNOB*=0, *PNI* is computed from simulations based on equation 33 of HRSG (2009, App. C); results depend on assumed values for h^2 and ω^2 and are not reported here. See Figure 2 for an example.

[8] Erratum: Original text read "The WSP column shows the expected proportions of natural origin-natural origin (NN) matings that would result in production of WSP-wild fish, and hatchery-natural hybrids (HN) and hatchery-hatchery (HH) matings. Matings are assumed to be random and are computed from $pHOS_{eff}$. γ, the proximal reproductive success of hatchery fish spawning in the wild, used to calculate $pHOS_{eff}$ was set to 0.80."

[9] Erratum: Cells in these columns revised to reflect corrected method for calculating pWILD.

4. MODELLING EFFECTS OF MANAGEMENT ACTIONS ON GENETIC RISK INDICATORS

4.1. ANALYTICAL APPROACH

To evaluate the behaviour of *PNI*, and the implications of the proposed standards for both population and hatchery management, a simple model was constructed that simulated a single Chinook Salmon population with an integrated hatchery program located in the same watershed. The purpose of the model was to gain an understanding of the dynamics of *PNI* and management actions in relation to performance indicators such as the *PNI* standards and natural and hatchery fish production. The model emulated a single moderate-sized population of ocean-type Chinook Salmon similar to those found in Georgia Strait, but was not designed to represent a specific population or hatchery.

Details of the model are provided in Appendix B, but are briefly summarized here (Fig. 6). A two life-stage population model was used to simulate the natural component of the population. The model was deterministic (no random or natural variation), and all parameters were fixed in each model run. A single age-at-maturity was assumed and simulations were done on a generation time step. The model was run for 100 generations and values at the end of the run were compiled for analysis. Thus the results cannot be used to evaluate time trends, or management actions aimed at conservation or recovery objectives where the goals are to achieve positive trends in population parameters.

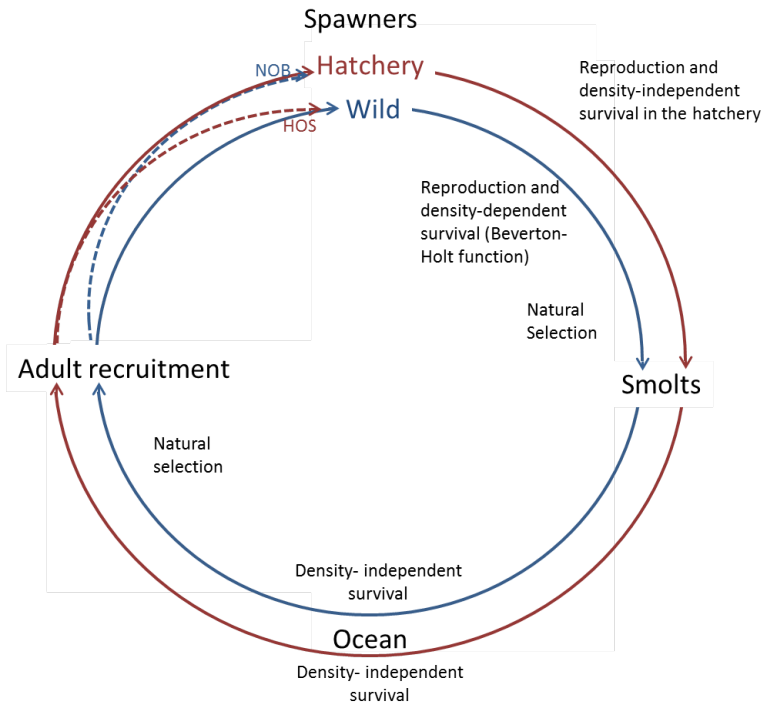

Figure 6. Schematic of model used to evaluate impacts of hatcheries on achieving biological objectives. NOB are natural-origin broodstock and HOS are hatchery-origin spawners in the river.

A Beverton-Holt function was employed to represent the production of underyearling smolts from the river, and was parameterized from data collected from streams from the east coast of Vancouver Island. Survival from smolt to returning adult (recruit) was assumed to be density-independent and the survival rate used in baseline simulations was chosen to ensure the

population was sustainable given current levels of exploitation for Chinook Salmon. A constant rate of harvest was used to generate annual catch.

The model hatchery collects broodstock from the river, and releases a constant number of underyearling smolts in a single release group each year. Estimates of the survival and fecundity of broodstock, and survival in the hatchery and after release were based on recent averages from four hatcheries located on the east coast of Vancouver Island.

Effects of the hatchery on population fitness were modelled using the approach of HSRG (2009). Fish adapted to the hatchery environment were assumed to have a different genotype and be less fit in the wild, and the breeding of hatchery-origin fish (including interbreeding with natural-origin fish) in the natural environment was assumed to result in a loss of fitness of the population. Fitness loss was assumed to decrease survival in both the freshwater and marine components of the model, and decrease the productivity of fish spawning in the natural environment. We used the same formulation as HSRG (2009) for the modelling of fitness.

The primary management actions we considered were three parameters of the hatchery program: the size of the program, brood stock composition, and selective removal of hatchery fish from the natural environment; the latter two actions are affected by the rate of marking, which we also examined. These parameters are the most relevant to the management of genetic impacts of the hatchery on the integrated spawning population, but we note that others may be important for evaluating hatchery performance (e.g., mating design, spawning practices, pedigree programs, release strategies). However, these were outside the scope of the current study.

The size of the hatchery program was indexed by the number of broodstock spawners taken, and was expressed as a proportion of the average (equilibrium) number of natural spawners in the river, in the absence of a hatchery. This served to scale the hatchery production to the size of the watershed accounting for existing harvest pressures to assist in generalizing the results. However, we limited the total broodstock to less than a third of the total returns to the river in any given year to avoid conservation concerns from removing too many fish for brood.

To minimize genetic impacts, we assumed that broodstock would be comprised of as many natural-origin spawners as possible to maximize *pNOB*. The selection of natural-origin spawners is affected by the marking rate as unmarked hatchery-origin fish are indistinguishable from natural-origin fish. If no fish are marked then it is assumed that the brood stock will be a mixture of hatchery- and natural-origin spawners in the same proportions as the river spawning component. We assumed that in cases where the number of marked fish in the escapement is high, no more than three times the broodstock quota would be searched for unmarked fish for broodstock, in order to limit the handling of fish. In practise, each hatchery program will vary in the methods of broodstock collection and the potential for selecting brood fish to meet *pNOB* objectives.

In some circumstances there may be potential to manage the number of hatchery-origin fish that can spawn in the model river through, for example, the use of a weir to select and remove hatchery fish. We modelled the removal of marked fish and added the removed fish to the catch.

For each simulation, outputs were the genetic parameters *PNI, $pHOS_{eff}$* and *pNOB*, and the predicted number of natural- and hatchery-origin fish produced by wild and hatchery spawning, and the catch.

Parameter values and sensitivity analyses

There is significant uncertainty about the appropriate values for some parameters in the model; sensitivity analyses were therefore conducted using a range of values to evaluate whether the general recommendations from the simulations were sensitive to input values.

The heritability of fitness (h^2) was assumed to be 0.5 by HSRG; however, various meta-analyses of heritability of life history traits linked to fitness yield much lower values (Mousseau and Roff 1987; Reed et al. 2015, Hoffman et al. 2016). For the baseline runs we used a value of 0.25, and then used $h^2 = 0.05$ in a sensitivity analysis to bracket the likely range.

The strength of selection is determined by the parameter ω^2 of the fitness function and is often expressed as a function of the phenotypic variation σ^2. Ford (2002) considered strong selection to be $\omega^2 = 10\ \sigma^2$ and very weak selection $100\ \sigma^2$. These are the values used by HSRG in their model. Summaries of estimates of selection suggest that $\omega^2 = 10\ \sigma^2$ is similar to the median of estimates for stabilizing selection and smaller values of ω^2 should be used in sensitivity analysis to span the likely range (Kingsolver et al. 2001; Kingsolver et al. 2012). In our analysis, since $\sigma^2 = 10$, we used $\omega^2 = 100$ as our baseline value, and values of 40 and 1000 in sensitivity analysis.

γ is the parameter that models the reduced reproductive success of hatchery-origin spawners in the wild due to factors other than selection on additive genetic variation. In the model, changes in fitness due to genetic selection is accounted for by *PNI* and associated fitness modelling; the intent of γ is to capture more proximal effects.

Initially HSRG used a proximal value of 0.8 for Chinook Salmon, but they have noted this value will need re-evaluation as more information becomes available. An extensive review of the reproductive success of hatchery fish in the wild suggests average values of 0.5 with a range that may extend as low as 0.2. However, in most field studies the contribution of selection on gene frequency cannot be separated from epigenetic, phenotypic and environmental factors that we are modelling with the γ parameter (Christie et al. 2014a). Also, most studies have been conducted on populations in which the Chinook Salmon juveniles spend a year or more in the hatchery; it is generally expected that γ will be higher in situations where juveniles spend less time the hatchery environment, though few data exist to confirm this expectation (Christie et al. 2014a).

Noting that estimates of relative reproductive success may have overestimated the non-genetic reduction in fitness, and may be too small for hatchery programs that hold fish for shorter periods, we used the HSRG value of 0.8 for γ in our baseline simulations as it is at the high end of observed values (resulting in small reduction in relative reproductive success), and a low value of 0.2 for sensitivity analysis. The high baseline value is considered risk-averse because it will result in increased gene flow from hatchery to the wild component of the population, which will lead to a reduction in *PNI* and fitness.

4.2. EFFECTS OF MANAGEMENT ACTIONS ON GENETIC RISK INDICATORS

The equilibrium effects of 3 management control measures, hatchery program size, proportion of hatchery fish marked, and proportion of marked fish selectively removed from natural spawning on performance metrics are shown in Figures 7-12. Figure 7 shows the impacts of 2 control measures on *PNI* in bivariate contour plots, assuming the third control measure is fixed (labeled at the top right corner of the panel). Base-case values are assumed for remaining biological and management parameters (Appendix B, Table B1). The shading of *PNI* values aligns with the 3 categories identified in Table 3, “integrated-wild” (light blue), “integrated-transition” (medium blue), “integrated-hatchery” (dark blue).

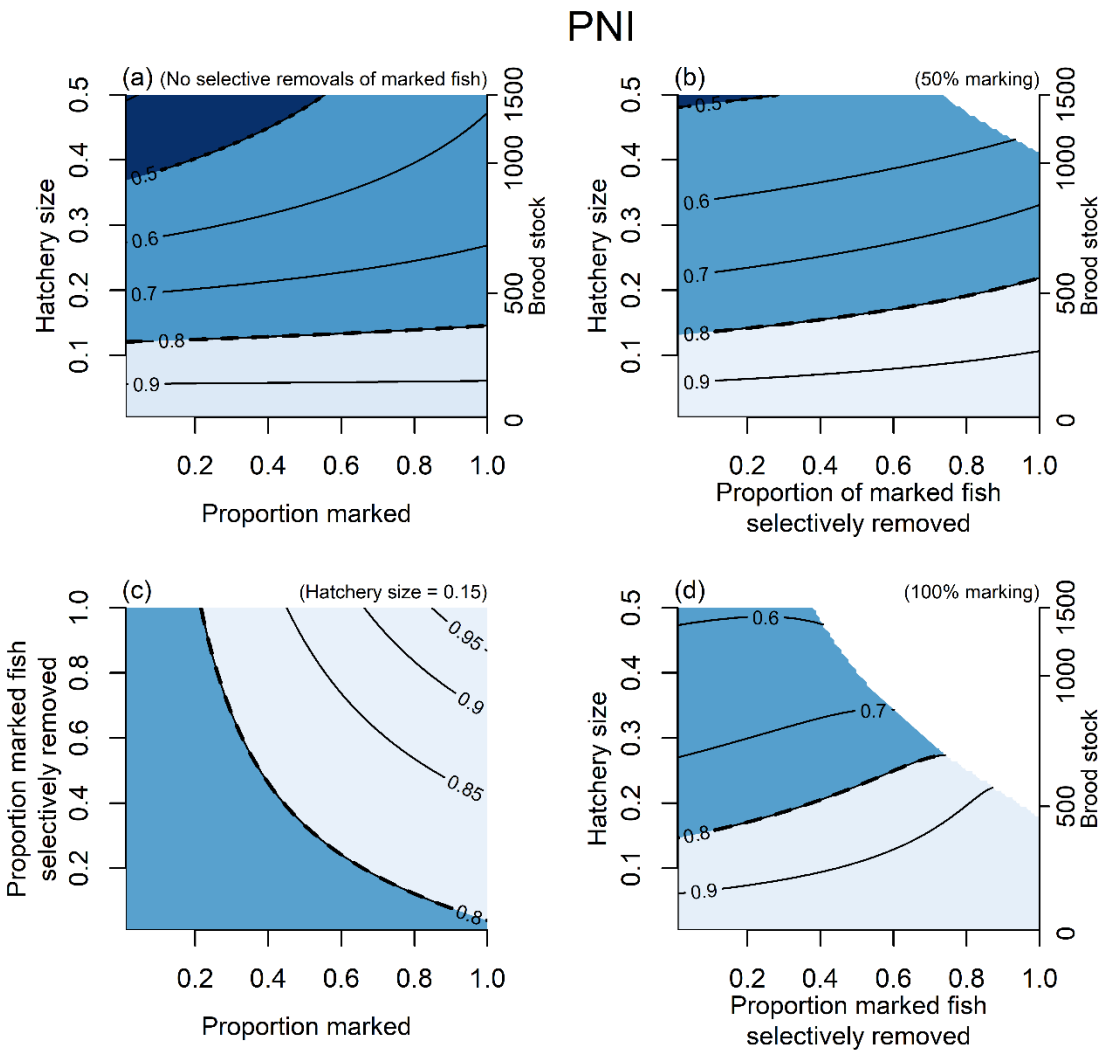

Figure 7.[10] Bivariate contour plots of proportionate natural influence, PNI, along gradients in three management levers, (a) proportion of hatchery fish that are marked and hatchery program size, as a proportion of average natural returns to the river, (b, d) proportion of marked fish that are selectively removed and hatchery program size, (c) proportion of hatchery fish marked and proportion of marked fish selectively removed. In each pairwise plot, the assumption about the third management lever is described in the top right corner of the panel. Panels (b) and (d) assume 50% and 100% marking respectively. The shading of PNI values aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery program.

In general, *PNI* values are largest for small hatchery programs, and are somewhat affected by proportion marked (Fig. 7a). To achieve *PNI* objectives for the "integrated-wild" category, the

[10] Erratum: Figure revised to reflect corrections to model and revisions to benchmarks for population categories.

upper limit of hatchery size (in terms of the broodstock taken) is about 15%[11] of average number of natural-origin spawners to the river for our base-case scenario, assuming no selective removal of marked fish. Larger hatchery programs are possible within the "integrated-wild" category when marked fish are selectively removed either at sea or in the river and marking rates are high (Fig. 7d). With 50-100%[12] marking and large removals of marked fish, the size of the hatchery program is limited by the constraint that brood take must be ≤ 1/3 of annual observed spawners returning to the river, limiting the size of the hatchery (white areas, Fig. 7c and d).[13]

Since *PNI* is calculated from *pNOB* and $pHOS_{eff}$, and those parameters are used with *PNI* to define categories of populations (Table 3), it is instructive to examine sensitivity of *pNOB* and $pHOS_{eff}$ to management control measures. Brood stock composition (*pNOB*) is sensitive to both the size of the hatchery program and the proportion marked (Fig 8a). Marking rates in excess of 60-80% are required to meet the "integrated-wild" goals for larger hatchery sizes under our base-case scenario. The selective removal of marked fish has a relatively small impact on brood composition when marking rates are <100% (Fig. 8b). When all fish are marked, hatchery brood is composed entirely of natural-origin fish (*pNOB* =1) (Fig. 8d).[14]

[11] Erratum: 10% corrected to 15% to reflect changes in model outputs.

[12] Erratum: 100% corrected to 50-100% to reflect changes in model outputs.

[13] Erratum: "white area, Fig. 7d" corrected to "white areas, Fig. 7c and d".

[14] Erratum: Text removed read "with the exception of large hatcheries where a maximum handling effort is applied when selecting unmarked fish for hatchery brood (Fig. 8d, top left corner). Above that handling effort (3 × target brood stock), marked and unmarked fish are taken for hatchery brood in the proportions in which they are found in the river, reducing *pNOB* below 1."

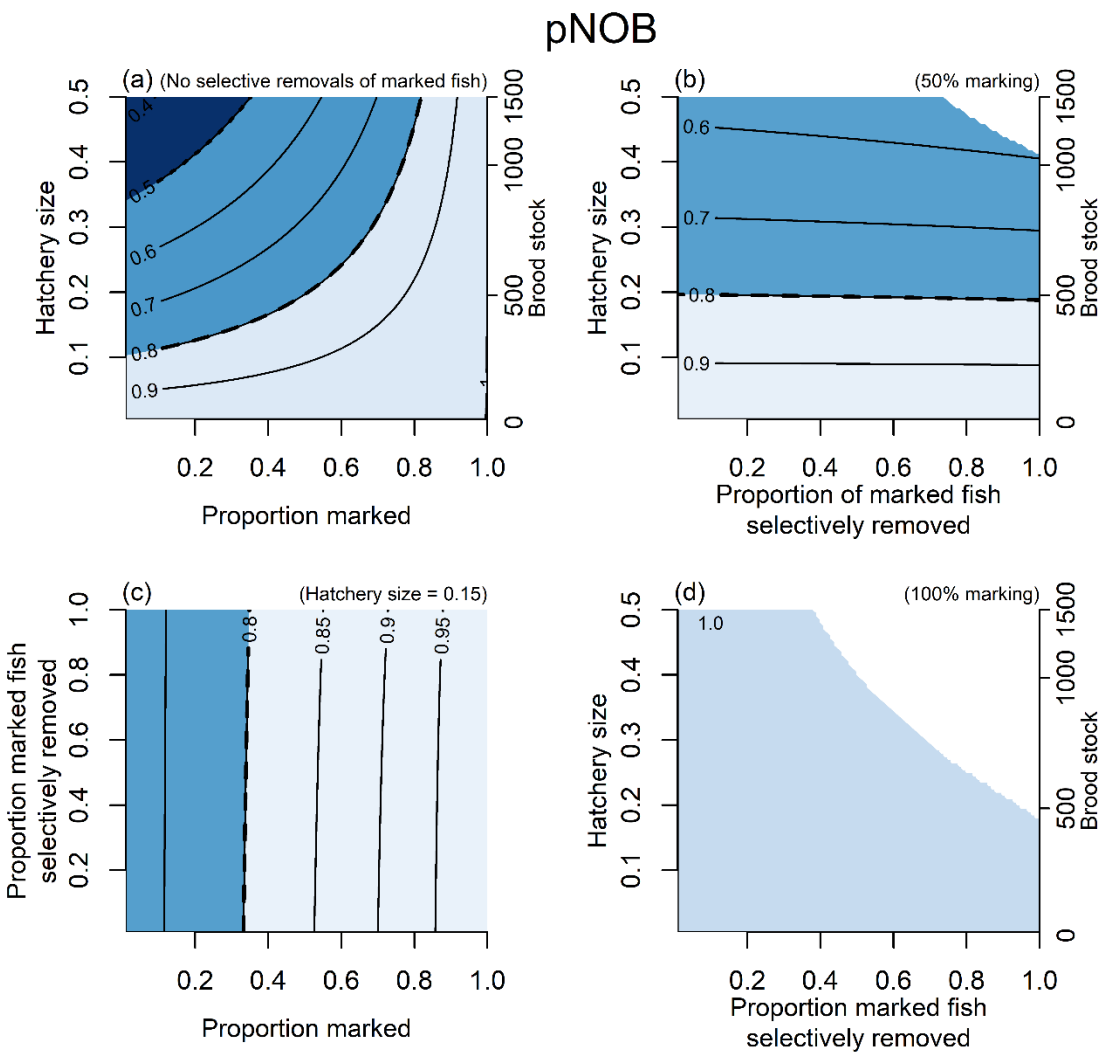

Figure 8.[15] *Bivariate contour plots of the proportion of natural-origin fish in the hatchery brood stock, pNOB, along gradients in three management levers, as described in the caption for Fig.7. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.*

The proportion of spawners in the river (natural spawners) that comprises effective hatchery spawners, $pHOS_{eff}$, is affected most significantly by hatchery program size (Fig. 9a). However, the exclusion of hatchery-origin fish from the spawning grounds through marking and selective harvest or removal at a weir reduces the $pHOS_{eff}$, especially when mark rates are high (Fig. 9c and d). Consistent with the *PNI* results, targets for $pHOS_{eff}$ for "integrated-wild" populations are met when hatchery size is less than about 15%[16] of average return of the natural population to the river without a hatchery in our base-case scenario, in the absence of selective removals of

[15] Erratum: Figure revised to reflect changes in model outputs.

[16] Erratum: 10% corrected to 15% to reflect changes in model outputs.

marked fish. Objectives for “integrated-transition” populations are met when the hatchery size is less than about 35-40%[17] without selective removals of marked fish in that scenario.

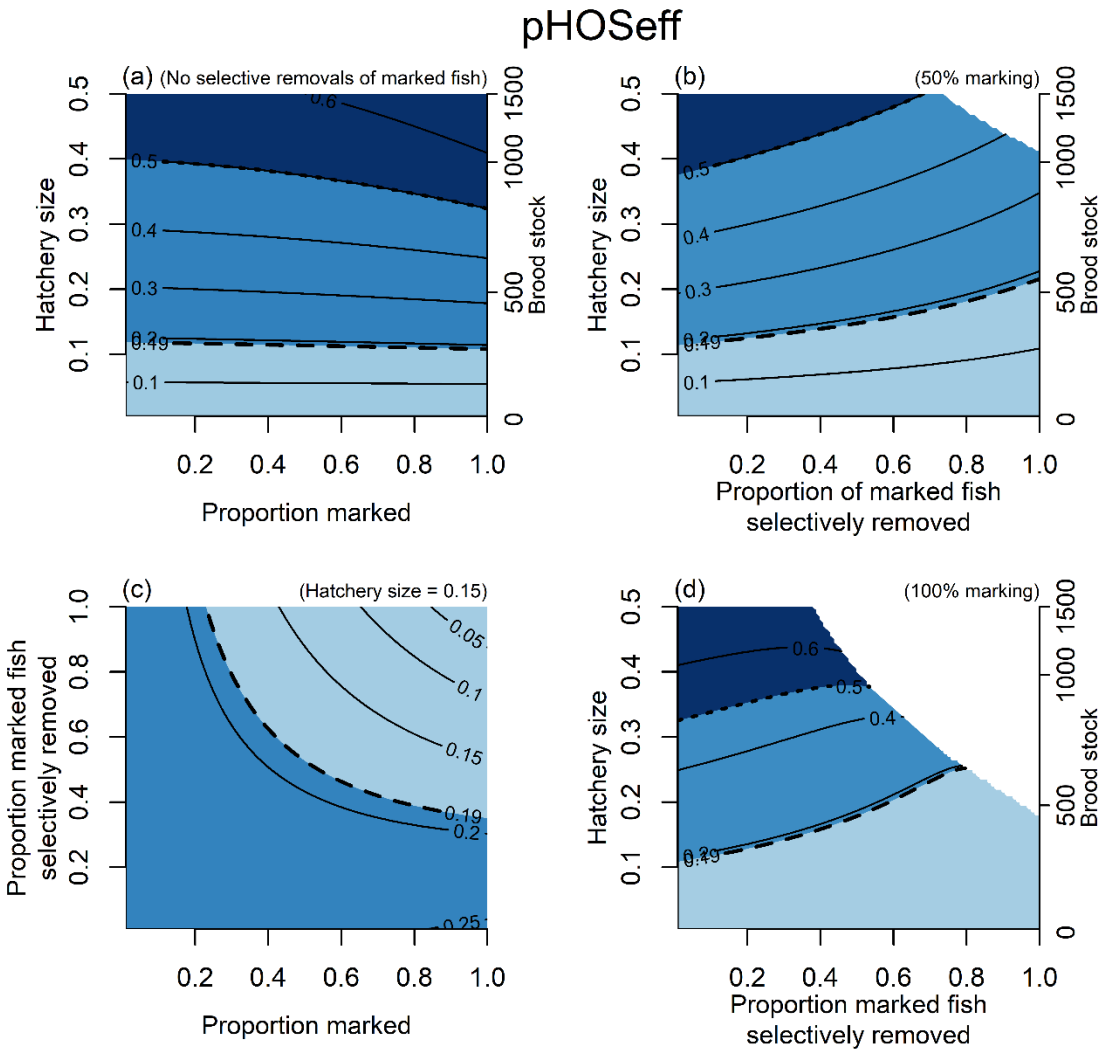

Figure 9.[15] Bivariate contour plots of the effective proportion of hatchery-origin spawners on the natural spawning grounds, $pHOS_{eff}$, along gradients in three management levers, as described in the caption for Fig.7. The shading aligns with the 3 categories of populations, “integrated-wild” (light blue), “integrated-transition” (medium blue), “integrated-hatchery” (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

From a management perspective, these results imply that the most effective way to meet objectives on genetic impacts is by scaling the size of the hatchery program to natural production. This ensures that abundance of hatchery-origin fish in the broodstock and on the natural spawning grounds is limited by natural capacity to sustain a population, according to different categories of populations. For the “integrated-wild” category, marking of hatchery-origin fish has only a marginal effect on achieving objectives, unless marking rates and selective

[17] Erratum: 25% corrected to 35-40% to reflect changes in model outputs.

removal of marked fish are both high. For the “integrated-transition” category, partial marking, potentially coupled with selective removal can play an important role in keeping within *PNI* guidelines. When hatchery-origin fish are more prevalent in the river, the ability to exclude them from brood stock through marking helps minimize impacts on *PNI*, allowing for larger hatchery sizes within *PNI* guidelines (Fig. 7a).

4.3. IMPACTS ON RECRUITMENT AND CATCH

Various combinations of hatchery program size, marking, and selective removal of marked fish have significant effects on natural production, defined as recruitment from river spawners (Fig. 10a). Natural production declines with increasing hatchery program size due to modelled genetic impacts on fitness (Fig. 10a) and the lowered reproductive success of hatchery fish in the wild. The component of the population spawning in the river becomes less-well adapted to the natural environment as the contribution of hatchery-origin fish to natural spawning grounds increases. Hatchery-origin spawners are assumed to be less successful at reproducing and their progeny are also assumed to be less fit, reducing recruitment. Complete marking of hatchery releases can prevent this decline in fitness with increasing hatchery production by allowing for the selection of unmarked natural-origin fish for broodstock (Fig. 10a, right side). Similarly, removal of marked hatchery-origin fish from the spawning grounds may reduce genetic impacts on natural-origin spawners, but these removals do not serve to increase recruitment to the river because of impacts on the number of spawners in the river (Figs. 10b,d). Maximum recruitment from river spawners is achieved with complete marking without removal of marked fish (Figs. 10a,c).

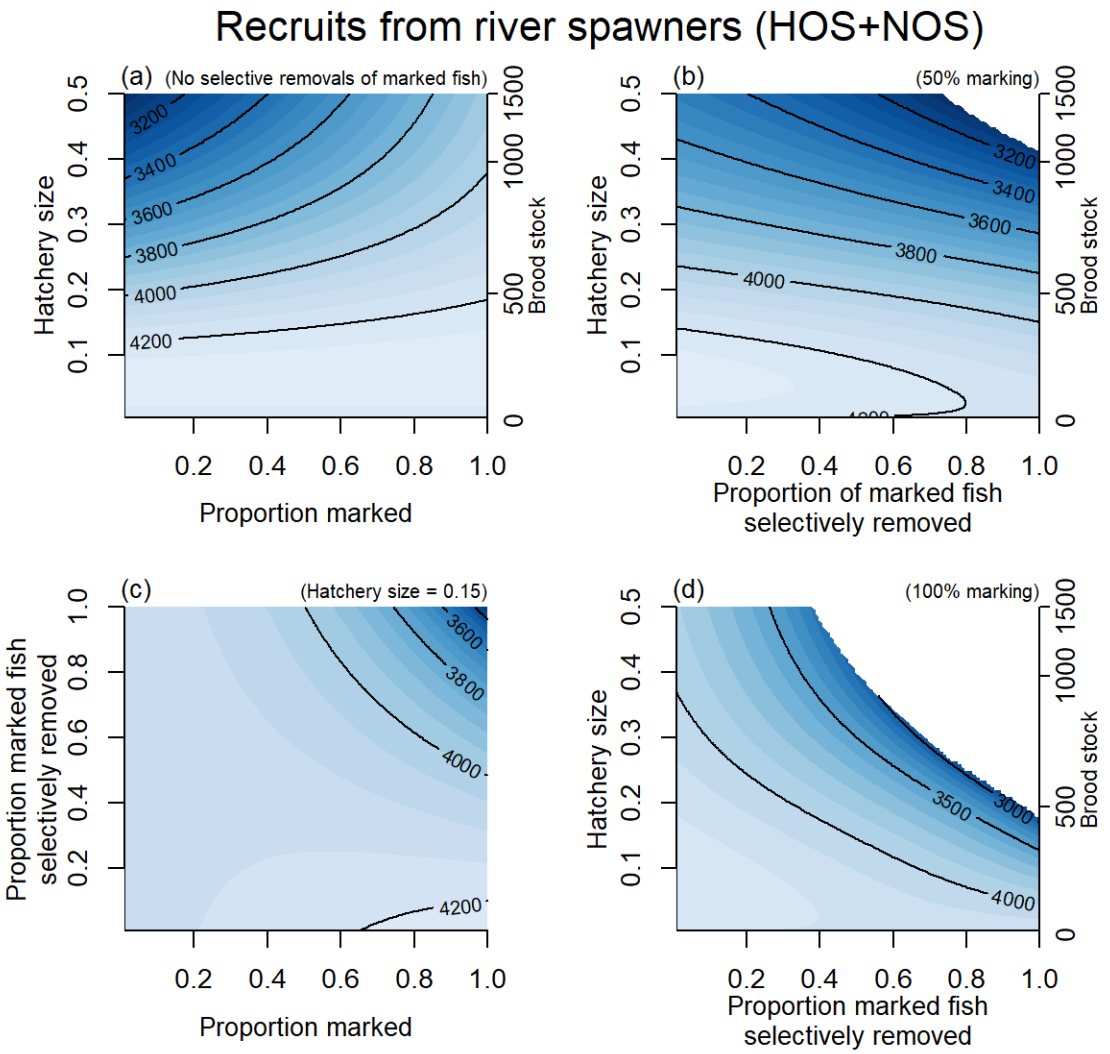

Figure 10.[15] Bivariate contour plots of the recruitment from river spawners (both hatchery-origin spawners, HOS, and natural-origin spawners, NOS) along gradients in three management levers, as described in the caption for Fig. 7. White areas occur where broodstock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

The production of adult recruits from hatcheries depends on hatchery program size only (Fig. 11), as our model assumed no changes in fitness in the hatchery environment (as in HSRG (2009). Under the base-case scenario of a 40% harvest rate, catch was maximized with large hatcheries, complete marking, and selective removal of marked fish, which were included in catch numbers (Fig. 12d). Selective removal of all marked fish was not possible for large hatchery programs in our model due to constraints on brood stock being less than 1/3 of annual returns to the river. Although genetic impacts of large hatcheries on population fitness can reduce recruitment from river spawners when some hatchery-origin fish are allowed to spawn naturally (Fig. 10d top, middle), these fitness impacts are small compared to the increases in hatchery production (Fig. 11d top, middle), resulting in relative large catches when hatchery programs are large (Fig. 12d top, middle).

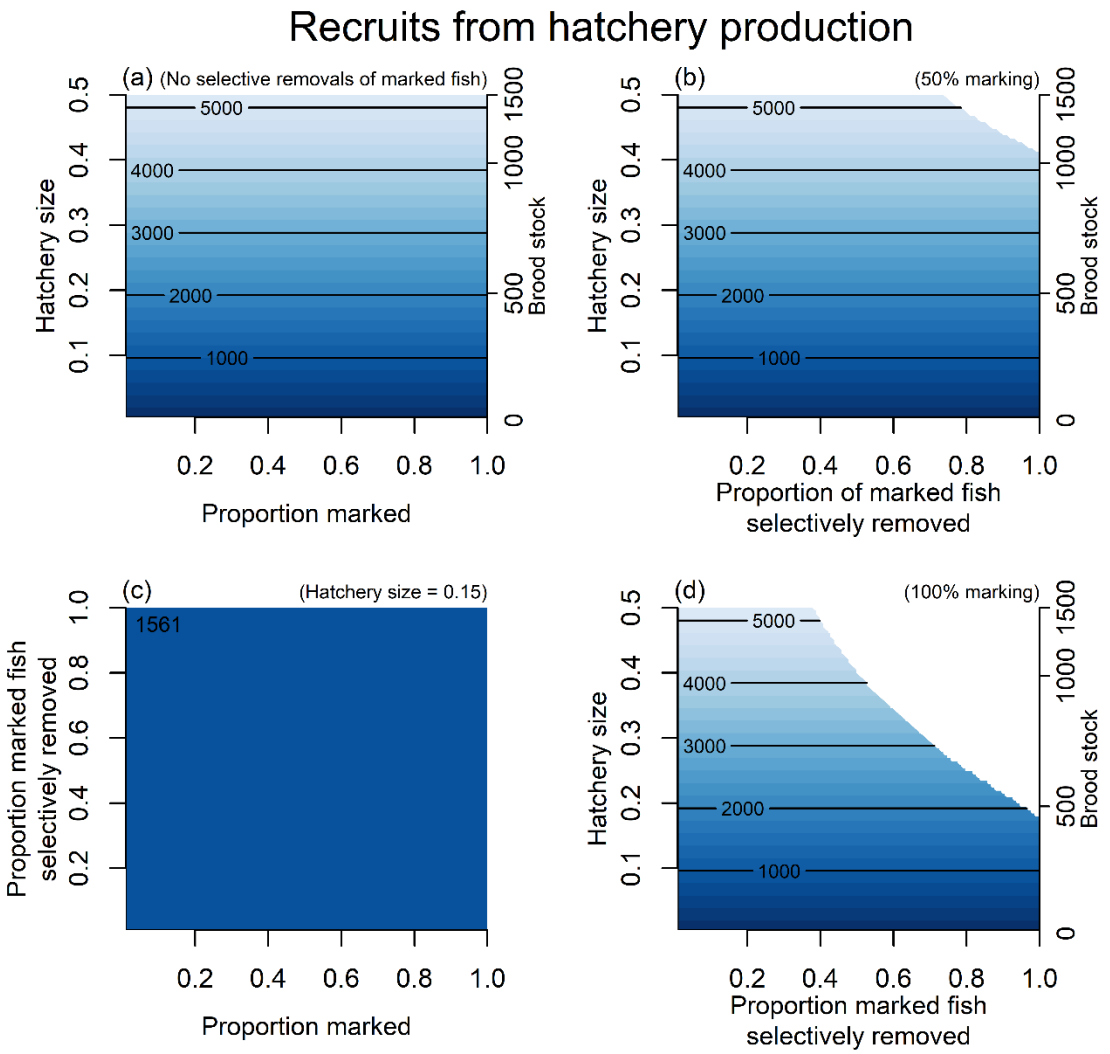

Figure 11.[15] Bivariate contour plots of the recruitment from hatchery production along gradients in three management levers, as described in the caption for Fig. 7. White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery program.

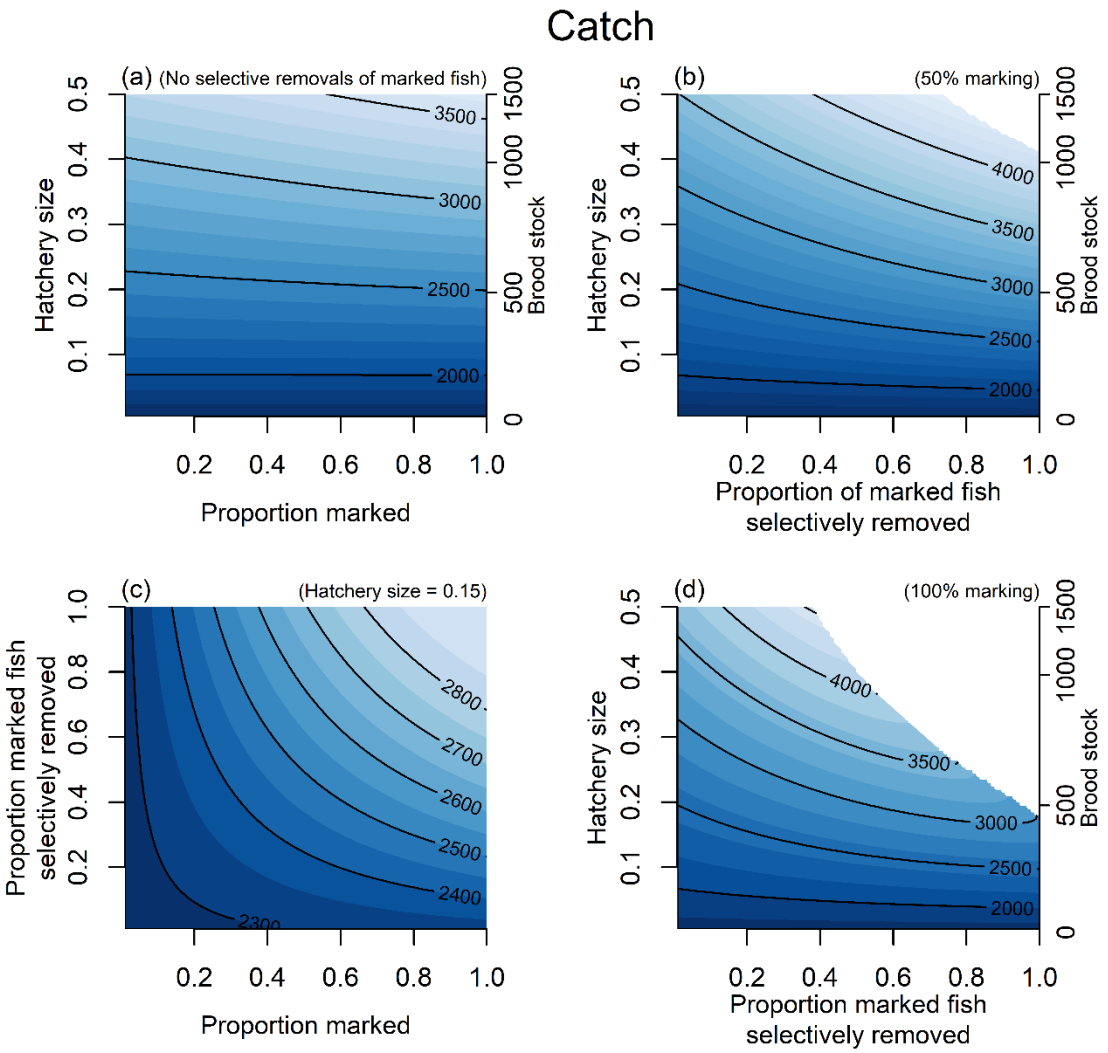

Figure 12.[15] Bivariate contour plots of total catch along gradients in three management levers, as described in the caption for Fig. 7. White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

4.4. SENSITIVITY ANALYSES

Our model of genetic impacts includes assumptions about hatchery and natural parameters which are uncertain: heritability of phenotypic traits, the relative reproductive success of hatchery vs natural-origin fish spawning in the natural environment, strength of selection, and survival rates. We found that varying the first two parameters related to fitness consequences within plausible ranges (Section 4.1.1., Appendix B, Table B1) had relatively minimal impacts on the ability to achieve *PNI* objectives with the management levers we examined (Figs. 13-14 for *PNI* results, Appendix B, Figs. B1-B10 for remaining performance metrics). The effect of hatchery program size on *PNI* was slightly larger under high heritability and weaker under[18] low relative reproductive success of hatchery-origin fish.

[18] Erratum: Added “and weaker under”.

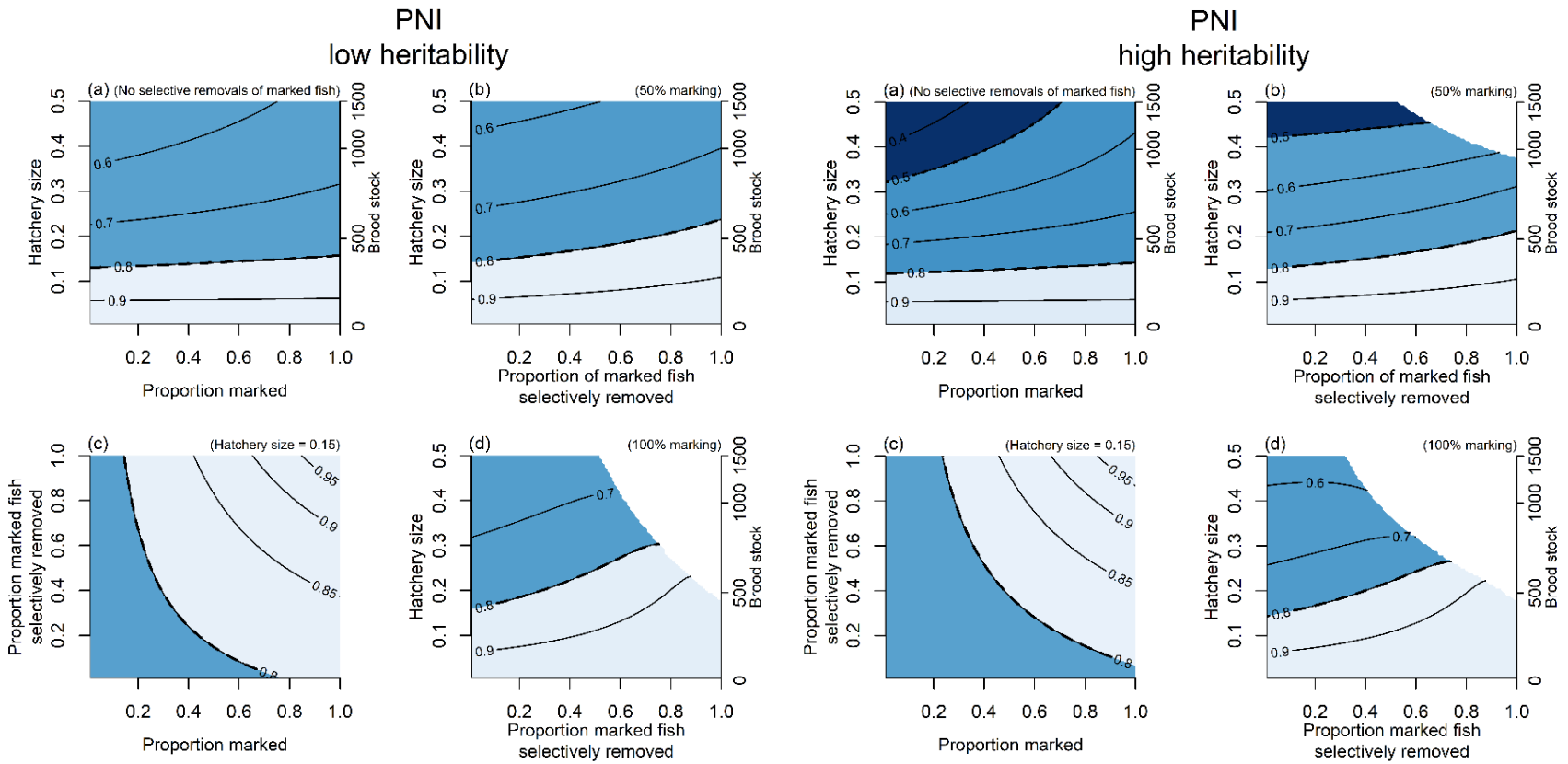

Figure 13.[15] Bivariate contour plots of PNI along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced heritability (h^2=0.05, a-d) and increased heritability (h^2=0.5, e-h) of phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

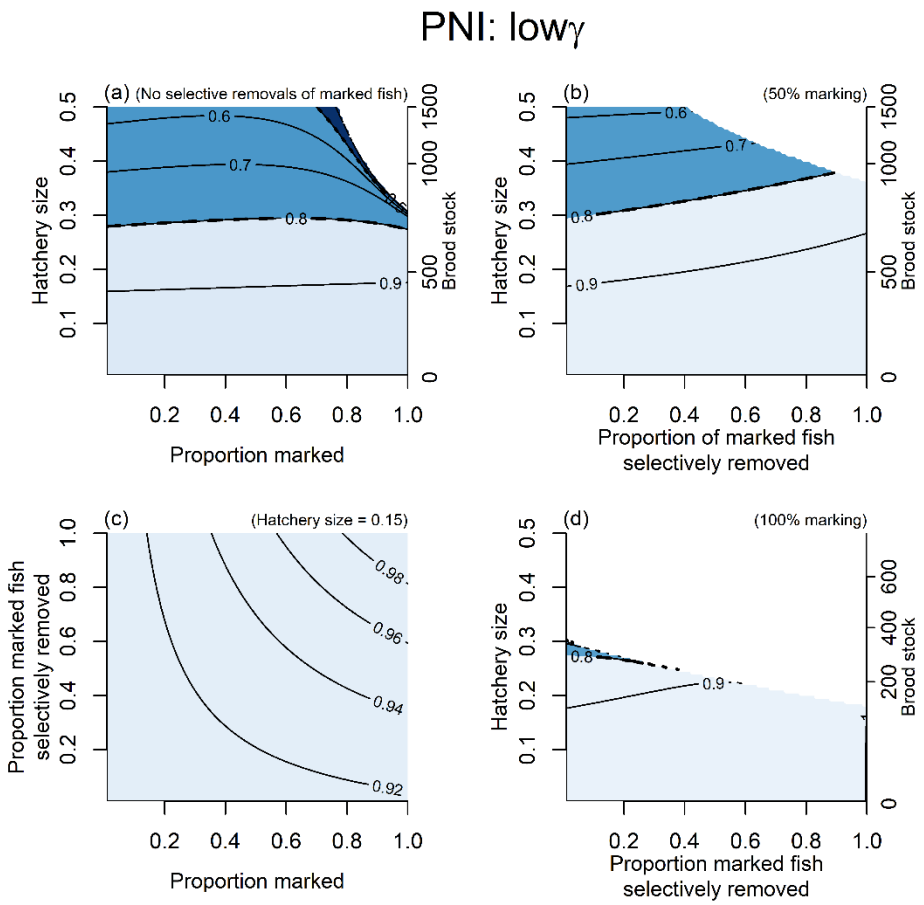

Figure 14.[15] Bivariate contour plots of PNI along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced proximal reproductive success (γ = 0.2, a-d) of hatchery-origin fish on natural spawning grounds. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

When we assumed the strength of selection for phenotypic traits was weak, the genetic impacts of the hatchery environment on population fitness were reduced to near zero, and natural production was little affected by the presence of hatchery spawners. With increased natural production, larger hatchery programs are possible within the "integrated-transition" zone[19] (Fig. 15a compared with Fig. 7a for *PNI* results, Appendix B, Figs. B 11-B 15 for remaining performance metrics). In contrast, strong selection limited size of hatchery programs because of the decrease in natural production resulting from the poor reproductive success of hatchery fish.

[19] Erratum: Original sentence read "With increased natural production, larger hatchery programs that contribute up to 35% of average returns to the river are possible within the "integrated-transition" zone (from about 20% in the base case)."

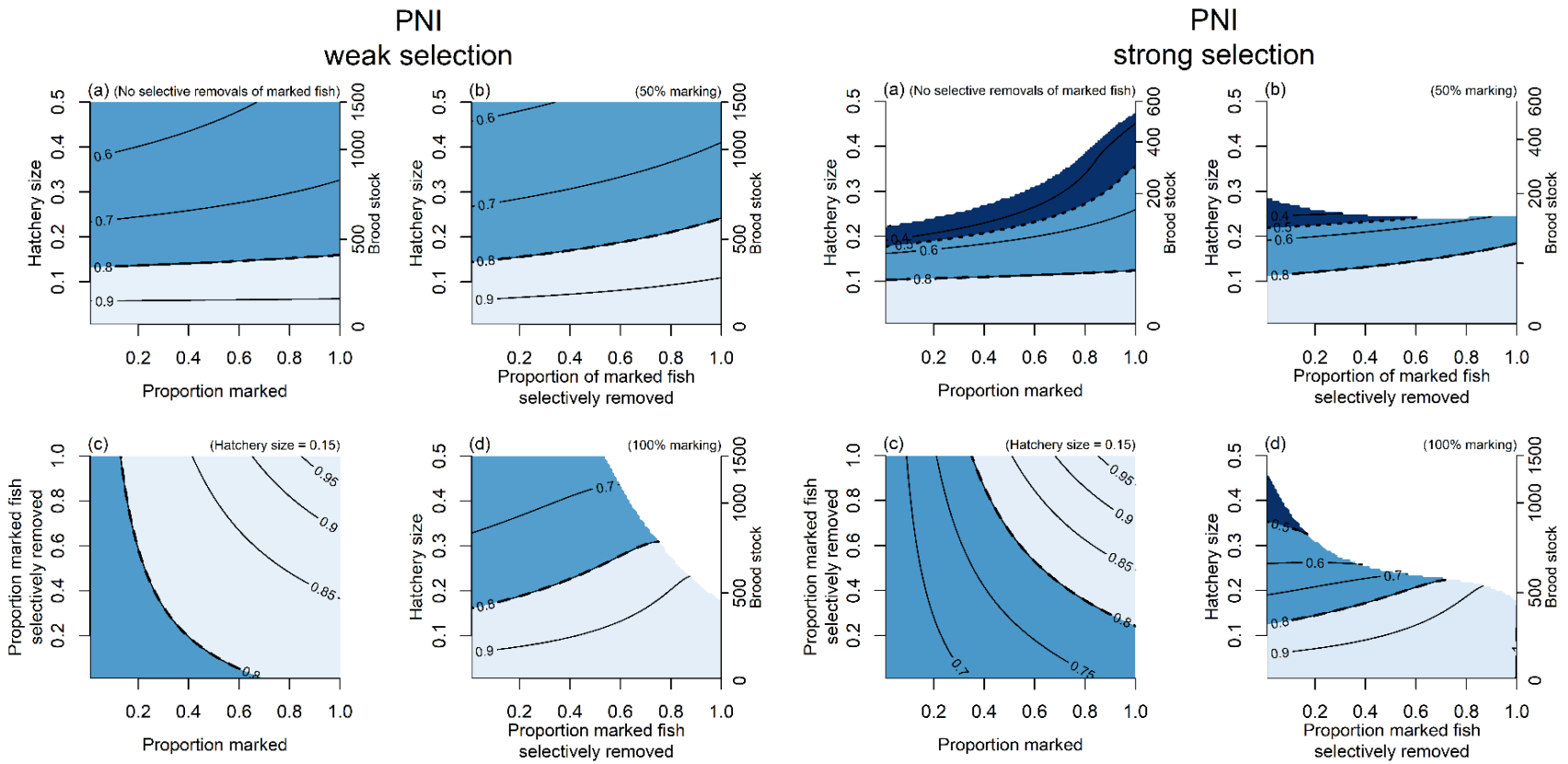

Figure 15.[15] Bivariate contour plots of PNI along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced strength of selection (ω^2=1000, a-d) and increased strength of selection (ω^2=40) for phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

Uncertainty in marine survival did not change our general conclusions about the importance of various management levers for achieving *PNI* objectives. Reducing marine survival of hatchery-origin fish from 0.0024 to 0.001 resulted in *PNI* objectives being met for relatively large hatchery programs[20] (Fig. 16a). Increasing marine survival of hatchery-origin fish to 0.005 resulted in a requirement for smaller hatchery releases to achieve *PNI* objectives (hatchery brood stock less than about 5% of average natural returns for "integrated-wild" category and less than 20%[21] for "integrated-transition" category). Reducing survival rate of natural-origin spawners by half reduced the allowable size of hatchery production within "integrated-wild" (Fig. 16g). Similarly, increasing survival of natural spawners from 0.02 to 0.05 resulted in an almost 50%[22] increase in maximum allowable hatchery program size to achieve *PNI* objectives for the "integrated-wild" category (Fig. 16j). See Appendix B, Figs. B 16-B 19 for sensitivity analyses on the remaining performance metrics (*pNOB*, $pHOS_{eff}$, returns to from river spawning, and returns from hatchery production). In these analyses, we assumed managers were not able to predict changes in marine survival, and scaled the size of the hatchery program to long-term average returns to river assuming moderate natural marine survival (0.02).

[20] Erratum: Text removed read "(up to about 20% of average natural returns for "integrated-wild" category and up to 40% for "integrated-transition" category, depending on brood composition)."

[21] Erratum: 10% corrected to 20% to reflect changes in model outputs.

[22] Erratum: ">50%" corrected to "an almost 50%" to reflect changes in model outputs.

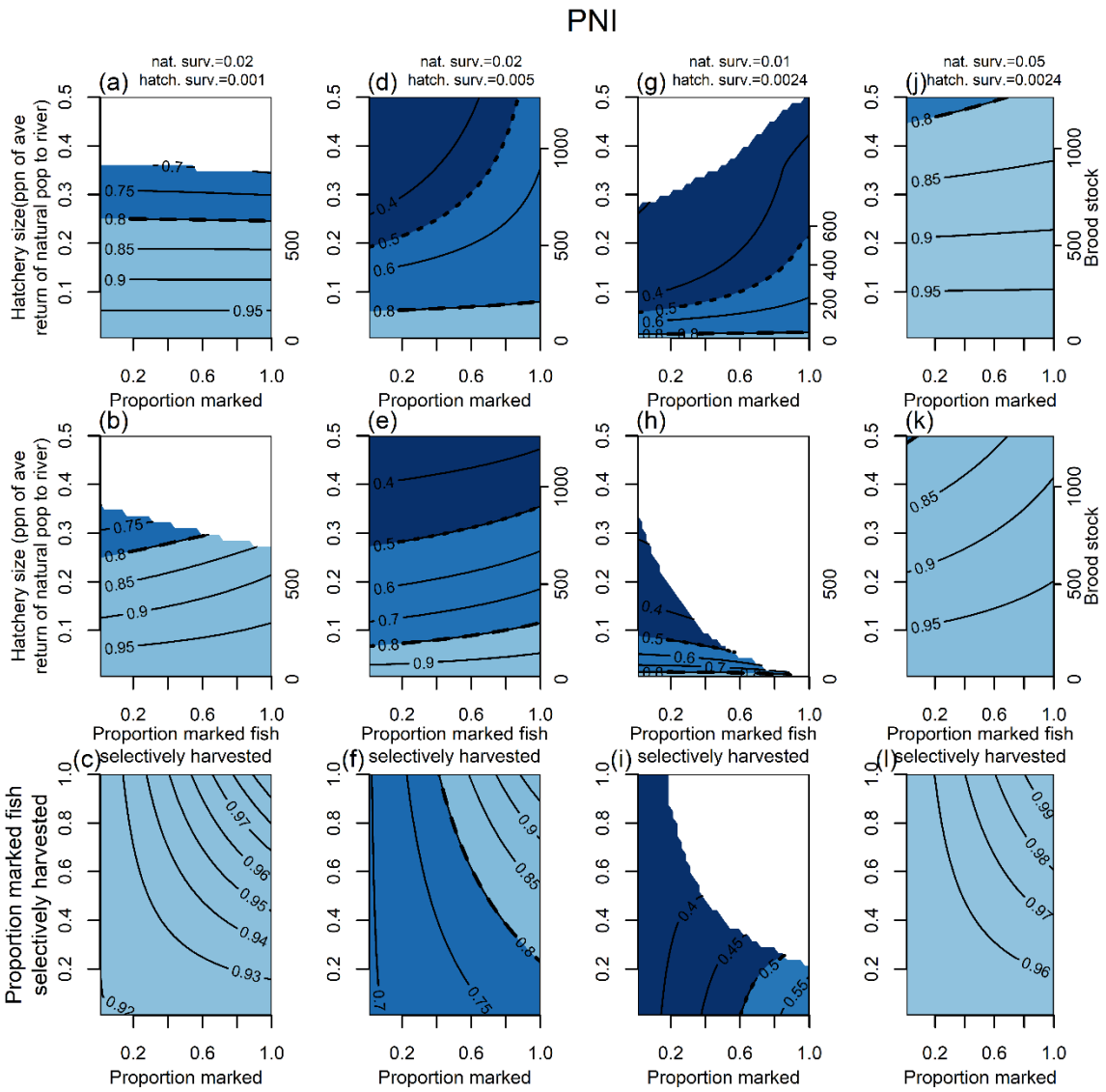

Figure 16.[15] Bivariate contour plots of PNI along gradients in three management levers, as described on axis labels under various assumptions about marine survival of natural-origin fish (nat.surv) and marine survival of hatchery-origin fish (hatch.surv). The first row depicts the effects of management levers: proportion marked and hatchery size, assuming no selective removal of marked fish. The second row (b,e,h,k) depicts effects of the proportion of marked fish selectively removed and hatchery size, assuming 50% marking. The third row (c,f,i,l) depicts the effects of proportion marked and proportion of marked fish selectively removed assuming hatchery size=0.15. Columns depict various assumptions about survival, labeled at the top. The shading is described in the caption to Fig. 7.

Impacts of variability in harvest rates and strength of density-dependence in the freshwater environment will scale to the survival rates, and were not investigated further here.

Overall, our results suggest scaling the size of the hatchery programs is required to achieve *PNI* objectives within the "integrated-wild" category, but for the "integrated-transition" category management of brood composition through marking of hatchery releases and possibly selective removal of marked fish from natural spawning grounds will become more important. These trends were robust to uncertainties in key parameters, though the absolute hatchery program

sizes, marking rates, and selective removals rates that define boundaries in genetic impacts among categories of populations ("integrated-wild", "integrated-transition", and "integrated-hatchery") will vary, especially with the strength of selection and marine survival rates.

This model describes long-term, equilibrium impacts on fitness of integrated hatchery system (Ford 2002). As such, it can provide strategic guidance on choice of the management levers to reduce genetic impacts on naturally spawning populations, but not short-term or tactical advice that requires information on time-trends or inter-generational variability in population fitness, genetic impacts, and/or *PNI*.

Stochasticity in population dynamics and fitness effects could be incorporated into the model to improve model realism in future iterations. Similarly, the component of the model pertaining to fitness effects could be extended from two-way interactions between hatchery-origin and naturally spawning fish, to three-way interactions, including for example that includes spawners originating from two different hatcheries and the natural environment.

5. OTHER CONSIDERATIONS

5.1. IMPLICATIONS FOR THE WILD SALMON POLICY

Under the WSP Chinook Salmon spawning sites (usually defined as rivers) are aggregated into CUs defined on the basis of common genetics, life history traits and other attributes. Within a CU one or more rivers may have a hatchery, and an associated integrated hatchery-natural origin population complex. As noted in section 1.3 "*Salmon are considered "wild" if they have spent their entire life cycle in the wild and originate from parents that were also produced by natural spawning and continuously lived in the wild. Salmon that originate directly from hatcheries and managed spawning channels are not considered wild in this policy, and are called "enhanced" salmon*" and "*The requirement in the definition that a wild salmon must complete more than one full generation in the wild safeguards against potential adverse effects resulting from artificial culture*."

This definition of wild is a precautionary approach for enhancement with respect to the first objective of the WSP "safeguard the genetic diversity of wild Pacific salmon" in that it recognizes that hatchery-origin spawners may present genetic risk to wild populations. Managing to higher *PNI* values has a similar goal but the indicators are developed using genetic theory in the context of hatchery-natural gene flow. *PNI* and the expected proportion of wild fish in a spawning population associated with an integrated hatchery program are related (Figure 17).

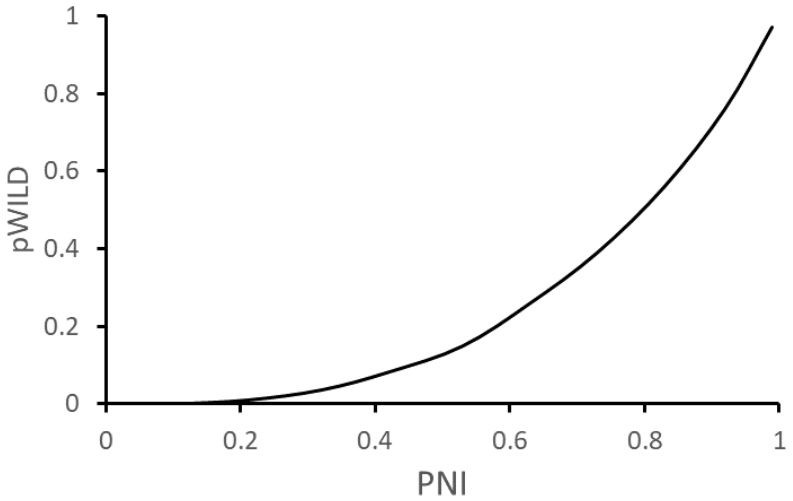

Figure 17.[23] Relation between PNI and the predicted proportion of wild spawners under the assumptions of no selection for broodstock composition, and random mating in the wild.

The biological status of a CU is assessed by considering the absolute and trend in abundance of spawners in the CU and, where there are multiple populations in the CU, the distribution of spawners among populations (DFO 2005). On the natural spawning grounds of populations with an integrated hatchery program there will be a mixture of hatchery-origin spawners, natural-origin spawners that are offspring of hatchery-origin spawners (transition spawners) and wild spawners that cannot be easily distinguished from transition spawners. There is no guidance in the WSP on the levels of hatchery production within a CU that are inconsistent with Objective 1, but a standardized approach to dealing with integrated hatchery programs within WSP assessments is recommended.

One approach to addressing hatchery production when evaluating the status of wild populations within CUs is to subdivide spawning populations into presumed wild, natural-origin, and hatchery-origin components and base WSP assessments on the wild or natural-origin component. However, the phenotypic and genotypic convergence of natural-origin (including wild) and hatchery-origin fish in an integrated hatchery program means there are not two distinct populations. Fish originating from both spawning locations become increasingly adapted to the more productive environment, a process that is indexed by *PNI*. Contemporaneous natural- and hatchery-origin fish within an integrated population do not differ greatly in fitness or genetic diversity. Thus all fish spawning in the natural environment contribute to the biological diversity and status of the population. However, when the *PNI* values are low and the population is dominated by gene flow from the hatchery to the natural environment the population will diverge from the original wild population in a manner inconsistent with the WSP Objective 1.

Whereas the biological categories for hatchery-influenced populations defined in Table 3 are characterized by the proportions of natural- and hatchery-origin fish they contain, it is the relative influence of the two environments on the equilibrium adaptive nature of all fish in the population that is reflected in the *PNI*. For assessment purposes, it is therefore most useful to assess the entire population based on the overall of level adaptation to the natural environment, rather than perform separate assessments for natural-origin or wild component versus the hatchery-origin component.

[23] Erratum: Figure revised to reflect corrected formula for pWILD.

Under this framework, populations that are clearly dominated by hatchery influences and have low *PNI* values would not be considered wild, and it is expected that they would not be included within a WSP status assessment. Conversely, populations with high *PNI* values may be considered wild because the hatchery is not anticipated to significantly alter the fitness and genetic integrity of the population. Table 4 provides proposed assessment guidelines for the integrated hatchery population categories defined in Table 3:

Table 4. Potential guidelines for the inclusion of integrated hatchery populations in WSP assessments based on their biological designation. The designations are described in Table 3.

Designation		***PNI***	**Inclusion in WSP assessment**	**Rationale**
A	Wild	n/a	Yes	No integrated hatchery; minimized risk from strays
B	Wild-stray influenced	n/a	Provisional	Most fish are wild, but long-term effects of one-way gene flow are expected to be risk factors
C	Integrated-wild	≥0.80[24]	Yes	Most fish are natural origin and >50% are wild; gene flow favours natural environment
D	Integrated-transition	≥0.5, <0.80[24]	Provisional	Gene flow favours natural environment but <50% of fish are wild. Hatchery program may be a risk factor to the wild population
E	Integrated-hatchery	<0.5	No	Hatchery selection dominates as most fish are hatchery origin; <15%[25] of spawners are wild.

There are two designations (B and D) in which a case-specific risk assessment, based in part on the *PNI* and related risk metrics but also on management options to increase *PNI*, will be needed to determine if these populations should be included in the CU during a WSP assessment. Populations in category B receive out-of-basin hatchery strays at a rate greater than those in category A and will be at greater risk of diverging from their wild adaptive state as straying (and immigration) rates increase. Further, the risk will increase if the donor population is a category E hatchery-dominated population relative to the risk from integrated-wild or integrated-transition populations with higher *PNI* values. Assessors should be aware that long-term *PNI* values decline rapidly at low rates of straying (*pHOS* < 0.1, Figure 2). Estimates of *pHOS* should be made available for WSP assessment of these populations.

The integrated-transition category is problematic as it is expected that wild fish will be in the minority yet most fish in the river will be of natural origin, with the resulting *PNI* values high enough to reflect a dominance of the natural environment as the primary adaptive influence. In the assessment process it may be appropriate to include such fish as part of the CU but recognize these populations may be at risk as a result of gene flow from hatchery-origin fish. The significance of the risk to the CU as a whole may depend on the importance of the population to the CU, trends in abundance, and potential trends in *PNI* that could occur as a result of changes in hatchery operations, the survival of hatchery releases or wild production.

5.2. INFORMATION NEEDS TO IMPLEMENT GENETIC RISK GUIDELINES

Managing integrated hatchery programs will require an integrated planning process that considers the status of the natural population and its habitats, impacts on biological diversity of the CU, and harvest goals. This ecosystem-based approach to hatchery planning was recognized as key to the HSRG process (Flagg 2015). The HSRG also recognized that precautionary management of genetic risk to wild salmon populations has associated information requirements. In an ecosystem management approach, information is required for

[24] Erratum: 0.72 corrected to 0.80 to reflect corrected method for calculating pWILD.

[25] Erratum: 25% corrected to 15% to reflect corrected method for calculating pWILD.

the comprehensive management of risks arising from synergistic hatchery, habitat and harvest pressures on wild populations.

Coordinated implementation of genetic risk guidelines for Pacific salmon in Canada requires that the biological significance of each population within a CU that is or may be impacted by enhancement be reflected in its assignment to the appropriate Table 3 biological category. In a large CU with many populations, the overall risk to the CU of an integrated-hatchery population managed primarily for harvest objectives may be deemed acceptable and one that can be managed with appropriate hatchery protocols and monitoring of surrounding wild populations. Conversely, in a CU with few populations, enhancement might be undertaken on populations managed to the more risk-averse biological goal of integrated-wild.

The geographic boundaries for each integrated population within the CU must be defined for the calculation of *pHOS*, and to identify distinct proximal populations not intended for enhancement. Those populations are most likely to be impacted by one-way gene flow from hatchery-influenced spawners. Defining the geographic scope of an enhanced population is relatively simple when there is a one-to-one correspondence between the integrated population and an entire watershed, but is more complex when an enhanced population is located in a large river network containing multiple populations among which increased migration of hatchery-origin fish might be expected.

Planning of new projects will require estimation of abundance for the average or expected natural-origin spawning population to be influenced by hatchery production. Natural-origin abundance can be estimated directly, or inferred from habitat characteristics such as watershed size (Liermann et al. 2010). Hatchery production can be estimated from the proposed brood collection, predicted survival rates in the hatchery and expected returns from releases. These estimates will then be used to adjust program size and develop hatchery, natural habitat and fishery management protocols to meet *PNI* goals.

For existing enhancement programs, marking of hatchery-produced juveniles provides a reliable means to estimate *pHOS* and *pNOB* from random samples of spawners in the river and broodstock. Partial marking of releases may be adequate if large enough samples of fish are recovered from natural spawning areas. For example, a population in the integrated-wild category has target *pHOS*<0.3. If 25% of hatchery releases are marked, then it is expected that <7.5% of river spawners will be marked; a fairly large sample of spawners will be required to produce a reliable estimate of the mark rate. Low rates of marking will also make estimation of straying to non-integrated populations more difficult. Higher marking rates may be required for other management measures such as mark-selective removals, broodstock management, or the estimation of fishery or population statistics.

The *PNI* guidelines provide “envelopes” for hatchery management and it is not intended that annual adjustments of releases and other measures will occur in relation to natural variation. However, *PNI* should be tracked over time as large-scale changes in productivity may require adjustments to production and release strategies. Persistent decreases in natural productivity will require reductions in hatchery releases, or management of *pHOS* and *pNOB* to maintain *PNI* goals. Monitoring of *PNI* will require coordination among all hatchery and salmon stock assessment activities to ensure appropriate information is being collected.

Tools have recently been developed through the HSRG process that can be adapted to any hatchery program, and that allow for evaluation of gene flow under multiple hatchery production scenarios, incorporating information on natural population abundance and productivity (HSRG 2017). These tools have the potential to be very useful if adapted for the Canadian enhancement program.

Additional information that may be useful in evaluating effects of the hatchery program on wild populations can be obtained from biological sampling. Measures such as size and age at return, run timing and spawning success (egg retention) can be monitored as part of standard stock assessment programs and can be useful indicators of changes in fitness that may be occurring.

5.3. CONSERVATION HATCHERY PROGRAMS

The genetic guidelines in Table 3 are for long-term steady state conditions based on biological goals for each integrated hatchery-river population complex. However, many conservation enhancement programs are initiated to assist in the recovery of populations that have declined to levels of concern. In these cases it is expected that the proportion of hatchery-origin spawners in both the hatchery and natural environments will exceed long-term targets during the early recovery phase when the primary focus is to increase abundance and minimize genetic drift, while temporarily relaxing the provisions to avoid domestication. HSRG (2015) define a recovery program in four phases, from prevention of extirpation to the long-term stable state (Table 5). Although this program was originally designed for a situation in which previously isolated habitats were being made available for recolonization, the sequence can be adapted to any recovery program.

Table 5. HSRG's four phases of a conservation-based hatchery program and the associated genetic risk guidelines (adapted from HSRG 2015).

Conservation phase	*PNI* target	Primary Objective	Comment
Preservation	None	Prevent extinction	Goal is to secure genetic diversity; population may not be self-sustaining under current conditions. Captive breeding may be used. *pHOS* > 0.5
Recolonization	None	Increase abundance	Restore habitats and maximize habitat utilization.
Local adaptation (or re-adaptation)	0.5 or 0.67*	Increase fitness and local adaptation	Habitats capable of supporting self-sustaining populations. Transition hatchery program to increase *PNI* to targets
Fully restored	0.5 or 0.67*	Maintain viable population	Hatchery provides additional harvest and safety net. Diversity and viability maintained

*Target depends whether population is designated as primary (0.67) or contributing (0.50).

HSRG (2014) also list conditions for success of conservation hatchery programs and the most relevant are paraphrased below:

- Develop clear, specific measureable goals for the integrated hatchery and natural population that have a sound scientific basis.
- Identify biologically-based triggers for initiating a conservation program, and moving among the phases of Table 5
- Include hatchery program as part of a larger program to address limitations to wild production or unsustainable exploitation.
- Implement a robust monitoring and evaluation program to evaluate progress in achieving goals, and to promote learning.

It is beyond the scope of this project to provide detailed guidelines for Canadian conservation enhancement programs. From the perspective of managing genetic risk, metrics, and guidelines, a similar approach to that of HSRG will be needed. The steps may include:

- Identifying the appropriate long-term biological designation for the recipient population and the associated genetic guidelines (Table 3).

- Establishing that the population meets triggering criteria for initiation of a conservation hatchery program as part of a larger recovery effort. This will include an assessment of current population status and an evaluation of factors that led to the poor status of the population so that the potential for recovery can be determined.
- During the early phases of a recovery action, natural-origin spawners will be in low abundance and a conservation hatchery program will have *PNI* values less than 0.5 and *pHOS*>0.3. Broodstock management and hatchery operational measures will be taken to minimize adverse genetic effects on the integrated population.
- Concurrent with the initiation of the hatchery program, measures to restore the productivity of the natural habitat and/or reduce the exploitation levels will be taken.
- As the population abundance increases, the hatchery program and associated recovery efforts will be adjusted to increase *PNI* and reduce *pHOS* to restore any loss of fitness due to domestication during the period of strong hatchery influence. This will be possible when the productivity of natural spawners increases as a result of habitat and harvest measures taken to reduce threats to population viability.

These steps should be integrated within a recovery planning process such as that envisioned by the WSP.

5.4. OTHER SPECIES AND TYPES OF ENHANCEMENT

The guidelines developed here are for Chinook Salmon hatcheries but have potential to be applied to other species or types of enhancement. The rationale for use of *PNI* is independent of species-specific details of the life history, and the nature of enhancement as it relies on standard genetic theory, and the assumption that the natural and artificial environments have different phenotypic optima that will influence fitness in populations over time. However, the rate and degree of domestication will vary among species and modes of enhancement.

It has been suggested that the strength of genetic and environmental effects of the hatchery environment depend on the length of time fish spends in artificial environments (Berejikian and Ford 2004). Thus species that are reared for a year or more (steelhead, Coho, stream-type Chinook Salmon) may be more affected than those that are released as fry (Pink, Chum, ocean-type Chinook Salmon). This may affect the difference in optimal phenotypes between hatchery and natural environments and the strength of selection caused by the hatchery environment. Unfortunately the available data are only suggestive of these differences as most studies have been conducted on populations with yearling or older smolts.

Pending further study and analysis, guidelines developed here for Chinook Salmon are considered highly appropriate for other yearling smolt/fed fry species (Coho, Sockeye Salmon) and can be used for Pink and Chum Salmon although they may be conservative with respect to the risks of the hatchery environment for the latter species. As previously mentioned, an important consideration for Pink and Chum Salmon will be meaningful biological and geographic population boundaries for the integrated hatchery-natural populations, given their increased propensity for migration among watersheds.

The WSP considers fish produced in spawning channels as enhanced, and therefore not wild (DFO 2005). Spawning channels have the potential to modify conditions for spawning, and may relax selection on the egg-fry stage as the result of increased survival. The effects of spawning channels on relative fitness are unknown, but are likely much less than for hatcheries. It is currently unclear whether *PNI* is a useful metric for spawning channels if the overall risk is small.

6. RECOMMENDATIONS

Wild Chinook Salmon exist in populations that are adapted to the natural environment on a localized geographic basis, and the genetic diversity underlying this variability within and among populations is the raw material for ongoing adaptation and persistence of the species. Hatchery-based Chinook Salmon enhancement programs can provide wild population conservation and harvest benefits but also pose risks of eroding the genetic diversity and fitness in wild populations. To manage genetic risks associated with DFO's Chinook Salmon hatcheries we recommend that the three principles articulated by HSRG be used to guide implementation of the approach outlined herein. We provide recommendations tailored to the Canadian context following each principle:

1. Develop clear biological goals for hatchery-influenced populations for use in the integrated planning process.

Recommendation 1. Define a wild population as one not affected by enhancement for two or more generations. These populations will have no hatchery releases or brood removals combined with a low immigration rate (<3%) of stray fish from hatchery-influenced populations over the two-generation interval.

Recommendation 2. Develop guidelines for the appropriate level and distribution of enhancement within a CU to be consistent with the WSP designation of a CU as an aggregation of wild salmon adapted to the natural environment and constituting an important element of intraspecific genetic diversity.

Recommendation 3. Within the integrated planning processes that develop guidance for enhancement, stock assessment, and fisheries management activities, establish biological goals for individual hatchery-influenced populations within CUs (Table 3) taking into consideration consequences of biological classification to the overall status of the CU.

Recommendation 4. In establishing goals for each population, document tradeoffs between increased genetic risk to wild populations from hatchery production and increased abundance required to support other objectives.

Recommendation 5. Develop guidelines for status assessments under the WSP for CUs that contain populations with hatchery contributions, including using *PNI* and *pHOS* values to evaluate potential degree of genetic impacts of hatcheries on hatchery-influenced populations.

2. Design and operate hatchery programs in a scientifically defensible manner.

Recommendation 6. Maintain the Canadian approach to Chinook Salmon hatchery production through the use of integrated hatchery programs based on local populations in which natural-origin fish are included in the hatchery broodstock.

Recommendation 7. Operate hatchery programs in accordance with natural population management practices, incorporating information on habitat quantity and quality, natural production, recruitment, straying and exploitation levels.

Recommendation 8. Evaluate options for hatchery operation to achieve the established biological goal for each population through the application of the proportionate natural influence (*PNI*) and associated metrics that are based on the numbers and proportions of hatchery- and natural-origin fish in the hatchery and natural spawning environments of an enhanced population.

Recommendation 9. Consider conservation-based hatchery programs for depleted populations within a broader recovery context, implementing staged reductions in hatchery influence as the population increases in abundance and limiting habitat and/or harvest pressures are eased.

Balance the risk of hatchery influence against the risk of diversity loss due to small population size.

3. Monitor, evaluate and adaptively manage hatchery programs.

Recommendation 10. Implement marking and monitoring measures to track *PNI* and other relevant parameters in the natural and hatchery environments; to capitalize on increased biological understanding, and adapt and respond to natural variation.

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APPENDIX A. GLOSSARY

Adaptation: Process of genetic change within a population due to natural selection, whereby the average state of a character becomes better suited to some feature of the environment.

Alleles: alternate versions of a given gene

Biodiversity: The variety of living organisms considered at a certain level of biological organization, such as the species, genus and higher taxonomic levels.

Conservation Units: Geographic regions representing ecological zones containing Pacific salmon populations characterized by specific life history types and genetic distinctiveness at neutral genetic loci. A CU contains a group of wild salmon sufficiently isolated from other groups that, if lost, is very unlikely to recolonize naturally within an acceptable timeframe (e.g., a human lifetime).

Effective Population Size: An ideal population that can equated to a real population. The ideal population has the same rate of genetic drift as the real population but factors as variation in the sex ratio of breeding individuals, the offspring number per individual, and numbers of breeding individuals in different generations are altered.

Assortative mating: Nonrandom mating systems in which like pairs with like.

Ecological Interactions: Ecological interactions between hatchery- and natural-origin fish include competition for feeding and spawning locations, predation of natural-origin fish by larger hatchery fish and the transfer of disease between hatchery- and natural-origin fish.

Enhancement: the use of hatchery-origin fish released to the wild to contribute fish for harvest and/or additional spawners in the natural environment (equivalent to Supplementation).

Epigenetic effect: a heritable chemical and/or structural alteration of DNA, often environmentally-induced, that is not reflected in the genotype (i.e. DNA sequence) of an individual.

Epistasis: The interaction of alleles at two or more loci in producing a phenotype.

Fitness: The relative number of offspring left by an individual after one generation.

Founder effects: Changes in the genetic composition of a new population due to its founding or origin from a small number of individuals from a larger source population.

Gene flow: movement of genes from one population to another, causing the populations to become more similar.

Genetic Diversity: genetic variability found in a population, or species, due to the genetic combinations of its individuals.

Genetic drift: Chance changes in allele frequencies that result from small population size, a force that reduces heterozygosity and polymorphism by the random loss of alleles.

Genetic integrity: A self-sustaining population, or assemblage of populations, that, if disturbed or impacted, maintains the ability to recover the adaptive state that is normal for that population.

Genotype: The set of DNA variants (alleles) found at one or more loci in an individual.

Habitat Restoration: Creation of new or restored fish habitat to allow spawning, rearing or passage.

Heritability: The proportion of observed variation in phenotype that can be attributed to differences in genotype.

Heterozygosity: The proportion of heterozygotes in a population.

Heterozygote: A diploid individual that carries two different alleles at a locus.

Homozygote: A diploid individual that carries two copies the same allele at a genetic locus.

Inbreeding: Mating between relatives.

Inbreeding Depression: Reduced vigour or fitness of inbred individuals.

Integrated Hatchery Program: Hatchery-origin and natural-origin fish are two components of a single population and spawn in both the hatchery and natural environments of the local watershed. The intent of an integrated program is for the natural environment to drive the adaptation of the combined hatchery-natural population.

Locus: A stretch of DNA at a particular place on a particular chromosome — often used for a 'gene.'

Mate Choice: Form of sexual selection in which one sex (usually females) determines whether mating occurs or not, often on the basis of phenotypic or behavioral characteristics of the opposite sex.

Mean Kinship: a measure of the relatedness of an animal with the entire current population (including itself). Individuals with low MK are considered important in conservation programs.

Migration: Movement of individuals to a new breeding location. A mechanism for gene flow.

Outbreeding: Mating with unrelated individuals, generally from an distinct population.

Mark Selective Fisheries: Harvest programs designed to target hatchery-origin adults to maximize catch of hatchery fish and reduce their abundance in natural spawning habitats. Hatchery-origin fish must be differentially marked.

Mutation: A spontaneous change in the genotype of an organism causing an altered DNA sequence and often resulting in a new allele.

Neutral Genetic Variation: Genetic variation (alleles or genotypes) that is apparently not subject to natural selection.

Natural production: recruitment from fish spawning in natural environment.

Natural Selection: The process by which differential reproductive success of individuals in a population results from differences in one or more hereditary characteristics.

Panmixia: Random breeding among individuals.

Pedigree: Multigenerational chart of parent–offspring relationships.

Pedigree Analysis: Use of pedigrees in captive propagation to avoid inbreeding and maximize genetic diversity.

Production Planning: The process by which hatchery production targets are set by managers, in consultation and collaboration with stakeholders, fishery managers, and scientists.

Proportionate Natural Influence (*PNI*): a metric that ranges between 0 and 1 to indicate the relative influences of the natural and hatchery environments on an salmon population. *PNI* values are approximated by *pNOB*/(*pNOB* + *pHOS*). Values <0.5 indicate that the hatchery environment is the primary environment influencing adaptation in the population whereas values >0.5 indicate that the natural environment is the primary environment influencing adaptation.

***pHOS*:** Mean proportion of natural spawners in a watershed or stream composed of hatchery-origin spawners. The census *pHOS* ($pHOS_{census}$) is the observed *pHOS* whereas the effective *pHOS* ($pHOS_{eff}$) is a discounted value accounting for the reduced reproductive success of hatchery-origin fish in the natural environment.

***pNOB*:** Mean proportion of a hatchery broodstock composed of natural-origin adults.

Phylogeographic: Geographic distribution of genetic lineages, useful in determining the origin and geographic dispersion of a species.

Polygamy: The practice of spawning with more than one mate.

Population: Group of interbreeding adults, typically confined to a geographic location that collectively interbreed and contain genetic material available for future adaptation.

Population structure: Any deviation from random breeding within a species, such as organization into populations among which gene flow is restricted.

Phenotype: the outward expression of a genotype.

Relative Reproductive Success: The reproductive success of hatchery-origin adults as relative to natural-origin adults measured as the contribution of individuals to the next generation of spawners. Factors that may influence the RRS include environmental modification due to the hatchery environment, domestication and epigenetic alteration of hatchery fish.

Segregated Hatchery Program: One which establishes a new hatchery-adapted population that is genetically distinct from all natural populations. Only hatchery-origin fish are used in the broodstock and the intent is to exclude hatchery fish from all natural spawning locations.

Sink Population: A population in a low-quality habitat in which the birth rate is generally lower than the death rate and population density is maintained by immigrants from source populations.

Source Population: A population in a high-quality habitat in which the birth rate greatly exceeds the death rate and the excess individuals leave as emigrants.

Stray: An adult salmon that returns to and remains in a non-natal breeding site.

Supplementation: the use of hatchery origin fish released to the wild to contribute fish for harvest and/or additional spawners in the natural environment.

APPENDIX B. TECHNICAL DOCUMENTATION ON MODELLING EFFECTS OF MANAGEMENT ACTIONS ON GENETIC RISK INDICATORS

Hatchery management decisions currently reflect hatchery-specific goals for production without explicitly considering genetic impacts on naturally spawning components of integrated hatchery salmon populations. Our goal was to evaluate the average, long-term effectiveness of management decisions on hatchery production, marking rates, and selective removal of marked fish in river for achieving biological objectives (Table 3). We further evaluated effects of those management decisions on recruitment from naturally and hatchery produced fish and catch. To do this, we adapted the population simulation model of HSRG (2009, Appendix C), previously used to compare the average, long-term effects of hatchery strategies on conservation and harvest goals for Upper Columbia River Chinook Salmon. Specifically, we adapted that model in four ways.

We focused on impacts of hatcheries on natural populations, and did not consider impacts of changes in habitat quality or harvest. In particular, we evaluated impacts of three decisions posed to hatchery managers: size of the hatchery relative to production of the natural population, marking rates of hatchery fish, and removal rates of marked fish from the river.

Two life-stages were included (instead of 5), which were adequate to capture the main hatchery effects on Chinook Salmon populations.

Harvest was aggregated into a single composite harvest rate, instead of segregated over multiple fisheries.

The hatchery production component of the model was simplified with assumptions of a 1:1 sex ratio and a single hatchery release group.

Our approach accounted for natural and hatchery production, survival in natural and hatchery environments, harvest, the composition of fish spawning in natural spawning grounds, relative reproductive success of natural and hatchery-origin fish on the spawning grounds, and genetic interactions between natural and hatchery-origin fish spawning in the natural environment. Genetic interactions were modelled based on Ford (2002)'s phenotypic fitness model of gene flow and selection in two environments, which was also used to develop the *PNI* metric. Our model simulated average, long-term effects over 100 generations, and is not meant to be interpreted on an annual or generational basis (Ford 2002; HSRG 2009).

MODEL DESCRIPTION

The model simulated production and survival of both hatchery-origin and natural-origin fish (Fig. 6 depicts a schematic for a single generation). A portion of natural-origin adult recruits was used as brood stock in the hatchery (blue dashed line, Fig. 6), and a portion of hatchery-origin fish returned to natural spawning grounds (red dashed line, Fig. 6). Reductions in fitness reduced survival for natural-origin fish in both freshwater and marine life stages.

Natural production

The abundance of smolts produced from natural-origin and hatchery-origin spawners in the natural environment (S_{NOS} and $S_{HOS,}$ respectively), Sm_{nat} in generation g, was simulated from a Beverton-Holt stock-recruitment relationship that accounted for density-dependent survival.

(Eqn. 1) $$Sm_{nat,g} = \frac{(S_{NOS,g}+S_{HOS,g}\cdot\gamma)\cdot p\cdot f_g}{1+(S_{NOS,g}+S_{HOS,g}\cdot\gamma)\cdot p/c},$$

where p is intrinsic freshwater productivity (i.e., smolts produced per spawner at low spawner abundances), c is the maximum number of smolts produced, γ is the proximal reduced

reproductive success of hatchery-origin spawners in nature[26], and *f* is the fitness of smolts derived from deviations in the equilibrium phenotype in the natural environment from the optimum (See Fitness sub-section below).

The number of adult recruits, Rec_{nat}, from fish spawning in the natural environment is,

(Eqn. 2) $Rec_{nat,g} = Sm_{nat,g} \cdot ms_{nat} \cdot f_g$,

where ms_{nat} is marine survival of fish spawning in the natural environment. The number of adults returning to the river (or natural spawning grounds) from fish spawning in the natural environment, after harvest, Ret_{nat} is,

(Eqn. 3) $Ret_{nat,g} = Rec_{nat,g} \cdot (1 - hr)$,

where *hr* is harvest rate. The number of natural-origin spawners in the natural environment in the subsequent generation, *g*+1, is the number of returns minus brood,

(Eqn. 4) $S_{NOS,g+1} = Ret_{nat,g} - B_{NO}$ ·,

where B_{NO} is the natural origin component of the brood take, B_T, .

(Eqn. 5) $B_{NO} = B_T \cdot \frac{Ret_{nat,g}}{Ret_{nat,g} + Ret_{hatch,g} \cdot (1-mr)}$

The brood take, B_T is from unmarked adults originating from both natural and hatchery environments when marking rates of hatchery-origin fish are <100%. *mr* is the marking rate of hatchery fish.

Broodstock and hatchery production

The number of hatchery smolts produced from the hatchery, $Sm_{hatch,g}$, is derived from the brood take, B_T, survival of brood take to spawning, *bs*, proportion of the brood stock that is female, *ppnF*,[27] fecundity of hatchery brood, *fec*, and survival from egg to smolt stage in the hatchery, *hs*.

(Eqn. 6) $Sm_{hatch,g} = B_T \cdot bs \cdot \ ppnF \cdot fec \cdot h$,[28]

The number of adult recruits from hatchery-origin fish prior to harvest, Rec_{hatch}, is,

(Eqn. 7) $Rec_{hatch,g} = Sm_{hatch,g} \cdot ms_{hatch}$,

and the number of adult returns to the natural spawning grounds from hatchery-origin fish after harvest, Ret_{hatch} , are the hatchery returns that escape the fishery,

(Eqn. 8) $Ret_{hatch,g} = Rec_{hatch,g} \cdot (1 - hr)$

Catch, *C*, includes both harvest from the fishery and the selective removal of marked fish in river,

(Eqn. 9) $C_g = \left(Rec_{hatch,g} + Rec_{nat,g}\right) \cdot hr + Rec_{hatch,g} \cdot (1 - hr) \cdot mr \cdot rr$.

[26] *γ* includes relative competition of hatchery fish compared with natural-origin spawners in freshwater environment, phenotypic and behavioural changes, and epigenetic effects that are not transmitted across generations.

[27] Erratum: Added text “proportion of the brood stock that is female, *ppnF*”.

[28] Erratum: Added $ppnF$ to equation to correct one of the errors in the original analysis.

The number of hatchery-origin spawners, S_{HOS} depends on the returns to hatchery and brood removals,

(Eqn. 10) $S_{HOS,g} = Ret_{hatch,g} \cdot (1 - mr \cdot rr) - B_{HO}$,

where B_{HO} is removals of unmarked hatchery-origin adults for brood take, and,

(Eqn. 11)$B_{HO} = B_T - B_{NO}$.

The proportion of spawners that are hatchery-origin in census, $pHOS_{(census)}$ is,

(Eqn. 12) $pHOS(census)_g = \frac{S_{HOS,g}}{S_{HOS,g}+S_{NOS,g}}$.

The proportion of effective hatchery spawners accounts for reduced reproductive success of hatchery origin spawners (HSRG 2014), and is calculated as:

(Eqn. 12b) $pHOS_{eff,g} = \frac{S_{HOS,g} \cdot \gamma}{S_{HOS,g} \cdot \gamma + S_{NOS,g}}$

The proportion of brood stock that is natural-origin, *pNOB*, is the ratio of unmarked returns that are natural origin to total number of unmarked returns.

(Eqn. 13) $pNOB_g = \frac{Ret_{nat,g}}{Ret_{nat,g}+Ret_{hatch,g} \cdot (1-mr)}$

The denominator includes both the natural returns and unmarked hatchery returns ($Ret_{hatch,g} \cdot (1 - mr)$). *PNI* is calculated as,

(Eqn. 14) $PNI_g = \frac{pNOB_g}{pHOS_{eff,g}+pNOB_g}$,

where $pNOB_g$>0.

Fitness

The fitness parameter in the stock-recruitment relationship, *f*, (Eqn. 1) ranges between 0-1, and is apportioned equally over two life stages (0.5 each for freshwater and marine stages),

(Eqn. 15) $f_g = F_g^{0.5}$.

Total fitness over both life stages, F_g, is derived from the mean phenotypic value in the natural population in generation, $\bar{P}_{Nat,g}$, the optimum phenotypic value in the natural environment, θ_{Nat}, the variance of the phenotypic trait, σ^2, and the variance in the probability distribution of fitness as a function of phenotypic values for individuals, ω^2,

(Eqn. 16) $F_g = \exp\left(-\frac{1}{2}\left(\frac{\left(\bar{P}_{Nat,g-\theta_{Nat}}\right)^2}{\omega^2+\sigma^2}\right)\right)$.

The mean phenotypic value varies over generations as selection drives phenotypes to equilibrium between natural and hatchery optimums, $\theta_{Nat}$and θ_{Hatch}, respectively.

(Eqn. 17) $\bar{P}_{Nat,g} =$

$\left(1 - pHOS_{eff,g-1}\right) \cdot \left[\bar{P}_{Nat,g-1} + \left(\left(\bar{P}_{Nat,g-1} \cdot \omega^2 + \theta_{Nat} \cdot \sigma^2\right)/(\omega^2 + \sigma^2) - \bar{P}_{Nat,g-1}\right) \cdot h^2\right]$

$+pHOS_{eff,g-1} \cdot \left[\bar{P}_{Hatch,g-1} + \left(\left(\bar{P}_{Hatch,g-1} \cdot \omega^2 + \theta_{Hatch} \cdot \sigma^2\right)/(\omega^2 + \sigma^2) - \bar{P}_{Hatch,g-1}\right) \cdot h^2\right]$,

where h^2 is the heritability of the trait (proportion of phenotypic variance resulting from heritable genetic variance), and $\bar{P}_{Hatch,g}$, is the mean phenotypic value in the hatchery population. $\bar{P}_{Hatch,g}$ is derived from,

(Eqn. 18) $\bar{P}_{Hatch,g} = \left(1 - pNOB_{g-1}\right)$

$$\cdot \left[\bar{P}_{Hatch,g-1} + \left(\left(\left(\bar{P}_{Hatch,g-1} \cdot \omega^2 + \theta_{Hatch} \cdot \sigma^2\right)/(\omega^2 + \sigma^2)\right) - \bar{P}_{Hatch,g-1}\right) \cdot h^2\right]$$

$$+pNOB_{g-1} \cdot \left[\bar{P}_{Nat,g-1} + \left(\left(\left(\bar{P}_{Nat,g-1} \cdot \omega^2 + \theta_{Nat} \cdot \sigma^2\right)/(\omega^2 + \sigma^2)\right) - \bar{P}_{Nat,g-1}\right) \cdot h^2\right].$$

Management decisions

We evaluated impacts of three parameters as decisions posed to hatchery managers: brood take, B_T, marking rates, *mr*, and removal rate of marked fish from river, *rr*. Brood take, B_T, was selected by the hatchery and comprised both hatchery-origin and natural-origin fish (Eqns. 5 and 11). We have assumed that only unmarked fish are selected for brood stock, with a constraint on handling < 3× the target brood stock when marking rates and hatchery production are high. If more than 3× target brood stock are handled before sufficient numbers of unmarked fish are recovered, then marked fish are used for the remaining brood take. An alternative assumption that both marked and unmarked (hatchery and natural origin) fish are taken for brood stock in the proportion at which they occur on the spawning grounds was considered under the scenario of 0% marking (see below). Brood take was scaled to a proportion of the long-term average returns to river for the natural population accounting for existing harvest, in the absence of a hatchery, but is constrained to ≤33% of observed annual returns to river. In sensitivity analyses, we varied brood take from 0-50% of average returns of the natural component of the population, and marking rates and removal rates of marked fish from 0-100%. We evaluated impacts of these management decisions on *PNI*, $pHOS_{eff}$, *pNOB*, recruitment from river spawning, Rec_{nat}, recruitment from the hatchery, Rec_{hatch}, and catch, *C*, in the final generation of the 100 generation simulation.

The model was developed and implemented using the software R, v.3.2.2.

Initial conditions and assumptions

Phenotypes were initialized at optimum values for natural population, and spawner abundances in the natural environment were initialized at equilibrium levels.

A single age-at-maturity is assumed. Reductions in fitness associated with changes in age-at-maturity of hatchery-origin fish can be considered by varying the reproductive success of hatchery-origin spawners in nature, *γ*.

Ecological interactions between hatchery and natural-origin spawners in natural environment resulting from competition are included in the *γ* parameter.

Genetic impacts of selection reflected in equilibrium conditions are derived in Ford (2002)

Genetic impacts depend on the composition of brood stock, composition of the naturally spawning population, ability of hatchery-origin fish to spawn successfully, survival of their progeny in nature, and strength of selection.

The model reflects long-term, average conditions, which are deterministic.

The hatchery program is assumed to be integrated since all hatchery-origin fish return to natural spawning grounds. However, the management option to selectively remove marked fish in the

river represents a scenario analogous to a segregated hatchery system if marking rates are high.

See Table B1 for parameter values.

Sensitivity analyses

Sensitivity of performance metrics to fitness parameters and marine survival of natural-origin spawners and hatchery-origin spawners were evaluated (Table B 1). Performance metrics, $pHOS_{eff}$, *pNOB*, recruitment from natural production, recruitment from hatchery production, and catch, were relatively insensitive to increase in heritability (Figs. B 1-B 5), the strength of selection (Figs. B6-B10), and reductions in the relative reproductive success of hatchery-origin spawners compared with natural-origin spawners (Figs. B 11-B 15).

The sensitivity of variability in marine survival rates on the performance metrics, $pHOS_{eff}$, *pNOB*, recruitment from natural production, and recruitment from hatchery production are shown in Figures B 16-B 19, and are consistent with results on *PNI* sensitivity described in Section 4.4.

Appendix B Figures

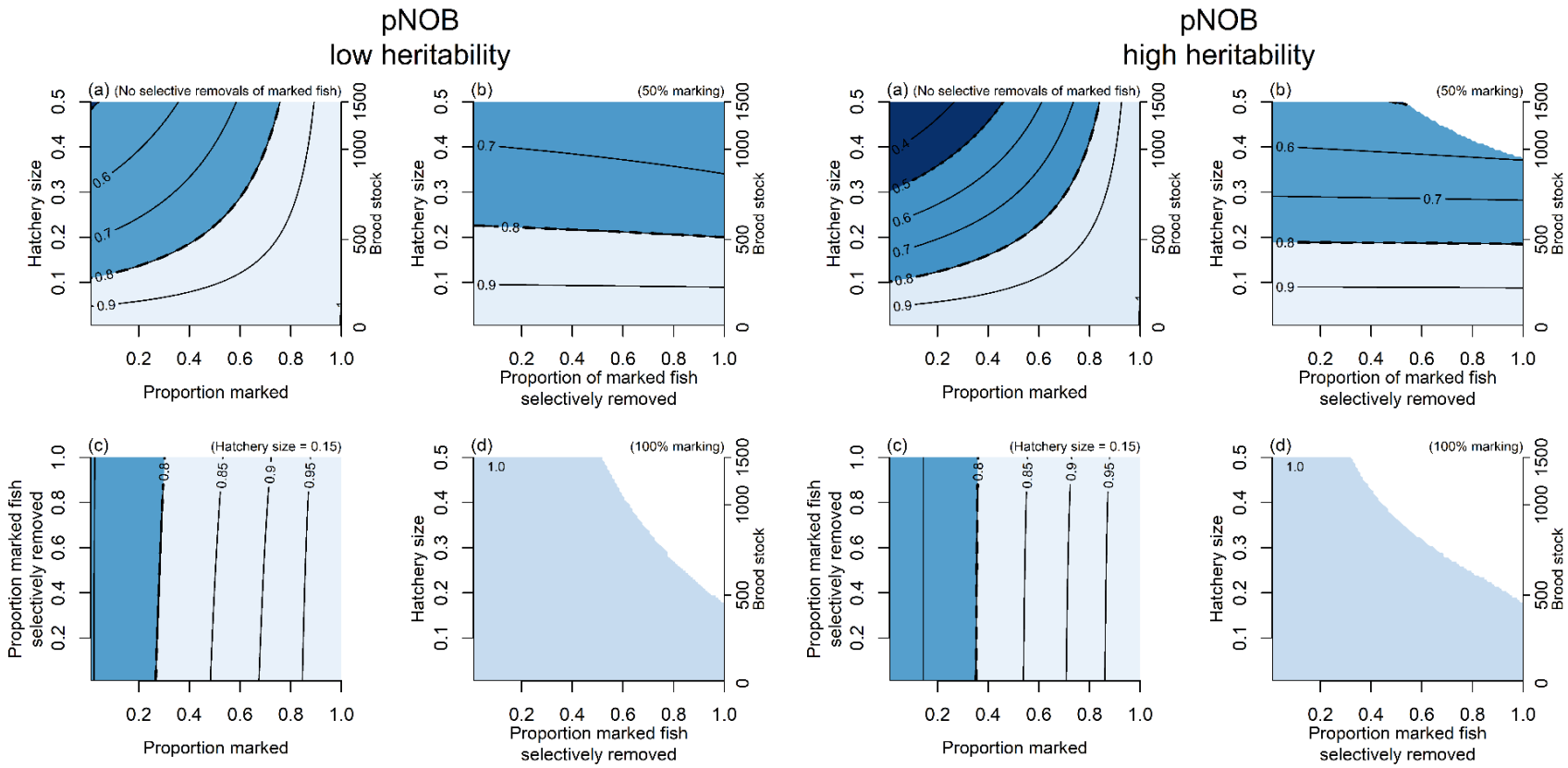

Figure B 1.[15] Bivariate contour plots of the proportion of natural-origin fish in the hatchery brood stock, pNOB, along gradients in three management levers, as described in the caption for Fig. 7 assuming low heritability (h^2=0.05, a-d) or high heritability (h^2=0.5, e-f) of phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

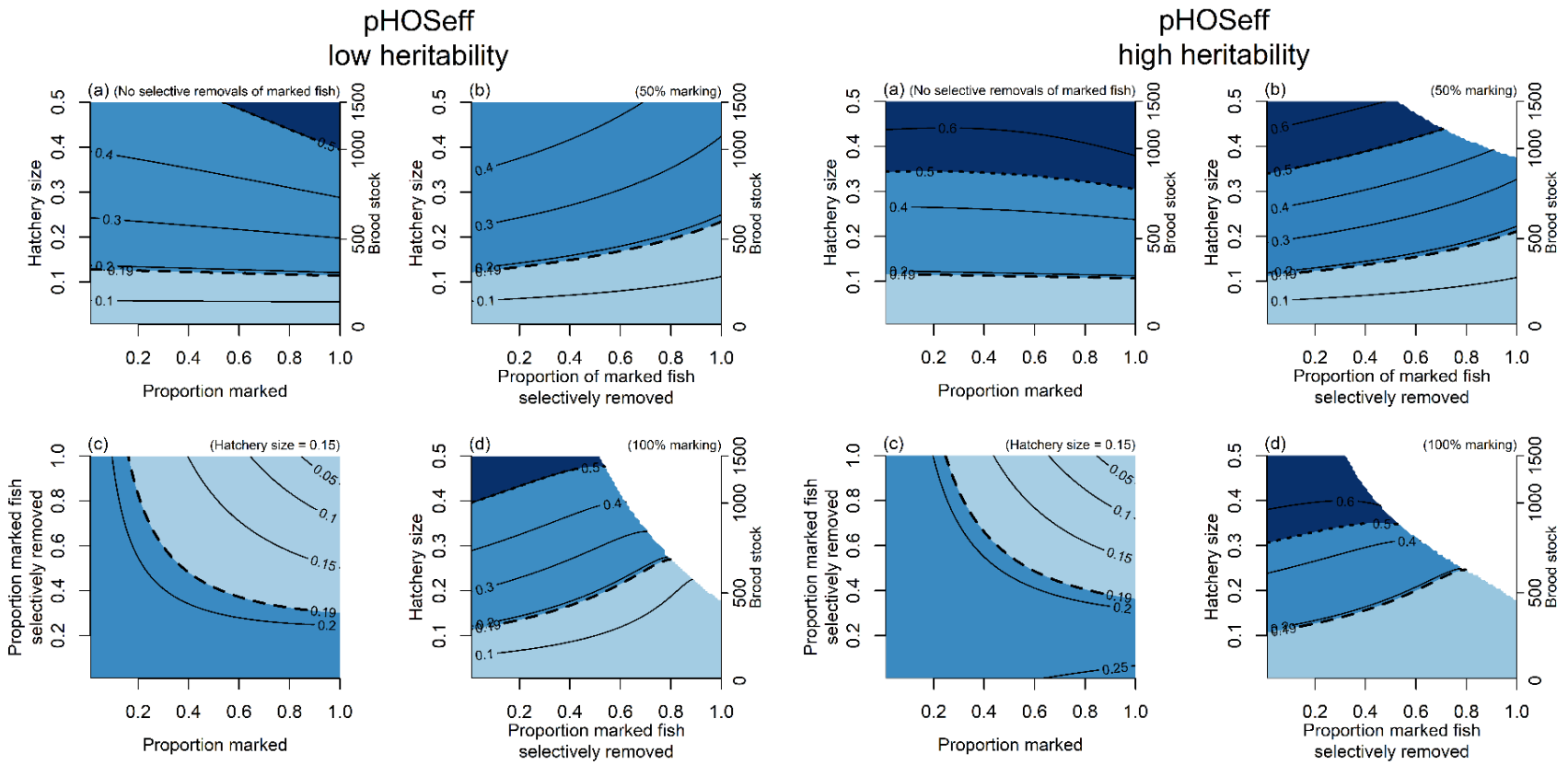

Figure B 2.[15] Bivariate contour plots of the effective proportion of hatchery-origin spawners on the natural spawning grounds, $pHOS_{eff}$, along gradients in three management levers, as described in the caption for Fig. 7 assuming low heritability (h^2=0.05, a-d) or high heritability (h^2=0.5, e-f) of phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

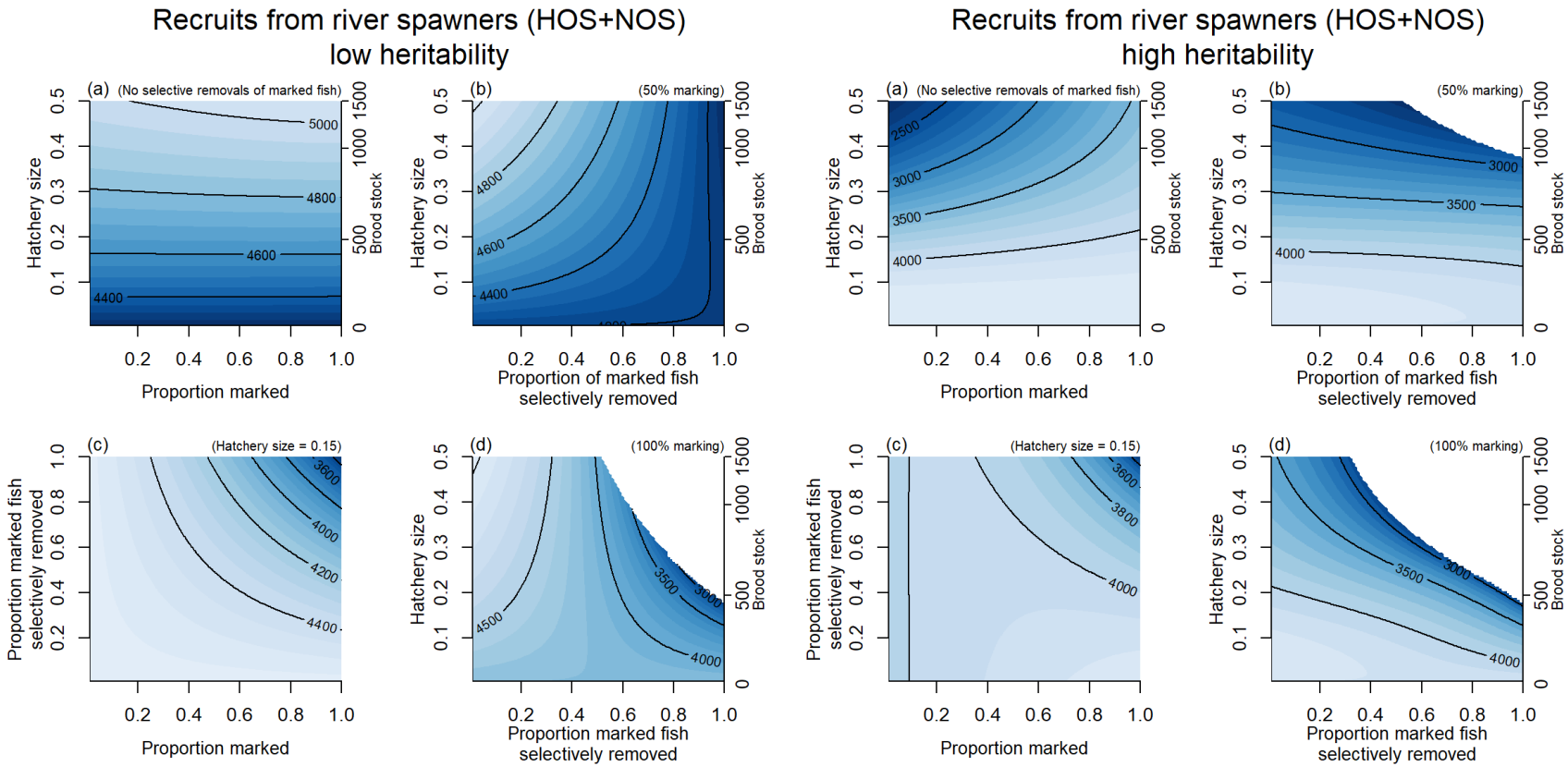

Figure B 3.[15] Bivariate contour plots of the recruitment from river spawners (both hatchery-origin spawners, HOS, and natural-origin spawners, NOS) along gradients in three management levers, as described in the caption for Fig. 7 assuming low heritability (h^2=0.05, a-d) or high heritability (h^2=0.5, e-f) of phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

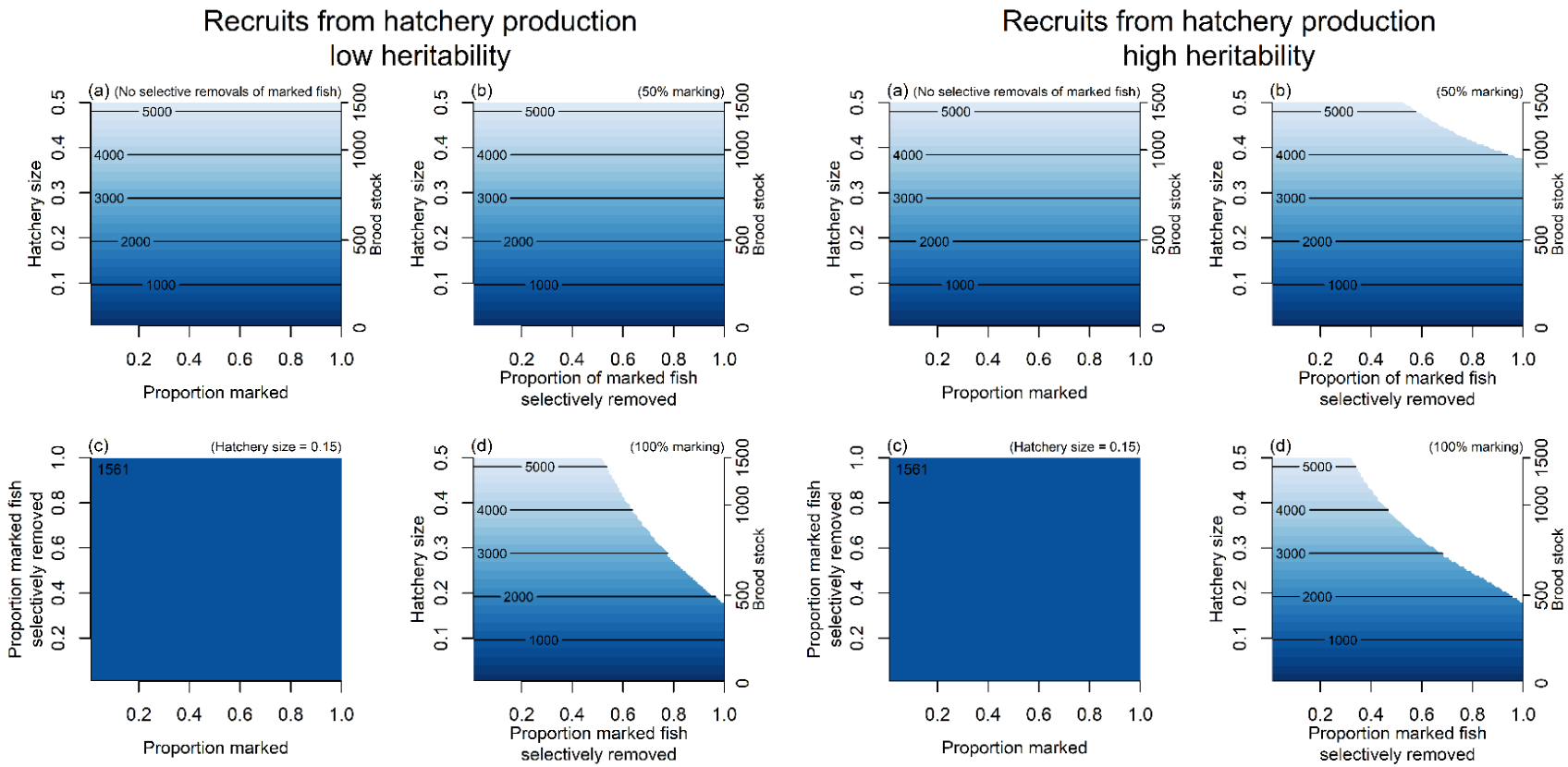

Figure B 4.[15] Bivariate contour plots of the recruitment from hatchery production along gradients in three management levers, as described in the caption for Fig. 7 assuming low heritability (h^2=0.05, a-d) or high heritability (h^2=0.5, e-f) of phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

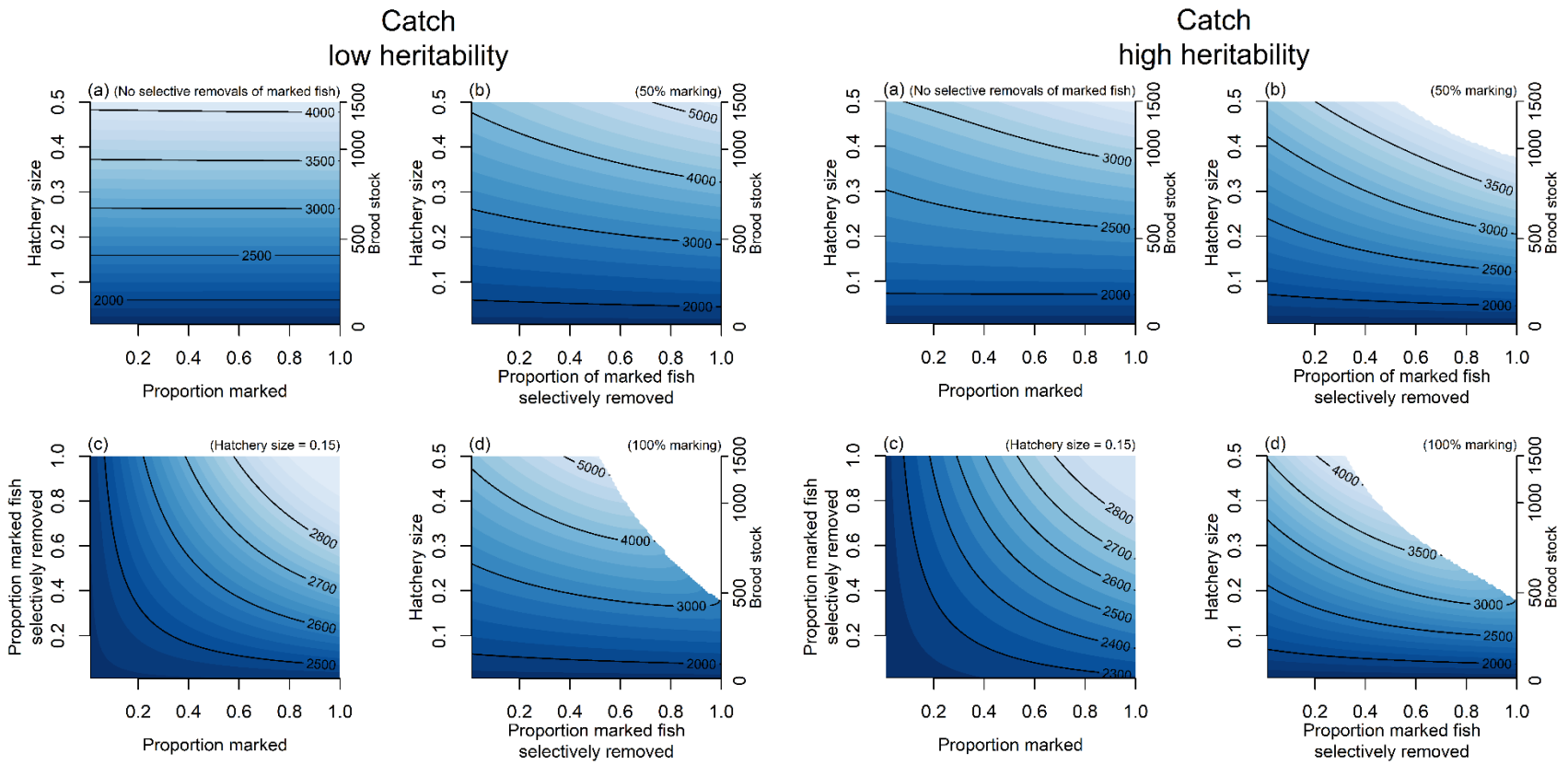

Figure B 5.[15] Bivariate contour plots of total catch along gradients in three management levers, as described in the caption for Fig. 7 assuming low heritability (h^2=0.05, a-d) or high heritability (h^2=0.5, e-f) of phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

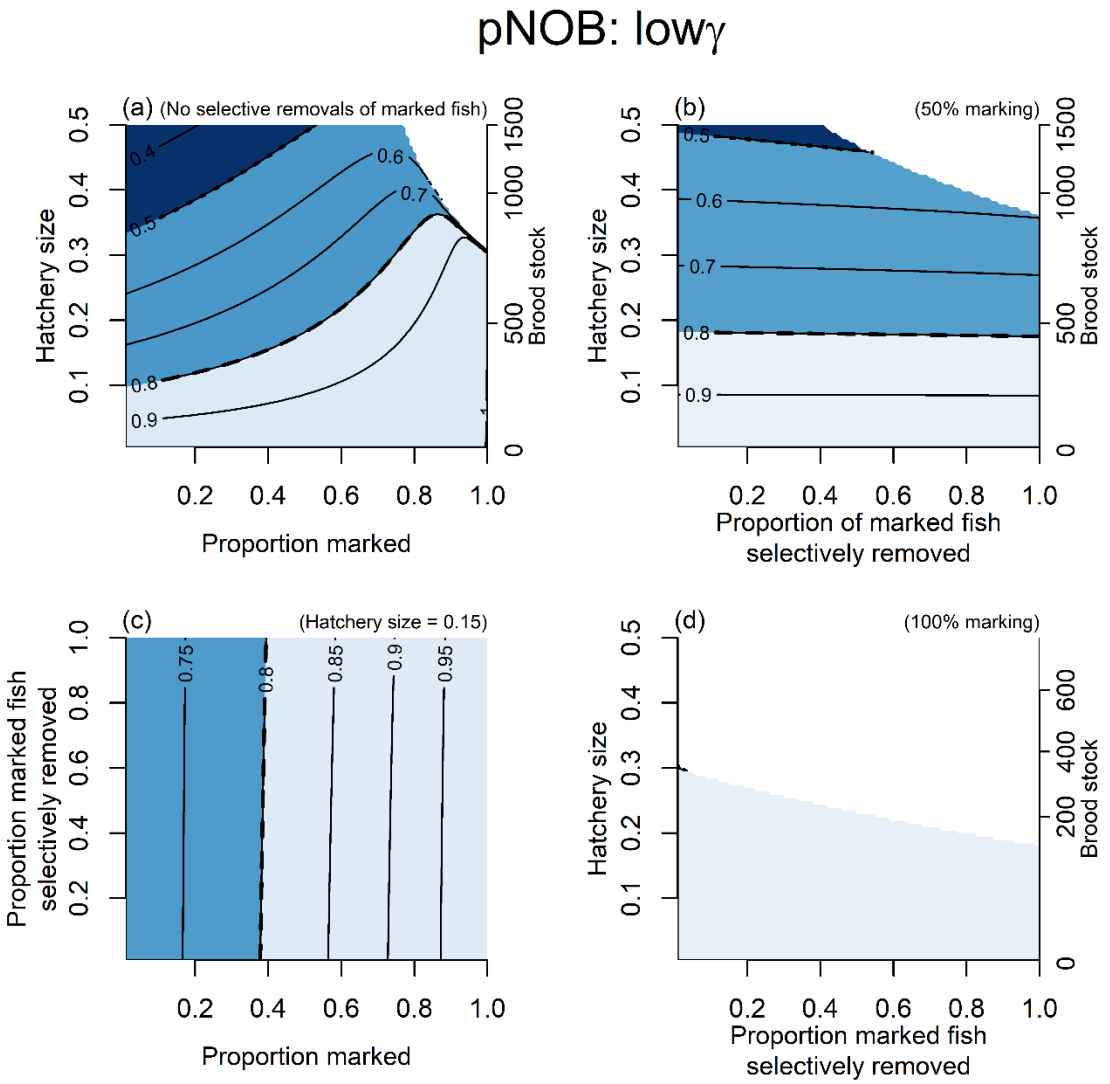

Figure B 6.[15] Bivariate contour plots of the proportion of natural-origin fish in the hatchery brood stock, pNOB, along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced proximal reproductive success of hatchery-origin spawners relative to the base case (γ = 0.2). The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

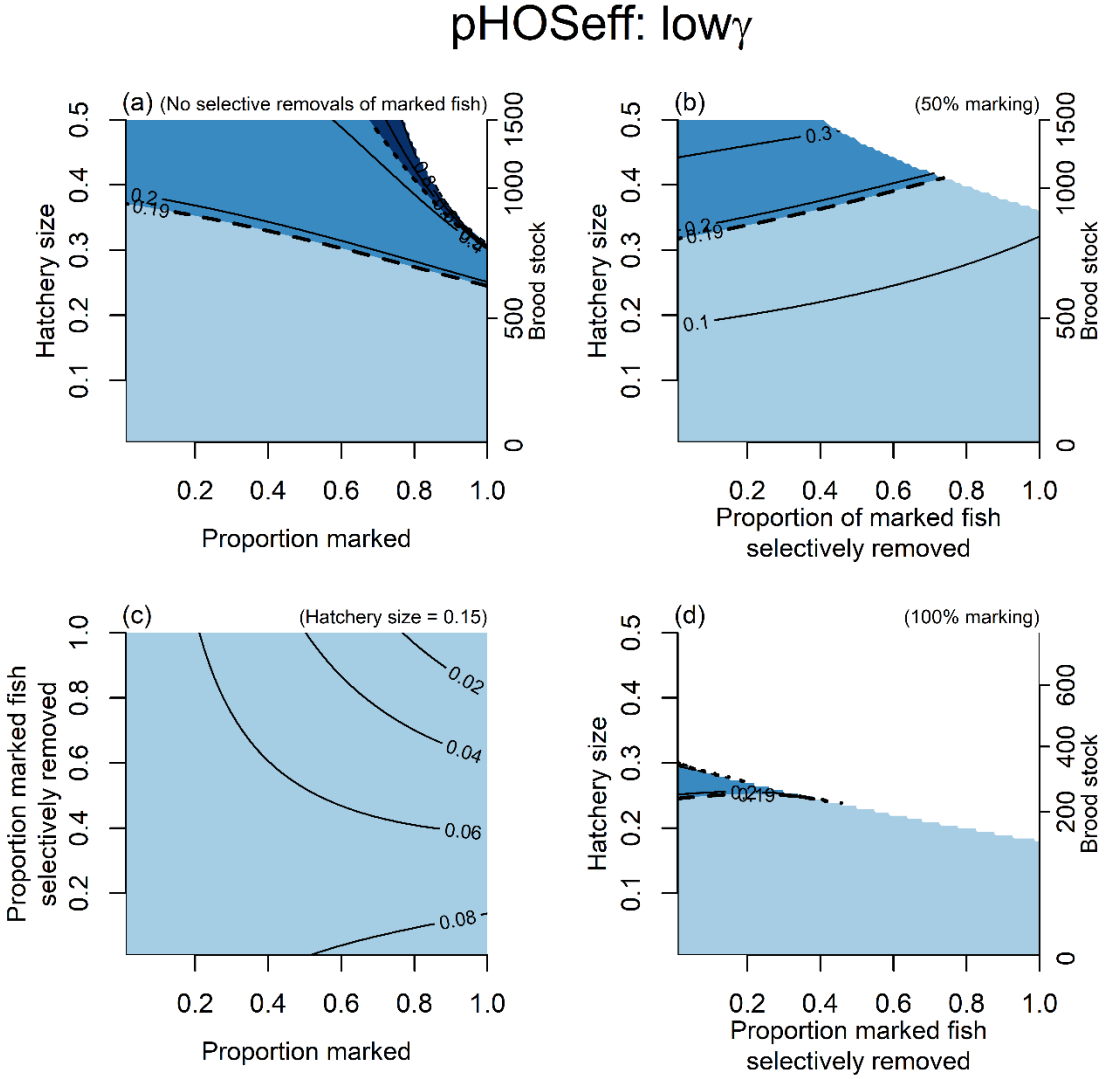

Figure B 7.[15] Bivariate contour plots the effective proportion of hatchery-origin spawners on the natural spawning grounds, $pHOS_{eff}$, along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced proximal reproductive success of hatchery-origin spawners relative to the base case ($\gamma = 0.2$). The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

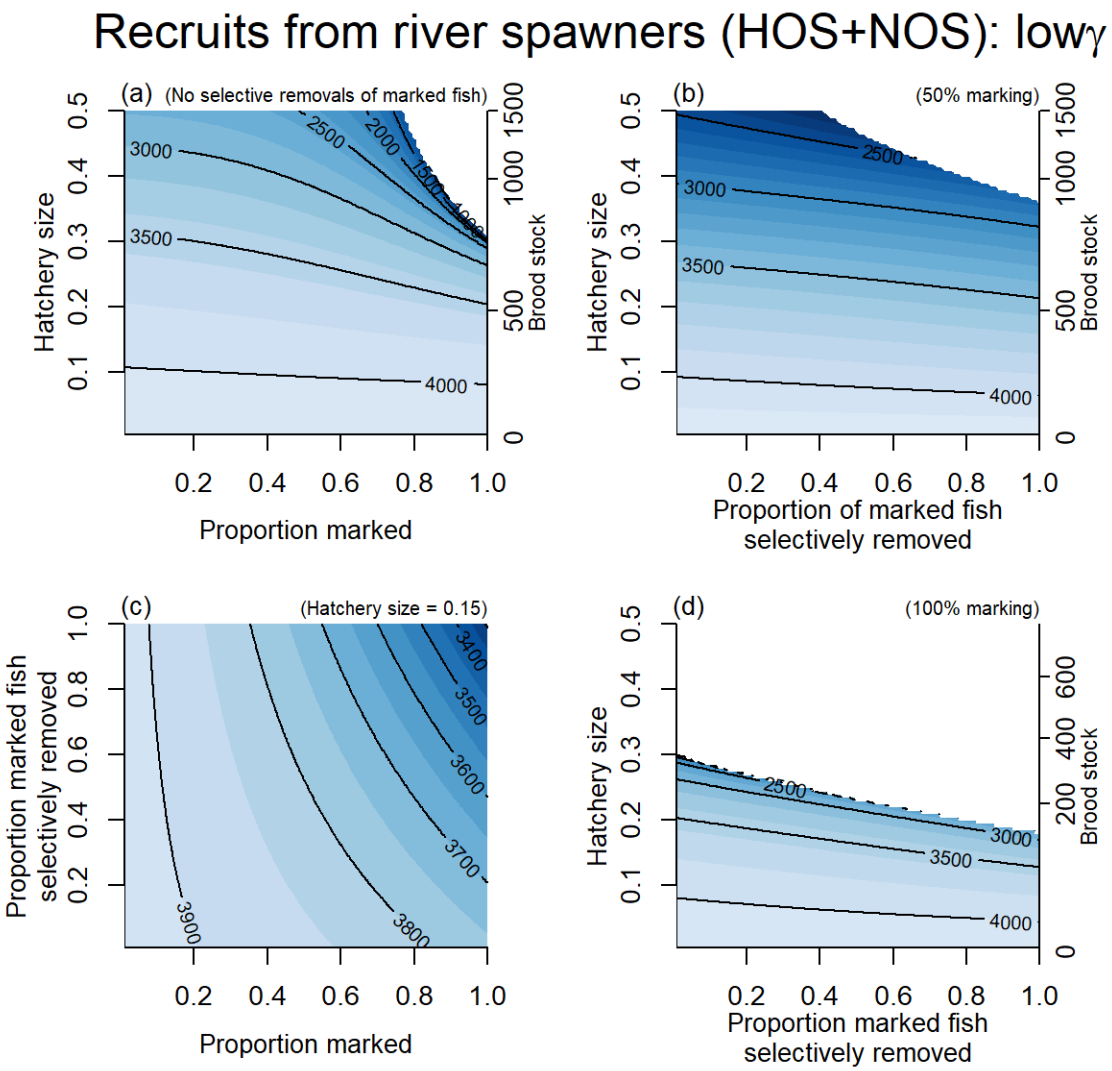

Figure B 8.[15] Bivariate contour plots the recruitment from river spawners (both hatchery-origin spawners, HOS, and natural-origin spawners, NOS) along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced proximal reproductive success of hatchery-origin spawners relative to the base case (γ = 0.2). The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

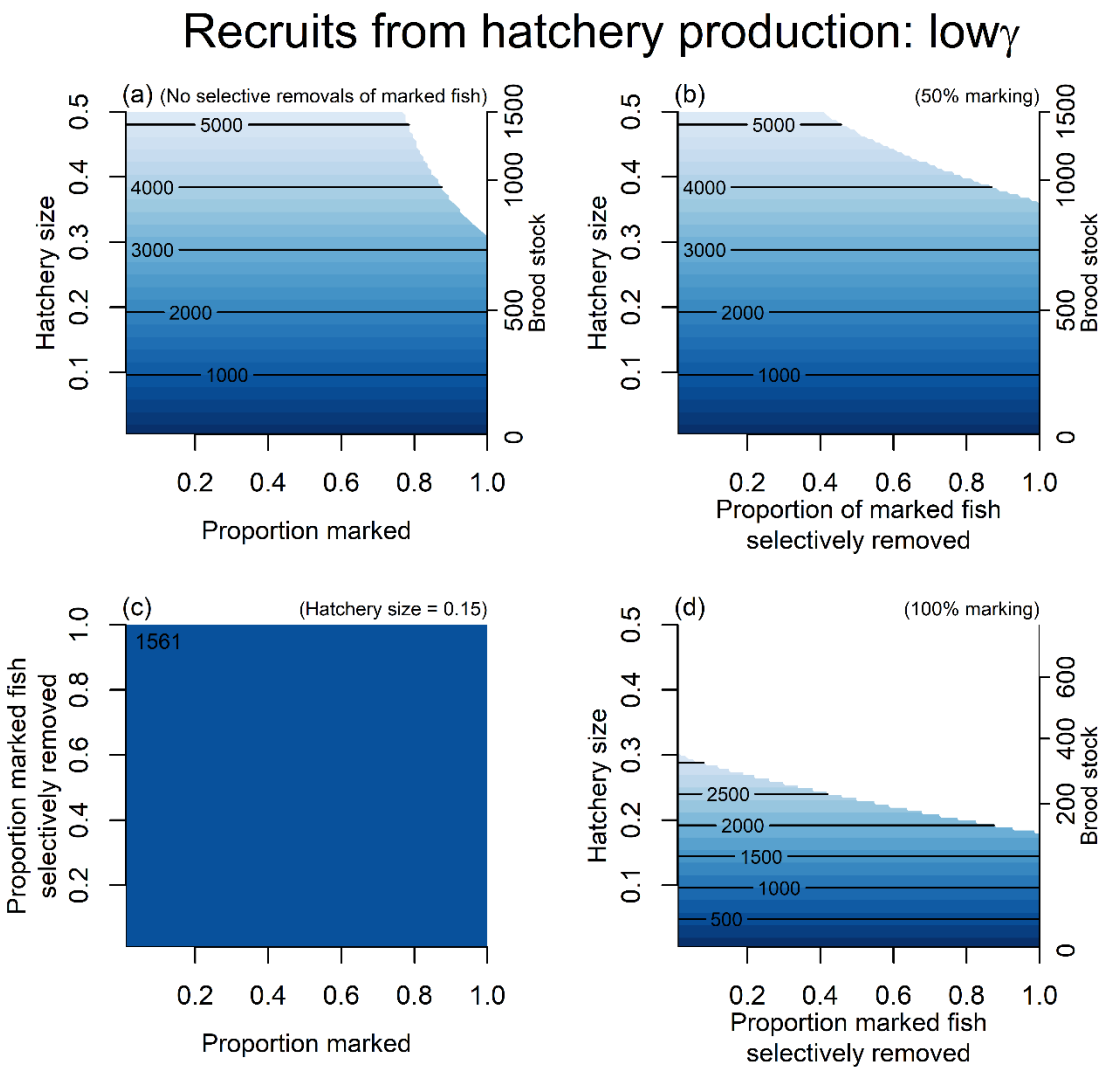

Figure B 9.[15] Bivariate contour plots the recruitment from hatchery production along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced proximal reproductive success of hatchery-origin spawners relative to the base case (γ = 0.2). The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

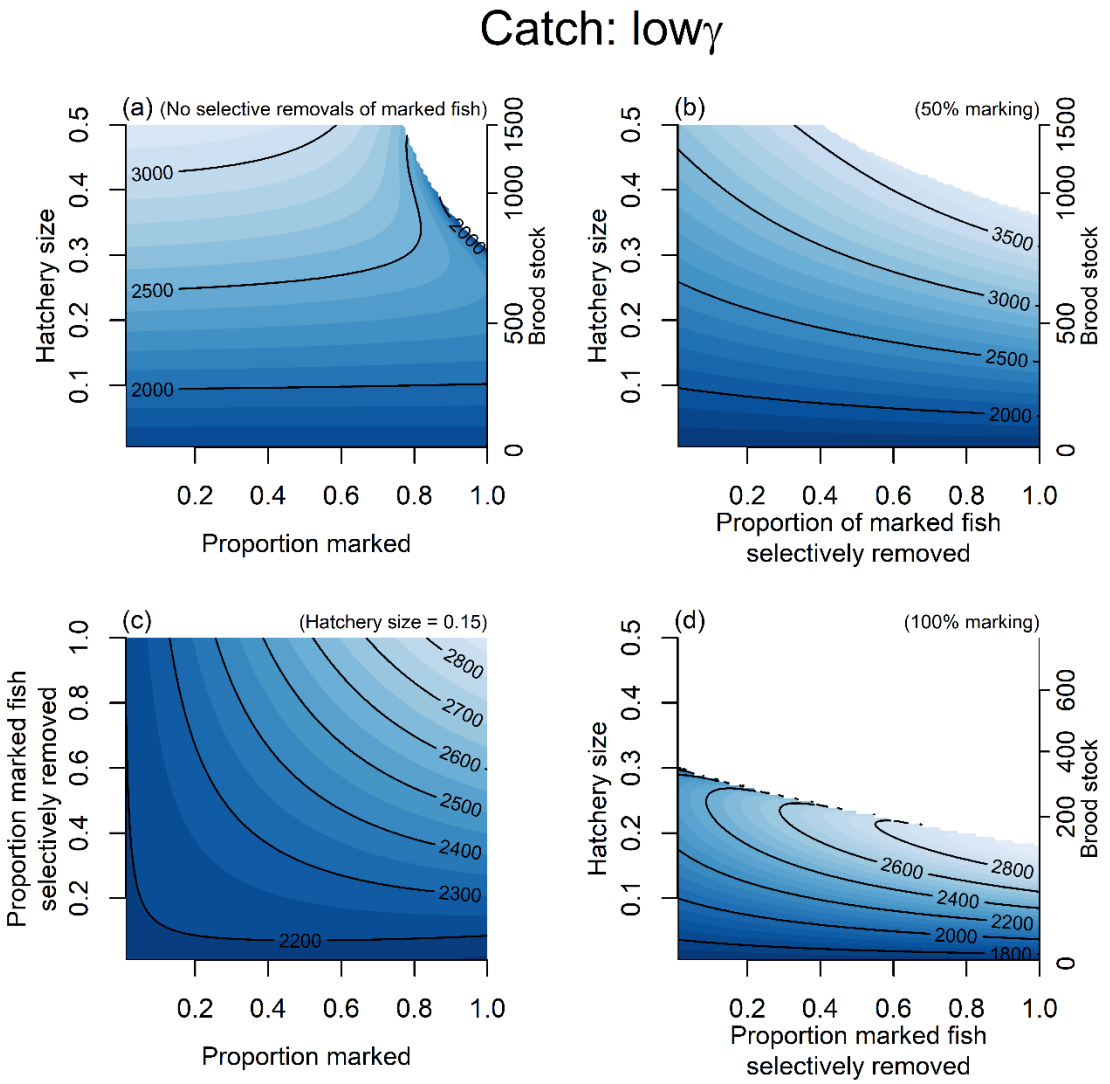

Figure B 10.[15] Bivariate contour plots total catch along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced proximal reproductive success of hatchery-origin spawners relative to the base case (γ = 0.2). The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

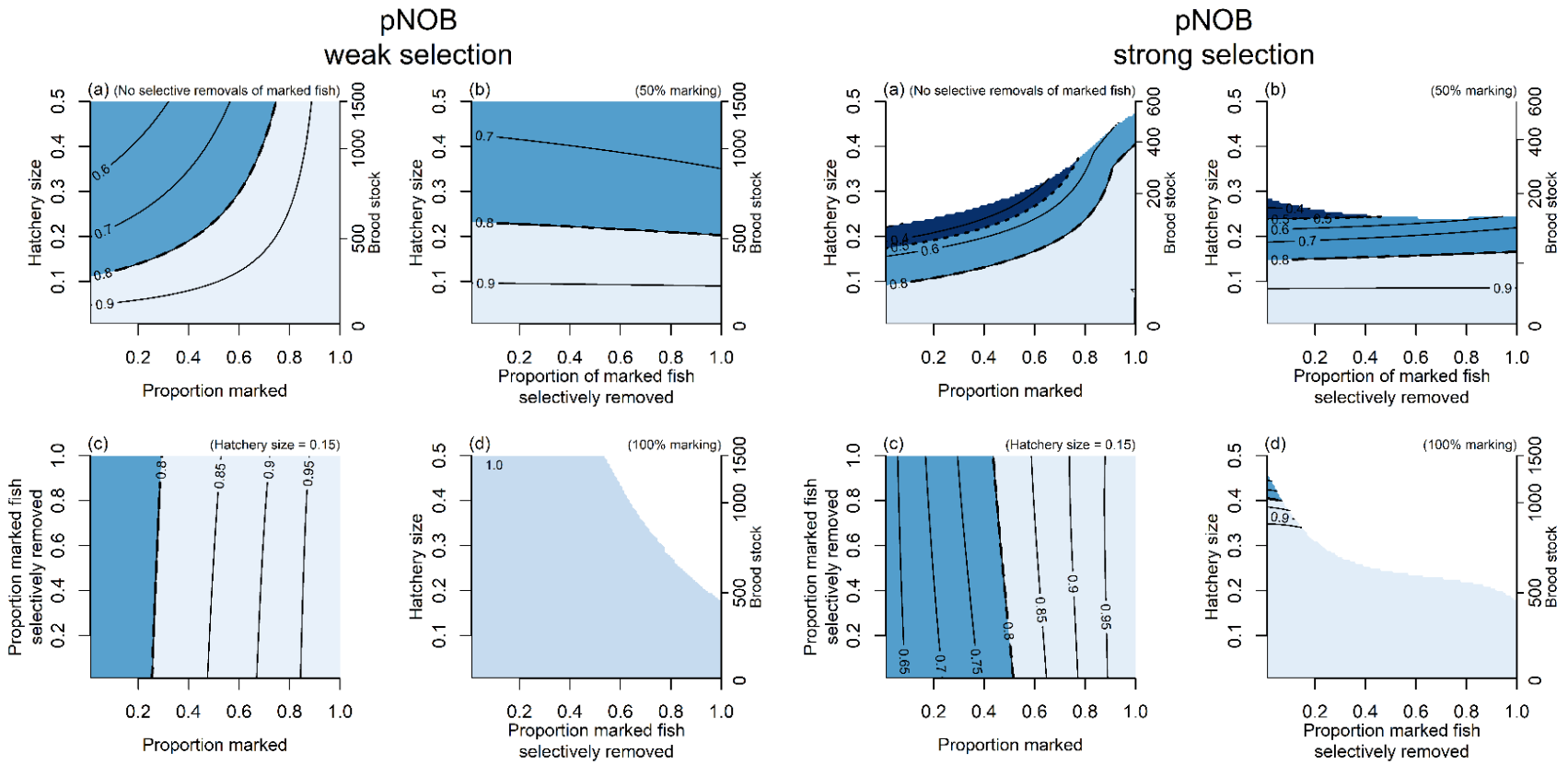

Figure B 11.[15] Bivariate contour plots of the proportion of natural-origin fish in the hatchery brood stock, pNOB, along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced strength of selection (ω^2=1000, a-d) and increased strength of selection (ω^2=40) for phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

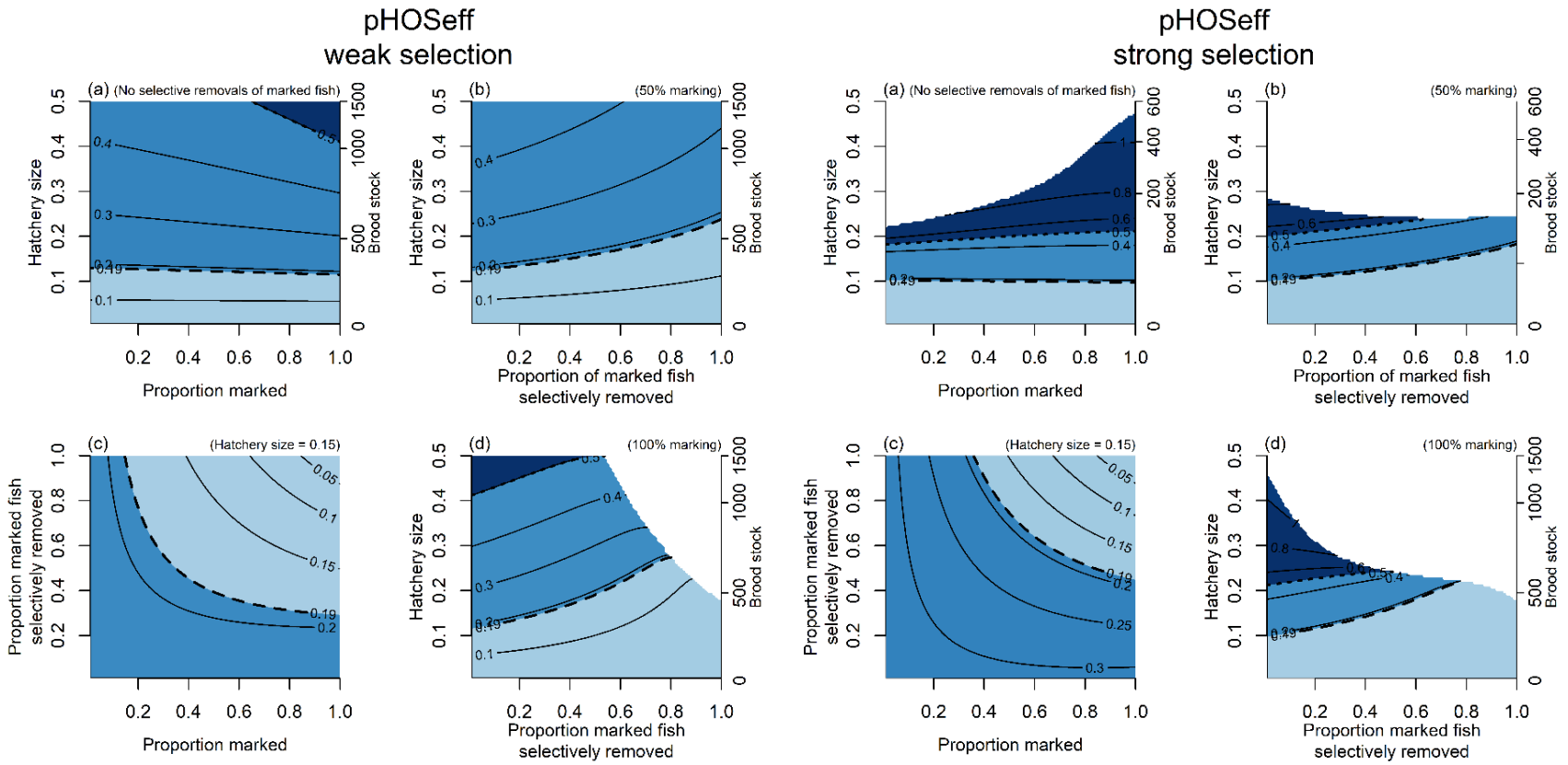

Figure B 12.[15] Bivariate contour plots of the effective proportion of hatchery-origin spawners on the natural spawning grounds, $pHOS_{eff}$, along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced strength of selection (ω^2=1000, a-d) and increased strength of selection (ω^2=40) for phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

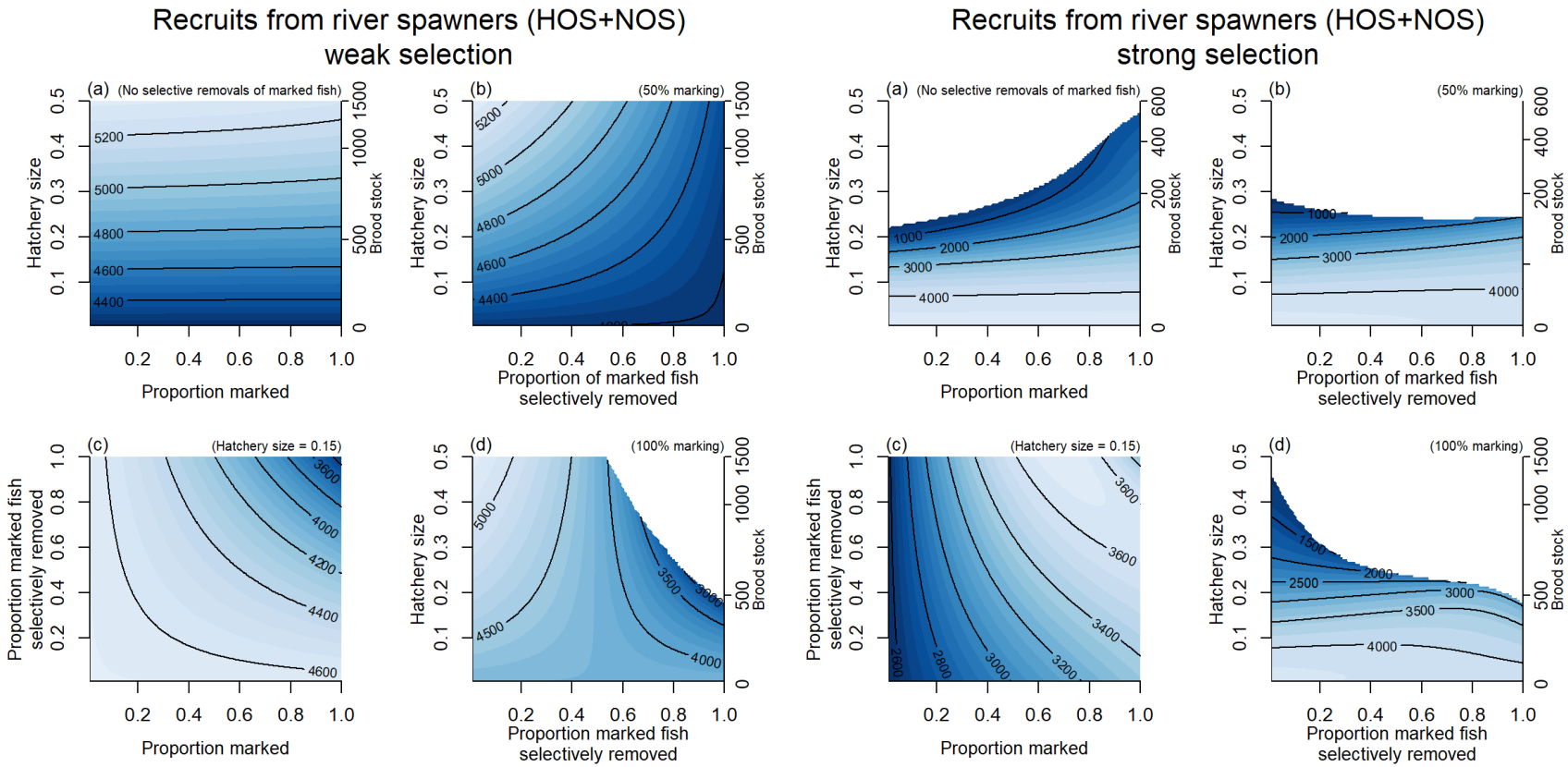

Figure B 13.[15] Bivariate contour plots of the recruitment from river spawners (both hatchery-origin spawners, HOS, and natural-origin spawners, NOS) along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced strength of selection (ω^2=1000, a-d) and increased strength of selection (ω^2=40) for phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

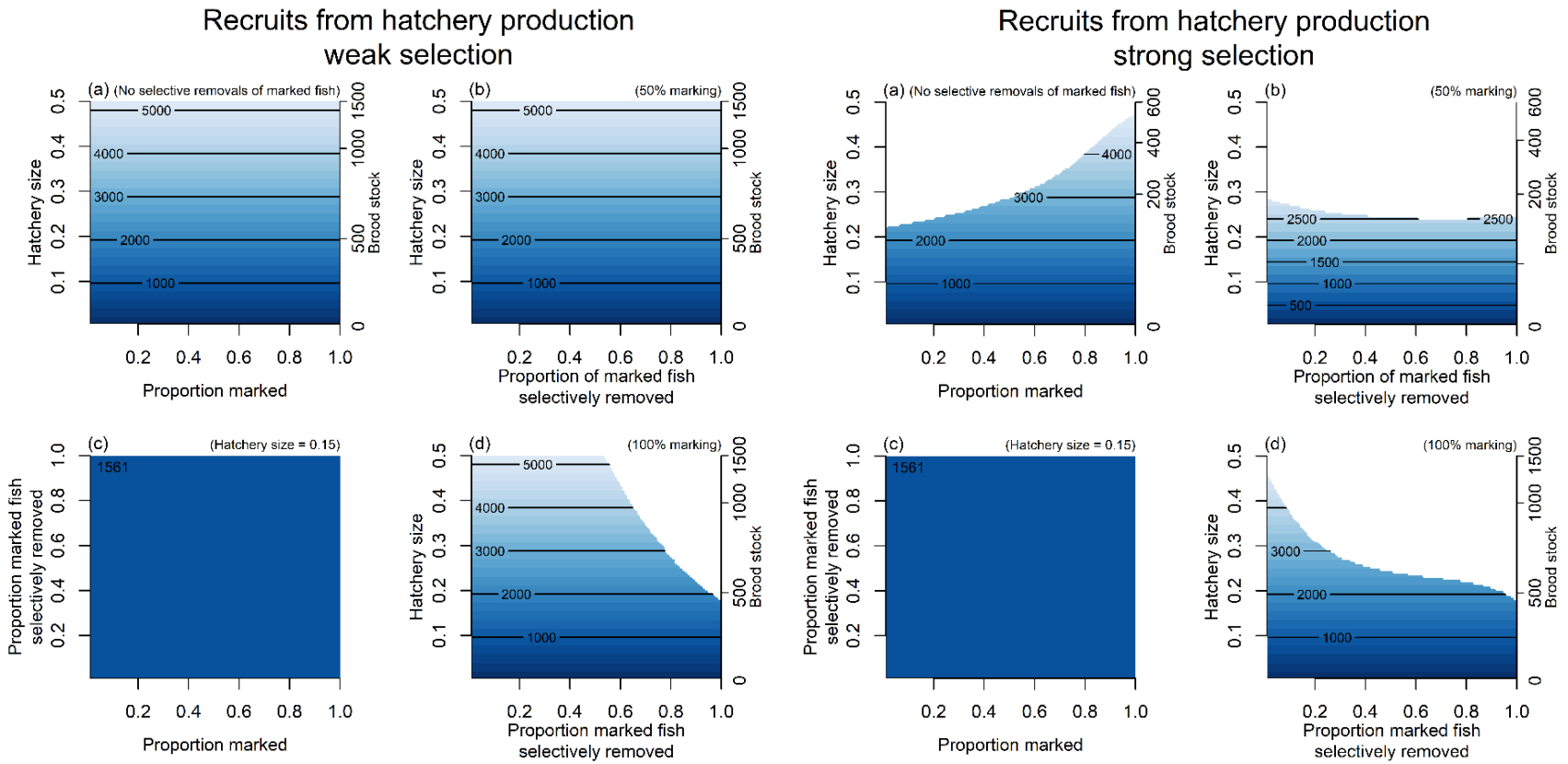

Figure B 14.[15] Bivariate contour plots of the recruitment from hatchery production along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced strength of selection (ω^2=1000, a-d) and increased strength of selection (ω^2=40) for phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

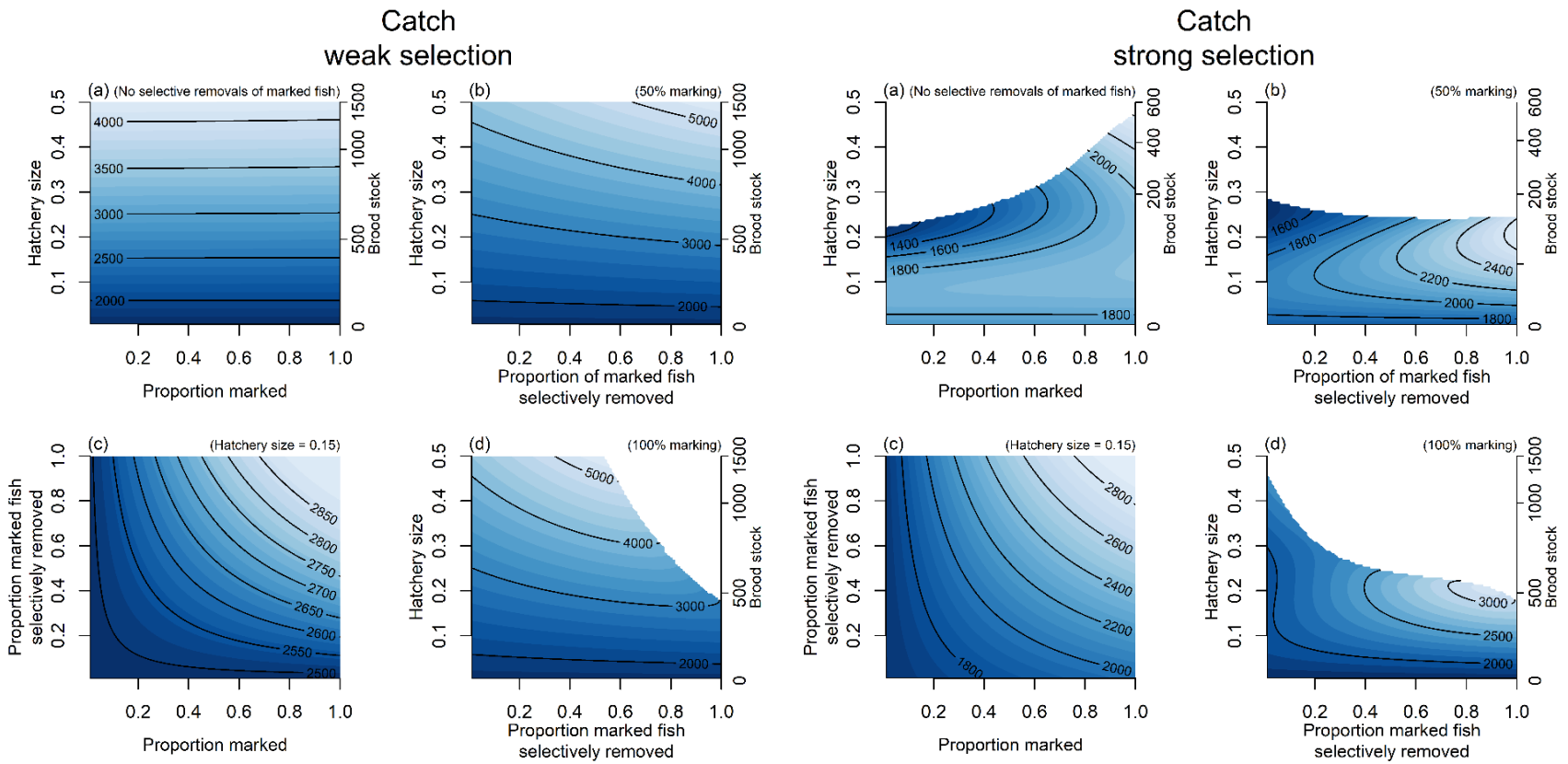

Figure B 15.[15] Bivariate contour plots of total catch along gradients in three management levers, as described in the caption for Fig. 7 assuming reduced strength of selection (ω^2=1000, a-d) and increased strength of selection (ω^2=40) for phenotypic traits. The shading aligns with the 3 categories of populations, "integrated-wild" (light blue), "integrated-transition" (medium blue), "integrated-hatchery" (dark blue). White areas occur where brood stock was constrained to be less than 1/3 annual returns to the river, limiting the size of the hatchery.

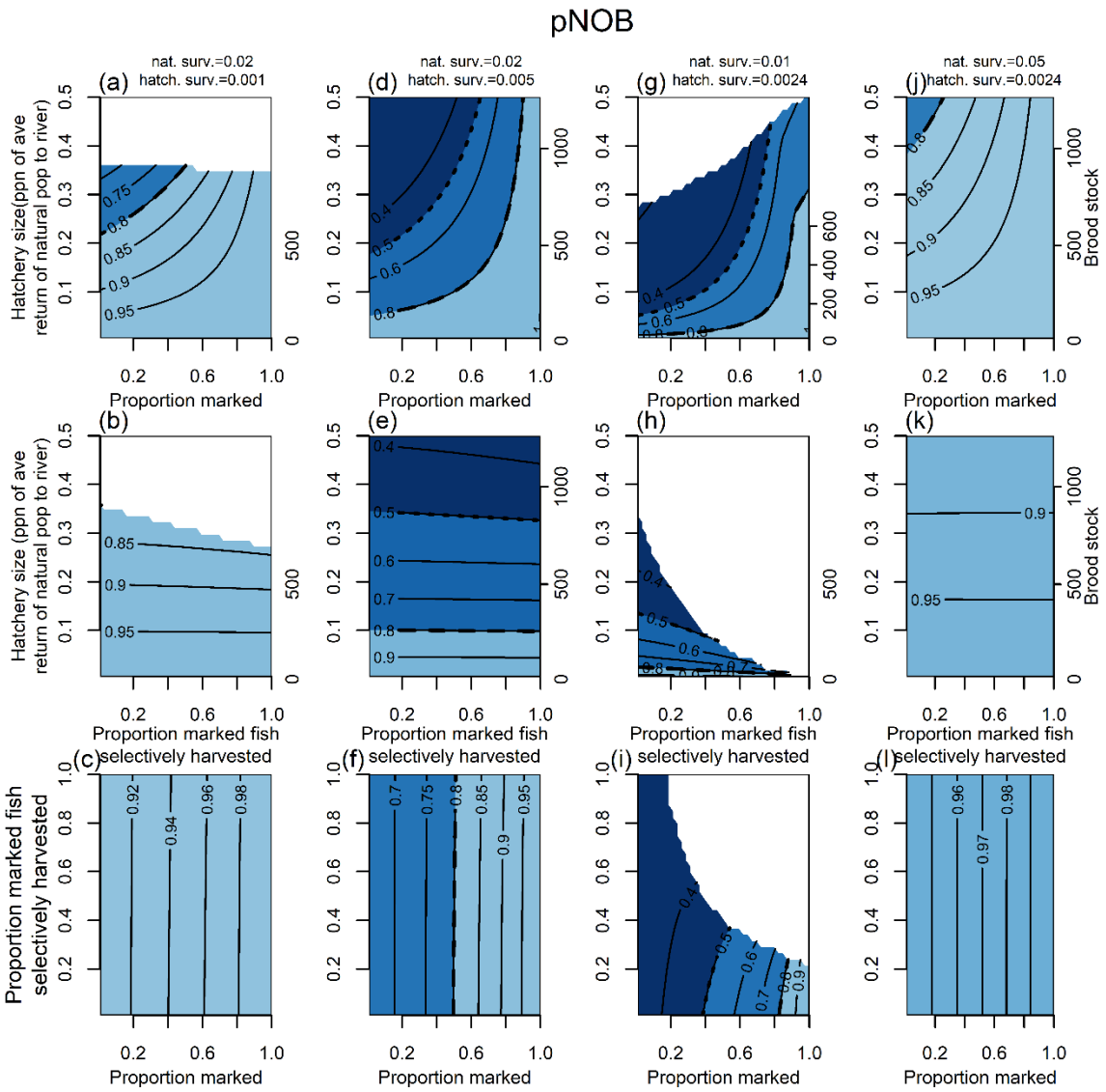

Figure B 16.[15] Bivariate contour plots of pNOB along gradients in three management levers, as described on axis labels under various assumptions about marine survival of natural-origin fish (nat.surv) and marine survival of hatchery-origin fish (hatch.surv). The first row depicts the effects of management levers: proportion marked and hatchery size, assuming no selective removal of marked fish. The second row (b,e,h,k) depicts effects of the proportion of marked fish selectively removed and hatchery size, assuming 50% marking. The third row (c,f,i,l) depicts the effects of proportion marked and proportion of marked fish selectively removed assuming hatchery size=0.15. Columns depict various assumptions about survival, labeled at the top. The shading is described in the caption to Fig. 7.

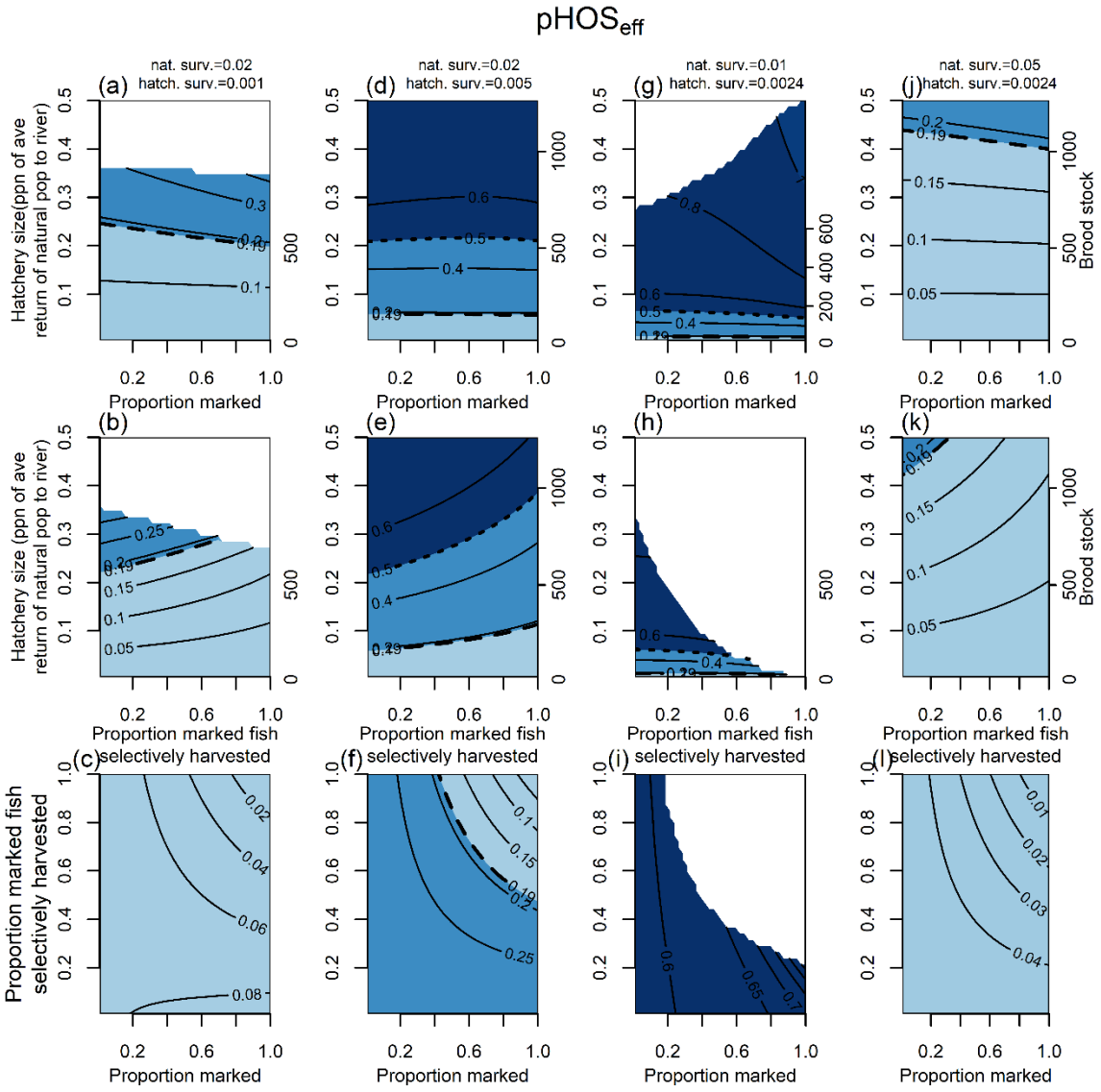

Figure B 17.[15] Bivariate contour plots of $pHOS_{eff}$ along gradients in three management levers, as described on axis labels under various assumptions about marine survival of natural-origin fish (nat.surv) and marine survival of hatchery-origin fish (hatch.surv). The first row depicts the effects of management levers: proportion marked and hatchery size, assuming no selective removal of marked fish. The second row (b,e,h,k) depicts effects of the proportion of marked fish selectively removed and hatchery size, assuming 50% marking. The third row (c,f,i,l) depicts the effects of proportion marked and proportion of marked fish selectively removed assuming hatchery size=0.15. Columns depict various assumptions about survival, labeled at the top. The shading is described in the caption to Fig. 7.

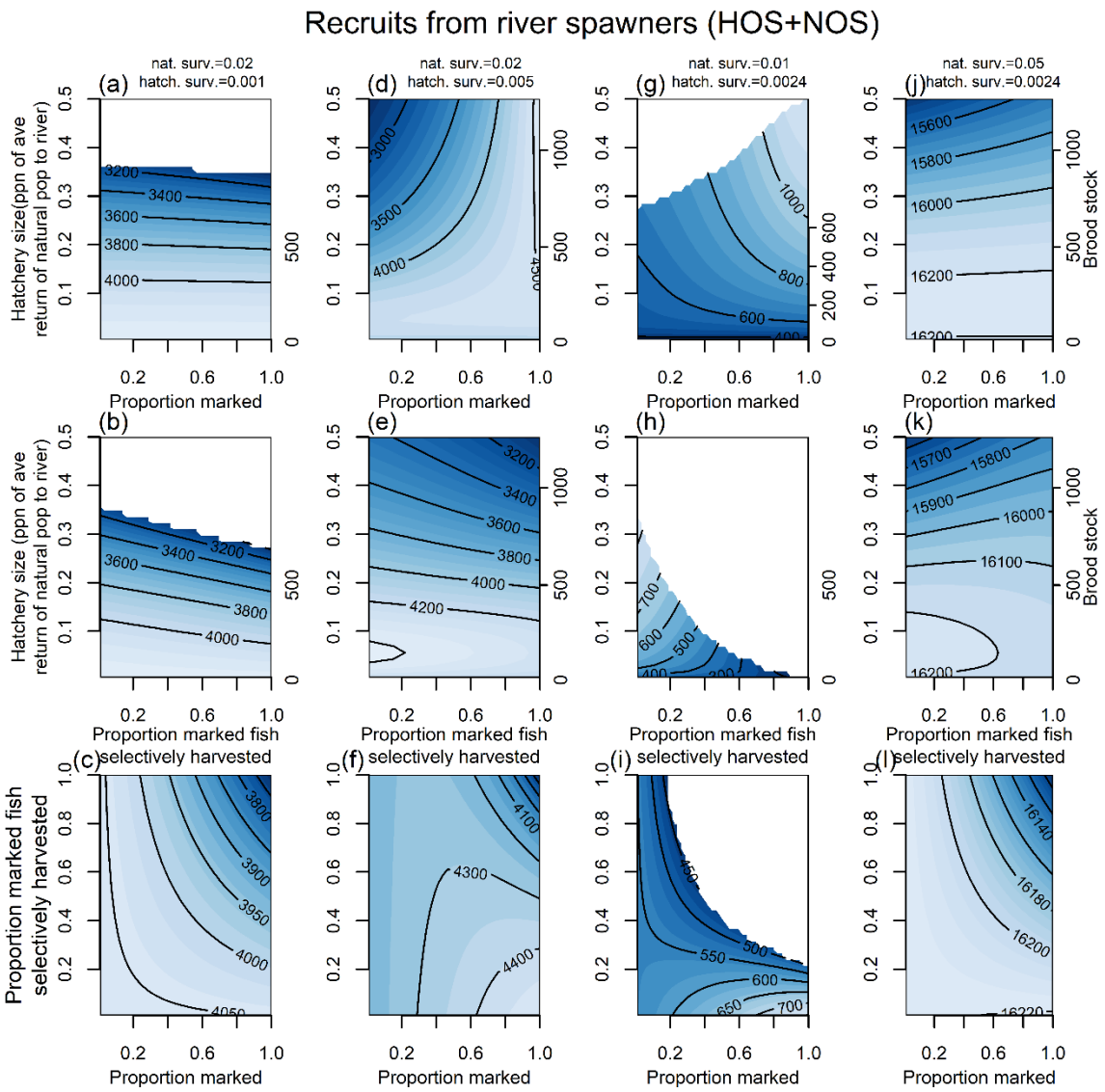

Figure B 18.[15] Bivariate contour plots of recruits from natural production along gradients in three management levers, as described on axis labels under various assumptions about marine survival of natural-origin fish (nat.surv) and marine survival of hatchery-origin fish (hatch.surv). The first row depicts the effects of management levers: proportion marked and hatchery size, assuming no selective removal of marked fish. The second row (b,e,h,k) depicts effects of the proportion of marked fish selectively removed and hatchery size, assuming 50% marking. The third row (c,f,i,l) depicts the effects of proportion marked and proportion of marked fish selectively removed assuming hatchery size=0.15. Columns depict various assumptions about survival, labeled at the top. The shading is described in the caption to Fig. 7.

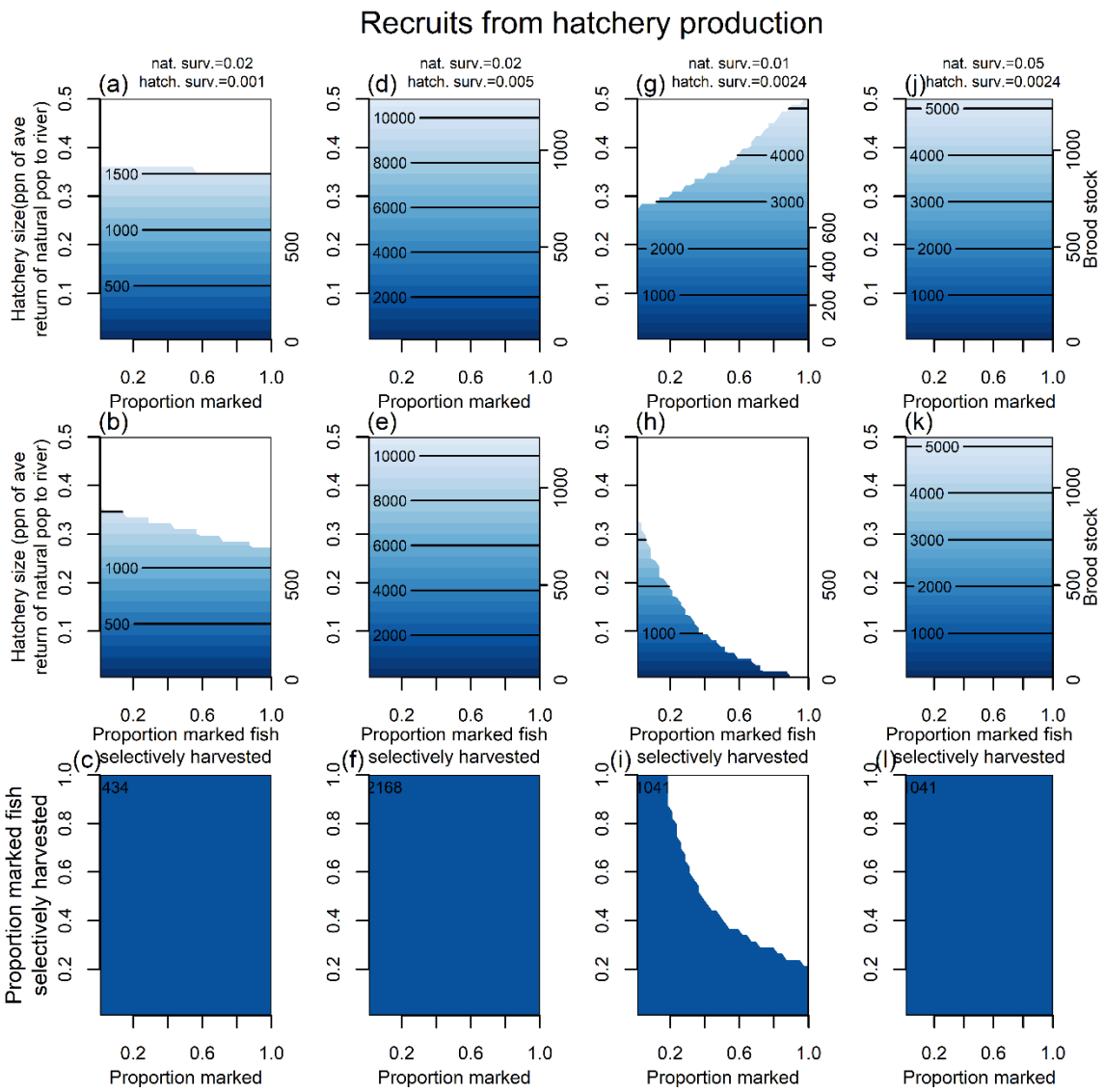

Figure B 19.[15] Bivariate contour plots of recruits from hatchery production along gradients in three management levers, as described on axis labels under various assumptions about marine survival of natural-origin fish (nat.surv) and marine survival of hatchery-origin fish (hatch.surv). The first row depicts the effects of management levers: proportion marked and hatchery size, assuming no selective removal of marked fish. The second row (b,e,h,k) depicts effects of the proportion of marked fish selectively removed and hatchery size, assuming 50% marking. The third row (c,f,i,l) depicts the effects of proportion marked and proportion of marked fish selectively removed assuming hatchery size=0.15. Columns depict various assumptions about survival, labeled at the top. The shading is described in the caption to Fig. 7.

Appendix B Tables

Table B 1. Model parameters and sensitivity analyses

(a) Parameters of natural production

Parameter	Value	Source	Sensitivity analyses	Comments
Beverton-Holt smolt productivity	175 smolts/spawner	Big Qualicum (Fraser et al. 1983; Tompkins et al. 2005)	-	The influence of Beverton-Holt parameters are linearly related to that of marine survival, below
Beverton-Holt smolt capacity, *c*	400,000 smolts	~Big Qualicum (Inferred from Fraser et al. 1983 data)	-	-
Marine survival	0.02	Chosen to generate sustainable dynamics given BH parameters and harvest rate	0.01 (low) and 0.05 (high)	-
Spawners at equilibrium accounting for harvest (S_{eq}) = long-term average recruitment (R_{eq}) of natural population	2514 (5714 without harvest)	Derived from BH parameters, marine survival and harvest rate	-	Marine survival =0.01, R_{eq}=114; Marine survival= 0.1, R_{eq}=21,714.

(b) Parameters of hatchery production

Parameter	Value	Source	Sensitivity analyses	Comments
Survival from brood collection to spawning	0.80	Big Q, Qualicum, Puntledge (fall) and Cowichan over the last 10 years (D. Willis, pers. comm.)	-	The influence of these parameters are linearly related to that of marine survival of hatchery smolts, below
Proportion of brood stock that is female[29]	0.5		-	
Fecundity of brood stock in the hatchery	4900 eggs/spawner		-	
Survival from egg to smolt in the hatchery	0.88		-	
Marine survival of hatchery smolts	0.0024		0.001 (low) and 0.005 (high)	-
Harvest rate	0.4	~Georgia Basin (PSC 2015, Fig 2.15)		-

[29] Erratum: Row added to include parameter that was omitted from the original model.

(c) Fitness parameters

Parameter	Value	Source	Sensitivity analyses	Comments
Relative reproductive success hatchery-origin spawners to natural-origin spawner on spawning grounds due to proximal effects (γ)	0.8	HSRG 2009	0.2(Christie et al. 2014a)	0.2 is the low end of observed values
Heritability (h^2)	0.25	HSRG 2009	0.05 (low heritability), 0.5 (high heritability)	-
Variance of probability distribution of fitness (ω^2)	100 (strong selection, given variance in phenotypic trait, and optimum trait values above)	HSRG 2009	40 (strong selection), 1000 (weak selection)	-
Variance in phenotypic trait (σ^2)	10	HSRG 2009	-	The influence of these parameters is linearly related to that of the probability distribution of fitness, above
Optimum phenotypic trait value in natural environment (θ_w)	100	HSRG 2009	-	
Optimum phenotypic trait value in hatchery (θ_h)	80	HSRG 2009	-	

(d) Management parameters

Management Levers (Scenarios)	Range considered in bivariate analyses
Percent marking of hatchery-origin fish	0-100%
Scale of hatchery expressed as proportion of average returns to river for the natural population	0-50%
Removal of marked fish from the river	0-100%

References for Appendix B

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