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Critical Habitat Case Study – Sakinaw Lake Sockeye Salmon

Étude de cas sur l'habitat essentiel – Saumon rouge du lac Sakinaw

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Abstract

Sockeye salmon (*Oncorhynchus nerka*) from Sakinaw Lake, southern British Columbia were considered for legal listing under the Species at Risk Act (SARA), which would have required that critical habitat be identified, to the extent feasible. Sakinaw sockeye were abundant 15 years ago, but have declined to such low levels that they have a high probability of extirpation.

We describe a methodology we developed to identify potential critical habitat for Sakinaw sockeye. Critical habitat is defined in SARA as the habitat necessary for the survival or recovery of the population. Our methodology consists of 1) describing the present status and life history of Sakinaw sockeye, 2) operationally defining critical habitat, and 3) modellling critical habitat requirements. A habitat was considered critical if the habitat (or improved habitat) was part of the minimal configuration leading to population viability, defined as a population with <10% probability of quasi-extinction and ≥ 95% probability of achieving recovery. To illustrate our approach we used a threshold of 250 female spawners by 2017 as a recovery goal. We recognize that this underestimates the habitat needed to meet longer term (~100 years) more ambitious recovery goals (e.g. 5000 spawners or 2500 female spawners).

We developed a stochastic age structured model using vital rate data chiefly from other (non-endangered) sockeye populations. We evaluated linkages between possible critical habitat combinations and management actions (e.g. levels of enhancement and fishery exploitation) using Monte Carlo simulation. Our habitat scenarios focused on the lake outlet and spawning beaches, both habitats likely to be limiting and where changes might result in improved survival. Changes at the outlet that might alter survival (e.g. predator control and flow adjustments) were modeled by varying pre-spawner survival rates while improvements to spawning beaches were modeled by increasing egg-to-fry survival rates and the carrying capacity for female spawners. Results from our preliminary model suggest that spawning habitat for 280 to 360 female spawners is required (depending on scenario) for Sakinaw sockeye to have <10% probability of quasi-extinction and ≥ 95% probability of meeting the recovery goal assuming no fishing exploitation. To offset 15% exploitation, spawning habitat for an additional 7-110 female spawners (depending on scenario) would be needed. All scenarios include artificial propagation. Potential critical habitat also includes habitat at the lake outlet sufficient to ensure that 90%-95% of the pre-spawners can reach the lake.

These results should be considered preliminary until more comprehensive sensibility analysis, evaluation of the effects of alternative density dependent responses, and criteria for quasi-extinction are completed. Retrospective simulations using relatively high initial population sizes (as occurred in the 1970’s and 1980’s) to investigate the degree to which vital rates must be reduced to mimic the rate of decline in abundance observed since 1987 should also be done. This will allow re-evaluation of the potential overall role of critical habitat on the ability of the population to survive and recover.

We suggest that this overall approach is applicable for other sockeye populations and, with some limitations, other species of salmon. However, success requires a good understanding of the life cycle of the species under investigation, and under what conditions, if any, that habitat may be limiting.

Résumé

Le saumon rouge (*Oncorhynchus nerka*) du lac Sakinaw, situé dans le sud de la Colombie-Britannique, a été étudié en vue de son inscription à la liste des espèces en péril en vertu de la *Loi sur les espèces en péril* (LEP), ce qui nécessiterait que son habitat essentiel soit identifié dans la mesure du possible. Le saumon rouge du lac Sakinaw était abondant il y a 15 ans, mais la population a diminué à des niveaux si bas que sa disparition est très probable.

Nous décrivons une méthode que nous avons mise au point pour identifier les habitats essentiels potentiels pour le saumon rouge. La LEP définit l'habitat essentiel comme l'habitat nécessaire à la survie ou au rétablissement d'une population. Notre méthode consiste 1) à décrire l'état actuel et le cycle vital du saumon du lac Sakinaw, 2) à proposer une définition opérationnelle de l'habitat essentiel et 3) à modéliser les exigences en matière d'habitat essentiel. Un habitat a été considéré comme essentiel s'il faisait partie de la configuration minimale qui permet la viabilité de la population, laquelle est définie comme une population qui présente une probabilité de quasi-extinction inférieure à 10 % et une probabilité de rétablissement d'au moins 95 %. Pour illustrer notre démarche, nous avons établi l'atteinte d'un seuil de 250 géniteurs femelles en 2017 comme objectif de rétablissement. Nous reconnaissons que cela sous-estime la quantité d'habitat nécessaire pour atteindre des objectifs de rétablissement à plus long terme (~100 ans) et plus ambitieux (p. ex. 5 000 géniteurs ou 2 500 géniteurs femelles).

Nous avons mis au point un modèle stochastique du cycle vital selon l'âge qui utilise des données vitales obtenues surtout sur d'autres populations (non en péril) de saumons rouges. Nous avons évalué les liens entre des combinaisons possibles d'habitats essentiels et des mesures de gestion (p. ex. niveaux d'ensemencement et de pêche) par simulation Monte Carlo. Nos scénarios d'habitat ont surtout porté sur la décharge du lac et les plages de fraie, deux habitats qui sont sans doute limitatifs et où des changements pourraient accroître la survie du saumon. Les changements à la décharge qui pourraient modifier la survie (p. ex. le contrôle des prédateurs et la régulation du débit) ont été modélisés en variant les taux de survie des prégéniteurs, tandis que les améliorations des plages de fraie ont été modélisées en accroissant les taux de survie des oeufs jusqu'au stade d'alevin et la capacité du milieu à soutenir des géniteurs femelles. Selon les résultats de notre modèle préliminaire, l'habitat de fraie devrait soutenir de 280 à 360 géniteurs femelles (selon le scénario) pour que la population présente une probabilité de quasi-extinction inférieure à 10 % et une probabilité de rétablissement d'au moins 95 % en l'absence de pêche. Pour compenser un taux d'exploitation de 15 %, l'habitat de fraie devrait soutenir de 7 à 110 géniteurs femelles supplémentaires (selon le scénario). Tous les scénarios comprennent de la multiplication artificielle. Les habitats essentiels potentiels comprennent aussi la décharge du lac pour que 90 à 95 % des prégéniteurs puissent atteindre le lac.

Ces résultats devraient être considérés comme préliminaire jusqu'à ce qu'une analyse de sensibilité plus exhaustive, l'évaluation des effets de différentes réponses dépendantes de la densité et l'établissement des critères de quasi-extinction soient effectués. Il faudrait aussi effectuer des simulations rétrospectives axées sur des tailles initiales relativement grandes de la population (comme c'était le cas dans les années 1970 et 1980) pour déterminer la mesure dans laquelle les taux vitaux doivent être réduits pour simuler la vitesse du déclin de l'abondance observée depuis 1987. Cela permettra de réévaluer l'effet global de l'habitat essentiel sur la capacité de la population à survivre et à se rétablir.

Nous suggérons d'appliquer cette approche générale à d'autres populations de saumons rouges et, dans certaines limites, à d'autres espèces de saumons. Toutefois, le succès de cette méthode nécessite une bonne compréhension du cycle vital de l'espèce étudiée et des conditions éventuelles dans lesquelles l'habitat pourrait être limitant.

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1. Introduction

1.1 Species and status

This investigation of critical habitat (CH) for sockeye salmon (*Oncorhynchus nerka*) from Sakinaw Lake in southern British Columbia (hereafter referred to as Sakinaw sockeye, Figure 1) is one of a series of CH studies being carried out across the country, and the first for Pacific salmon. Like many other salmonids, Sakinaw sockeye reproduce in freshwater and spend most of their adult lives at sea. We selected Sakinaw sockeye because: this population has a restricted freshwater distribution that we felt would be relatively easy to model; the status of Sakinaw sockeye is poor and habitat perturbations are implicated in their decline; and Sakinaw sockeye are the topic of other ongoing investigations.

The status of Sakinaw sockeye was evaluated in 2002 during an emergency assessment by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The COSEWIC Emergency Assessment Subcommittee reviewed all available information, including a report by Murray and Wood (2002), and concluded that this genetically unique and geographically distinct population had declined so drastically that the unit was at imminent risk of extinction. Subsequently, a complete status report (COSEWIC 2003) was presented to COSEWIC and the endangered designation was confirmed. COSEWIC (2003) concluded that Sakinaw sockeye salmon are a listable unit of biodiversity because they are genetically distinct from all other sockeye populations based on analyses of protein-coding (allozyme), mitochondrial, and microsatellite DNA; they inhabit freshwater habitat that is unusual in its physical, chemical, and biological characteristics; and they possess local adaptations such as protracted adult run timing, extended lake residence prior to spawning, small body size, low fecundity and large smolts.

Wood and Parken (2004) reviewed the status of Sakinaw sockeye, forecasting a median return in 2004 of 390 individuals, and concluded that COSEWIC's endangered designation for these fish would almost certainly remain if their forecast was accurate. Approximately 100 spawners returned to Sakinaw Lake in 2004, only 26% of the median forecast.

In anticipation of a decision to legally list Sakinaw sockeye under the Species at Risk Act (SARA, Government of Canada 2004), a recovery team was formed in 2002 to re-evaluate the status of these fish and the main threats to their viability, and to propose specific recovery goals, objectives and actions (Sakinaw Sockeye Recovery Team 2004). Ultimately Sakinaw sockeye were not listed under SARA, but Fisheries and Oceans Canada (DFO) has committed to the development of comprehensive recovery plans and an action plan to protect and rebuild the population (http://www.ec.gc.ca/press/2005/050121_n_e.htm).

1.2 Objectives of study

Under SARA, critical habitat must be identified in the recovery strategy or action plan for legally listed species. The draft recovery strategy (Sakinaw Sockeye Recovery Team 2004) describes population modelling intended to identify critical habitat. Here we provide more details on, and preliminary results from, this modelling exercise.

The primary objective of this research was to develop a procedure that can be used to:

1- Identify habitats critical for the survival and recovery of Sakinaw sockeye

2- Rank these habitats according to their impacts on the survival and recovery of Sakinaw sockeye considering associated implementation costs (sensitivity analysis)

3- Model possible fishery management actions and assess their linkages with critical habitat and their dual impacts on species survival and recovery

This study is a limited case study, and as such, does not specifically identify critical habitat for Sakinaw sockeye. After a brief review of the study area and pertinent research we describe the model and present preliminary findings.

1.3 Study Area

This study focuses on freshwater habitats that may be critical to the survival and recovery of Sakinaw sockeye. Sakinaw Lake (Figure 1) is at an elevation of 5 m, is ~8 km long, and has a surface area of ~6.9 km^2. It is highly unusual compared to other lakes in the region. The main (southwest) basin is meromictic (fresh water over salt water) and does not undergo seasonal mixing (Murray and Wood 2002). The 64 km^2 drainage basin contains various small lakes, none of which contain anadromous sockeye salmon although the largest tributary lake, Ruby Lake, contains non-anadromous sockeye salmon (i.e. kokanee).

The short (~ 0.2 km) outlet stream has been dammed intermittently from the early 1900's to the mid 1930's and a dam and fishway have been operated since the mid 1950's (Sakinaw Sockeye Recovery Team 2004). Lakes within the drainage provide drinking water for various hotels, cottages and small communities. In 2002 and 2003, insufficient water was discharged to provide continual water flow for the outlet stream's fishway. Domestic water demands are expected to continue to increase, and improved water storage and release strategies are being investigated (McBain 2004).

2.0 Background Research

2.1 Abundance

Numbers of Sakinaw sockeye have declined precipitously since the mid-1980's (Figure 2). The average decline in the number of mature individuals was 33% per year during 1990-2002 (COSEWIC 2003). Only 3 adults returned in 2003 and 100 in 2004, fewer than the number of parents in 1999 and 2000 that gave rise to these returning adults. COSEWIC (2003) concluded that Sakinaw sockeye had collapsed primarily due to over-fishing, exacerbated by reduced productivity due to freshwater habitat degradation, and that the unit was at high risk of extinction from fishing, poaching, natural predation and impediments to spawning migration including low water flow.

2.2 Life History

Sakinaw sockeye salmon are anadromous, reproducing and dying in fresh water but spending much of their life in the ocean. Adult sockeye return to Sakinaw Lake between May and October; most arrive in July and August. The adults remain in the lake without feeding until they spawn, which occurs primarily in mid-November. At that time, the adults seek out groundwater fed beaches (Figure 1) to construct redds that will provide incubation habitat for the eggs and resulting alevins. These beaches appear essential to Sakinaw sockeye; spawning has never been observed in tributaries to Sakinaw Lake.

After emerging from the redds the following spring, most juvenile Sakinaw sockeye spend 1 year (occasionally 2) feeding and growing in this unusual lake before exiting to the Strait of Georgia during March to June (peak in May). A small estuary at the mouth of Sakinaw Lake Creek provides a transition zone for smolts although the extent that it is utilized is unknown.

Once at sea, juvenile Sakinaw sockeye are presumed to follow a similar migratory pattern as other nearby, better-studied sockeye populations. They probably move mostly northwest out of the Strait of Georgia along the coast of British Columbia toward the Gulf of Alaska, feeding and growing for another 2 to 3 years before migrating back to the Strait of Georgia (Burgner 1991).

During their return migration, Sakinaw sockeye can be captured in fisheries within Johnstone and Georgia Strait that are targeting other more productive populations of sockeye and pink salmon (*O. gorbuscha*). Fish that reach the mouth of Sakinaw Creek appear to hold there until tide and flow conditions permit their passage through the stream. Adult Sakinaw sockeye must swim up this shallow, short stream and through a water control weir before they arrive in the lake. En route, mortality due to predation (seals and otters) may be significant, and once in the lake, Sakinaw sockeye may be subject to mortality from lampreys.

2.3 Critical Habitat and Recovery Goals

Before identifying habitats potentially critical for Sakinaw sockeye, we need to consider what is meant by CH. The broad definition in SARA of habitat for aquatic species means that anywhere that Sakinaw sockeye lives is considered habitat (Environment Canada 2004):

> *"spawning grounds and nursery, rearing, food supply, migration and any other areas on which aquatic species depend directly or indirectly in order to carry out their life processes"* (Section 2(1)).

According to SARA, habitat becomes "critical" when its loss jeopardizes the survival of a species or population. Critical habitat is formally defined in SARA as:

> *"the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species"* (Section 2(1)).

Critical habitat therefore is the minimum extent and configuration of habitat throughout the life history of Sakinaw sockeye necessary to provide an acceptable probability that Sakinaw sockeye will survive or recover according to specific recovery objectives. It follows that certain amounts of habitat at each life stage may be critical. Potential critical habitat is the habitat necessary to achieve recovery goals identified by the Sakinaw Sockeye Recovery Team (2004) including: "*Ensure that by 2017, the mean population abundance in any four year period exceeds 1,000 naturally produced spawners, with no fewer than 500 naturally produced spawners*[1] *in a year*." In this report we focus on the identification of habitat(s) required to generate 500 naturally produced spawners by 2017 with 95% probability.

2.4 Habitat Necessary for Survival and Recovery[2]

A qualitative evaluation of the various habitats occupied by Sakinaw sockeye and their potential as CH was undertaken. A habitat was proposed as critical if, in its current state, it limited production or was judged to potentially do so as a result of human activities.

2.4.1 Outlet Stream and Estuarine Habitat for Migrating Smolts and Adults

The short (<0.2 km) outlet stream from Sakinaw Lake is used by smolts en route to the sea, and pre-spawning adults when they return to Sakinaw Lake, and the estuary is presumably used as a staging area for both adults and smolts. Adult sockeye often have trouble reaching the lake because the limited lake water storage makes it difficult to release enough water during the typically dry summers for fish to access the fishway. Elevated water temperatures that reach 24°C during the peak of the migration may further affect the entry of adult sockeye. Logging in the early 20th century impacted the

[1] Spawned and reared in natural fish habitat; not released from a hatchery and excluding non-anadromous fish.
[2] Most of he information in this section is adapted from the draft report by the Sakinaw Sockeye Recovery Team (2004)

Sakinaw estuary although, the degree of disturbance and implications to Sakinaw sockeye is not known.

Observations indicate that sockeye primarily migrate into the lake during high tides at night. This may be a behavioral response to predation by otters and seals that move to the base of the dam and fishway in pursuit of adult sockeye and coho salmon (*O. kisutch*). Returning adult sockeye in 2003 and 2004 required up to one hour to move through the fishway, and were extremely vulnerable to predation during this time.

Low flows in the spring may also make it difficult for the smolts to find the outlet, thereby delaying or preventing emigration. Outlet stream temperatures exceeding 20^{o}C in late May and June may increase the propensity for young sockeye to remain a second year in the lake, which may increase survival but decrease fecundity.

For these reasons, the outlet of Sakinaw Lake and its small estuary are considered as proposed critical habitat for Sakinaw Lake sockeye.

2.4.2 Beach Habitat for Spawning and Egg Incubation

High egg and alevin survival depends on clean spawning gravel and sufficient flow for the delivery of oxygenated water and the removal of metabolic wastes (Foerster 1968). Sakinaw sockeye spawn exclusively along the lake shoreline. Spawning grounds are near the mouths of streams where alluvial material and upwelling groundwater exist, or on the lake bottom that is exposed to currents created by strong wave action.

Five beaches are reported to have been used for spawning: Sharon's (Beach 1), Haskins (Beach 2), Ruby Creek (Beach 3), Kokomo Bay (Beach 4), and Prospector Bay (Beach 5) (Figure 1). In recent years, Beach 1 has been the primary beach used by spawning sockeye (G. McBain, DFO Sechelt, pers. communication). It is difficult to predict which of the other beaches would be utilized if the population rebuilds, and thus, which are most critical to recovery. For this reason, all the five known spawning beaches plus the catchments for the streams entering Sakinaw Lake at these beaches are proposed critical habitat for Sakinaw sockeye (Figure 1).

2.4.3 Pelagic Lake: Habitat for Juvenile Sockeye

Since sockeye live in Sakinaw Lake for one and occasionally two years, we need to consider the possibility that the lake is critical habitat for juvenile sockeye. Results are somewhat confusing. Sakinaw Lake appears to be one of the most productive lakes in coastal BC, which generally are unproductive (Shortreed et al. 2000, 2003) Zooplankton prey species seem relatively abundant and Sakinaw sockeye smolts are large (mean size: 13.1 cm and 23.6 g during 1992-1995 brood years). The abundance of favoured prey and the strong growth of sockeye suggest that the lake rearing capacity is not a major limitation. This conclusion is supported by data showing very good survival of fry (~ 30%) in the lake in 2002. However, the incidence of lamprey scars on smolts can be high, and few smolts left the lake in 2004, although observations were not made over the whole migration time period. The latter may indicate poor survival; alternatively, juveniles may have survived and will leave during 2005 or remains as non-anadromous fish ("residuals"). In summary, although evidence is not clear-cut, most information suggests that the pelagic zone is not critical habitat for juvenile sockeye but this assumption should be reassessed in the future.

2.4.4 Pelagic Lake Habitat for Adult Sockeye

Sakinaw Lake is often used by adult sockeye for several months prior to spawning. It is unknown where the sockeye reside in the lake and whether parasitism by lamprey is a significant threat to their survival. Nevertheless, the pelagic lake habitat is not considered to be critical habitat for adult sockeye at this time.

2.4.5 Offshore Marine Habitat

Loss of marine habitat for sockeye seems plausible, or even probable. However, since marine habitat impacts on Sakinaw sockeye are not documented, and it would appear impracticable to manage marine offshore habitat for Sakinaw sockeye, we do not consider offshore marine habitat to be critical habitat.

An interesting consideration is the habitat occupied by returning sockeye. As mentioned, Sakinaw sockeye can be caught in fisheries targeting other populations of salmon, and fishery impacts are strongly implicated in the decline of this population (COSEWIC 2003). We do not propose that the migratory corridor for Sakinaw sockeye to be critical habitat, but we do examine the influence of fishery exploitation on survival and recovery.

3.0 Modelling Critical Habitat Requirements

To quantify the importance of habitats as critical we assessed the importance of habitat quantity and quality using population viability analysis (PVA). A habitat was considered critical if the habitat or improved habitat was essential for the viability of the species.

We followed guidelines developed by Environment Canada (2004) to identify critical habitat (Figure 3). Once the recovery goals (step 1) and acceptable level of risk (step 2) have been identified by the recovery team, a model is developed to determine if the population is viable and which habitat(s) might be critical (step 3). The probability that the projected population is above the recovery threshold is then estimated (step 4). If the population is below the threshold (i.e., not viable), then we investigate which improvements to the habitats and/or management actions (e.g., supplementation, fishery) are necessary for the population to be viable (step 5).

3.1 Operational definition of critical habitat

We expand on the definition of viability in the guidelines by adding the requirement that the population should also have a low probability of quasi-extinction for any year while in the process of recovery.

A habitat is therefore critical if this habitat in its current or improved state is necessary for the viability of the population, where viability is defined as a population state having less than 10% probability of quasi-extinction and at least 95% probability of meeting the recovery goal.

3.2 Critical habitat identification steps

3.2.1 Recovery Goals (step 1)

Recovery is often perceived as a single number that the population must reach within a certain period and be maintained thereafter for an acceptable period. In contrast, we advocate a staged approach with specific goals at various time intervals during the expected recovery period.

Since multiple goals were not finalized in time for our study, we used a single recovery goal but the approach could be easily expanded. In this report we focus on the identification of habitat(s) required to generate 500 naturally produced spawners by 2017.

3.2.2 Acceptable level of risk (step 2)

We used 10% and 95% as acceptable thresholds for the probability of quasi-extinction and recovery, respectively.

3.2.3 Model building (step 3)

In PVA, a population dynamic model projects the population through time and determines the probabilities of quasi-extinction and recovery.

We assessed Sakinaw Lake sockeye viability by building an age structured model (Caswell 2001). This model had 5 classes (ages 1- 5, Figure 4) and tracked the annual contribution of individuals in each class at one census to all classes in the following census. We assumed a 0.5 sex ratio and modelled only females to avoid underestimating extinction risk (Brook et al. 2000). Note that class 1 is named fry and corresponds to the period between spawning and fry emergence while class 2 is named smolt and corresponds to the period from fry emergence to migration to the sea as smolts.

The life cycle graph along with the transition matrix is in Figure 5. For each class, the probability of surviving and entering the next age class at time t+1 is given by S_{a+1} where *a* is an age class. Fecundities are the average number of female fry born to a single female in each age class and are given by N_{Fry4} to N_{Fry5}. The densities of individuals at time t+1 in each class “a” ($N_{a, t+1}$) is given by the product of the transition matrix (L_t) whose elements incorporate fecundity ($N_{Fry4\ to}$ N_{Fry5}) and survival for each class (S_1 to S_{a-1}) by a vector $N_{a, t}$ (whose elements represent the abundance of individuals in each class ‘a’ at time ‘t’).

Structured models have advantages over simpler models. First, using a structured model makes it possible to assess the influence that vital rates of particular classes have on the growth of the population as a whole. Second, they are particularly well suited to evaluating management alternatives, provided that demographic data from contrasting situations exist. Lastly, manipulation of the parameters of structured models allows one to perform computer “experiments” to predict the likely effects of proposed management practices. The main shortcoming of structured models is that they required finer data detail such as age or stage specific survival rates.

Vital rates for the transition matrix were estimated as follows:

$N_{Fry4} = P_{mat4} \times S_{lake} \times S_{lamprey} \times S_{eggs} \times N_0 \times P_{fem}$ **(1)**
$N_{Fry5} = P_{mat5} \times S_{lake} \times S_{lamprey} \times S_{eggs} \times N_0 \times P_{fem}$ **(2)**

where

N_{Fry4}: number of female fry born to a single age 4 female
N_{Fry5}: number of female fry born to a single age 5 female
P_{mat4} and P_{mat5} : proportion of fish that are mature by age 4 and 5, respectively.
S_{lake}: pre-spawners survival through the lake outlet
$S_{lamprey}$: pre-spawners survival in the lake
S_{eggs}: egg-to-fry survival
N_0: number of eggs per female
P_{fem}: proportion of female

$S1 = S_{fry\_smolt}$ **(3)**
$S2 = S_{smolt\_age3}$ **(4)**
$S3 = S_{o\_age3}$ **(5)**
$S4 = S_{o\_age4} \times (1- P_{mat4})$ **(6)**

where S1 to S4 are survival rates from one class to the next, and S_{o_age3} and S_{o_age4} are ocean survival of 3 and 4 year-old.

We used RAMAS METAPOP as a framework to perform the population projection (Akçakaya 2002). RAMAS allows users to define the following key elements: transition matrix, initial abundance in each class, amount of environmental stochasticity for vital rates; type of density dependence and stages/classes affected by it, population segment threshold, fishing exploitation, supplementation, and the number and duration of projections. Population segment refers to the portion of the population that is targeted by the recovery goal. In the case of Sakinaw sockeye, the population segment corresponds to the 4 and 5 year-old female fish as these are potential spawners. We developed a FORTRAN program to perform the simulation scenarios that provided input and extracted output from RAMAS.

Parameter estimates and stochasticity

We parameterized the age structured model using data primarily from Murray and Wood (2002), COSEWIC (2003), Wood and Parken (2004), and Sakinaw Sockeye Recovery Team (2004). Given the lack of age specific survival rates for Sakinaw sockeye, we used the mean and variance of egg-to-fry (S_{eggs}) and fry-to-smolt (S_{fry_smolt}) survivals from typical sockeye populations in British Columbia (Bradford 1995). In the absence of age specific marine survival rates, we made the following plausible assumptions: a) the marine survival (MS) of sockeye from Chilko lake was representative of the marine survival of Sakinaw sockeye, b) 3 year-old (S_{o_age3}) and 4 year-old (S_{o_age4}) females have the same ocean survival, and c) that all 5 year old females that survived fishing will spawn. We simplify the model further by assuming that all the variability in marine survival occurred at the smolt stage; this procedure avoided potential errors associated with improperly specifying interactions in survival rate among marine stages.

Procedures for estimating age specific marine survival rates and the proportion of fish that mature by age 4 (P_{mat4}) are described in Appendix 1.

We modelled the effect of both environmental and demographic stochasticity. Since the observed variance of the vital rates includes environmental variation and measurement error (total variance), we estimated the variance due to environmental stochasticity as 50% of the total variance (Akçakaya et al. 2003). We assumed independent lognormal distributions for pre-spawner survival by lamprey predation ($S_{lamprey}$) and other predators in the lake outlet (S_{lake}) (Bradford 1995) and also for S_{eggs}. We assumed that the coefficient of variation on both $S_{lamprey}$ and S_{lake} was 20%. The effect of environmental variation in fecundity rates ($N_{Fry4,}$ N_{Fry5}) was therefore estimated as 50% of the sum of the variance of $S_{lamprey}$, S_{lake} and S_{eggs}. Variable definitions, sources, and parameters values are in Tables 1a and 1b.

Demographic stochasticity refers to the variability in population growth rates arising from random differences among individuals. This produces random fluctuations in mean fitness or population growth rates that are inversely proportional to population size (Lande 2002). Demographic stochasticity was modelled by drawing the number of survivors for the i^{th} age from a binomial distribution with parameters Si (survival rate) and Ni(t) (as sample size) and the number of young produced by the i^{th} stage from a Poisson distribution with mean Fi(t)Ni(t) (Akçakaya 1991).

Model structure, density dependent and initial population size

Because of a paucity of vital rate estimates and knowledge of how density dependent processes operate for Sakinaw sockeye, our model should be viewed as exploratory. We kept the model as simple as possible so that it would be relatively easy to keep track of its mechanics. This simplification seems acceptable since our goal is to rank the importance of various habitats in light of various management actions rather than to provide an accurate probability of meeting particular recovery goals. Although population abundance is currently very low and depensation is possible - we do not explicitly model depensation. Until we better understand whether and how depensation operates, our approach has been to estimate the probability of quasi-extinction, i.e. the probability that at least once during the projection period the number of spawners goes below a threshold judged to be critical. We used 20 female spawners as the critical threshold for quasi-extinction. If there is a high probability of quasi-extinction, it is unlikely that the population will survive or recover even if there is a high probability of reaching the recovery threshold by 2017. As a result, when we identify CH, we take account of both the probability of quasi-extinction and the probability of recovery.

We modelled the effect of density dependence (D-D) on the spawning process by varying the carrying capacity for the population segment available to contribute to spawning (i.e. 4 and 5 year-old females) using a ceiling type D-D. The ceiling type D-D implies that density-dependent reduction in vital rates (compensation) does not occur until the population abundance reaches the ceiling.

To mimic the Sakinaw sockeye population in 2000, we used as initial abundances, 64 and 1 females at age 4 and 5, respectively. We back-calculated the number of females in age classes 1 to 3 as 4735, 1051, and 105 individuals, respectively. The simulation was carried for 17 years (~4 generations); the probability of quasi-extinction was estimated each year while the probability of recovery was estimated in the last year of the simulation.

Supplementation

Hatchery-fed fry put into the lake from 2002 to 2006 were introduced into the model as smolts estimated as 30% of the number of hatchery fry (G. Bonnell, DFO, pers. communication) in years 2003 to 2007. By 2010, all spawners will be naturally produced. The number of hatchery fry for 2002, 2003 and 2004, were 32,710, 13,300 and 0. We assumed that beyond the smolt stage, hatchery and wild fish had equivalent survival.

Model evaluation

It is impossible at this stage to evaluate the model as data from Sakinaw are very limited. Our approach has been to use vital rate estimates for a typical sockeye population to determine the potential for recovery given favourable conditions. We plan re-evaluation and improvement of the model (step 3) as new information becomes available (step 9).

Sensitivity analysis

A sensitivity analysis was carried out as follows: a simulation was performed using extreme values (± 1SD) for fry-per age 4 female (N_{Fry4}), fry-per age 5 female (N_{Fry5}), fry (S_{fry_smolt}) and smolt (S_{smolt_age3}) survival rates, one parameter at a time and setting the standard deviation to zero. Note that for N_{Fry4} and N_{Fry5} we only considered extreme values for egg-to-fry survival. The model used to perform the sensitivity analysis was the "base" condition with an adult carrying capacity of 500, a level of supplementation for both 2005 and 2006 of 84,000 hatchery fry, and a fishing exploitation of 10%. The goal of this analysis was to identify which vital rates had the most impact on model predictions and hence, which should receive future research priority, e.g., field studies associated with those parameters having the greatest impact on probabilities of quasi-extinction and on reaching the recovery goals.

3.2.4 Assessing viability and critical habitat (Step 4 and 5)

Since the model did not explicitly track the number of spawners per se, we estimated the number of age 4 and 5 female adults to reflect the desired threshold for spawners using the procedure described in Appendix 2. For instance, under a fishing exploitation of 10%, a threshold of 292 adult females is equivalent to 250 adult female spawners.

To identify critical habitat we focused on habitats that had the potential to be improved: i.e., spawning beaches and the lake outlet. Spawning success could potentially be improved through beach restoration that might increase egg-to-fry survival (S_{eggs}). Predator control and flow adjustments at the lake outlet could increase pre-spawner survival (S_{lake}). We assessed the importance of various habitat configurations along with management possibilities (exploitation and hatchery fry supplementation) on the probability of quasi-extinctions and the probability of meeting the recovery threshold.

The basic set of simulation scenarios is summarized as follow: ceiling type density dependence, nine levels of fishing exploitation (μ) ranging from 0.0 to 0.4 in increments of 0.05, and 3 levels of supplementation for 2005 and 2006 (50,000, 84,000, and 120,000 fry).

This basic scheme was repeated for various habitat improvements and carrying capacity (see the list below) for a total of 2160 configurations[3]. The baseline habitat conditions yield an egg-to fry survival rate (S_{eggs}) of 0.13 and a pre-spawner survival in the lake outlet of 0.90 (S_{lake}). The baseline conditions also included the actual levels of supplementation with fed fry in 2002 to 2004.

An improvement of habitat quality in the lake outlet increased mean pre-spawner survival (S_{lake}) from 0.90 to 0.95 while improvement of habitat quality on the spawning beaches increased mean egg-to-fry survival (S_{eggs}) from 0.13 to 0.18. Variation in the parameters remained the same with these improvements. Improvements to spawning beaches were assessed by varying the carrying capacity for 4 and 5 year-old adults from 50 to 1000 females in increments of 50. It would be desirable to quantify the spawning area needed to support the spawner thresholds used in the recovery goals but this was not practicable at this time. Each simulation was run for 17 years (~4 generations) with 10,000 replications.

scenario	S_{lake}	S_{eggs}	Carrying capacity of female spawners (in increment of)	Exploitation (in increments of)
base	0.90	0.13	50 to 1000 (50)	0 to 0.4 (0.05)
S_{lake}	0.95	0.13	50 to 1000 (50)	0 to 0.4 (0.05)
S_{eggs}	0.90	0.18	50 to 1000 (50)	0 to 0.4 (0.05)
S_{eggsl}	0.95	0.18	50 to 1000 (50)	0 to 0.4 (0.05)

Contour plots of the probability of quasi-extinction and the probability of reaching the recovery threshold under various scenarios were used to identify critical habitat. Critical habitat would be described by the intersection of contour lines for a 10% probability of quasi-extinction and 95% probability of reaching the recovery threshold. The carrying capacity of female spawners was estimated by converting the carrying capacity of 4 and 5 year-old adults using equation (Appendix 2). Interpolation and contour plots were created using S-PLUS (2001).

[3] 9 levels of exploitation x 3 levels of supplementation x 4 habitat configurations x 20 levels of carrying capacity

4.0 Results

4.1 Sensitivity analysis

Figure 6 illustrates the probabilities of quasi-extinction and of reaching the recovery goal for the lowest and highest values for each vital rate assumed in this study. Uncertainty in the number of fry per age 4 female (N_{Fry4}) has the greatest impact in that both probabilities are above the acceptable level of risk when N_{Fry4} is at its lowest selected value (37). When only 37 fry survive per age-4 female, the probability of quasi-extinction is 16% and the probability of reaching the recovery threshold is only 36%. Uncertainty in fry and smolts survival rates is also important. The probability of quasi-extinction is acceptably low ($\leq$ 0.1) when the survival rates of fry and smolt are 12% and 5%, respectively. However, at these low survivals, there is only a ~75% probability of reaching the recovery threshold (250 female spawners by 2017). Low values of Fry per age 5 female (N_{Fry5}) had much less impact on the identification of CH, which is not surprising since most spawners are 4 years old.

4.2 Identification of critical habitat

Figures 7a to 7d illustrate the profile of the probabilities of quasi-extinction for various combinations of fishing exploitation, habitats and levels of supplementation. The shaded area corresponds to configurations that have an acceptable risk of quasi-extinction. As expected, for any given level of carrying capacity of female spawners, the probability of quasi-extinction increases with an increase in fishing exploitation. In contrast, the level of supplementation does not seem to affect the habitat configuration needed to meet the threshold probability of quasi-extinction. Under the current habitat configuration and improved flow at the lake outlet (5% increase in pre-spawner survival at the lake outlet), there are two zones with an acceptable probability of quasi-extinction ($\leq$ 10%) (Figure 7a and 7b). The first zone is defined by a carrying capacity of 50 to 100 female spawners and a corresponding fishing exploitation of 0.1- 0.13. The second zone corresponds to a carrying capacity of $\geq$ 100 female spawners and a fishing exploitation of roughly $\leq$ 15%. Under the beach restoration scenario (5% increase in egg-to-fry survival), there are two zones with an acceptable probability of quasi-extinction (Figure 7c). The first zone is defined by a carrying capacity of 50-100 female spawners and a corresponding fishing exploitation of 0.15. The second zone corresponds to a carrying capacity of $\geq$ 100 female spawners and a fishing exploitation of roughly $\leq$ 17.5%. Under the beach restoration scenario (5% increase in egg-to-fry survival) and improved flow at the lake outlet (5% increase of pre-spawner survival at the lake outlet) there is one zone with an acceptable level of probability of quasi-extinction (Figure 7d). This zone is defined by a carrying capacity of $\geq$ 50 female spawners and fishing exploitation of $\leq$ 17.5%.

In summary, depending of the habitat configuration, a population with vital rates used in this study would have $\leq$10% probability of quasi-extinction under exploitations of 11.0% - 17.5% and a carrying capacity of $\geq$ 50 female spawners.

Figures 8a to 8d illustrate the profile of the probabilities of recovery for various combinations of fishing exploitation, carrying capacity of female spawners, habitat combinations, and levels of supplementation. These plots show that a minimum carrying capacity of 280 female spawners is required to meet the recovery goal of at least 250 female spawners by 2017, and is obtained under both improved flow at the lake outlet and beach restoration (Figure 8d). To identify and compare the amount of critical habitat under various habitat configurations we used 15% fishing exploitation as our maximum allowable level of exploitation (since for the 4 habitat configurations, a carrying capacity of >100 females would have ≤ 10% probability of quasi-extinction with 15% exploitation).

The critical habitat is therefore the intersection of the zone with an acceptable risk of quasi-extinction (shaded area) and the 95% probability of recovery (Figures 8a-8d). We found that the level of supplementation had little effect on the probability of reaching the recovery threshold, while habitat did. Figure 9 summarizes the critical habitat express in term of carrying capacity of female spawners for various habitat configurations. With the current habitat configuration and no exploitation, a carrying capacity of 360 female spawners is needed to meet the recovery threshold whereas habitat for an additional 101 female spawners is necessary with 15% fishing exploitation (Figure 8a). With improved flow at lake outlet conditions) (5% increase pre-spawner survival), a carrying capacity of 320 and 438 female spawners will be critical to meet the recovery goal under 0% and 15% exploitation, respectively. With beach restoration (5% increase egg-to-fry), a carrying capacity of 280 and 321 female spawners will be needed to meet the recovery goal under 0% and 15% exploitation, respectively. Finally, with improved flow and beach restoration, a carrying capacity of 280 and 287 female spawners will be needed to meet the recovery goal under 0% and 15% exploitation, respectively.

5. Discussion

In this report we described the modeling approach we developed to help identify potential critical habitat (and management actions) needed to provide a high probability of achieving a recovery goal for Sakinaw sockeye, while ensuring a low probability of quasi-extinction. As mentioned earlier, our research is preliminary. Although our approach appears promising, further investigation is needed to analyze the consequences of using alternative parameter values, density-dependent functions, simulation scenarios, a more comprehensive sensitivity analysis, and alternative criteria for quasi-extinction. Furthermore, we describe procedures to identify potential critical habitat as the habitat required to meet the stated recovery goal by 2017, but we recognize that this underestimates the habitat needed to meet the long term (~100 years) recovery goal of 5000 spawners (2500 females) (Bradford and Wood 2004).

Critical habitats

We are unable to quantify the exact amount and location of critical spawning habitat at this time, in part because we have little observation data from years when spawner densities were high, and there are few relevant published data. However, our model suggests that spawning habitat for 280 to 360 female spawners is required (depending on scenario) for Sakinaw sockeye to have <10% probability of quasi-extinction and ≥ 95% probability of meeting the recovery goal (i.e. 250 female spawners by 2017), with no fishing exploitation. To offset 15% exploitation, spawning habitat for additional 7-101 female spawners (depending on the scenario) would be needed to meet the same criteria. Note that all of these scenarios include artificial propagation proposed by the recovery team. Potential critical habitat would also include the lake outlet so that 90%-95% of the pre-spawners can reach the lake.

Critical habitat should be identified as that necessary to sustain a wild population, and not be dependent on supplementation with artificially reared fry. Accordingly, we ran additional simulation scenarios to explore the "maintenance requirement" for spawning habitat assuming that fry supplementation would be discontinued once the Sakinaw sockeye population had been restored to the minimum abundance targets set for 2017. In these simulations, the initial "restored" population comprised 55,792 females at age 1, 9,862 at age 2, 1,173 at age 3, 413, at age 4 and 10 at age 5 based on a typical result from a previous simulation under a successful rebuilding scenario. Extent of spawning habitat had a large effect on the probability of maintaining abundance above the minimum target level of 250 spawners (Figure 10). However, annual variation in survival rates, especially smolt to age 3 (marine) survival, ultimately constrained the effectiveness of increasing spawning habitat as a strategy to maintain abundance. For the example scenario with 15% fishing mortality, no artificial propagation of fry, and enough spawning habitat for 600 females, the probability of falling below 250 female spawners within 6 generations was decreased from 40% to 10% by reducing annual variability in marine survival by 50%. No comparable improvement in viability could be achieved simply by adding spawning habitat without reducing variability in survival rates. Based on recent recommendations by Bradford and Wood (2004), further work on modeling CH should consider multiple goals and both minimum abundance and quasi-extinction should be computed as generational averages.

The delimitation of the critical spawning habitat is obviously more complex than simply estimating the spawning habitat as the number of redds by the average area occupied by a redd. For instance, there is a high variation in the quality of the beaches – within the beach areas used for spawning are pockets of habitat that are highly suitable, and many other areas that are less suitable. Some of these other areas may be used at higher spawner densities. Additional field observations are clearly needed to describe egg-to-fry survival as a function of spawner density, habitat quality and location. Alternatively, an experimental approach where spawning sockeye within large enclosures are monitored may be required. For the time being, Sharon's beach, the only beach that sockeye have consistently selected for spawning at recent low spawner abundances should be considered part of the potential critical habitat. Since the utility of the spawning beaches depends on ground water input from adjacent stream watersheds, the watersheds themselves may also be potential critical habitat. A better understanding of the origin of ground water at the spawning beaches is necessary to determine whether stream watersheds should be considered as CH.

Model expansion and retrospective analysis

Although we focused on few habitats (lake outlet, spawning beaches) and their impact on the survival of certain stages (pre-spawners and egg-to-fry survival) and ultimately on the recovery of Sakinaw sockeye - our model like others (Greene and Beechie 2004) could be expanded to include other habitats such as lake rearing habitat and associated life stages.

The addition of a spatial structure to our model might be useful to delimitate the spawning beaches that are needed for the recovery of Sakinaw sockeye. Application of a habitat-based metapopulation modeling approach (Akçakaya and Atwood 1997 and Akçakaya 2000) to our situation would require a predictive model to describe if a particular location is likely to be used for spawning. This model of habitat suitability for spawning could be based on environmental factors related to the substrate attributes susceptible to affecting spawning quality (e.g. substrate type-temperature-oxygen-slope-surficial groundwater flow, proximity to stream mouth). Once such a model is available, RAMAS GIS and other software could be used to identify habitat patches that may support subpopulations, based on the spatial distribution of suitable habitat. The demographic parameters (survival and fecundity) of subpopulations may differ, and may be based on the habitat characteristics of the beach occupied by that subpopulation. The carrying capacity for each major area may also differ, and may depend on both habitat quality and area of each beach (see Akçakaya 2002 for details). Other spatial factors that operate at the metapopulation level such as distances and the rates of dispersal among populations, and the degree of environmental fluctuation by different populations would also be required. Unfortunately, we do not yet have sufficient data to develop such an approach.

A simpler alternative would be to use a single-population model in conjunction with a habitat model. This would consist of weighting egg-to-fry survival according to spawner abundance, amount of spawning habitat of various qualities and their respective egg-to-fry survival. For example, areas of low, medium, and high spawning quality could be estimated from a habitat model and their corresponding egg-to-fry survival from experiments or expert opinion. A weighted egg-to-fry survival could be estimated under the assumptions that spawning areas are selected according to their quality from high to low, spawners dispersal is not limited, environmental fluctuations among the spawning areas are correlated, and egg-to-fry survival within each habitat spawning type is independent of spawners density.

We know Sakinaw sockeye were relatively abundant until the late 1980's (average escapement ~ 5000) but the population crashed in recent years (Figure 2). We plan to be able to re-run our model using initial population sizes from this earlier period and then experiment with parameter values (e.g. fishing exploitation, marine survival, freshwater survival) to determine what conditions might cause the population to crash. For instance, we suspect that survivals of pre-spawners swimming up the outlet stream may sometimes have been considerably lower than we permitted in our model. This retrospective analysis may also give us a better idea of what parameter values are realistic at present, especially parameters related to marine survival. We would then re-run our model to evaluate the potential role of critical habitat on the ability of the population to survive and recover.

Model parameters

Sakinaw sockeye can be categorized as data-limited. We populated our model chiefly using parameter values from other better studied populations. Are these values therefore appropriate for Sakinaw sockeye? We don't know yet - but it seems likely that Sakinaw sockeye declined rapidly in the 1990s because they had lower survival than most other populations. Our assumption that the variation in vital rates between populations adequately represents the variation for Sakinaw sockeye may be faulty. Empirical relationships are required to make use of information from other populations. Sensitivity analysis are needed to explore the implications of the variation, trend and correlation in vital parameters that might be induced by various factors (e.g. climate change, fishing, etc.) on the identification of CH.

The model allowed us to evaluate possible fishery management actions, and investigate their linkages with critical habitat, and their dual impacts on species survival and recovery. The approach was useful, although it is not clear if we will ever be able to differentiate between marine fishing and freshwater habitat effects based on the data we have.

Model applicability

We chose Sakinaw sockeye to carry out this case study in part because they have a restricted freshwater distribution. How applicable is our approach then to other sockeye populations, and other species of Pacific salmon? We think this approach is applicable for other sockeye populations and, with some limitations, other species of salmon. However, for this approach to work, one needs to have a good understanding of the life cycle of the species under investigation, and to know under what conditions, if any, habitat becomes limiting.

Acknowledgements

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Table 1a. Variable definitions and names used in the age structured model for Sakinaw sockeye.

Variable Description	Variable Name
Number of eggs/female	N_0
Proportion of female that breed by age 4	P_{mat4}
Proportion of female that breed by age 5	P_{mat5}
fishing exploitation	μ
Survival of pre-spawners migrating up the lake outlet	S_{lake}
Survival of pre-spawners in the lake (main source of mortality thought to be due to lamprey predation)	$S_{lamprey}$
Egg-to-fry survival	S_{eggs}
Ratio: female/total	P_{fem}
Fry-to-smolt survival	S_{fry_smolt}
Smolt (age 2) - age 3-survival	S_{smolt_age3}
Ocean survival of age 3 female	S_{o_age3}
Ocean survival of age 4 female	S_{o_age4}
Number of female fry born to a single age 4 female	N_{Fry4}
Number of female fry born to a single age 5 female	N_{Fry5}

Table 1b. Parametrization of an age structured model for Sakinaw sockeye: variable names, source, population(s), mean and standard deviation due to environmental variation (SD). BC stands for British Columbia and EO for expert opinion.

Variable Name	Source	Population(s)	mean	SD
N_0	Murray and Wood (2002)	Sakinaw - brood stock	2500	0.0
P_{mat4}	EO		(>0.9)	0.0
	Simulation (see appendix 1)		0.95	0.0
P_{mat5}	EO		1.0	0.0
S_{lake}	EO		0.90	0.18
$S_{lamprey}$	EO		0.95	0.19
P_{fem}	EO		0.5	0.0
S_{eggs}	Bradford 1995	11 from BC	.131	0.034
S_{fry_smolt}	Bradford 1995	5 from BC	.25	0.12
$S2=S_{smolt\_age3}$	Simulation (see Appendix 1)		0.0989	0.049
S_{o_age3}	Assumption		0.8	0.0
S_{o_age4}	assumption		0.8	0.0
N_{Fry4}	Equation (1)		132	0.144
N_{Fry5}	Equation (2)		139	0.144

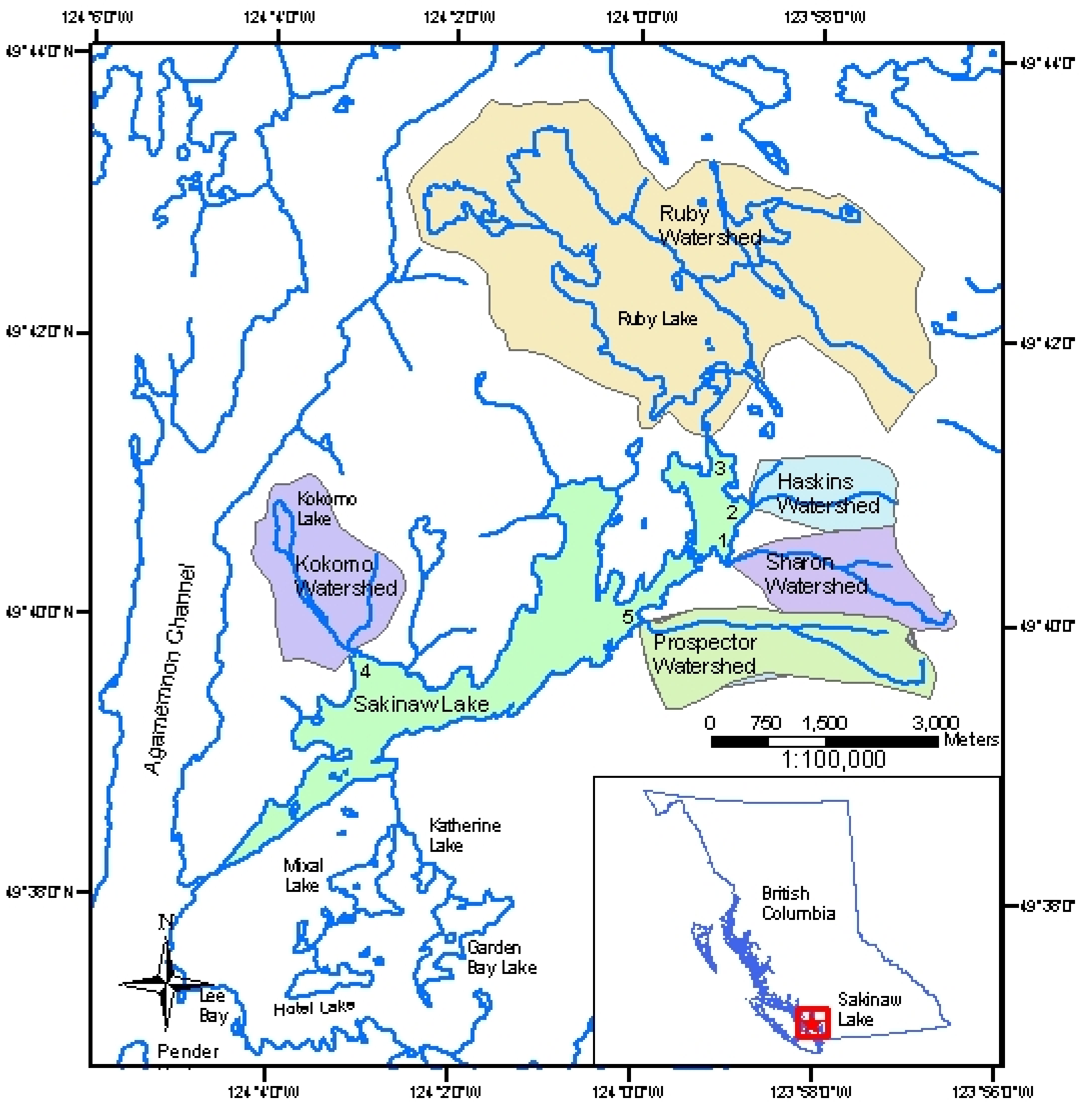


Figure 1. Sakinaw Lake, its tributaries, known sockeye spawning beaches and their watersheds: Beach 1 (Sharon's); Beach 2 (Haskins); Beach 3 (Ruby Creek Bay); Beach 4 (Kokomo Creek Bay) and Beach 5 (Unnamed creek). Inset shows location of Sakinaw Lake within southern British Columbia.

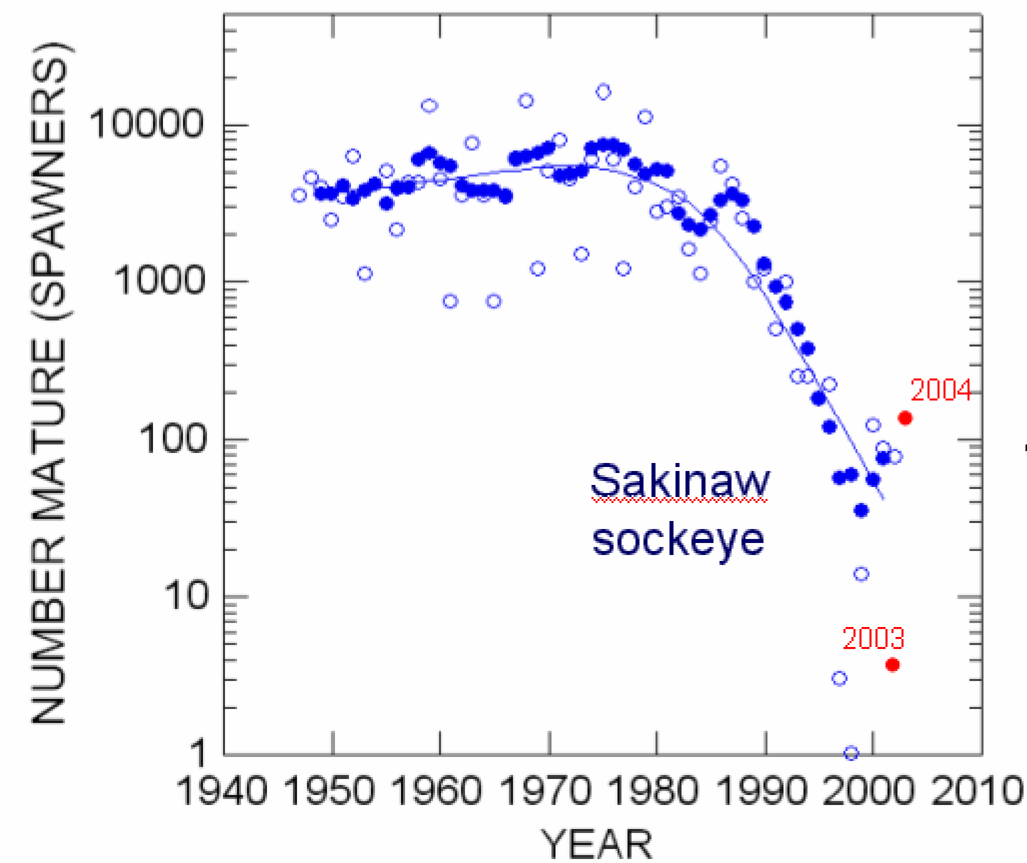


Figure 2. Trends in number of mature individuals in the Sakinaw Lake sockeye salmon population. Open circles are annual estimates of spawning escapement; filled circles are the corresponding estimates smoothed over one-generation (4 yr); line is fitted to smoothed data by LOWESS.

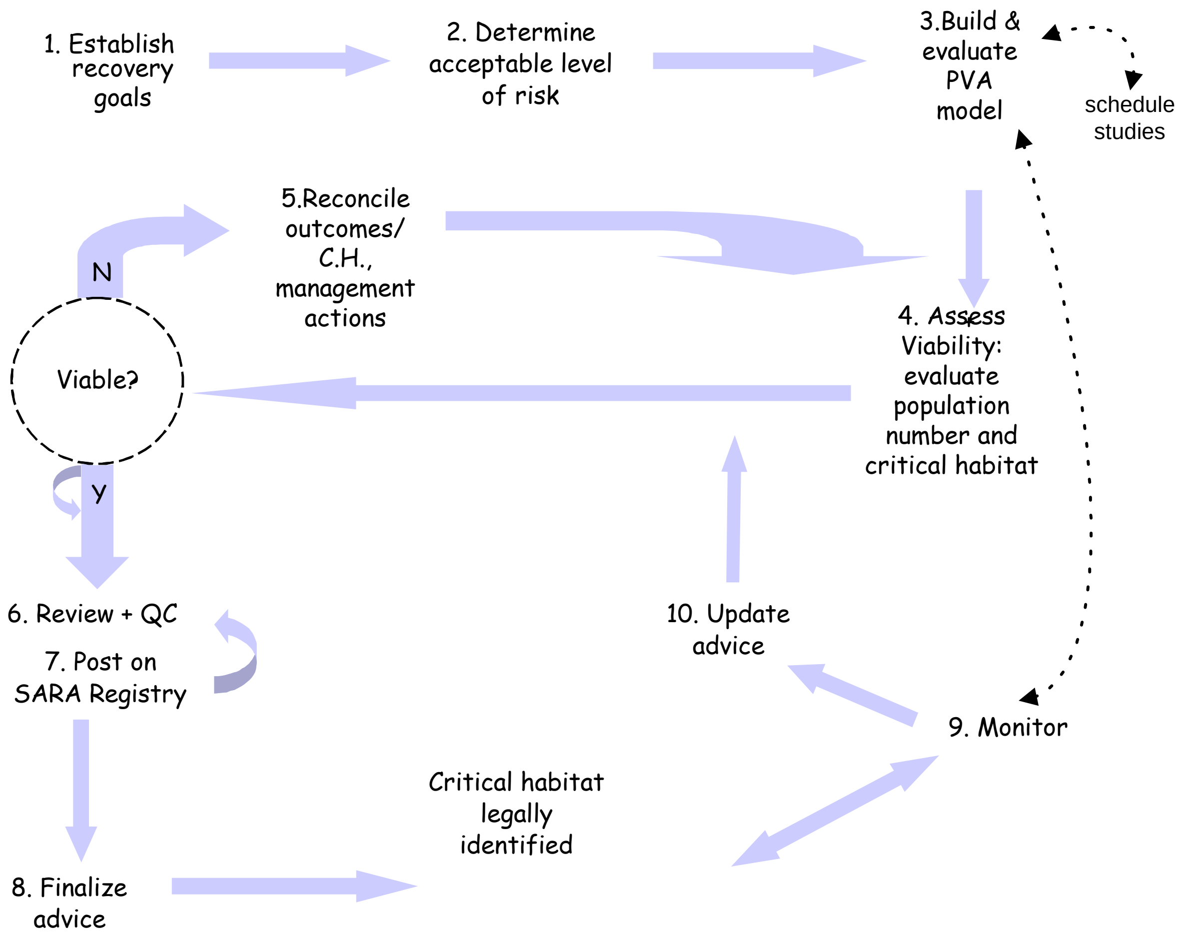


Figure 3. Ten step approach for establishing critical habitat (C.H.) and management actions (after Environment Canada 2004).

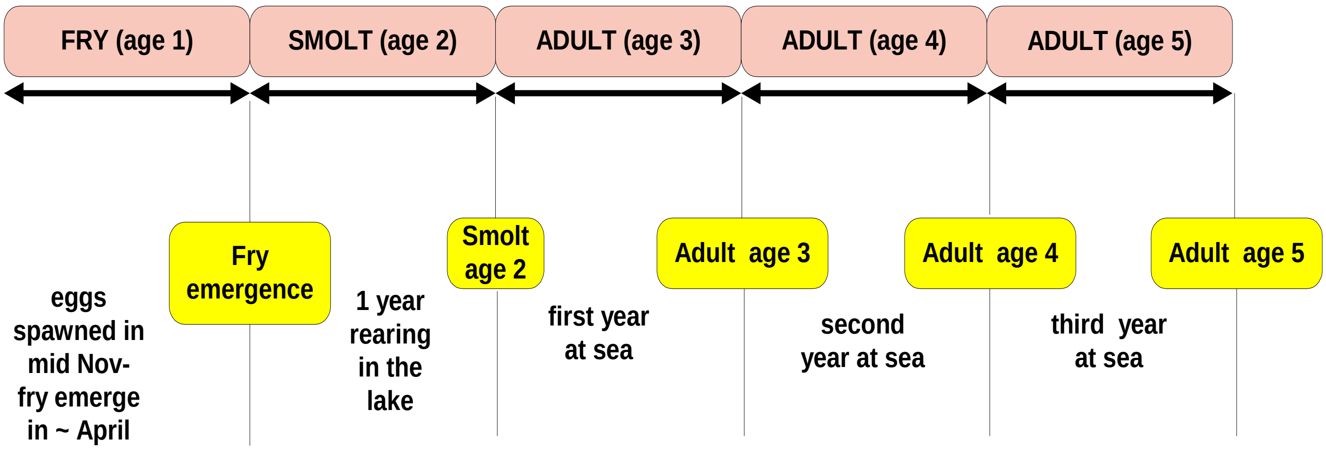
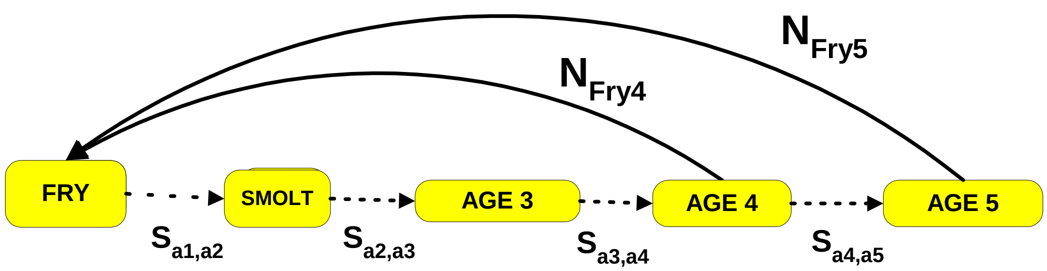


Figure 4. Explanation of the five age classes in the age structured model developed for Sakinaw sockeye. Only female are modelled. Age classes (1-5): fry, smolt, adult age 3, adult age 4 and adult 5.



$$\begin{bmatrix} 0 & 0 & 0 & N_{Fry4} & N_{Fry5} \\ S_{a1,a2} & 0 & 0 & 0 & 0 \\ 0 & S_{a2,a3} & 0 & 0 & 0 \\ 0 & 0 & S_{a3,a4} & 0 & 0 \\ 0 & 0 & 0 & S_{a4,a5} & 0 \end{bmatrix} \times \begin{bmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \\ N_4(t) \\ N_5(t) \end{bmatrix} = \begin{bmatrix} N_1(t+1) \\ N_2(t+1) \\ N_3(t+1) \\ N_4(t+1) \\ N_5(t+1) \end{bmatrix}$$

$$L(t) \times N(t) = N(t+1)$$

Figure 5. Age structured model for Sakinaw sockeye showing the relationship between the probability of survival from one age class at time ‘t’ to the next ($S_{a,a+1}$) at time ‘t+1’ (dashed line), numbers of fry per age 4 and age 5 female (N_{Fry4} and N_{Fry5}, black arrow full line), the transition matrix L(t), initial abundance matrix (N(t)), and abundance at time ‘t+1’ (N (t+1)).

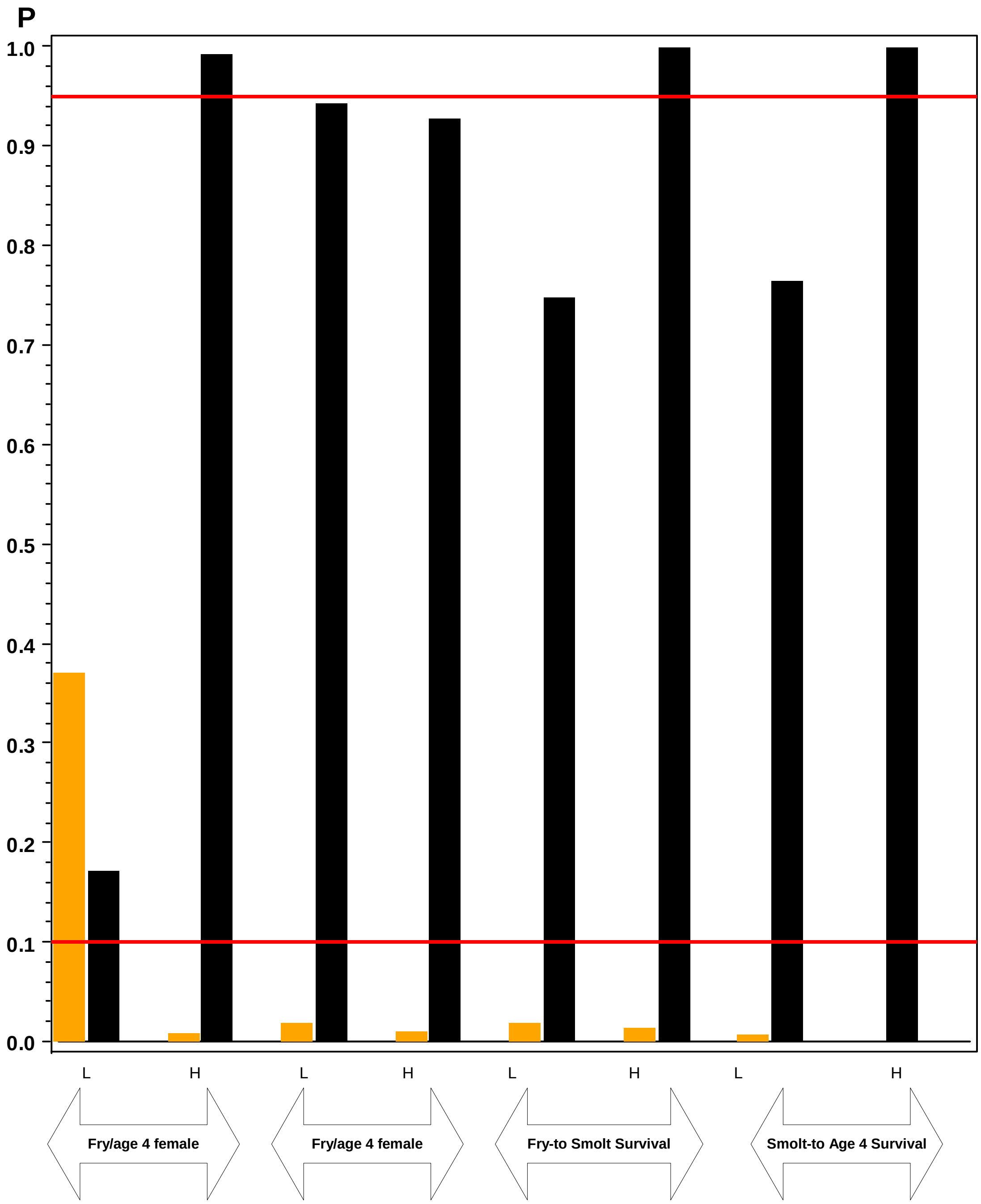


Figure 6. Results from sensitivity analyses examining the effects of low (L) and high (H) survivals on probabilities of quasi-extinction (light histograms) and of meeting the recovery goal of 250 female spawners by 2017 (dark histograms). Lower horizontal line is a reference probability (0.1) for quasi-extinction and upper horizontal line is a reference level for achieving the recovery goal (0.95). Low and high egg-to-fry survivals of 0.037 and 0.223 correspond to low and high values of N_{Fry4}, N_{Fry5} of 37,224; 39, 245, respectively. Low and high values of fry to smolt survival and smolt to age 3 were 0.128, 0.372; and 0.05, 0.148 respectively.

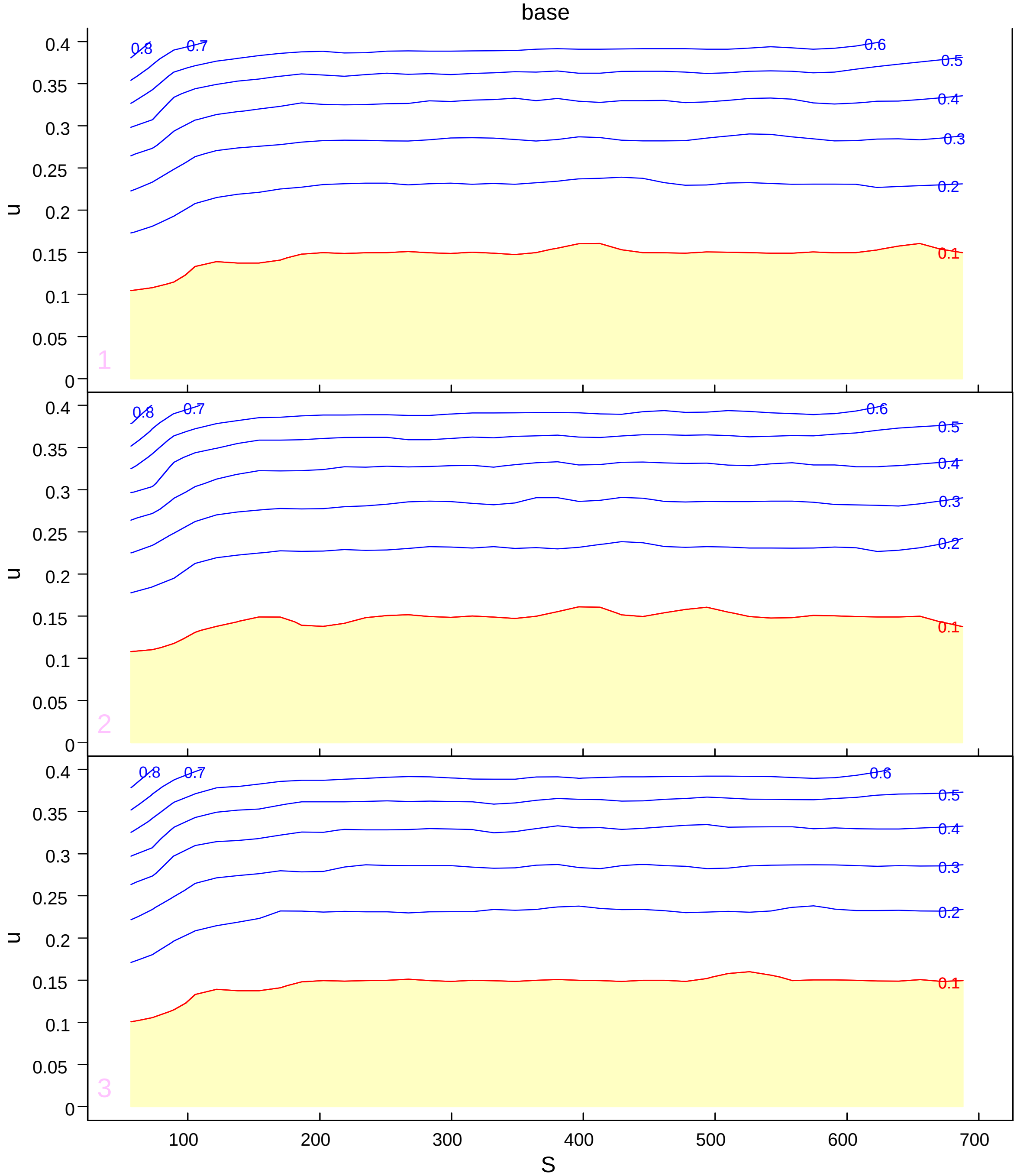


Figure 7a. Probabilities of quasi-extinction for combinations of fishery exploitation (µ, Y axis) and carrying capacity of female spawners (S, X axis). Levels 1-3 for each of the habitat configurations (base, lake, eggs, and eggsl) represent three levels of fed-fry supplementation in 2005 and 2006 (50,000, 84,000, and 120,000 respectively). The shaded area corresponds to the zone with an acceptable probability for quasi-extinction (≤0.1). The 'base' configuration used an egg-to-fry survival (S_{eggs}) of 0.13 and a pre-spawners survival rate in the lake outlet (S_{lake}) of 0.90.

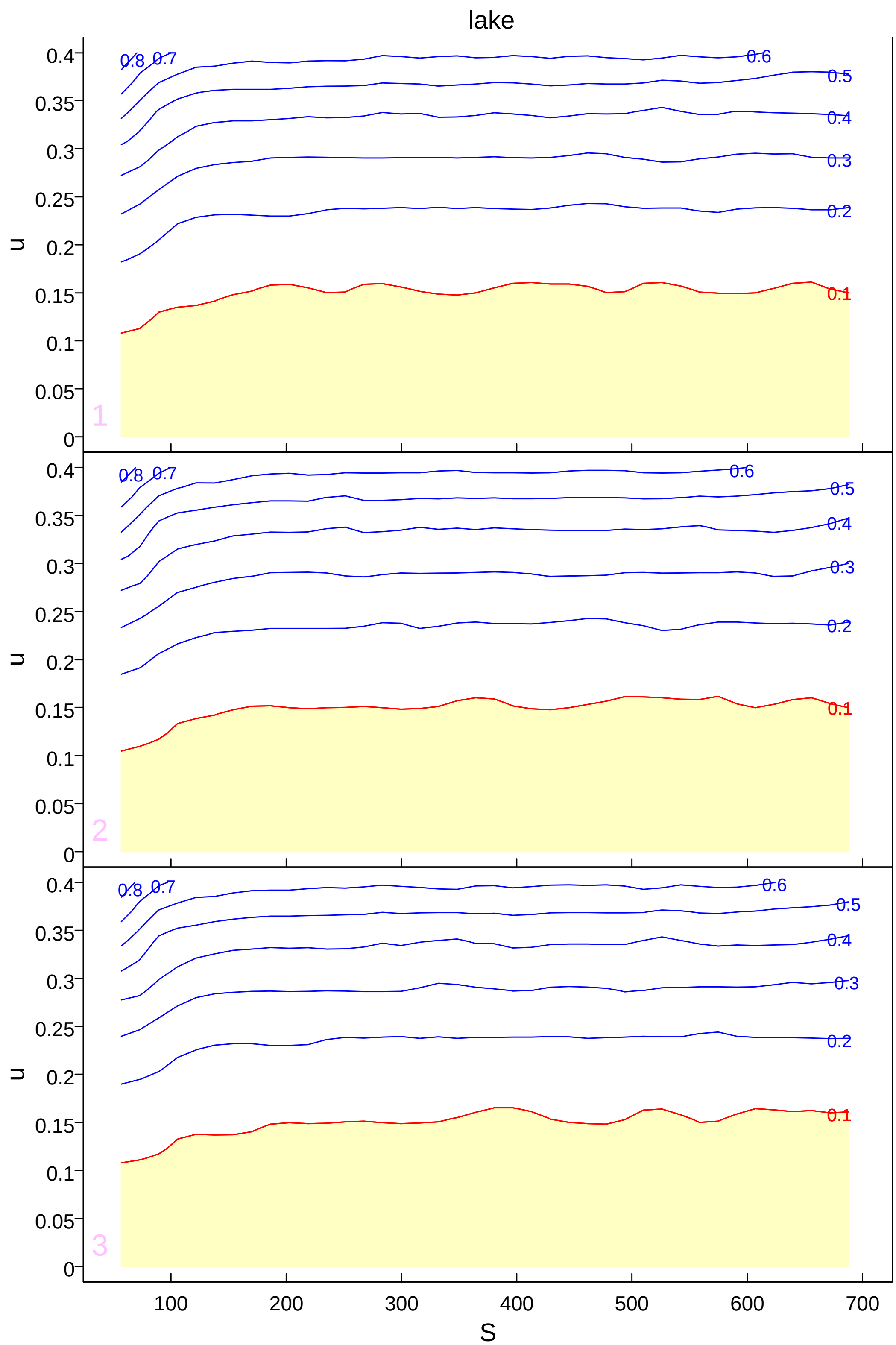


Figure 7b. As 7a except that ‘lake’ habitat configuration used a pre-spawners survival rate in the lake outlet (Slake) of 0.95. The shaded area corresponds to configurations that have an acceptable risk of quasi-extinction.

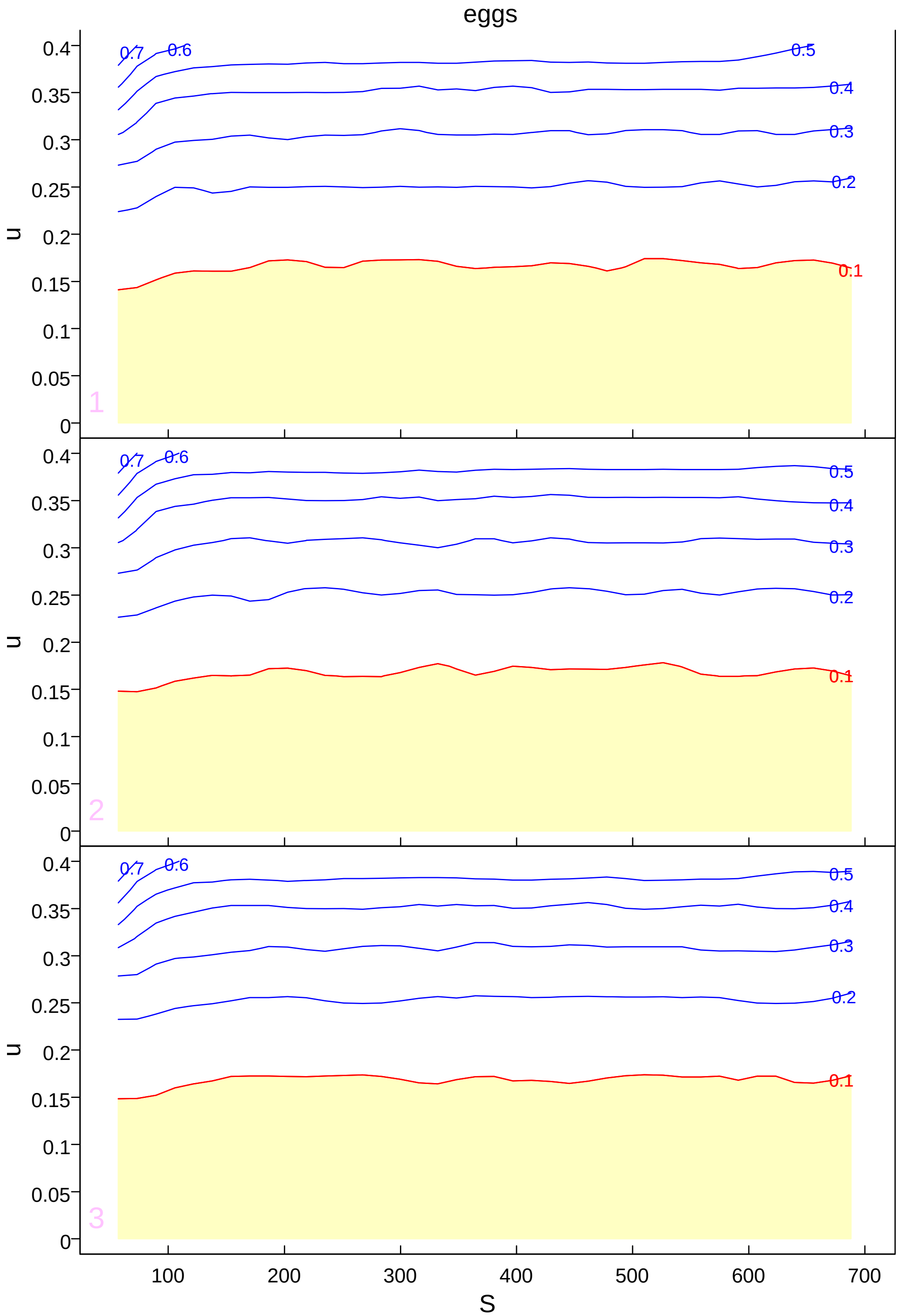


Figure 7c. As 7a except, except that 'eggs' habitat configuration refers to an egg-to-fry survival (S_{eggs}) of 0.18. The shaded area corresponds to configurations that have an acceptable risk of quasi-extinction.

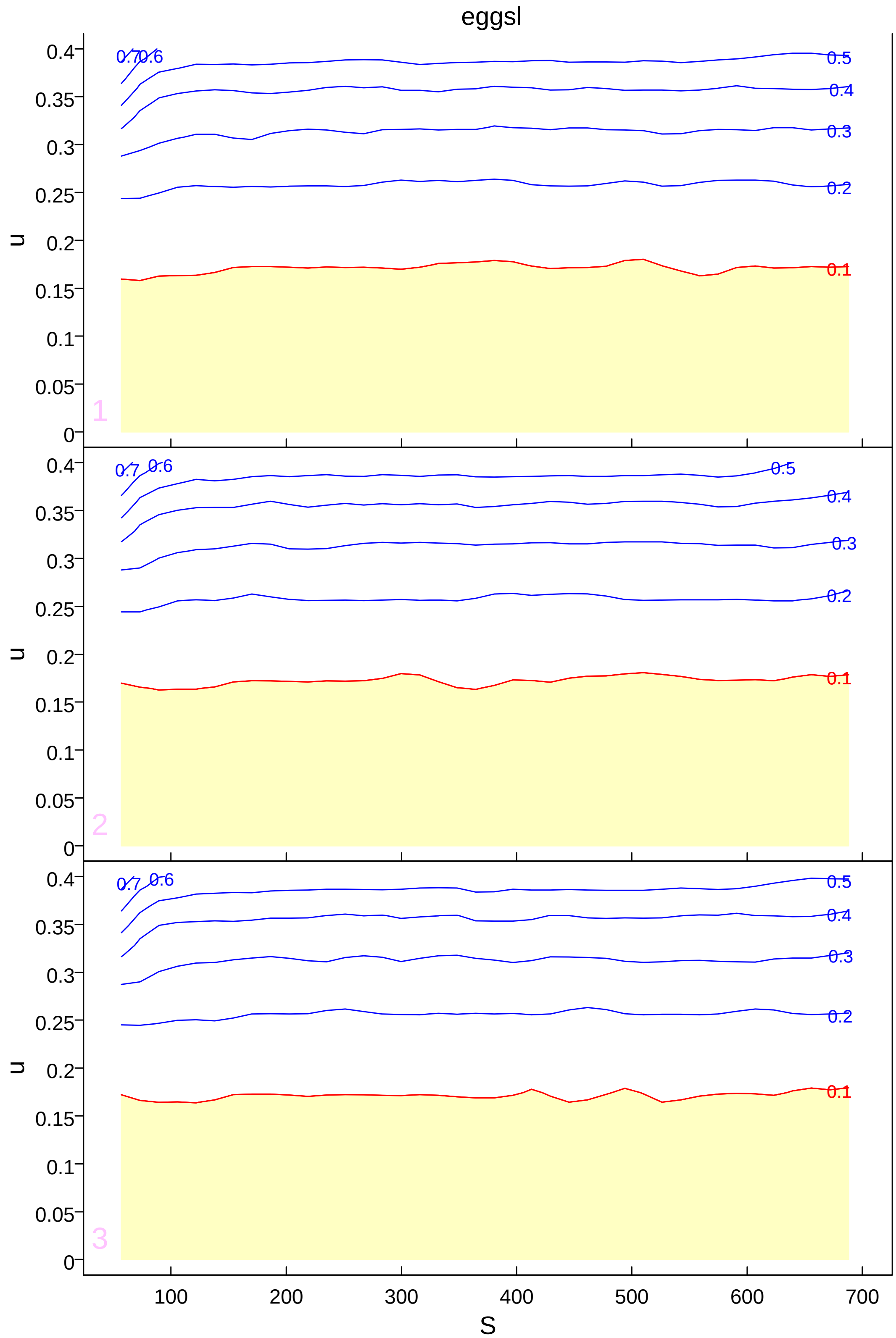


Figure 7d. As 7a except, except that 'eggsl' habitat configuration refers to an egg-to-fry survival (S_{eggs}) of 0.18 and a pre-spawners survival rate in the lake outlet (S_{lake}) of 0.95. The shaded area corresponds to configurations that have an acceptable risk of quasi-extinction.

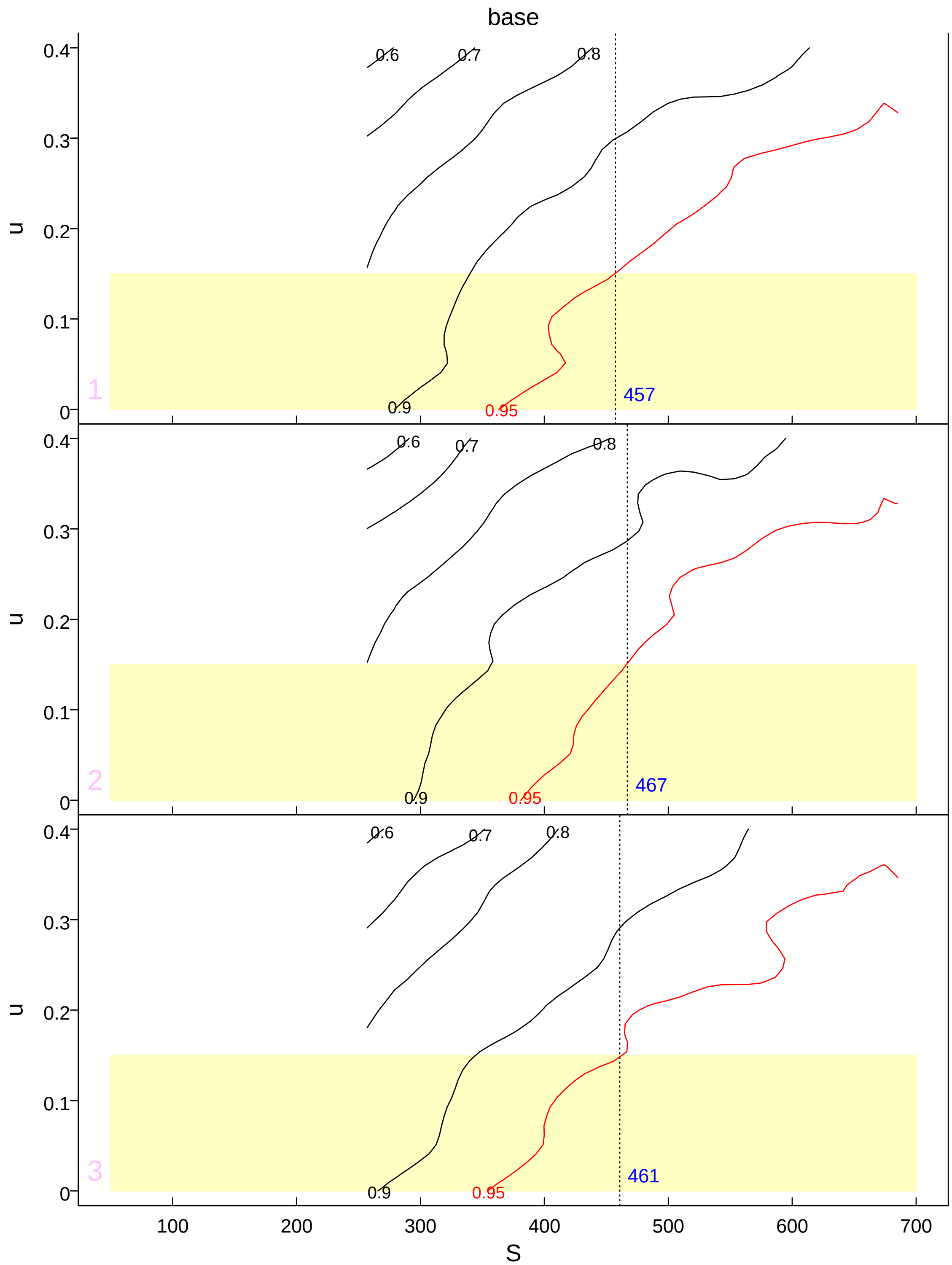


Figure 8a. Probability of meeting the recovery threshold of 250 female spawners by 2017 under the same scenarios as in Figure 7a. The shaded area corresponds to configurations that have an acceptable risk of quasi-extinction. The area corresponding to a probability of at least 0.95 corresponds to habitat configurations that have an acceptable level of meeting the recovery goal. The habitat configuration described by the line of interception between these 2 areas corresponds to critical habitat. For example, for the “base” configuration, 120,000 fed-fry in 2005 and 2006 and 15% fishing exploitation, the habitat necessary for 461 female spawners is critical.

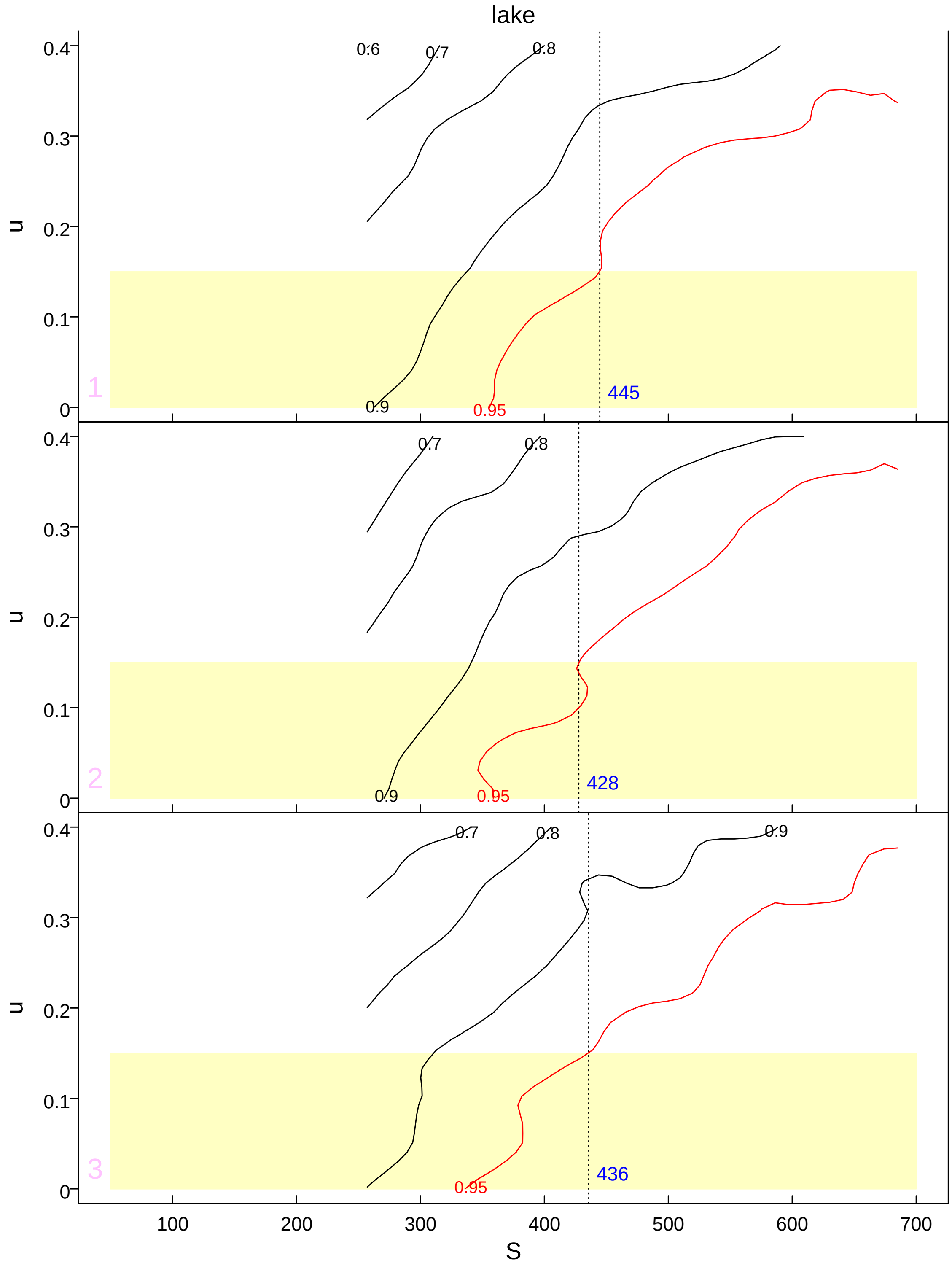


Figure 8b. As 8a except that 'lake' habitat configuration used a pre-spawners survival rate in the lake outlet (S_{lake}) of 0.95. For example, for the "lake" configuration, 120,000 fed-fry in 2005 and 2006 and 15% fishing exploitation, the habitat necessary for 436 female spawners is critical.

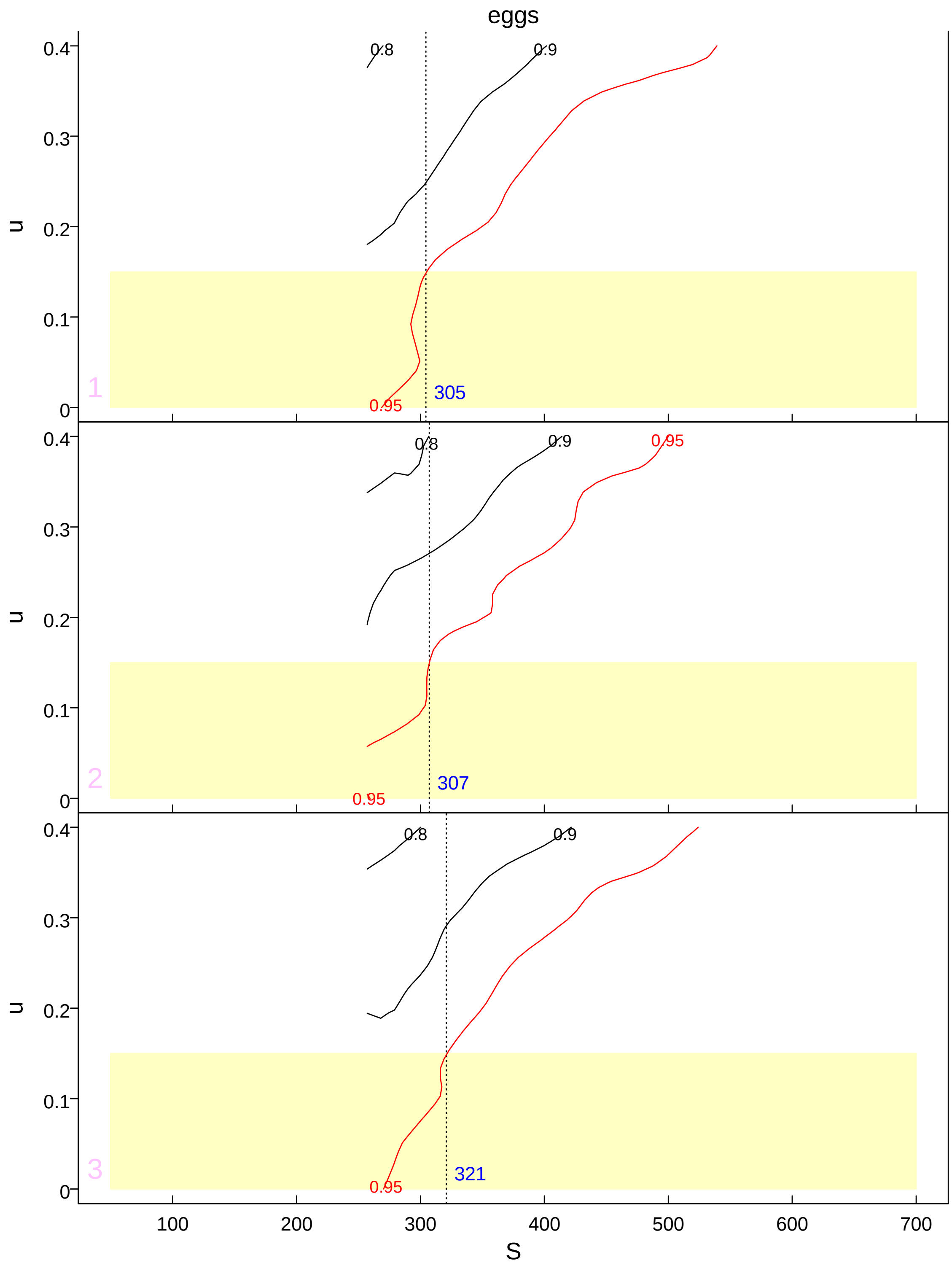


Figure 8c. As 8a except that 'eggs' habitat configuration used an egg-to-fry survival (S_{eggs}) of 0.18. For example, for the "eggs" configuration, 120,000 fed-fry in 2005 and 2006 and 15% fishing exploitation, the habitat necessary for 321 female spawners is critical.

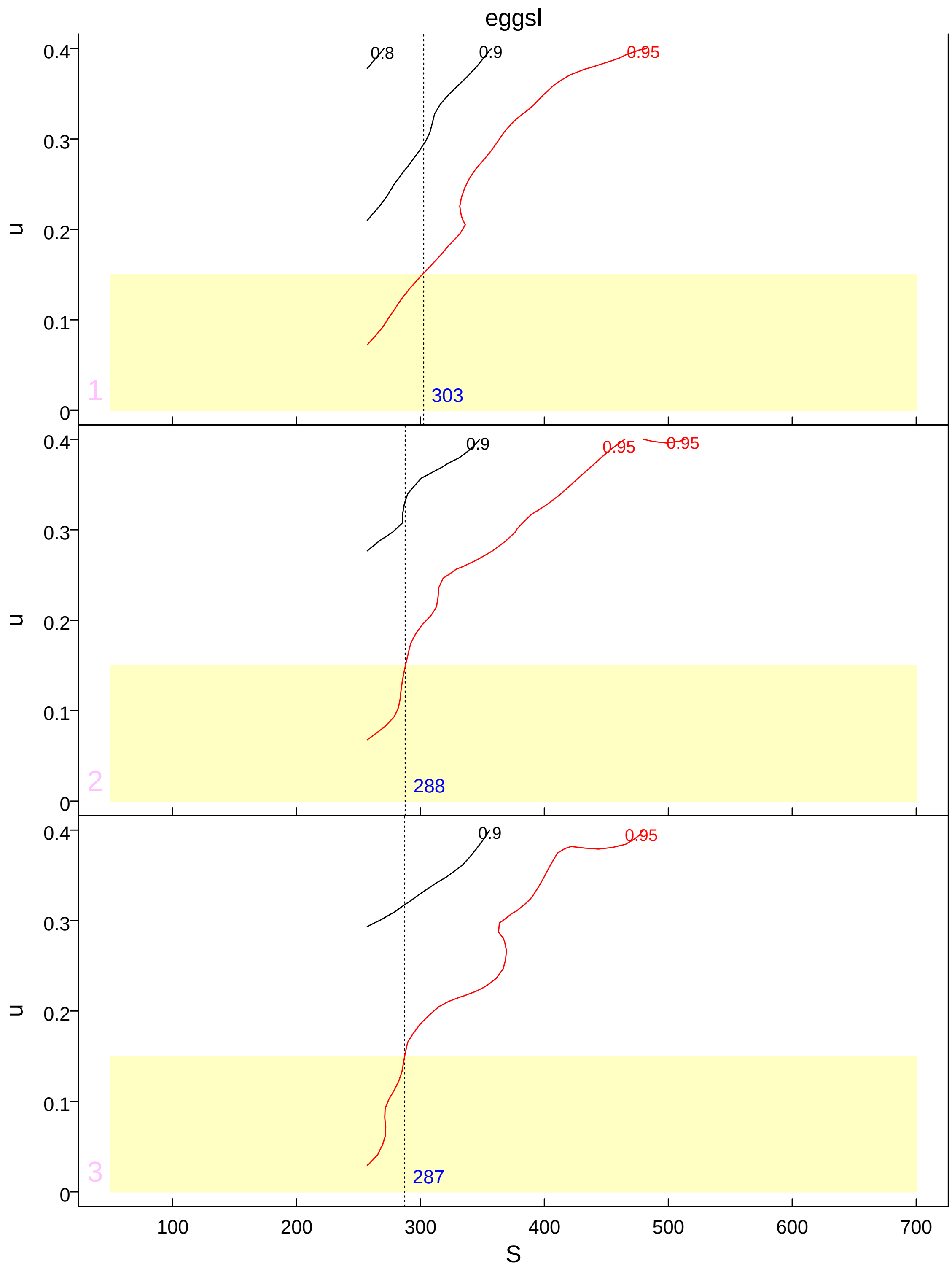


Figure 8d. As 8a except, except that ‘eggsl’ habitat configuration refer to an egg-to-fry survival of 0.18 (S_{eggs}) and a pre-spawners survival rate in the lake outlet (S_{lake}) of 0.95. For example, for the “eggsl” configuration, 120,000 fed-fry in 2005 and 2006 and 15% fishing exploitation, the habitat necessary for 287 female spawners is critical.

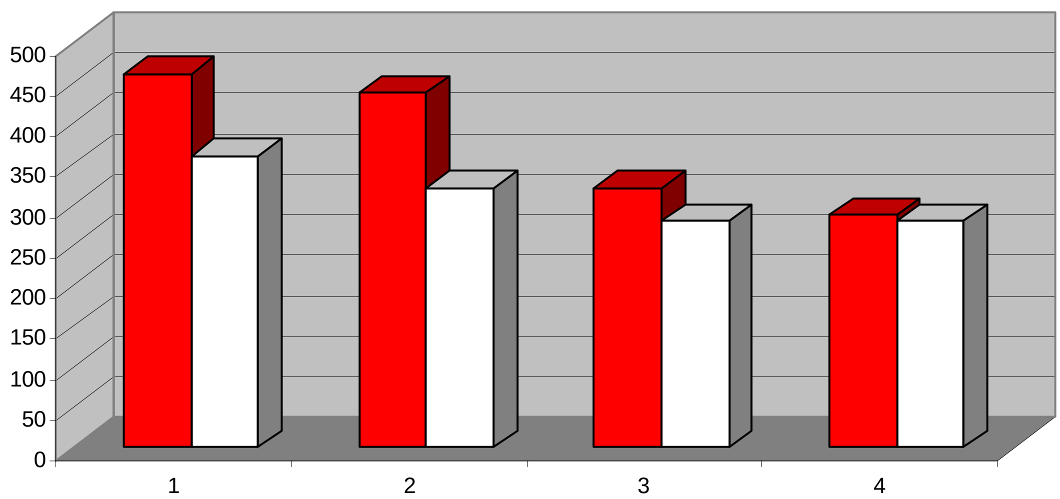


Figure 9. Critical carrying capacity of female spawners (Y axis) under current habitat configuration (1), improved flow at the lake outlet (2), beach restoration (3) and of improved flow at the lake outlet and beach restoration (4) under no fishing (light) and 15% fishing exploitation (dark).

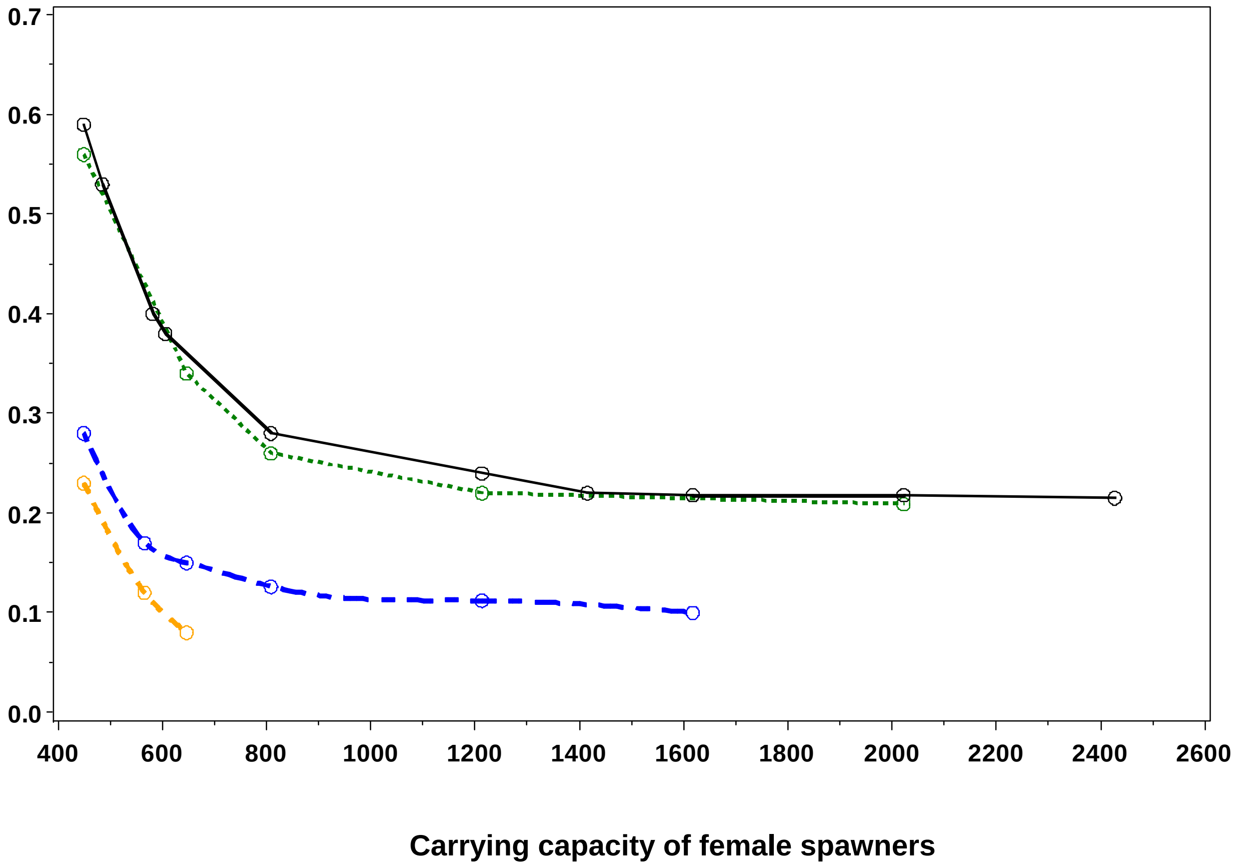


Figure 10. Probability of remaining above minimum target of 250 female spawners (Y axis) every year from 2017- to 2041 (6 generations) if fry supplementation is discontinued and fishing mortality remains at 15%, plotted as a function of carrying capacity of female spawners (X axis). All simulations began with a "restored" population based on previous simulation results for 2017 under successful rebuilding scenarios (55,792 females at age 1, 9,862 at age 2, 1,173 at age 3, 413, at age 4 and 10 at age 5). Other parameters are the same as in the previous base case (solid line), or with variability reduced by 50% in fecundity (dotted line), survival from fry to smolt (long dashed line), or survival from smolt to age3 (short dashed line).

Appendix 1. Procedure used to estimate the proportion of age 4 females that are mature and age specific ocean survival rates. Below are age specific related variables: number, survival, and proportion of mature fish.

Variable Description	Variable Name
Number of females in class 2	N_2
Number of females in class 3	N_3
Number of females in class 4	N_4
Number of females in class 5	N_5
Proportion of females that breed by age 4	P_{mat4}
Proportion of females that breed by age 5	P_{mat5}
Proportion of age-4 female spawners	PS_4
Fishery exploitation	μ
Pre-spawner survival in lake outlet	S_{lake}
Pre-spawners survival to lamprey predation	$S_{lamprey}$
Egg-to-fry survival	S_{eggs}
Ratio: female/total	P_{fem}
Fry-to-smolt survival	S_{fry_smolt}
Smolt (age 2)-to- age 3 survival	S_{smolt_age3}
Ocean survival of age 3 female	S_{o_age3}
Number of female spawners at age-4	NS_4
Ocean Survival of age 4 female	S_{o_age4}
Number of female spawners at age-5	NS_5
Marine survival of females	MS

The equations 1 to 12[4] describe how these variables are related.

0. $S_z = S_3 = S_4$ (assume survival of age 3 and 4 is the same)

1. $S_r = \dfrac{S_z}{S_2}$

2. $N_3 = N_2 \cdot S_2$

3. $N_4 = N_3 \cdot S_3 = (N_2 \cdot S_2) \cdot S_z$

4. $N_5 = N_4 \cdot S_4 \cdot (1 - P_{MAT4}) = (N_2 \cdot S_2) \cdot S_3 \cdot S_4 \cdot (1 - P_{MAT4}) = (N_2 \cdot S_2) \cdot S_z^{\,2} \cdot (1 - P_{MAT4})$

5. $NS_4 = N_4 \cdot P_{MAT4} \cdot (1 - \mu) = (N_2 \cdot S_2) \cdot S_z \cdot P_{MAT4} \cdot (1 - \mu)$

[4] Note that S_3 and S_4 refers to So_age3 and So_age4, respectively.

6. $NS_5 = N_5 \cdot (1-\mu) = (N_2 \cdot S_2) \cdot S_z^{\ 2} \cdot (1 - P_{MAT4}) \cdot (1-\mu)$

7. $MS = \dfrac{N_4 \cdot P_{MAT4} + N_5}{N_2}$

8. $PS_4 = \dfrac{NS_4}{NS_4 + NS_5}$

Substituting eq. (3) and eq. (4) into eq. (7), and S_2 by S_z/S_r, and simplifying, we get:

9a.

$$MS = \frac{(N_2 \cdot S_2) \cdot S_z \cdot P_{MAT4} + (N_2 \cdot S_2) \cdot S_z^{\ 2} \cdot (1 - P_{MAT4})}{N_2} = \frac{S_z^{\ 2}}{S_r} \cdot [P_{MAT4} + S_z \cdot (1 - P_{MAT4})]$$

9b MS = $\dfrac{S_z^{\ 2}}{S_z / S_2}.\ [P_{MAT4} + S_z \cdot (1 - P_{MAT4}) = S_2 . S_z [P_{MAT4} + S_z \cdot (1 - P_{MAT4})]$

Substituting eq. (5) and eq. (6) into eq. (8) and simplifying, we get:

$$10.\ PS_4 = \frac{(N_2 \cdot S_2) \cdot S_z \cdot P_{MAT4} \cdot (1-\mu)}{(N_2 \cdot S_2) \cdot S_z \cdot P_{MAT4} \cdot (1-\mu) + (N_2 \cdot S_2) \cdot S_z^{\ 2} \cdot (1 - P_{MAT4}) \cdot (1-\mu)} =$$

$$= \frac{P_{MAT4}}{P_{MAT4} + S_z \cdot (1 - P_{MAT4})}$$

Rearranging eq. (10) to isolate S_z as:

$$11.\ S_z = \frac{P_{MAT4} - PS_4 \cdot P_{MAT4}}{PS_4 \cdot (1 - P_{MAT4})}$$

Substituting eq. (11) into eq. (9), we get:

$$12.\ MS = \frac{1}{S_r} \cdot \left(\frac{P_{MAT4} - PS_4 \cdot P_{MAT4}}{PS_4 (1 - P_{MAT4})} \right)^2 \cdot \left[P_{MAT4} + \left(\frac{P_{MAT4} - PS_4 \cdot P_{MAT4}}{PS_4 \cdot (1 - P_{MAT4})} \right) \cdot (1 - P_{MAT4}) \right] =$$

$$= \frac{P_{MAT4}^{\ 3}}{S_r \cdot P_{S4}^{\ 3}} \cdot \left(\frac{1 - PS_4}{1 - P_{MAT4}} \right)^2$$

Estimation of P_{MAT4} using equation 11 and values of PS_4 and S_z

Rearranging equation 11 as follow.

$$S_z \cdot PS_4 \cdot (1-P_{MAT4}) = P_{MAT4} - PS_4 \cdot P_{MAT4}$$

$$S_z \cdot PS_4 - S_z \cdot PS_4 \cdot P_{MAT4} = P_{MAT4} - PS_4 \cdot P_{MAT4}$$

$$S_z \cdot PS_4 = P_{MAT4} + S_z \cdot PS_4 \cdot P_{MAT4} - PS_4 \cdot P_{MAT4}$$

$$P_{MAT4} \cdot (1 + S_z \cdot PS_4 - PS_4) = S_z \cdot PS_4$$

$$P_{MAT4} = \frac{S_z \cdot PS_4}{1 + S_z \cdot PS_4 - PS_4}$$

We estimated P_{MAT4}=0.950495 using values that have been observed in the field (PS_4=0.96) or seemed reasonable (S_z=0.8)

Estimation of S_2 using equation 9b, and values for S_z, PS_4, P_{MAT4}, and MS

We assumed that the marine survival (MS) of sockeye from Chilko lake is representative of the marine survival of Sakinaw sockeye, all the variability in marine survival occurred at the smolt stage,.and that the ocean survival of age-3 and age-4 are the same and equal 0.8 (0).

Rearranging equation 9b as

$$S_2 = \frac{MS}{S_z[P_{MAT4} + S_z \cdot (1 - P_{MAT4})}$$

Using PS_4 (0.96), S_z(.8) ,and P_{MAT4} (0.95) and 1000 values of MS draw at random from Chilko log normal distribution of marine survival , we estimated the mean and standard deviation of S2 as 0.0989 and 0.0693, respectively.

Appendix 2. Procedure used to estimate the number of age 4 and 5 female adults to corresponding to the number of age 4 and 5 female spawners.

Given

(3) $N_4 = N_3 \cdot S_3 = (N_2 \cdot S_2) \cdot S_z$

(4) $N_5 = N_4 \cdot S_4 \cdot (1 - P_{MAT4}) = (N_2 \cdot S_2) \cdot S_3 \cdot S_4 \cdot (1 - P_{MAT4}) = (N_2 \cdot S_2) \cdot S_z^{\,2} \cdot (1 - P_{MAT4})$

(5) $NS_4 = N_4 \cdot P_{MAT4} \cdot (1 - \mu) = (N_2 \cdot S_2) \cdot S_z \cdot P_{MAT4} \cdot (1 - \mu)$

(6) $NS_5 = N_5 \cdot (1 - \mu) = (N_2 \cdot S_2) \cdot S_z^{\,2} \cdot (1 - P_{MAT4}) \cdot (1 - \mu)$

Expressing (N_4+ N_5) in terms of N_4 using (4)

$N_4 + N_5 = N_4 \cdot S_4 \cdot (1 - P_{MAT4})$ **(a)**

and NS_5 in terms of NS_4

Substitute NS_4 (4) and NS_5 (5)

$$NS_5 / NS_4 = \frac{(N_2 \cdot S_2) \cdot S_z^{\,2} \cdot (1 - P_{MAT4}) \cdot (1 - \mu)}{(N_2 \cdot S_2) \cdot S_z \cdot P_{MAT4} \cdot (1 - \mu)} = \frac{S_z\ (1 - P_{MAT4})}{P_{MAT4}} \quad \textbf{(b)}$$

$$NS_5 = \frac{S_z\ (1 - P_{MAT4})}{P_{MAT4}} . NS_4 \quad \textbf{(c)}$$

Expressing (NS_4 + NS_5) in terms of N_4 using (5) and (c)

$$N_4 + N_5 = N_4 \cdot P_{MAT4} \cdot (1 - \mu) + \frac{S_z\ (1 - P_{MAT4})}{P_{MAT4}} \text{X}\ N_4 \cdot P_{MAT4} \cdot (1 - \mu) \quad \textbf{(d)}$$

Then

$$\frac{N_4 + N_5}{NS_4 + NS_5} = \frac{(a)}{(d)} = \frac{N_4 + N_4 . S_z\ (1 - P_{MAT4}\ )}{N_4 . P_{MAT4} . (1 - \mu) + \dfrac{S_z (1 - P_{MAT4}}{P_{MAT4}}\ \text{X}\ N_4 . P_{MAT4} . (1 - \mu)`}$$

Dividing numerator and denominator by N4

$$\frac{N_4 + N_5}{NS_4 + NS_5} = \frac{1 + S_z . (1 - P_{MAT4})}{P_{MAT4} . (1 - \mu) + S_z (1 - P_{MAT4}) (1 - \mu)}$$

For example, given S_z=.8, μ=0.2, P_{MAT4}=.95, the ratio is 1.31 - and 328 adults (age 4 and 5) would correspond to 250 spawners (age 4 and 5).

Conversely, for and μ=0.1, the ratio is 1.167, and 292 adults (age 4 and 5) would correspond to 250 spawners (age 4 and 5).