Fisheries and Oceans Science | Pêches et Océans Sciences

C S A S | **S C É S**

Canadian Stock Assessment Secretariat | **Secrétariat canadien pour l'évaluation des stocks**

Research Document 2000/126 | **Document de recherche 2000/126**

Not to be cited without permission of the authors [1]

Ne pas citer sans autorisation des auteurs [1]

Biological Reference Points for the Conservation and Management of Steelhead, *Oncorhynchus mykiss*

N.T. Johnston, E.A. Parkinson, A.F. Tautz, and B.R. Ward

Fisheries Management Branch
BC Ministry of Agriculture, Food, and Fisheries
2204 Main Mall, Vancouver, B.C., V6T 1Z4

[1] This series documents the scientific basis for the evaluation of fisheries resources 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.

[1] La présente série documente les bases scientifiques des évaluations des ressources halieutiques du Canada. Elle traite des problèmes courants selon les échéanciers dictés. Les documents qu'elle contient ne doivent pas être considérés comme des énoncés définitifs sur les sujets traités, mais plutôt comme des rapports d'étape sur les études en cours.

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

Les documents de recherche sont publiés dans la langue officielle utilisée dans le manuscrit envoyé au Secrétariat.

This document is available on the Internet at: Ce document est disponible sur l'Internet à:
http://www.dfo-mpo.gc.ca/csas/

ISSN 1480-4883
Ottawa, 2000

Canada

Abstract

We derive two simple biological reference points from a Beverton-Holt stock-recruitment relationship. We then compare the performance of several biological reference points as thresholds in single threshold and dual threshold harvest control rules, using an age-structured population model based on Keogh River steelhead that incorporates realistic levels of process error and implementation error.

Simple harvest control rules that use abundance thresholds to initiate reductions in harvest rates below the threshold can considerably reduce the risk of quasi-extinction for small populations of steelhead at low abundance compared to constant exploitation rate (CER) harvesting policies. Threshold harvesting policies can also reduce recovery time and increase both catch and escapement compared to a CER policy. A CER policy will maximize ln(catch) and reduce the frequency of fishing closures, but it will also increase the risk of quasi-extinction for low productivity stocks compared to threshold harvesting policies. "Constant" exploitation rate control rules that use abundance thresholds can perform similarly to proportional threshold harvesting under conditions of strongly autocorrelated environmental variability and realistic levels of prediction error and implementation error. Harvest control rules that have both an upper precautionary threshold and a limit reference point reduce extinction risk at low stock productivity. The thresholds and harvest rates that maximize catch change with stock productivity, variance in smolt-to-adult survival, temporal autocorrelation in survival deviations, maximum population size, uncertainty in the asymptotic maximum recruitment, and the form of the spawner-smolt recruitment function, but the qualitative results hold true. N_{LRP}, the abundance threshold from which a population can recover to $0.25 \cdot B$ in one generation in the absence of harvesting, increased escapement and lowered extinction risk at low stock productivity with only small reductions to maximum catches. Empirical estimates of the catch-maximizing LRP for the Keogh River steelhead were about $0.17 \cdot B$ to $0.18 \cdot B$ for both Beverton-Holt and rectilinear "hockey stick" stock-recruitment functions.

Résumé

Les auteurs déterminent deux points de référence biologiques simples dérivés d'un rapport de recrutement aux stocks du type Beverton-Holt. Ils comparent ensuite la capacité de plusieurs points de référence biologiques comme seuils employés dans les règles de régulation de la récolte à simple ou double seuil, en utilisant un modèle de population à structure par âge, basé sur la population de saumons arc-en-ciel de Keogh River, qui intègre des niveaux réalistes d'erreurs de méthode et d'application.

Les règles simples de régulation de la récolte qui utilisent des seuils d'abondance pour amorcer la diminution des taux de récolte jusqu'à des valeurs inférieures au seuil peuvent grandement réduire le risque de quasi-disparition de petites populations de saumons arc-en-ciel en faible abondance, par rapport aux politiques de récolte à taux constant d'exploitation (TCE «CER»). Les politiques de récolte employant les seuils permettent aussi de réduire la période de rétablissement et d'augmenter la prise et l'échappement, en comparaison d'une politique TCE. Cette dernière maximise la fonction ln(prise) et réduit la fréquence des fermetures de la pêche, mais elle entraîne aussi l'augmentation du risque de quasi-disparition des stocks à faible rendement, par rapport aux politiques de récolte employant les seuils. Les règles de régulation à taux « constant » d'exploitation qui emploient des seuils d'abondance peuvent donner des résultats semblables au cas de récolte à seuil proportionnel, lorsqu'il existe des conditions de variabilité environnementale à autocorrélation élevée et des niveaux réalistes d'erreurs de prévision et d'application. Les règles de régulation de la récolte qui emploient à la fois un seuil préventif supérieur et un point de référence limite réduisent le risque de disparition des stocks à faible rendement. Les seuils et les niveaux de récolte qui maximisent les prises varient en fonction de nombreux facteurs : la production des stocks, la variance du taux de survie saumoneau-adulte, l'autocorrélation temporelle dans les écarts des taux de survie, la taille maximale de la population, l'incertitude relative au recrutement maximum asymptotique et la forme de la fonction de recrutement géniteur-saumoneau. Les résultats qualitatifs sont toutefois valables. Le seuil d'abondance N_{LRP}, à partir duquel une population peut se reconstituer jusqu'à une valeur de 0,25·B en une génération, en l'absence de toute activité de récolte, accroît l'échappement et réduit le risque de disparition des stocks de faible rendement, et il n'entraîne cependant que de légères réductions des prises maximales. Les estimations empiriques du seuil LRP de maximisation des prises, pour les saumons arc-en-ciel de Keogh River, sont d'environ 0,17·B à 0,18·B, dans le cas de la fonction de recrutement aux stocks du type Beverton-Holt, comme dans celui de la fonction rectiligne du type « bâton de hockey ».

Introduction

Fisheries agencies ensure the conservation and sustainable use of fisheries resources by attempting to "maintain or restore stocks at levels capable of producing maximum sustainable yield" (FAO 1995). These management objectives have typically been implemented as harvest control rules designed to maximize the (potential) long-term average yield from the fishery with little risk of recruitment overfishing. Many fisheries have been overexploited nonetheless, partly because environmental variability and measurement error make decreases in abundance difficult to detect initially, and partly because there are strong institutional disincentives to reducing harvest rates as abundance declines (Ludwig et al. 1993). Recently a precautionary approach to fisheries management "based on stock-specific reference points and predefined decision rules" (Richards and Maguire 1998) and an explicit consideration of the effects of uncertainty has been advocated to maintain the long-term viability of fisheries (e.g., FAO 1995).

Biological reference points are biologically derived indices of stock status, which are used to initiate management actions to achieve particular management objectives (Gabriel and Mace 1999). Many fisheries agencies have adopted reference points as a conceptual framework for implementing a precautionary approach to fisheries management (reviewed in Serchuk et al. 1999). Minimally, the framework consists of a target reference point (TRP) that defines a desired state, a limit reference point (LRP) that defines a highly undesired state, and a set of control rules for the three regions thus defined below, between, and above the reference points which constrains the stock to states near the TRP (Garcia 1996). A precautionary threshold or buffer reference point (PRT) may be inserted between the LRP and the TRP to reduce the risk that the LRP will be reached without corrective action being taken (Serchuk et al. 1999). The reference points can be expressed as harvest rates or as biomass levels, and are intended to avoid severe recruitment overfishing (Mace 1994). The desired relationship among biomass reference points is: average system state ≈ TRP > PRT >> LRP. The control rules can take many functional forms (Thompson 1999), but threshold harvesting, i.e. harvesting only above a LRP, reduces extinction risk and increases average yield compared to constant harvest rate strategies (Quinn et al. 1990, Lande et al. 1997, Cass and Riddell 1999).

There is no consensus on appropriate definitions for LRPs and TRPs, which could vary with specific management objectives, available data, and perceptions of risk. Because maintaining the productive capacity of a stock is a common goal, the fishing mortality rate that produces the maximum sustainable yield, F_{MSY}, and the associated stock biomass, B_{MSY}, are common reference points, however F_{MSY} and B_{MSY} have been used both as LRPs and as TRPs (Mace and Gabriel 1999). Unfortunately, MSY-derived reference points require estimates of stock-recruitment parameters, which are often poorly known (Gabriel and Mace 1999). Many other biological reference points have been defined and applied, often as heuristic approximations to F_{MSY} or B_{MSY} for data-poor situations (summarized in Mace 1994, Gabriel and Mace 1999, Serchuk et al. 1999). There are, however, few evaluations of their effectiveness under realistic levels of uncertainty (but see Quinn et al. 1990, Myers et al. 1994, Thompson 1999).

Defining effective reference points for steelhead and other species that exist as numerous small, discrete populations is difficult because normally there is little or no quantitative information available for a given population from which commonly-used reference points can be calculated. Even where stock-recruitment data exist, estimates of productivity may be very imprecise (see below). Determining LRPs by quantitative risk assessment methods such as population viability analysis (e.g., Botsford and Brittnacher 1998) will rarely be possible or reliable (Taylor 1995, Ludwig 1999) in these data-poor situations. In any event, using minimum viable populations as LRPs may not adequately meet a management goal of maintaining stocks near levels capable of producing MSY. Establishing effective LRPs is particularly important for steelhead because the small size of many populations increases their vulnerability to extirpation (Routledge and Irvine 1999), which has occurred (Slaney et al. 1996).

We present a simple method for defining effective, stock-specific TRPs and LRPs for steelhead and other territorial, stream-rearing salmonids whose stock-recruitment relationship (SRR) approximates a Beverton-Holt model. The method assumes that there is an upper limit to smolt production that is determined by the amount and quality of freshwater spawning and rearing habitat, and that the maximum smolt recruitment is, in principle, predictable from habitat characteristics (e.g., Nickelson 1998). We derive a simple approximation to the spawner abundance at MSY, N_{MSY}, and show that it depends little on stock productivity over the most likely range of stock productivity for steelhead. We determine a LRP by considering the rate of recovery of a depressed population to N_{MSY}, and show that this LRP ensures equal resilience to increases in density-independent mortality for all stock productivity values. We then use an age-structured population model based on Keogh River steelhead (Ward and Slaney 1988) that incorporates realistic levels of parameter uncertainty and implementation error to compare the performance of this LRP and other common biological reference points under different harvest control rules and management goals.

Methods

Conceptual framework for a simple LRP

A simple analytic relation between the maximum recruitment *B* and N_{MSY} exists for a stationary, deterministic Beverton-Holt stock-recruitment relationship. N_{MSY} can be approximated over a wide range of stock productivity values by a fixed proportion of *B*. We then define the spawner abundance from which the population returns to N_{MSY} within one generation as a LRP, show that this LRP has the same resilience for all stock productivity values, and that the resilience is directly related to the spawner threshold defined by N_{MSY}.

We separate the stock dynamics of steelhead into freshwater and marine phases. Assume that the freshwater dynamics can be represented by a stationary Beverton-Holt stock-recruitment relation (Ward 1996, 2000) with discrete generations, relating smolts in generation $t+1$ to spawners in generation t:

$$R_{t+1} = \frac{\alpha \cdot N_t}{\left[1 + \alpha \cdot N_t / \beta\right]}$$

where:

R_{t+1} = the number of smolts produced in generation $t+1$,

N_t = the number of adult spawners in generation t,

α is the "freshwater productivity", i.e., the number of smolts produced per spawner as spawner numbers approach zero, and

β is the "habitat capacity", the asymptotic number of smolts produced at very large spawner numbers.

Assume also a density-independent marine phase (Ward 2000),

$$N_{t+1} = s \cdot R_{t+1}$$

where:

N_{t+1} = the number of adult spawners returning in generation $t+1$, and

s is the marine survival from smolt to adult, and is constant for a given oceanic regime.

The stock-recruitment relation for adult fish is:

$$N_{t+1} = \frac{a \cdot N_t}{[1 + a \cdot N_t / B]}$$

where

$a = s \cdot \alpha$ = the number of adult recruits per spawner ("stock productivity") and

$B = s \cdot \beta$ = the asymptotic number of adult recruits at very high spawner abundance.

The spawner abundance that produces the maximum sustainable yield is:

$$N_{MSY} = \frac{B}{a} \cdot \left[\sqrt{a} - 1\right].$$

Note that N_{MSY} depends on a and B but is linear in B. Define P_{MSY} as the ratio of N_{MSY} to the asymptotic adult recruitment B:

$$P_{MSY} \equiv \frac{N_{MSY}}{B} = \left[\frac{1}{\sqrt{a}} - \frac{1}{a}\right]$$

P_{MSY} is independent of B and is maximized at a stock productivity of $a = 4$ (Fig. 1). Consequently, $N_{MSY} \leq \frac{B}{4} = \frac{s \cdot \beta}{4}$ for all a and α and we can set an upper bound on N_{MSY} if we can estimate habitat capacity and the average smolt-to-adult survival. We propose that a spawner abundance of $N_{CCT} = 0.25 \cdot B$ be a "conservation concern threshold" below which recruitment overfishing occurs for a population whose SRR resembles the Beverton-Holt model. The ratio of $0.25 \cdot B$ to the true N_{MSY} is:

$$P_{0.25B} = \frac{a}{4 \cdot (\sqrt{a} - 1)}$$

and the N_{CCT} will be equal to or greater than N_{MSY} for all $a > 1$. N_{CCT} is within 20% of N_{MSY} for $2 < a < 10$, but the yield from N_{CCT} is within 3% of the MSY over this range of stock productivity.

More generally, let $N_{CCT} = q \cdot B$ define a conservation concern threshold (CCT), where $0 < q < 1$, and let $N_{LRP} = p \cdot B$ be a LRP, where $0 < p < q$. If the population is initially at $N_{t=0} = p \cdot B$ spawners, then the spawner abundance after n generations is:

$$N_n = \frac{a^n \cdot (1-h)^n \cdot p \cdot B}{1 + p \cdot \sum_{i=1}^{n} a^n \cdot (1-h)^{n-1}}$$

where h is a fixed harvest rate. If the population is to recover from the LRP to the CCT in n generations, then $N_n \geq q \cdot B$, whence:

$$p \geq \frac{q}{a^n \cdot (1-h)^n - q \cdot \sum_{i=1}^{n} a^n \cdot (1-h)^{n-1}}.$$

Consider a LRP that is defined as the spawner abundance from which the population will recover to the CCT in one generation. Then

$$p = \frac{q}{a \cdot (1-q-h)}$$

and

$$N_{LRP} = p \cdot B = \frac{q \cdot B}{a \cdot (1-q-h)}.$$

Note that the LRP defined by the spawner abundance for recovery to $q \cdot B$ in one generation varies with stock productivity (Fig. 1). We will show that this LRP implies equal resilience across all stock productivity, i.e., that a population at the LRP can withstand the same increase in density-independent mortality before going extinct, independently of the stock productivity.

First, consider the density-independent mortality, m_1, that will hold an unfished population at the LRP. In the absence of this mortality, a population at the LRP would recover to the CCT in one generation. Thus,

$$(1-m_1)\cdot q\cdot B = N_{LRP} = \frac{q\cdot B}{a\cdot(1-q)}$$

whence

$$m_1 = 1-\frac{1}{a\cdot(1-q)}.$$

Recall that as the population approaches zero, the SRR is approximately linear and $N_{t+1} \cong a \cdot N_t$. Thus, the effect of the density-independent mortality m_1 is to reduce the stock productivity for populations at the LRP from a to an effective stock productivity of:

$$a' = (1-m_1)\cdot a$$

Substituting for m_1,

$$a' = \frac{1}{(1-q)}.$$

Next consider the additional density-independent mortality, m_2, that will cause a population that is at the LRP to go extinct over time. The extinction criterion is $\frac{N_{t+1}}{N_t} < 1$ for a small population. Thus,

$$(1-m_2)\cdot N_{t+1} < N_t.$$

But for a very small population, $N_{t+1} \cong a' \cdot N_t$, whence

$$(1-m_2)\cdot a'\cdot N_t = (1-m_2)\cdot(1-m_1)\cdot a\cdot N_t < N_t$$

and after substituting for m_1 and solving,

$$m_2 > q \; .$$

Thus, a population at N_{LRP}, the spawner abundance from which the unfished population will recover to $q \cdot B$ in one generation, can withstand the same increase in density-independent mortality without going extinct regardless of the stock productivity. The magnitude of the additional density-independent mortality required to cause the extinction of a population at the LRP, is directly related to the recovery target that defines the LRP, and is numerically equal to the ratio, q, of the fixed recovery threshold (the CCT or TRP) to the asymptotic recruitment.

Although we have implicitly defined N_{LRP} in terms of adult spawners, N_{LRP} can be determined solely from smolt production parameters as:

$$N_{LRP} \equiv \frac{q \cdot B}{a \cdot (1-q)} = \frac{q \cdot s \cdot \beta}{s \cdot \alpha \cdot (1-q)} = \frac{q \cdot \beta}{\alpha \cdot (1-q)} \; .$$

Empirical approximations for N_{CCT} and N_{LRP}

Uncertainty in estimates of the parameters of the stock-recruitment relationship introduces uncertainty into estimates of N_{CCT} and N_{LRP}. Where empirical stock-recruitment data exist, the uncertainty can easily be accommodated by Bayesian statistical methods. We use the results of a Bayesian analysis of steelhead spawner-smolt data for Keogh River, British Columbia and for Snow Creek, Washington to suggest simple empirical approximations that may be useful where stock-recruitment data are lacking but β is estimable by other means.

Ward (2000) gives the spawner-smolt data for the Keogh River and discusses how it was obtained; we reproduce the data in Appendix 1. We omitted data for brood years between 1982-1985, which were affected by stream fertilization. The spawner-smolt data for Snow Creek upstream of the weir was provided by Randy Cooper (Washington Department of Fish and Wildlife, 283 236 Highway 101, Port Townsend, Washington WA98368); we omitted one point which we believed was implausible (4 spawners, 2052 smolts). Measurement error is low for both data sets because adults and smolts are directly enumerated at weirs. We used a grid technique (200 × 300) to calculate the relative likelihood of various plausible combinations of α and β for a Beverton-Holt SRR, given the observed data. We restricted α to the range from 0 to about 4 times the maximum observed smolts per spawner, and β to the range from 0 to about twice the maximum observed smolt output. We assumed a uniform prior, lognormal process error, and used a likelihood kernel (Walters and Ludwig 1994) that implicitly integrated over variances to calculate relative likelihood values from which we obtained the posterior marginal distributions of α and β, their expected values, and the expected value of N_{LRP} as a weighted mean over the parameter grid.

Performance of reference-point-based management policies under uncertainty

We used simulation to assess the performance of reference-point-based management policies under "realistic" scenarios of environmental variability, prediction error, and implementation error. The simulation was based on the population dynamics of Keogh River steelhead, which is typical of inner South Coast winter run steelhead populations. Many of these populations have declined considerably over the last decade (Smith and Ward 2000). We considered several harvest control rules and a range of reference point definitions from the literature.

Ward and Slaney (1988) and Ward (1996) document the population dynamics of steelhead in the Keogh River. The number of returning adults has varied between 31 and 4 248 (Fig. 2). Mature adult winter run steelhead enter the Keogh River between November and May. Kelts emigrate from March to June. Fry emerge in mid-June to late-June, rear in freshwater for 1 to 5 years, and emigrate as smolts in May. Virgin adults return after 1 to 4 winters at sea, after migrating widely throughout the North Pacific. The modal smolt age is 3 years and the modal sea age is 2 years, but adult fish could be up to 9 years old at first spawning. Smolt-to-adult survival varies with smolt size, and shows strong temporal trends (Ward 2000). We list the overall smolt survival data by year of smolt emigration (Fig. 2) in Appendix 1. Sea age at maturity varies among smolt ages and between the sexes. Fecundity varies with female size. Returning steelhead are caught by sport fisheries (angling) in their natal rivers, and some stocks may be caught as bycatch in net fisheries that target other salmon species, both at sea and in river.

We modeled steelhead population dynamics in annual time steps as a density-dependent egg-to-smolt function followed by a density-independent marine survival function; empirical data (Ward 2000) support this model. Unless otherwise noted, all parameters and variances were estimated from the Keogh River data set. Smolt production from a given egg deposition was described by a Beverton-Holt type stock-recruitment relationship, which is the most probable empirical SRR for the Keogh data (see Appendix A1). We commenced each simulation by fixing the initial spawning population size at $0.1 \cdot B$ for 10 years, where B is the asymptotic adult recruitment at the average smolt-to-adult survival. We set B at 1 000 adults for most runs; this value approximates the observed B for Keogh River steelhead under the regime of good ocean survival seen between 1977 and 1991.

To initialize the abundance-at-age distribution, we first partitioned the initial spawner populations into males and females with the long-term average spawner sex ratio of 1:1. We used the mean eggs per spawner data observed for the last 10 brood years during which the river did not receive experimental inorganic nutrient additions to calculate egg deposition during the initial 10-year period. Smolt production from a given egg deposition was estimated from a Beverton-Holt SRR, as described below. During the initialization period we used the observed proportions of smolts from each brood year that emigrated at freshwater ages 1 to 5 to calculate the number of smolts of a given age emigrating in a given year. The total number of adult fish returning from all smolts (ages 1 to 5) that emigrated in a year was determined by applying a year-specific ocean survival. The relative survival of smolts of different ages was calculated from an empirical smolt size-survival relation and mean size-at-age data (Ward and Slaney 1988, their equation 1 and Table 6) to give year- and smolt-age specific survival rates. Adult recruits with a common life history were assumed to have a 1:1 sex ratio. Surviving smolts of a given freshwater age returned as mature spawners according to a fixed, sex-specific maturation schedule (Ward and Slaney 1988, their Table 3).

After the initial age-abundance distribution was established, we compared different management policies by generating 500 trials under each policy, a trial being 50 years (i.e., 10 generations at a modal generation time of 5 years). Egg deposition in brood year t was estimated from the female spawners as:

$$Eggs_t = \sum_{i=1}^{4} fecundity_i \cdot NF_{i,t} + RS \cdot Eggs_{t-1}$$

where $fecundity_i$ is the average fecundity of females of ocean age i, $NF_{i,t}$ is the number of virgin females of ocean age i in brood year t, and RS is the average proportion of repeat spawners. Mean fecundity was estimated as 296 for 1-ocean females, 3 274 for 2-ocean females, and 4 800 for 3-ocean and 4-ocean females. RS was 0.092 for the Keogh data. The number of smolts produced from the brood year was:

$$NSmolt_t = \left(\frac{\alpha \cdot Eggs_t}{(1 + \alpha \cdot Eggs_t / \beta)} \right) \cdot e^{\varepsilon_t} \cdot e^{-(\sigma_0^2 / 2)}$$

where ε_t was drawn from a normal distribution, $N(0,\sigma_0)$. The second exponential term ensures that the random error will have a mean of 1.We estimated σ_0 as 0.52 from the observed SRR. The asymptotic maximum smolt production β was calculated from the maximum adult recruitment as $\beta = B / s$ where s is the long-term average smolt-to-adult survival. Smolt productivity α was calculated from the adult productivity, a, for the policy under examination. Because productivity is imprecisely estimated from empirical data (see below), we varied a over the range from 1 to 5 recruits·spawner^{-1} to search for policies that were little affected by stock productivity.

The numbers of smolts from a given brood year t that emigrated at age i in year $t+i$ was calculated from mean proportions by age Psm_i observed at the Keogh River, so the total number of smolts of all ages emigrating in year t was:

$$NTSmolt_t = \sum_{i=1}^{5} Psm_i \cdot NSmolt_{t-i} \, .$$

The mean proportions of smolts emigrating at freshwater ages 1 through 5 were 0.000, 0.347, 0.536, 0.115, and 0.002 for broods that were not affected by stream fertilization (Table A1). The number of adult recruits $NRecruits_t$ from all smolts that emigrated in year t was:

$$NRecruits_t = s_t \cdot NTSmolts_t$$

where $s_t = e^{-M_t}$ is a year-specific smolt-to-adult survival and M_t is a year-specific mortality rate.

We used a parametric resampling procedure to model marine survival. The overall survival of all smolts emigrating from the Keogh River in a given year has varied about 10-fold, between 0.024 and 0.26, but the data show two distinct "regimes" of variable high survival between 1977 and 1990 and variable low survival from 1991 onward (Ward 2000). We modeled environmental variation in survival by an autoregressive random process (Walters and Parma 1996), as $M_t = \overline{M} + d_t$ where $e^{-\overline{M}}$ is the geometric mean survival, $d_t = \rho \cdot d_{t-1} + \omega_t$, $0 < \rho < 1$ is a lag-1 autocorrelation, and ω_t is a normally-distributed random process, $N(0,\sigma)$, with a mean of zero and a standard deviation of σ. Using this model, we estimated $\rho = 0.72$ from the lag-1 autocorrelation in the observed time series of *ln*(survival) (Table A2). The lag-1 autocorrelation in the survival, s_t, is 0.57.

The expected sample variance of an autoregressive process varies with the autocorrelation ρ and the series length T (Heino et al. 2000). We estimated σ, corrected for the observed autocorrelation (Heino et al. 2000, their equation 3), to be 0.629; the unadjusted value was 0.808. To ensure that the standard deviation remained constant for all simulations, we scaled σ as:

$$\sigma_{\rho,T} = \sigma \cdot \sqrt{\frac{(1-\rho^2)\cdot(T-1)}{T - \left\{\frac{2+2\cdot\rho+\rho^2-\rho^{2T}}{1-\rho^2}\right\} + \left\{\frac{(1-\rho^T)\cdot(1+2\cdot\rho-\rho^T}{T\cdot(1-\rho)^2}\right\}}}$$

We used $e^{-\overline{M}} = 0.083$ from the Keogh survival data, so that the arithmetic mean survival was 0.11. We used $\rho = 0.7$ to approximate the current survival pattern. We also examined less correlated survival patterns ($\rho = 0.0$ and 0.4) and a range of variation in survival ($\sigma = 0.2$, 0.4, 0.629, and 0.8). Because the autoregressive process can generate unreasonably high survivals, we capped s_t at 0.60, about twice the highest observed smolt-to-adult survival.

We calculated age- and emigration year-specific survival rates $S_{i,t}$ for smolts of freshwater age i that emigrated in year t from the year-specific overall smolt survival s_t, the known abundance of different smolt ages in the smolt emigration, and fixed relative survivals of 0.0, 0.049, 0.170, 0.404, and 0.692 for smolts aged 1 through 5. We used a fixed sex- and freshwater age-specific maturation schedule $Pmat_{i,j}$ to assign surviving smolts to an ocean age at return, j. The number of adult recruits returning to spawn in any year t is then:

$$NR_t = \sum_{i=1}^{5}\sum_{j=1}^{4} NSmolt_{t-i-j} \cdot Psm_i \cdot S_{i,t-j} \cdot Pmat_{i,j} \,.$$

Returning adults of all ages were harvested at the same year-specific exploitation rate, which was determined by the harvest control rule under consideration. The harvest control rule calculated a target harvest rate $h_{target,t}$ from imprecise estimates of the number of returning adults. Adult returns were forecast from the prior year's returns as:

$$NEst_t = 1.398 \cdot (N_{t-1})^{0.926} \cdot e^{\mu_t} \cdot e^{-(\sigma_N^2/2)} \qquad (r^2 = 0.66, N = 22)$$

where μ_t is drawn from the normal distribution $N(0, \sigma_N)$ and $\sigma_N = 0.362$. The target harvest rate was implemented with error to give an actual harvest rate:

$$h_t = h_{target,t} \cdot (1 + v_t)$$

where v_t was drawn from the normal distribution $N(0, \sigma_h)$. We estimated σ_h as 0.063 from exploitation rate data for Skeena River steelhead reported in Cox-Rogers (1994). The catch was:

$$Catch_t = h_t \cdot N_t$$

and the escapement in year t was:

$$N_t = NR_t - Catch_t \,.$$

We examined two common classes of harvest control rules: (1) a constant exploitation rate (CER) policy with a minimum spawning escapement (Kope 1999), and (2) a "proportional threshold harvesting" policy (PTH, Lande et al. 1997) which harvested a constant proportion of the estimated surplus spawners above a minimum spawning escapement (Fig. 3). Within each class of harvest control rule, we compared a "single threshold" policy (i.e., a LRP below which forecast abundance there was no harvest) and a "dual threshold" policy (a LRP and a precautionary threshold) in which the harvest rate (CER) or the proportion of surplus fish harvested (PTH) declined linearly with forecast abundance from the nominal value at the precautionary threshold to zero at the LRP. Note that a constant exploitation rate policy with no minimum escapement and a constant escapement policy are special cases of the above, and were included in the set of harvest control rules that we compared.

We compared the performance of several LRPs within the above harvest control policies. We used two common LRPs (Myers et al. 1994): 20% of the unfished equilibrium population ($0.2 \cdot N_{equil}$) and the spawner abundance that produces 50% of the maximum recruitment, $N_{50\%}$ (Mace 1994). We also considered N_{LRP} (defined above) and fixed proportions of the asymptotic maximum recruitment between $0.0 \cdot B$ and $0.20 \cdot B$. We used a PRT of $0.25 \cdot B$, which approximated N_{MSY}. We also examined PRTs of $0.2 \cdot B$, $0.3 \cdot B$, and $0.35 \cdot B$ for some cases. A no fishing policy provided baseline values for some evaluations. To reduce the many possible comparisons, we used the following parameter set as a standard case where appropriate: $a = 2.2$, $B = 1\,000$, $\sigma = 0.629$, $\rho = 0.7$, $N_0 = 0.1 \cdot B$, $h = 0.5$, PRT = $N_{CCT} = 0.25 \cdot B$. The productivity value and variances approximate those of the Keogh River steelhead population.

Harvest control rules for the different combinations of policies and thresholds are given in Table 1. The harvest policy used imprecise estimates of the LRP and PRT and the forecasted returns to determine an appropriate harvest rate for the estimated surplus spawners. Because all the LRPs and PRTs were linear functions of B, we used error in the estimate of B to generate imprecision in the estimated LRP or PRT. We assumed lognormal error in B:

$$B_{estimated} = B \cdot e^{\upsilon_{trial}} \cdot e^{-(\sigma_B^2/2)}$$

where υ_{trial} was drawn from the normal distribution $N(0,\sigma_B)$. We estimated $\sigma_B = 0.243$ for the Keogh River stock (Fig. 4). We also considered reduced ($\sigma_B = 0.122$) and increased ($\sigma_B = 0.486$ and 0.972) uncertainty in B. We did not update $B_{estimated}$ during a trial, nor did we consider systematic bias in the estimates. We assumed that all returning fish encountered the fishery.

We used several performance indicators to evaluate alternative control rules and thresholds: (1) the probability of "quasi-extinction" within 10 generations, (2) the mean catch over the 10-generation time series, (3) the CV of catch, (4) the mean ln(catch + 1) over the time series, (5) the mean spawner abundance over the last generation of the time series, (6) the time to recover to the PRT from the initial abundance, and (7) the frequency of fishing closures during the time series. We used the median value of an indicator from 500 replicate time series to characterize its response under a given policy. A population was extirpated if the average annual escapement over a generation was less than 10 spawners. This "extinction" definition is arbitrary, but it is adequate to identify policies that produce very low abundance only infrequently. We also examined quasi-extinction thresholds 1, 2, 5, 15, 20 and 25 spawners to assess the sensitivity of our results to the "extinction" definition.

We considered two plausible management scenarios that differed in management goals. The first scenario adjusted the control rule, harvest rates, and thresholds to maximize an objective function. We used mean catch and ln(catch + 1) as objective functions to compare harvest control rules under "risk neutral" and "risk adverse" management strategies (Deriso 1985). Although steelhead fisheries are not managed to maximize long-term average yield, we wish to know the conditions that are necessary for this management option. This scenario can also be considered as the general case for an exploited salmonid population. We found the maxima numerically, using a grid search method. The grid used harvest rates at 0.05 units between 0 and 1, and LRPs at $0.01 \cdot B$ units between $0.01 \cdot B$ and $0.25 \cdot B$. The computed maxima may be imprecise, however, because of the coarse grid spacing and the flat response surface (see Fig. 10). The second scenario examined the situation where steelhead are caught as a bycatch in another fishery, e.g., as in the Skeena River sockeye fishery or the Fraser River chum salmon fishery. Bycatch harvest rates can be considerable, e.g., 0.5 to 0.6 for Skeena River steelhead (Cox-Rogers 1994). We compared the performance of different harvest control rules and thresholds in maintaining desired attributes of the steelhead population under a fixed maximum harvest rate. The harvest control rule reduced the externally defined maximum harvest rate, depending on steelhead abundance. We attached particular importance to the probability of quasi-extinction and to the final spawner abundance as performance indicators because the quality of catch-and-release sport fisheries is roughly proportional to abundance, and because abundant salmon may be required to sustain important ecological processes within their natal watersheds (Cederholm et al. 1999).

Results

Empirical approximations for N_{CCT} and N_{LRP}

The Bayesian analysis produced precise estimates of β but very imprecise estimates of α for both the Keogh River and Snow Creek data sets if a Beverton-Holt stock-recruitment function was assumed (Fig. 4). The expected value of β was 6 741 smolts for the Keogh River, with an upper 90% bound of approximately 9 550. For Snow Creek, the expected value of β was 1 594 with an upper 90% bound of about 2 060. Note that for the Keogh River data, $0.35 \cdot \beta_{estimated}$ approximates 0.25 times the upper 90% distribution limit for the estimate. Using $0.35 \cdot \beta_{estimated}$ rather than $0.25 \cdot \beta_{estimated}$ for N_{CCT} would thus result in a less than 10% probability that N_{CCT} is less than the MSY escapement, N_{MSY}. This adjustment has less than a 10% effect on potential yield if the adult stock productivity is greater than 3 recruits·spawner^{-1}. For Snow Creek steelhead $0.32 \cdot \beta_{estimated}$ similarly approximates 0.25 times the 90% bound, and adjusting N_{CCT} from $0.25 \cdot \beta_{estimated}$ to $0.32 \cdot \beta_{estimated}$ would result in a less than 10% probability that N_{CCT} is less than N_{MSY}. If these two data sets are representative of steelhead SRR, then we suggest approximating N_{CCT} by $0.35 \cdot \beta$ as a rule of thumb that will usually exceed N_{MSY}.

The expected value of N_{LRP} was 94 adult spawners for the Keogh River for a recovery target of $0.25 \cdot \beta$, so that p is 0.127 at a long-term average smolt-to-adult survival of 0.11. Estimates of N_{LRP} for Snow Creek were unreliable because α is poorly specified (Fig. 4). As a tentative rule of thumb, we suggest that a p value of 0.10 to 0.15 be used if α is unknown.

Performance of reference-point-based management policies under uncertainty

Increasing variation in smolt-to-adult survival reduced the unfished equilibrium spawner abundance at all stock productivity values, and increased the probability of extinction for stock productivity values below 1.4 recruits·spawner^{-1} (Fig. 5). The effects were proportionately greater at lower stock productivity values. At the observed variance in survival ($\sigma = 0.629$), increasing the temporal autocorrelation in survival deviations further reduced the unfished equilibrium abundance for all stock productivity values, and greatly increased the probability of extinction for stock productivity values below about 2 recruits·spawner^{-1} (Fig. 6). The modeled extinction probabilities were sensitive to the abundance used as the quasi-extinction threshold, but under current conditions ($\sigma = 0.629$ and $\rho = 0.7$) the modeled extinction probability for depressed populations increased rapidly below stock productivity values of 2 recruits·spawner^{-1} for all extinction thresholds between 1 and 25 spawners (Fig. 7). The choice of quasi-extinction threshold had little effect on values of the LRP and nominal harvest rate that maximized long-term catch, except below stock productivity values of about 1.4 recruits·spawner^{-1} (Fig. 8).

For depressed populations with characteristics similar to Keogh River steelhead, harvest control rules that used a LRP greatly reduced the risk of extinction, reduced the time to recover to N_{CCT}, increased the final escapement, and increased the catch compared to a constant exploitation rate policy (Fig. 9 and 10). However, a CER policy with no LRP minimized the frequency of fishing closures and usually maximized ln(catch) for a given harvest rate (Fig. 9 and 10). At low LRP values, a dual threshold policy (i.e., both a LRP and a precautionary threshold) gave increased escapement, reduced extinction risk, higher catch, lower frequency of fishing closures, and a shorter recovery period than a single threshold policy (Fig. 9 and 11). Single threshold and dual threshold policies performed similarly at high LRP values because at high LRP values and/or high harvest rates both harvest control rules converge to the maximum harvest rate that is consistent with the LRP (Fig. 3). Neither extinction risk nor catch varied much with the LRP under a dual threshold policy, except at very high nominal harvest rates (Fig. 9 and 11). The upper precautionary threshold influenced the performance of the dual threshold policy at low LRP values for a given harvest rate: escapement and catch increased while recovery time and frequency of fishing closures decreased with increasing precautionary thresholds (Fig. 12). The probability of quasi-extinction and ln(catch) were little affected by the location of the precautionary threshold within the range from $0.2 \cdot B$ to $0.35 \cdot B$.

Proportional threshold harvesting rules with either a single LRP or with both a LRP and a precautionary threshold gave results that were qualitatively similar to the corresponding CER policies (Fig. 13). Note that single threshold CER and PTH rules coincide for a LRP of zero. In general, a PTH policy increased escapement, reduced extinction probability, increased catch, reduced the frequency of fishing closures, and reduced the time to recover to N_{CCT} compared to a CER policy without a LRP. A precautionary threshold further increased escapement, reduced extinction risk, increased catch, decreased fishing closures, and shortened recovery periods at low LRP values.

For the harvest policies considered, thresholds greater than about $0.1 \cdot B$ greatly reduced the risk of quasi-extinction, even at low stock productivity (Fig. 9 to 13).

The combinations of LRP and either nominal harvest rate (for CER policies) or harvest fraction on surplus fish (for proportional threshold policies) that maximized catch over the 10-generation time horizon varied among harvest policies (Fig. 14). The catch-maximizing LRP and nominal harvest rate values for "constant" exploitation rate policies with single or dual thresholds differed only at low stock productivity (below 1.6 recruits·spawner^{-1}), where the dual threshold policy had lower LRP values and higher nominal harvest rates (Fig. 14). Catch-maximizing LRPs for proportional threshold harvesting policies were lower than those for CER policies at the same stock productivity. The nominal harvest fractions on surplus fish for single- and dual threshold PTH policies were generally similar. The average harvest rates actually applied during fishing openings to maximize the long-term average catch increased with increasing stock productivity, but were similar for all policies at high stock productivity. At low stock productivity values, the dual threshold CER and PTH policies applied lower average harvest rates than the single threshold policies. At very low stock productivity, the catch-maximizing single threshold policies were to harvest all the initial population.

The various catch-maximizing single and dual threshold CER and PTH policies produced similar catches and final escapements at all stock productivity values (Fig. 15). The probability of quasi-extinction increased rapidly with decreasing stock productivity at the catch-maximizing combinations of LRPs and harvest rates for all policies. Extinction probabilities at low stock productivity were reduced for the dual threshold policies (Fig. 15). In all cases, however, the risk of extinction for the catch-maximizing policy at stock productivity values below 1.8 recruits·spawner^{-1} was considerably greater than that of the unharvested population (compare Fig. 6 and Fig. 15). The frequencies of fishing closures were lower and ln(catch) was generally higher for the catch-maximizing PTH policies than for CER policies (Fig. 15). Escapements were similar to or slightly below the LRPs at low stock productivity, but escapements exceeded the LRPs at high stock productivity.

Maximizing discounted catch (3% per annum rate) gave results that were similar to those obtained by maximizing catch, except that LRPs were slightly lower (Fig. 16) and extinction probabilities slightly higher (Fig. 17).

Ln(catch) was maximized by a LRP at or near zero for all policies and stock productivity values (Fig. 18); consequently CER and PTH policies coincided, and all single threshold policies became pure CER policies with no LRP. Although nominal harvest rates were higher for the dual threshold policies, the average harvest rates applied during fishing openings were lower for the dual threshold policies than for the single LRP policies (Fig. 18). The dual threshold policies that maximized ln(catch) produced higher escapement, lower probability of extinction, higher catch, shorter recovery times, and lower frequencies of fishing closures than pure CER policies (Fig. 19). The single threshold (i.e., pure CER) policies always maximized ln(catch).

Harvest control rules that maximized ln(catch) targeted considerably lower nominal harvest rates than policies that maximized catch, but applied only slightly lower average harvest rates at the same stock productivity (compare Fig. 14 and Fig. 18). Escapements and catches were lower for policies that maximized ln(catch), but the reduction in catch was only 10-20% (Fig. 15 and 19). Extinction risk was greatly increased for policies that maximized ln(catch), except below stock productivity values of 1.2 recruits·spawner^{-1} where catch-maximizing policies harvested all the initial population (Fig. 15 and 19). However, policies to maximize ln(catch) greatly reduced the frequency of fishing closures (Fig. 15 and 19).

The magnitude of the temporal autocorrelation in survival deviations affected the catch-maximizing LRPs and nominal harvest rates for a single-threshold CER policy. At the observed variance in survival, the catch-maximizing LRPs and nominal harvest rates both increased as the autocorrelation increased (Fig. 20). The average harvest rate applied during fishing openings also increases as ρ increases. “Optimal” LRPs at moderate and high stock productivity values declined from about $0.2 \cdot B$ at the observed autocorrelation ($\rho = 0.7$) to about $0.12 \cdot B$ for uncorrelated survival deviations. The effect of increasing autocorrelation was to increase escapements, catches, and the frequency of fishing closures and to decrease ln(catch) and recovery time at the catch-maximizing LRPs and harvest rates (Fig. 21). The risk of quasi-extinction generally increased at low stock productivity as the autocorrelation increased.

At the currently observed autocorrelation in smolt-to-adult survival deviations, the magnitude of the variance in smolt-to-adult survival also affected the catch-maximizing LRPs and harvest rates for a single-threshold CER policy (Fig. 22). Catch-maximizing LRPs and harvest rates both generally increased as the variation in survival increased (Fig. 22). Increasing variation in survival at the current autocorrelation decreased escapements, catches, and ln(catch) while increasing the probability of extinction, recovery time, and the frequency of fishing closures (Fig. 23). At current conditions, the effects of changes in survival variation on extinction risk were considerably larger than proportionate changes in autocorrelation (compare Fig. 21 and Fig. 23).

Two-fold variation in the observed uncertainty in the estimate of the asymptotic recruitment slightly changed the catch-maximizing LRPs for a single threshold CER policy (Fig. 24), but had little effect on the performance of the catch-maximizing LRPs and harvest rates (Fig. 25). Larger uncertainty (a 4-fold increase in σ_B) greatly altered the catch-maximizing LRPs and harvest rates, however (Fig. 24). Two-fold and 4-fold increases in the observed σ_B slightly reduced escapement and catches, but halving σ_B had little effect (Fig. 25). Increased population size (i.e., asymptotic maximum adult recruitment) reduced the catch-maximizing LRP values, but had little effect on harvest rates, except at very low stock productivity, where they declined (Fig. 26). The risk of extinction at maximum catch increased considerably for low productivity populations as B declined, but escapement and catch changed little or not at all (Fig. 27).

Increasing the precautionary threshold for a dual threshold policy slightly decreased the catch-maximizing LRP value at low stock productivity, and resulted in lower average harvest rates (Fig. 28). Recovery time (to $0.25 \cdot B$) was greatly reduced at a higher precautionary threshold, but escapement, extinction risk, and catch were unchanged at the catch-maximizing conditions (Fig. 29).

The performance of different limit reference points (i.e., N_{LRP}, $0.2N_{equil}$, $N_{50\%}$, fixed proportions of B) varied with nominal harvest rate, stock productivity, and harvest policy (Fig. 30 to 33). $N_{50\%}$ generally maintained the highest escapement, the lowest probability of quasi-extinction, and the lowest recovery time; however, it also produced the lowest catch and the highest frequency of fishing closures. At low stock productivity, $N_{50\%}$ rarely permitted fishing, and the risk of extinction closely approximated the unfished equilibrium value (Fig. 6). $0.2N_{equil}$ gave low escapement, very high extinction risk, and long recovery time at stock productivity values below 2 recruits·spawner^{-1}, but it maintained fishing opportunities and produced larger catch. N_{LRP} generally gave results that were intermediate between $N_{50\%}$ and $0.2N_{equil}$. At stock productivity below 1.6 recruits·spawner^{-1}, N_{LRP} produced high escapement and low extinction risk similar to $N_{50\%}$ while maintaining higher catch and fewer fishing closures. Recovery time was intermediate between $N_{50\%}$ and $0.2N_{equil}$. At low nominal harvest rates and high stock productivity, all LRPs gave similar results. At high nominal harvest rates and high productivity, catches were similar for the different LRPs but escapements and recovery times differed, with N_{LRP} producing slightly lower escapements and slightly longer recovery times. Harvest policies with both a precautionary threshold and a LRP greatly reduced the differences in performance among different LRP definitions (Fig. 30 to 33).

N_{LRP}, $0.2N_{equil}$, and $N_{50\%}$ all vary with stock productivity and differed considerably, especially at low stock productivity values where N_{LRP} and $N_{50\%}$ increased (Fig. 34). The nominal harvest rates that maximized catches for N_{LRP}, $0.2N_{equil}$, and $N_{50\%}$ were relatively constant above stock productivity values of about 2 recruits·spawner^{-1}, but both nominal harvest rates and the average harvest rates applied during fishing periods declined sharply at low stock productivity for N_{LRP} and $N_{50\%}$ (Fig. 34). Consequently, escapement was higher and the probability of quasi-extinction was much lower at low stock productivity values for N_{LRP} and $N_{50\%}$ than for either $0.2N_{equil}$ (Fig. 35) or the LRP and harvest rate combinations that maximized catch (Fig. 15). Except at very low stock productivity, however, maximum catches using N_{LRP} or $0.2N_{equil}$ were only slightly less than the absolute maxima (Fig. 15 and Fig. 35). Recovery times were lowest for $N_{50\%}$, which approximated a no-fishing policy below 2 recruits· spawner^{-1} (Fig. 34 and 35).

The qualitative performance of CER harvest control rules did not change under a "hockey stick"-type (Barrowman and Myers 2000) spawner-smolt recruitment function (Fig. 36). Harvest control rules that incorporated thresholds greatly decreased the risk of quasi-extinction and increased escapement and catch compared to CER policies without LRPs (Fig. 36). At low LRP values, control rules with both a LRP and a precautionary threshold gave higher escapement, increased catch, and lower frequency of fishing closures than either a single threshold policy or a no threshold policy. The functional form of the spawner-smolt recruitment relationship did, however, considerably alter the quantitative performance of different harvest control rules (compare Fig. 9 and Fig. 36). Under corresponding control rules and thresholds, the "hockey-stick" stock-recruitment function gave considerably higher escapement and catches, lower extinction risk, and fewer fishing closures than the Beverton-Holt stock-recruitment function. The limit reference points and harvest rates that maximized catches for the "hockey-stick" SRR (Fig. 37) were higher than those for the Beverton-Holt SRR (Fig. 14), especially at low stock productivity. Catch-maximizing LRP values for the "hockey stick" SRR varied more with stock productivity than those for the Beverton-Holt SRR, which were relatively constant above a productivity of 2.5 recruits·spawner^{-1} (Fig. 14 and Fig. 36). Proportional threshold harvesting maximized catches at lower LRPs and higher nominal harvest fractions than CER policies for both stock-recruitment relationships. Maximum catches at a given stock productivity were 2- to 3-fold higher for the "hockey stick" SRR than for the Beverton-Holt SRR (Fig. 15 and Fig. 37). Similarly, escapement was considerably higher, extinction risk at low productivity was lower, recovery time was lower, and the frequency of fishing closures was lower for the "hockey stick" SRR (Fig. 38).

Despite the difference between Beverton-Holt and "hockey stick" SRRs in the catch-maximizing LRP values at a given stock productivity (Fig. 14 and Fig. 37), "optimal" LRP values under a CER policy with a single abundance threshold were similar for Beverton-Holt and "hockey stick" SRRs for the Keogh River steelhead data. We estimated the "optimal" LRP by weighting the catch-maximizing LRP value at a given stock productivity for the SRR by the posterior marginal probability of the stock productivity for the SRR (Fig. 4). The "optimal" LRP values were $0.178 \cdot B$ for a Beverton-Holt SRR and $0.183 \cdot B$ for a "hockey-stick" SRR for the Keogh River data, where we have used the long-term average smolt-to-adult survival to convert smolts per spawner to adult recruits per spawner. Because we have ignored variation in the LRPs with B, these values are only approximately correct.

Discussion

Harvest management policies for steelhead fisheries must address 6 major constraints: (1) many steelhead populations are small and may be vulnerable to extirpation, (2) production parameters for individual populations are uncertain, (3) temporal variability in adult recruitment is high and can be strongly autocorrelated, (4) populations may be harvested by fisheries directed at other species, (5) management objectives are stated imprecisely, and (6) prediction and implementation errors may degrade the performance of a given policy. We have used simulation to compare the performance of simple harvest control rules under these constraints. Our goal was to assess the impacts of realistic levels of variability and uncertainty on the performance of different harvest policies and thus to identify policies that perform "well" under a broad range of plausible conditions. Our general conclusion is that threshold harvesting provides a suitable management framework to conserve and manage small populations of steelhead in variable and uncertain environments.

Simple harvest control rules that use abundance thresholds to initiate reductions in harvest rates below the threshold can considerably reduce the risk of quasi-extinction for small populations of steelhead at low abundance compared to constant exploitation rate harvesting policies. Threshold harvesting policies can also reduce recovery time and increase both catch and escapement compared to a CER policy. A CER policy will maximize ln(catch) and reduce the frequency of fishing closures, but it will also increase the risk of quasi-extinction for low productivity stocks compared to threshold harvesting policies. "Constant" exploitation rate control rules that use abundance thresholds can perform similarly to proportional threshold harvesting under conditions of strongly autocorrelated environmental variability and realistic levels of prediction error and implementation error. Harvest control rules that have both an upper precautionary threshold and a limit reference point reduce extinction risk at low stock productivity. The thresholds and harvest rates that maximize catch change with stock productivity, variance in smolt-to-adult survival, temporal autocorrelation in survival deviations, maximum population size, uncertainty in the asymptotic maximum recruitment, and the form of the spawner-smolt recruitment function, but the qualitative results hold true. N_{LRP}, the abundance threshold from which a population can recover to $0.25 \cdot B$ in one generation in the absence of harvesting, increased escapement and lowered extinction risk at low stock productivity with only small reductions to maximum catches. Empirical estimates of the catch-maximizing LRP for the Keogh River steelhead were about $0.17 \cdot B$ to $0.18 \cdot B$ for both Beverton-Holt and rectilinear "hockey stick" stock-recruitment functions.

Long-term average catch generally declines as environmental variability increases (Lande et al. 1997), and temporal autocorrelation in recruitment variability further decreases average catch and increases extinction risk for depressed small populations (Cass and Riddell 1999). Harvest control rules that incorporate a limit reference point to establish a minimum spawning escapement generally increase the long-term average catch and reduce the risk of extinction in fluctuating environments compared to constant exploitation rate policies (Ricker 1958, Larkin and Ricker 1964, Quinn et al. 1990, Lande et al. 1997, Cass and Riddell 1999). Our results generally support these conclusions. If extinction risk can be ignored, however, a constant exploitation rate policy can produce catches that are within 15% of the theoretical optimum where there are strongly autocorrelated environmental effects on recruitment (Parma and Walters 1996). In our simulations, CER policies reduced maximum catches by 10-20% compared to threshold policies, but extinction risk increased several-fold to many-fold at low stock productivity. CER policies also led to lower escapements and longer recovery times. We argue that an increased probability of quasi-extinction and lower abundance make CER policies unsuitable for small populations of steelhead with uncertain production parameters.

Proportional threshold harvesting and CER harvesting with a LRP gave similar maximum catches when smolt-to-adult survival deviations were strongly autocorrelated ($\rho = 0.7$), despite slightly different control rules (Fig. 3). Nevertheless, PTH policies may be preferable. PTH harvesting allowed lower LRPs, applied lower average harvest rates, and imposed fewer fishing closures than threshold CER policies (Fig. 14 and Fig. 15). The nominal harvest fraction that maximized catch for a PTH policy was generally in the range from 0.8 to 0.9 in simulations that used empirical estimates of prediction and implementation error. This fraction is less than the expected optimal value of one (i.e., a constant escapement policy) to maximize annual yield (Lande et al. 1997), but Lande et al. (1997) also note that the optimal harvest fraction may be substantially less than one if there is large uncertainty in the population size. Dual threshold CER and PTH policies performed similarly to single threshold policies, except that they reduced extinction risk at very low stock productivity. Despite generally similar performance, dual threshold harvest control rules may be preferable to either single threshold or no threshold policies because they reduce harvest rates sooner during periods of declining abundance. Dual threshold harvest control rules may also be preferable in circumstances where another fishery harvests steelhead as bycatch. A nominal harvest rate will be established by the other fishery, but may be reduced according to a harvest control rule based on steelhead abundance to ensure that some minimum steelhead abundance is maintained. At low LRP values, dual threshold harvest rules increase escapement, greatly lower extinction risk, and reduce closure frequency while maintaining much of the maximum catch (Fig. 9 and Fig. 13).

Fixed LRPs that maximized catch for a single threshold CER policy were usually in the range from $0.15 \cdot B$ to $0.2 \cdot B$ for long term average stock productivity values greater than 2 recruits·spawner^{-1} under a wide range of conditions. Only the functional form of the stock-recruitment relation, temporal autocorrelation in survival deviations, and maximum population size strongly influenced the catch-maximizing LRPs. Because both increased autocorrelation and lower maximum population size increased the catch-maximizing LRP values (Fig. 20 and Fig. 26), a conservative management policy might adopt LRPs near $0.2 \cdot B$. The flatness of the catch response surface near the maximum (Fig. 10 and Fig. 11) suggests that precise optimization is not required; near-maximal catches can be obtained from a range of LRP values. Catch-maximizing LRP values decline at low stock productivity (Fig. 14), however, catch maximization will be an inappropriate management goal for small, unproductive populations whose relative extinction risk is high even without harvest (Fig. 7) and is increased greatly by catch-maximizing harvest policies (Fig. 15). Using N_{LRP} or $N_{50\%}$ as a LRP greatly reduces extinction risk for small unproductive populations (Fig. 35) by reducing harvest rates at low stock productivity (Fig. 34). N_{LRP} also maintains much of the maximum catch. $N_{50\%}$ is a very conservative LRP that significantly reduces catch at low and moderate stock productivity values. Myers et al. (1994) showed that $N_{50\%}$ effectively avoids recruitment overfishing for a wide variety of fish stocks. The $0.2{\cdot}N_{equil}$ LRP, which is commonly recommended (Francis 1993) and widely applied (Myers et al. 1994), generally performed poorly compared to the other LRPs. Myers et al. (1994) recommend against using $0.2{\cdot}N_{equil}$ as a threshold because it also performed poorly in empirical tests and because it does not account adequately for differences in density-dependence among stocks.

N_{LRP} is effective in reducing extinction risk because it is tied conceptually both to the processes that cause extinction and to a recovery trajectory. N_{LRP} explicitly links the maximum sustainable increase in density-independent mortality from all sources to a specified rate of recovery to a desired abundance level. Populations are driven extinct by systematic changes in fecundity or density-independent mortality that produce sustained periods of negative population growth rates. These types of changes may result from reduced growth and survival in the marine phase of the life history (e.g., from climate change, incidental harvest) or from decreased freshwater habitat quality (e.g., from logging, urbanization) which reduces freshwater survival. Extinction from purely stochastic processes occurs only at very low abundance (Routledge and Irvine 1999). Except for very small populations, N_{LRP} defines conditions that generally permit rapid recovery to a CCT and identifies a maximum additional mortality to avoid extinction. Simulation confirms its effectiveness.

Information on stock productivity is required to determine N_{LRP}. Estimates of a are often highly uncertain, especially if uncertainty in the underlying stock-recruitment model is admitted. Simple approximations to N_{LRP} seem possible, however. Empirical smolt production data for the Keogh River steelhead population suggests that N_{LRP} is approximately $0.13{\cdot}B$. In our simulations, fixed proportions of B in the range from about 0.15 to 0.2 performed well, especially under the dual threshold harvest policy. B is generally better specified than a from steelhead stock-recruitment data, and can also be estimated with habitat capability models. Both a and B vary with marine survival, but N_{LRP} can be determined from the α and β parameters of the spawner-smolt relation. Two-fold uncertainty in the estimate of B does not greatly alter catch-maximizing LRPs and harvest rates.

Stock productivity must be greater than about 2 recruits·spawner^{-1} for 0.25·B to be a good approximation to N_{MSY}. Smolt productivity data for the Keogh River and Snow Creek (Fig. 4) imply stock productivity values greater than 2 recruits·spawner^{-1} at their average smolt-to-adult survival values of 0.11 and 0.051. Harvest rates for the Skeena steelhead stock aggregate are about 55% (Cox-Rogers 1994), which implies a minimum stock productivity of at least 2.5 recruits·spawner^{-1}. Bjorn (1977) suggests that steelhead in the Clearwater River, Idaho formerly sustained harvest rates of 80%, which requires a stock productivity of 5 recruits·spawner^{-1}. The limited data suggest that approximating N_{MSY} by for 0.25·B will frequently be valid.

We have not considered genetic effects that might reduce the viability of very small populations, nor have we considered depensatory mechanisms in the stock-recruitment relationship. There is no clear empirical evidence for or against depensation in salmon (Liermann and Hilborn 1997). However, small populations of salmonids (10's to 100's of spawners) have persisted for long periods (e.g., coho and steelhead in Carnation Creek, B.C., Hartman and Scrivener 1990). Inbreeding and loss of genetic material may occur at very small population size, but the abundance at which these effects become important is uncertain, and even low rates of straying among populations may reduce their consequences.

Management implications

The simple relationship between N_{LRP}, N_{CCT}, and B for a population with a Beverton-Holt type SRR provides the conceptual framework for a conservation policy for steelhead that is based on a dual threshold harvesting policy. The policy would use N_{CCT} as a minimum abundance target and N_{LRP} as a LRP to establish three management zones based on abundance: (1) a routine management zone at abundances above N_{CCT}, (2) a conservation concern zone between N_{LRP} and N_{CCT}, and (3) an extreme conservation concern zone at abundances below N_{LRP}. N_{CCT} is a good approximation to N_{MSY} over the range of plausible stock productivity indicated for the Keogh River and Snow Creek steelhead populations. A population whose abundance is at or above N_{CCT} can be managed to optimize agreed-upon societal goals. In the conservation concern zone, the population is recognized as overfished, and management activities increasingly reduce harvest and other controllable sources of mortality as abundance declines towards N_{LRP}. Near or below N_{LRP} it is recognized that the viability of the population may be at risk. Management actions could include extraordinary measures to increase stock productivity (e.g., hatchery supplementation, fertilization, habitat enhancement, or coarse fish removal) or to reduce all mortality sources (e.g., predator control). We suggest that N_{LRP}

be 0.15·B to 0.2·B, from our simulations. We suggest that N_{CCT} be 0.35·B to ensure that there is a high (> 90%) probability that an empirically-estimated N_{CCT} equals or exceeds the true N_{MSY}; this value is based on the uncertainty observed in empirical estimates of β for the Keogh River and Snow Creek steelhead stocks.

The definitions of N_{LRP} and N_{CCT} result in several options for monitoring stock status. First, if spawners are at N_{LRP}, then the resulting smolts will be at the N_{CCT}, expressed in smolt equivalents. Thus, if the adult population is at N_{LRP}, smolt abundance will be at q (i.e., 25%) of the maximum smolt abundance. If smolt abundance can be determined as a fraction of habitat capacity, then N_{LRP} can be monitored by an indicator that does not require a direct estimate of productivity. If the spawner population is at 0.25·B, then smolt abundance will be 50 to 75% of the maximum for stock productivity values between 1.1 and 10. Thus, an index of smolt abundance that is less than 50% of the habitat capacity implies that the adult population is below N_{CCT}. Alternatively, adult recruits can be used directly to assess stock status.

In summary, a dual threshold harvesting policy based on N_{LRP} and N_{CCT} is likely to avoid high risk of quasi-extinction while maintaining adequate escapement and catch. Fixed proportions of the asymptotic maximum recruitment provide good approximations to N_{LRP} and N_{CCT} and allow relatively easy monitoring of population status using either smolts or adults. The proposed policy performed well under realistic levels of variation for small, moderately productive populations.

Acknowledgements

We thank Pat Slaney and the various Keogh fence crews for generating the primary data on steelhead population dynamics. We thank Rick Cooper for providing the Snow Creek data. We are grateful to Al Cass and Paul McElhany for their helpful criticisms of an earlier draft of the paper. We are very grateful to Janice Burns for her patience.

References

Barrowman, N.J. and Myers, R.A. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Can. J. Fish. Aquat. Sci. 57: 665-676.

Bjorn, T.C. 1977. Mixed stocks of wild and hatchery steelhead trout: a management problem in Idaho. *In* Genetic implications of steelhead management. *Edited by* T.J. Hassler and R.R. Van Kirk. Calif. Coop. Fish. Res. Unit Spec. Rep. 77-1.

Botsford, L.W., and Brittnacher, J.G. 1998. Viability of Sacramento River winter-run chinook salmon. Conservation Biol. 12: 65-79.

Cass, A., and Riddell, B. 1999. A life history model for assessing alternative management policies for depressed chinook salmon. ICES J. mar. Sci. 56: 414-421.

Cederholm, C.J., Kunze, M.D., Murota, T., and Sibatani, A. 1999. Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. Fisheries 24, No.10: 6-15.

Cox-Rogers, S. 1994. Description of a daily simulation model for the Area 4 (Skeena) commercial gillnet fishery. Can. MS. Rep. Fish. Aquat. Sci. 2256: 46 pp.

Deriso, R. 1985. Risk adverse harvesting strategies. *In* Resource management. Proceedings of the second Ralf Yorque workshop held in Ashland, Oregon, July 23-25, 1984. *Edited* by M. Mangel. Lecture Notes in Biomathematics No. 61: 65-73. Springer-Verlag, Berlin.

FAO (Food and Agricultural Organization of the United Nations). 1995. Code of conduct for responsible fisheries. FAO, Rome. http://www.fao.org/fi/agreem/codecond/ficonde.asp

Francis, R.I.C.C. 1993. Monte Carlo evaluation of risks for biological reference points used in New Zealand fishery assessments. *In* Risk evaluation and biological reference points for fisheries management. *Edited by* S.J. Smith, J.J. Hunt, and D. Rivard. Can. Spec. Publ. Fish. Aquat. Sci. 120. Pp. 221-230.

Gabriel, W.L., and Mace. P.M. 1999. A review of biological reference points in the context of the precautionary approach. *In* Proceedings of the Fifth National Stock Assessment Workshop. Providing scientific advice to implement the precautionary approach under the Magnuson-Stevens Fishery Conservation and Management Act. *Edited by* V.R. Restrepo. U.S. Department of Commerce, National Marine Fisheries Service, NOAA Technical Memorandum NMFS-F/SPO-40. Pp. 34-45.

Garcia, S.M. 1996. The precautionary approach to fisheries and its implications for fishery research, technology and management: an updated review. FAO Fisheries Technical Paper No. 350, Part 2: 1-63.

Hartman, G.F. and Scrivener, J.C. 1990. Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia. Can. Bull. Fish. Aquat. Sci. 223: 148 pp.

Heino, M., Ripa, J., and Kaitala, V. 2000. Extinction risk under coloured environmental noise. Ecography 23: 177-184.

Kope, R. 1999. Proposed changes to the fishery management plan for Pacific salmon. *In* Proceedings of the Fifth National Stock Assessment Workshop. Providing scientific advice to implement the precautionary approach under the Magnuson-Stevens Fishery Conservation and Management Act. *Edited by* V.R. Restrepo. U.S. Department of Commerce, National Marine Fisheries Service, NOAA Technical Memorandum NMFS-F/SPO-40. Pp. 52.

Lande, R., Sæther, B.-E., and Engen, S. 1997. Threshold harvesting for sustainability of fluctuating resources. Ecology 78: 1341-1350.

Larkin, PA. and Ricker, W.E. 1964. Further information on sustained yields from fluctuating environments. J. Fish. Res. Bd. Canada 21: 1-7.

Liermann, M. and Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. Can. J. Fish. Aquat. Sci. 54: 1976-1984.

Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? Ecology 80: 298-310.

Ludwig, D., Hilborn, R., and Walters, C. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science 260: 17, 36.

Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Can. J. Fish. Aquat. Sci. 51: 110-122.

Mace, P.M., and Gabriel, W.L. 1999. Evolution, scope, and current applications of the precautionary approach in fisheries. *In* Proceedings of the Fifth National Stock Assessment Workshop. Providing scientific advice to implement the precautionary approach under the Magnuson-Stevens Fishery Conservation and Management Act. *Edited by* V.R. Restrepo. U.S. Department of Commerce, National Marine Fisheries Service, NOAA Technical Memorandum NMFS-F/SPO-40. Pp. 65-73.

Myers, R.A., Rosenberg, A.A., Mace, P.M., Barrowman, N., and Restrepo, V.R. 1994. In search of thresholds for recruitment overfishing. ICES J. mar. Sci. 51: 191-205.

Nickelson, T.E. 1998. A habitat-based assessment of coho salmon production potential and spawner escapement needs for Oregon coastal streams. Oregon Dep. Fish Wildl. Fish. Div. Info. Rep. 98-4, 15 pp.

Quinn II, T.J., Fagen, R., and Zheng, J. 1990. Threshold management policies for exploited populations. Can. J. Fish. Aquat. Sci. 47: 2016-2029.

Richards, L.J., and Maguire, J.-J. 1998. Recent international agreements and the precautionary approach: new directions for fisheries management science. Can. J. Fish. Aquat. Sci. 55: 1545-1552.

Ricker, W.E. 1958. Maximum sustained yields from fluctuating environments and mixed stocks. J. Fish. Res. Bd. Canada 15: 991-1006.

Routledge, R.D., and Irvine, J.R. 1999. Chance fluctuations and the survival of small salmon stocks. Can. J. Fish. Aquat. Sci. 56: 1512-1519.

Serchuk, F.M., Rivard, D., Casey, J., and Mayo, R.K. 1999. A conceptual framework for the implementation of the precautionary approach to fisheries management within the Northwest Atlantic Fisheries Organization (NAFO). *In* Proceedings of the Fifth National Stock Assessment Workshop. Providing scientific advice to implement the precautionary approach under the Magnuson-Stevens Fishery Conservation and Management Act. *Edited by* V.R. Restrepo. U.S. Department of Commerce, National Marine Fisheries Service, NOAA Technical Memorandum NMFS-F/SPO-40. Pp. 103-119.

Slaney, T.L., Hyatt, K.D., Northcote, T.G., and Feldon, R.J. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. Fisheries 21, No. 10: 20-35.

Smith, B.D., and Ward, B.R. 2000. Trends in wild adult steelhead (*Oncorhynchus mykiss*) abundance for coastal regions of British Columbia support the variable marine survival hypothesis. Can. J. Fish. Aquat. Sci. 57: 271-284.

Taylor, B.L. 1995. The reliability of using population viability analysis for risk classification of species. Conservation Biol. 9: 551-558.

Thompson, G.G. 1999. Optimizing harvest control rules in the presence of natural variability and parameter uncertainty. *In* Proceedings of the Fifth National Stock Assessment Workshop. Providing scientific advice to implement the precautionary approach under the Magnuson-Stevens Fishery Conservation and Management Act. *Edited by* V.R. Restrepo. U.S. Department of Commerce, National Marine Fisheries Service, NOAA Technical Memorandum NMFS-F/SPO-40. Pp. 124-145.

Walters, C., and Ludwig, D. 1994. Calculation of Bayes posterior probability distributions for key population parameters. Can. J. Fish. Aquat. Sci. 51: 713-722.

Walters, C., and Parma, A.M. 1996. Fixed exploitation rate strategies for coping with effects of climate change. Can. J. Fish. Aquat. Sci. 53: 148-158.

Ward, B.R. 1996. Population dynamics of steelhead trout in a coastal stream, the Keogh River, British Columbia. *In* Stock assessment in inland fisheries. *Edited by* I. Cowx. Fishing News Books, Blackwell Scientific Publications, Oxford, U.K. pp. 308-323.

Ward, B.R. 2000. Declivity in steelhead (*Oncorhynchus mykiss*) recruitment at the Keogh River over the past decade. Can. J. Fish. Aquat. Sci. 57: 298-306.

Ward, B.R., and Slaney, P.A. 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Can. J. Fish. Aquat. Sci. 45: 1110-1122.

Table 1. Harvest control rules for constant exploitation rate (CER) and for proportional threshold harvesting (PTH) policies with a single minimum escapement threshold at LRP, or with an additional precautionary abundance threshold at CCT. h_t is the target harvest rate at time t for a predicted recruitment of $NEst_t$, h_{policy} is the nominal harvest rate for the CER policy, and p_{policy} is the nominal proportion of surplus spawners to be harvested for the PTH policy.

		Predicted Recruitment		
Harvest Policy	Thresholds	$NEst_t <$ LRP	LRP $<$ $NEst_t$ $<$ CCT	CCT $<$ $NEst_t$
Constant exploitation rate	LRP	$h_{target} = 0$	$h_{target} = min(h_{policy}, \frac{NEst_t - LRP}{NEst_t})$	$h_{target} = min(h_{policy}, \frac{NEst_t - LRP}{NEst_t})$
Constant exploitation rate	LRP and CCT	$h_{target} = 0$	$h_{target} = min(\frac{h_{policy}}{(CCT - LRP)} \cdot (NEst_t - LRP), \frac{NEst_t - LRP}{Nest_t})$	$h_{target} = min(h_{policy}, \frac{NEst_t - LRP}{NEst_t})$
Proportional threshold harvesting	LRP	$h_{target} = 0$	$h_{target} = p_{policy} \cdot \left(\frac{NEst_t - LRP}{NEst_t}\right)$	$h_{target} = p_{policy} \cdot \left(\frac{NEst_t - LRP}{NEst_t}\right)$
Proportional threshold harvesting	LRP and CCT	$h_{target} = 0$	$h_{target} = \frac{p_{policy}}{(CCT - LRP)} \cdot \frac{(NEst_t - LRP)^2}{NEst_t}$	$h_{target} = p_{policy} \cdot \left(\frac{NEst_t - LRP}{NEst_t}\right)$

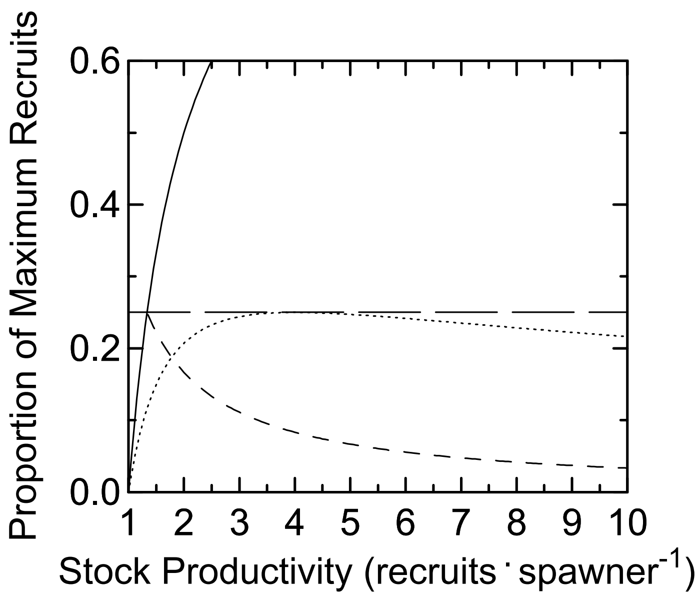

Fig. 1. The unfished equilibrium abundance, N_{equil} (——); the spawner abundance at MSY, N_{MSY} (······); the conservation concern threshold defined by $N_{CCT} = 0.25 \cdot B$ (— — —) where B is the asymptotic maximum adult recruitment; and the limit reference point, N_{LRP} (– – –), defined as the spawner abundance from which the population will recover to the conservation concern threshold in one generation in the absence of harvest, as functions of the stock productivity parameter of the Beverton-Holt stock-recruitment relationship,

$$N_{t+1} = \frac{\alpha \cdot N_t}{(1 + \alpha \cdot N_t / \beta)}.$$

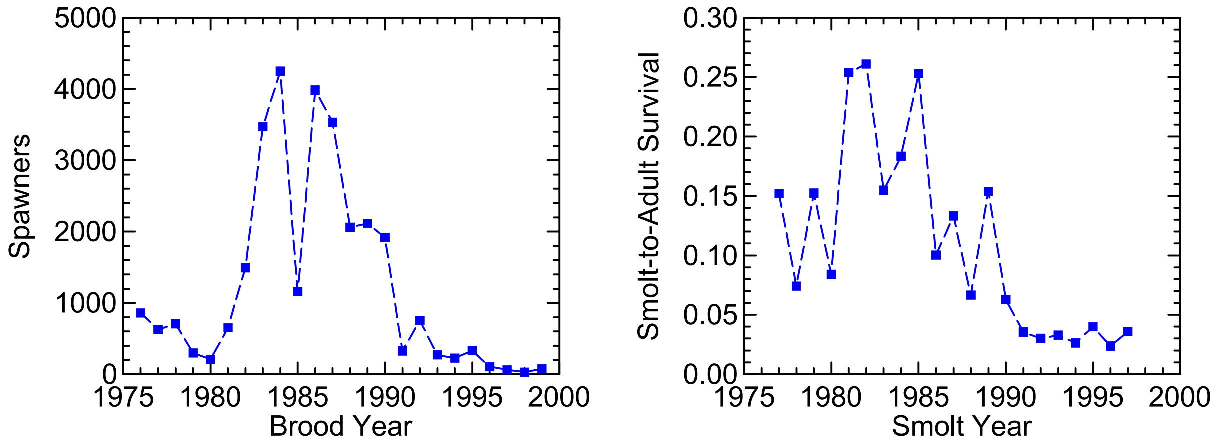

Fig. 2. (left panel) Spawner abundance by brood year for Keogh River steelhead.

(right panel) Overall smolt-to-adult survival by year of smolt emigration for Keogh River steelhead. Outmigrant smolts are a variable mixture of ages 1 to 5.

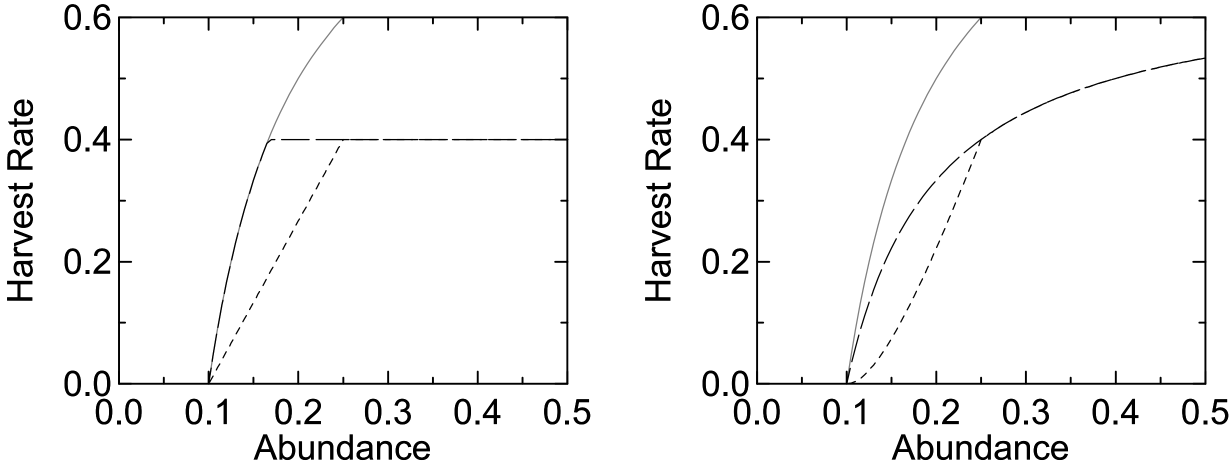

Fig. 3. (left panel) Harvest control rules for constant exploitation rate (CER) harvest policies with a single minimum escapement threshold at 0.1B (— —) or with a minimum escapement threshold at 0.1·B and a precautionary threshold at 0.25B (- -) below which the harvest rate declines linearly to zero at the minimum escapement threshold. The harvest rates are bounded by a maximum rate (——) if a minimum escapement must be maintained. Abundance is in units of B, the asymptotic maximum recruitment.

(right panel) Harvest control rules for proportional threshold harvesting (PTH) policies with a single minimum escapement threshold at 0.1B (— —) or with a minimum escapement threshold at 0.1·B and a precautionary threshold at 0.25B (- -) below which the proportion of surplus fish that are harvested declines linearly to zero at the minimum escapement threshold. The CER and PTH policies have been adjusted to have the same harvest rate (0.4) at the precautionary threshold in this example; the nominal harvest fraction on surplus fish is 0.67 for this PTH policy. In the region between the minimum escapement threshold and the precautionary threshold, the harvest rate for the PTH policy at a given recruitment is always lower than or equal to the harvest rate under the CER policy.

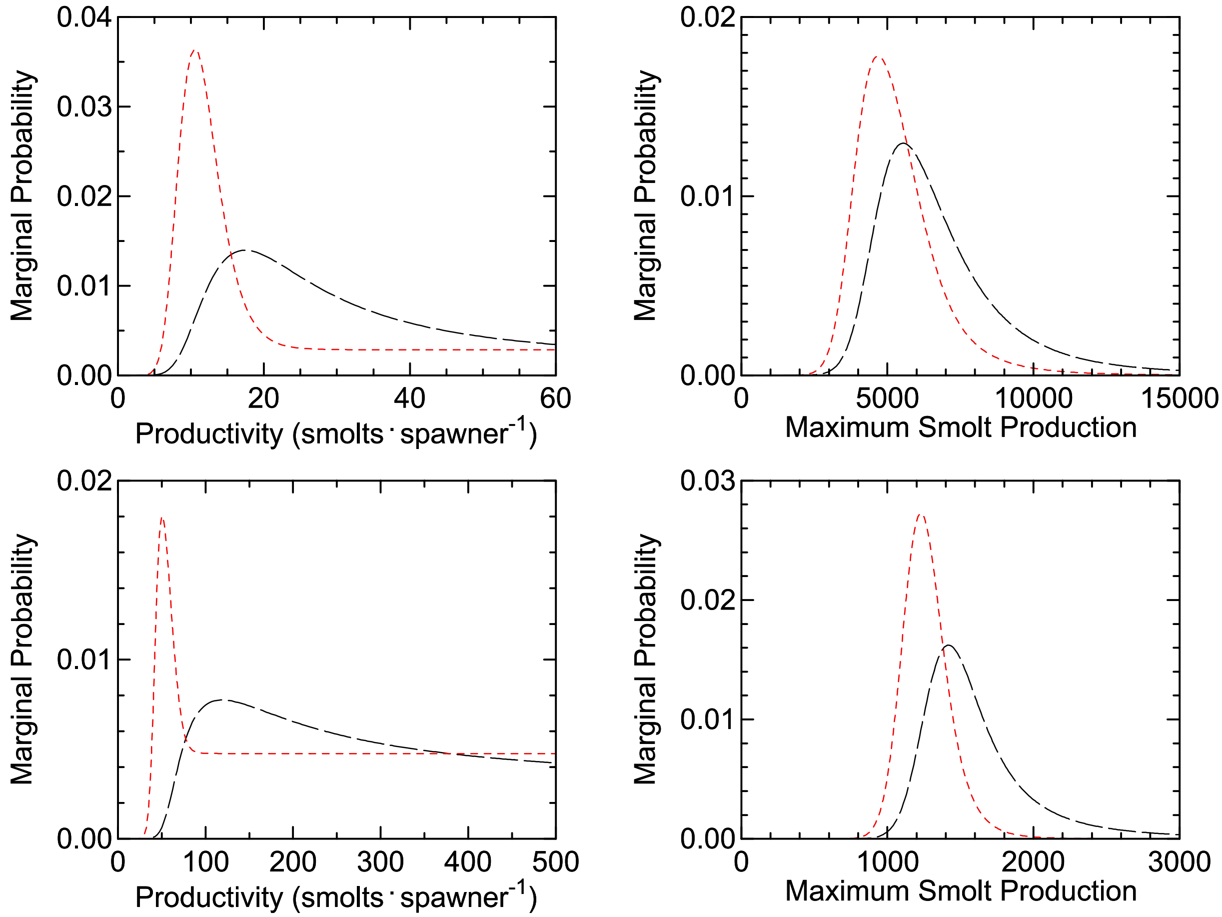

Fig. 4. Posterior probabilities of smolt productivity values and maximum smolt recruitment for steelhead in the Keogh River, British Columbia (upper panels) and in Snow Creek, Washington (lower panels) for Beverton-Holt (— — —) and rectilinear "hockey stick" (- - -) stock-recruitment functions.

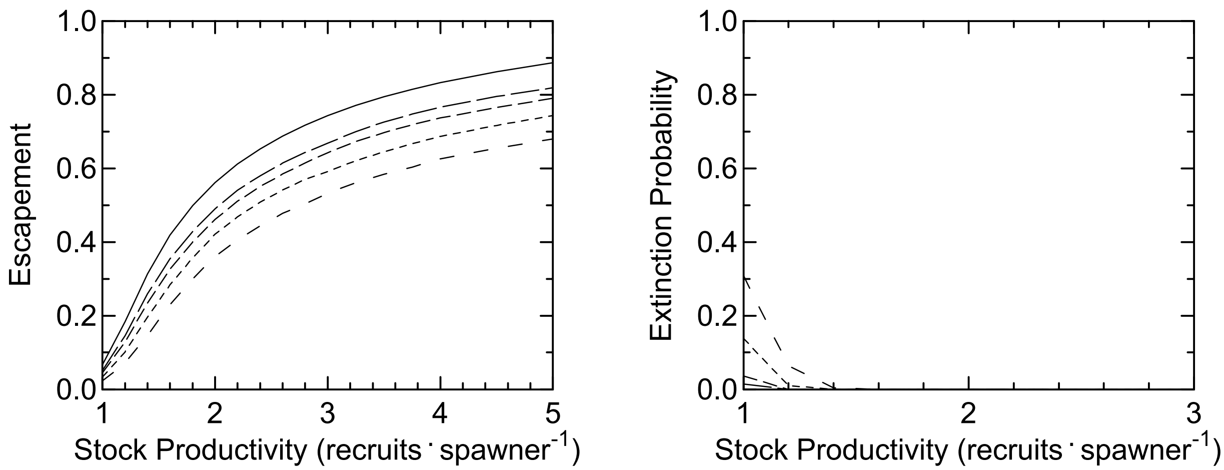

Fig. 5. The effects of variation in smolt-to-adult survival on the unfished equilibrium spawner abundance (left panel) and the probability of quasi-extinction (right panel) at different stock productivity values. Survival deviations are uncorrelated in time ($\rho = 0$). Results are based on 500 trials using the stochastic, age-structured steelhead population model described in the text. Lines represent: $\sigma_{survival}$ = 0.0 (——), 0.2 (— — —), 0.4 (– – –), 0.6 (- - -), and 0.8 (– – –). The initial population size was N_0 = 0.1B where B = 1 000.

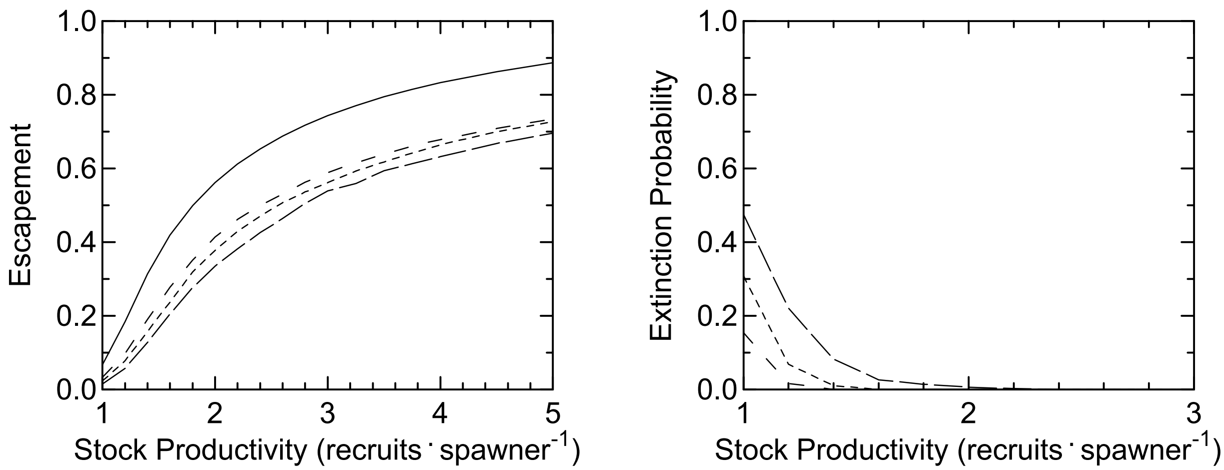

Fig. 5. The effects of temporal autocorrelation in smolt-to-adult survival deviations on the unfished equilibrium abundance (left panel) and the probability of quasi-extinction (right panel) at different stock productivity values for the stochastic, age-structured steelhead population dynamics model described in the text. Results are based on 500 50-year trials with the observed variation in smolt-to-adult survival ($\sigma_{survival}$ = 0.629). Lines are: ρ = 0.0 (– – –), 0.4 (- - -), and 0.7 (— — —). Deterministic model results ($\sigma_{survival}$ = 0, ρ = 0) are shown for comparison (——). Initial population size is N_0 = 0.1B where B = 1 000.

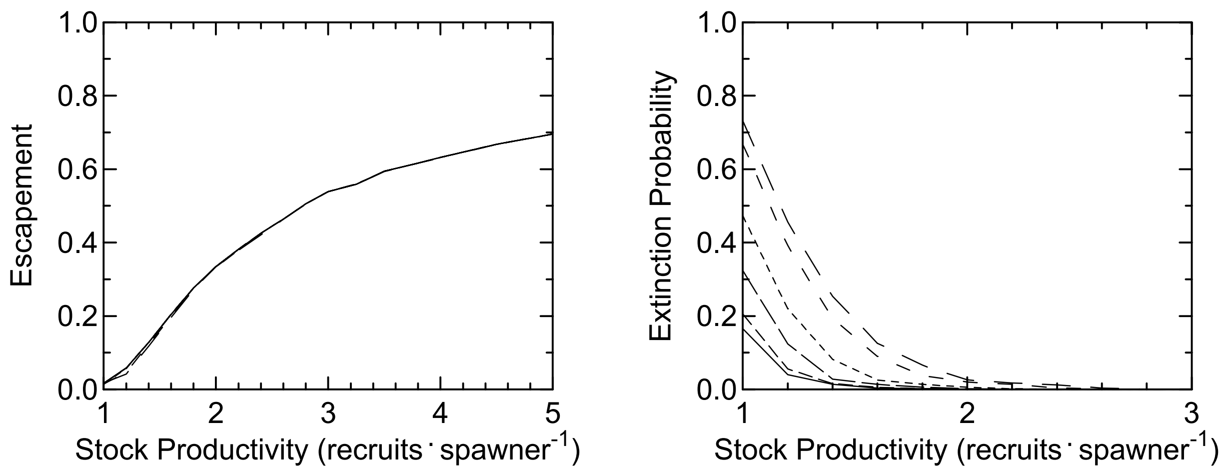

Fig. 7. Effects of the quasi-extinction threshold on the unfished equilibrium spawner abundance (left panel) and the probability of quasi-extinction (right panel) at different stock productivity values for the steelhead population dynamics model described in the text. Quasi-extinction thresholds are: 1 (——), 2 (– – –), 5 = (— — —), 10 (- - -), 20 (– – –), and 25 (— — —) fish. Results are based on 500 trials using the observed smolt-to-adult survival variation ($\sigma_{survival}$ = 0.629) and temporal auto-correlation in survival deviations (ρ = 0.7). The initial population size is $N_0 = 0.1B$ where B = 1 000.

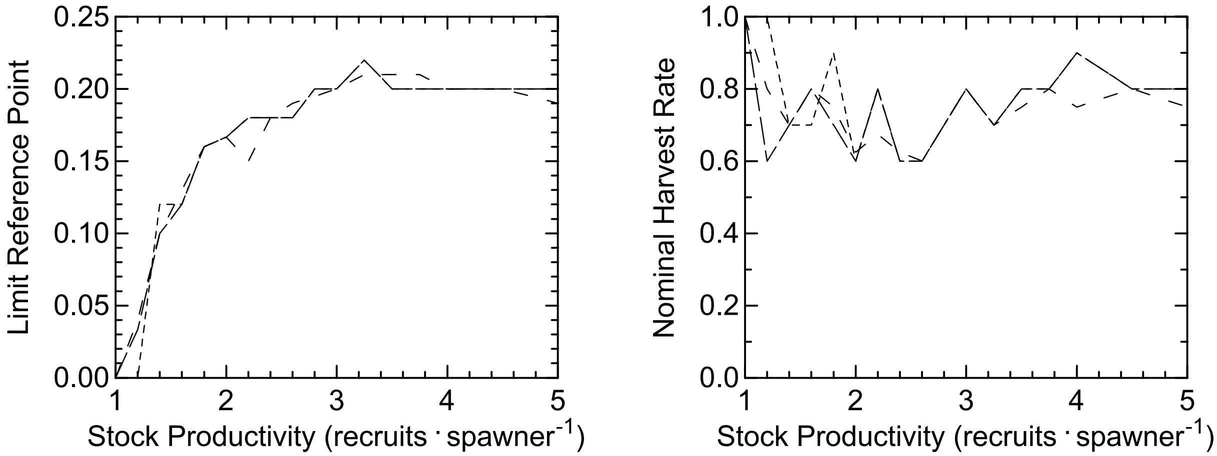

Fig. 8. Effects of the quasi-extinction threshold on the limit reference point abundance (left panel) and nominal harvest rate (right panel) values that maximize the long-term catch under a "constant" exploitation rate harvest policy with a single limit reference point below which forecast abundance the harvesting ceases. Extinction thresholds are: 2 (— — —), 10 (– – –), and 25 (- - -) fish. Results are based on 500 trials using the observed smolt-to-adult survival variation ($\sigma_{survival}$ = 0.629) and temporal autocorrelation in survival deviations (ρ = 0.7). The initial population size is $N_0 = 0.1B$ where B = 1 000.

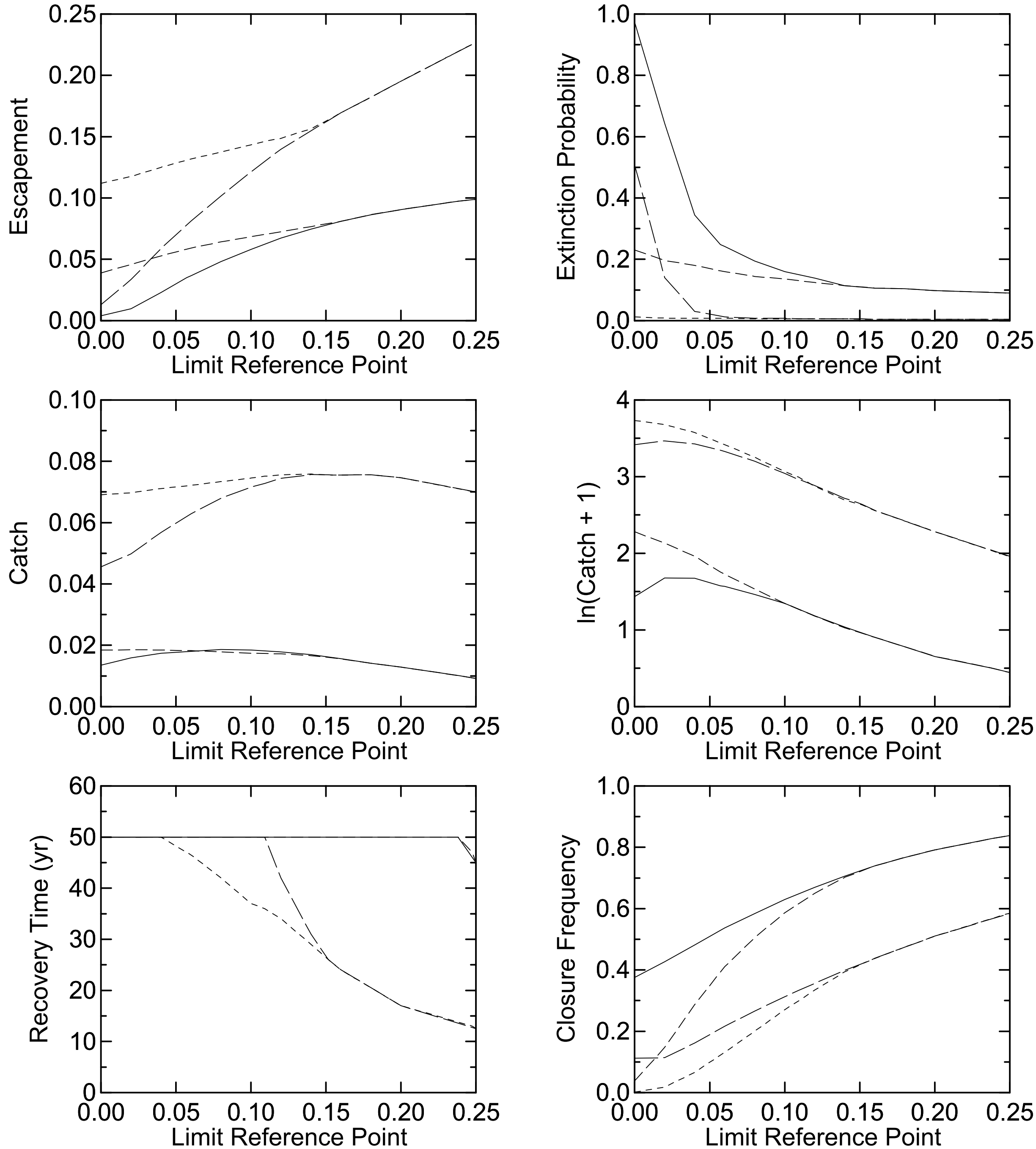

Fig. 9. The effects of limit reference point definitions and stock productivity on performance indicators under a "constant" exploitation rate harvesting rule with either: a single abundance threshold (limit reference point, LRP) below which forecast abundance the harvesting ceases (—— and — — —), or a limit reference point and a precautionary reference point at 0.25B (– – – and - - -) below which forecast abundance the

nominal harvest rate declines linearly to zero at the LRP. Data are shown for low stock productivity (1.4 recruits·spawner^{-1}, —— and – – –) and for moderate stock productivity (2.2 recruits·spawner^{-1}, — — — and - - -). Limit reference points, escapement, and catch are in units of B, the asymptotic maximum adult recruitment. The nominal harvest rate is 0.5, the initial population size is $N_0 = 0.1B$, B = 1 000, the variation in smolt-to-adult survival is $\sigma_{survival} = 0.629$, and temporal autocorrelation in survival deviations is $\rho = 0.7$ in this example. Note that a LRP of zero is a conventional constant exploitation rate harvesting rule.

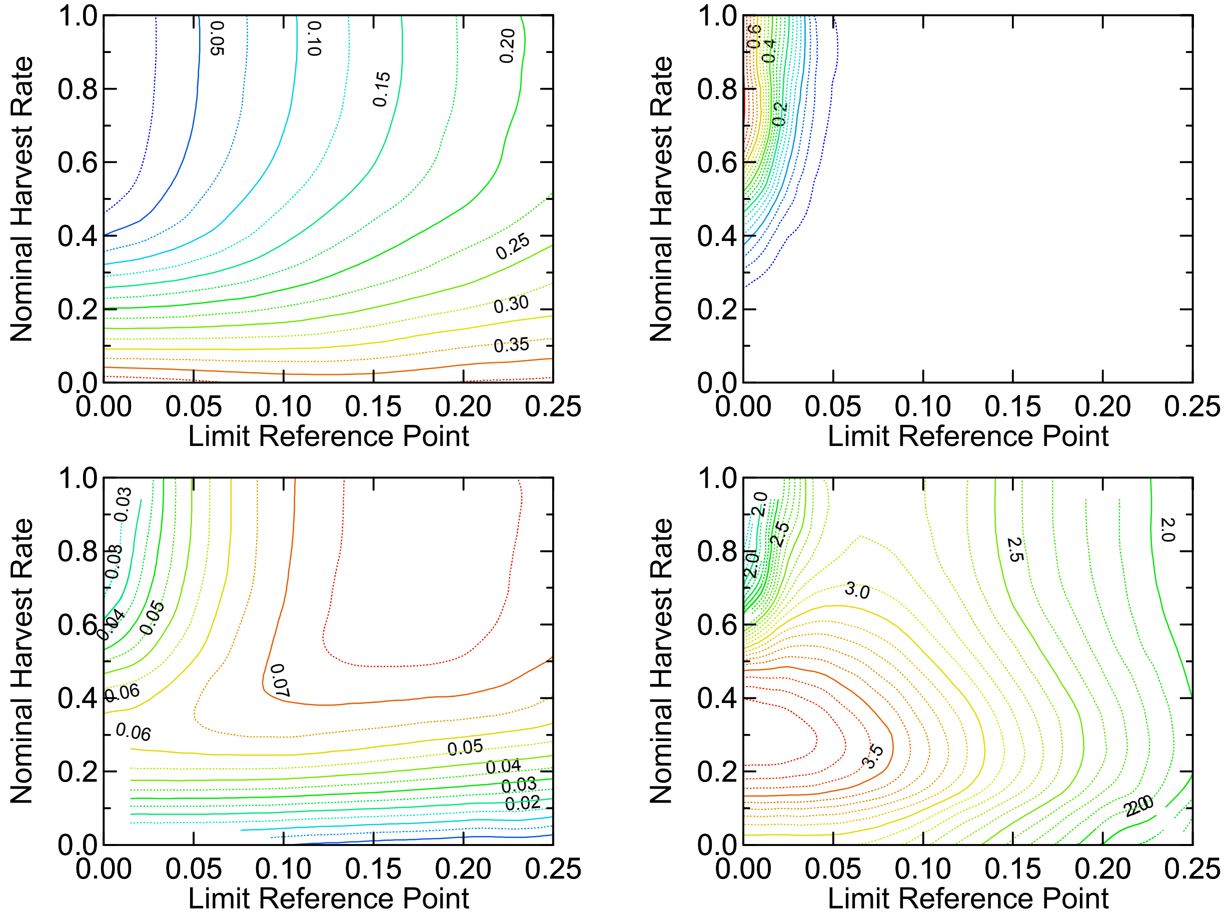

Fig. 10. The dependence of escapement (upper left), extinction probability (upper right), catch (lower left) and ln(catch) (lower right) on the limit reference point (LRP) and nominal harvest rate under a constant exploitation rate harvesting policy with a single LRP below which forecast abundance the harvesting ceases. Abundance is in units of B, the asymptotic maximum adult recruitment. B = 1 000, N_0 = 0.1B, $\sigma_{survival}$ = 0.629, ρ = 0.7, and a = 2.2 recruits·spawner^{-1}.

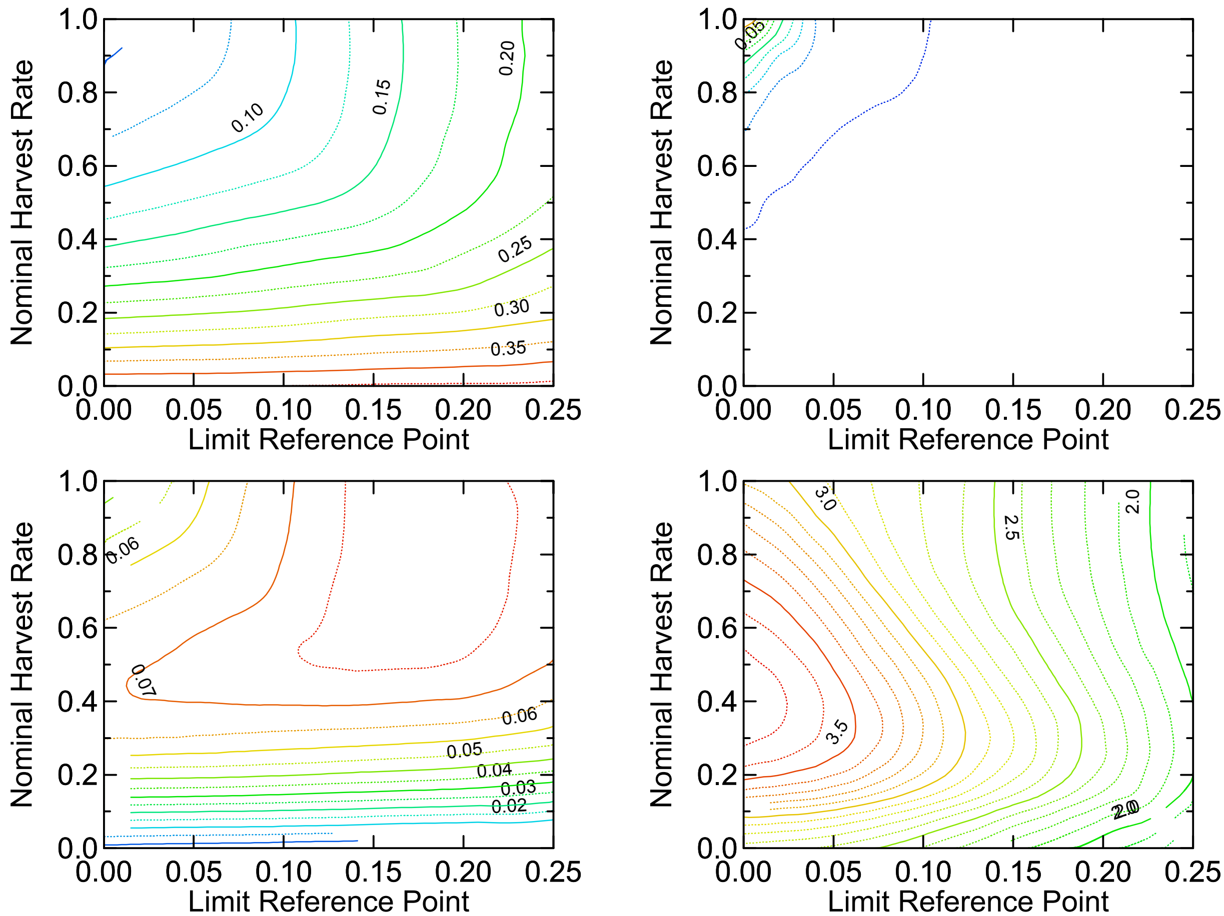

Fig. 11. The dependence of escapement (upper left), extinction probability (upper right), catch (lower left) and ln(catch) (lower right) on the limit reference point (LRP) and nominal harvest rate under a "constant" exploitation rate harvesting policy with a precautionary threshold at 0.25B below which forecast abundance the harvest rate declines linearly to zero at the limit reference point. Abundance is in units of B, the asymptotic maximum adult recruitment. B = 1 000, $N_0 = 0.1B$, $\sigma_{survival} = 0.629$, $\rho = 0.7$, and a = 2.2 recruits·spawner^{-1}.

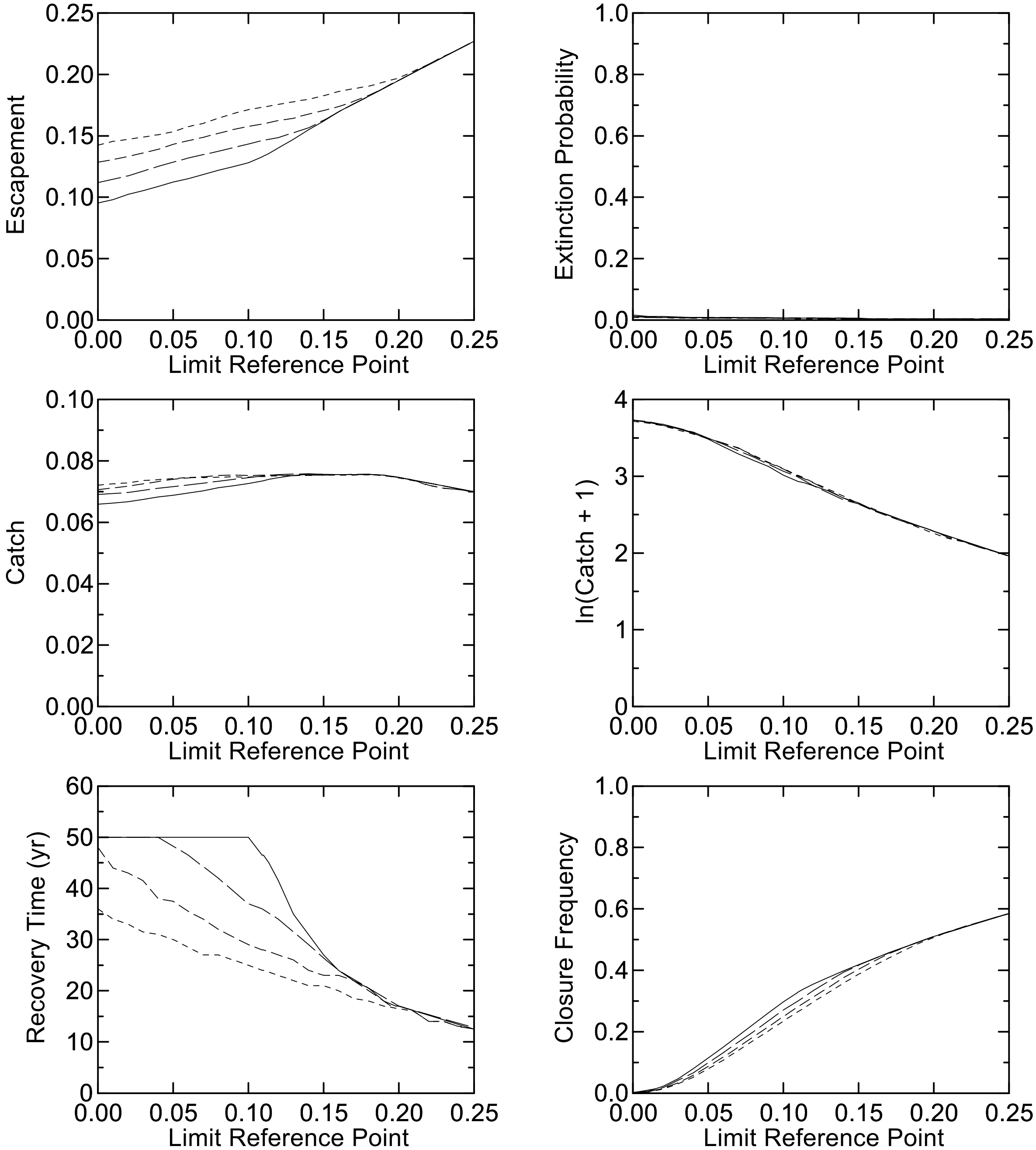

Fig. 12. The effect of limit reference point definition on performance indicators under a "constant" exploitation rate harvesting rule with a precautionary threshold below which forecast abundance the harvest rate declines linearly to zero at the limit reference point. Precautionary thresholds are: 0.20B (——), 0.25B (— — —), 0.30B (– – –), and 0.35B (- - -). Abundance is in units of B, the asymptotic maximum adult

recruitment. The nominal harvest rate is 0.5, $N_0 = 0.1B$, $B = 1\ 000$, $\sigma_{survival} = 0.629$, $\rho = 0.7$, and $a = 2.2$ recruits·spawner^{-1}.

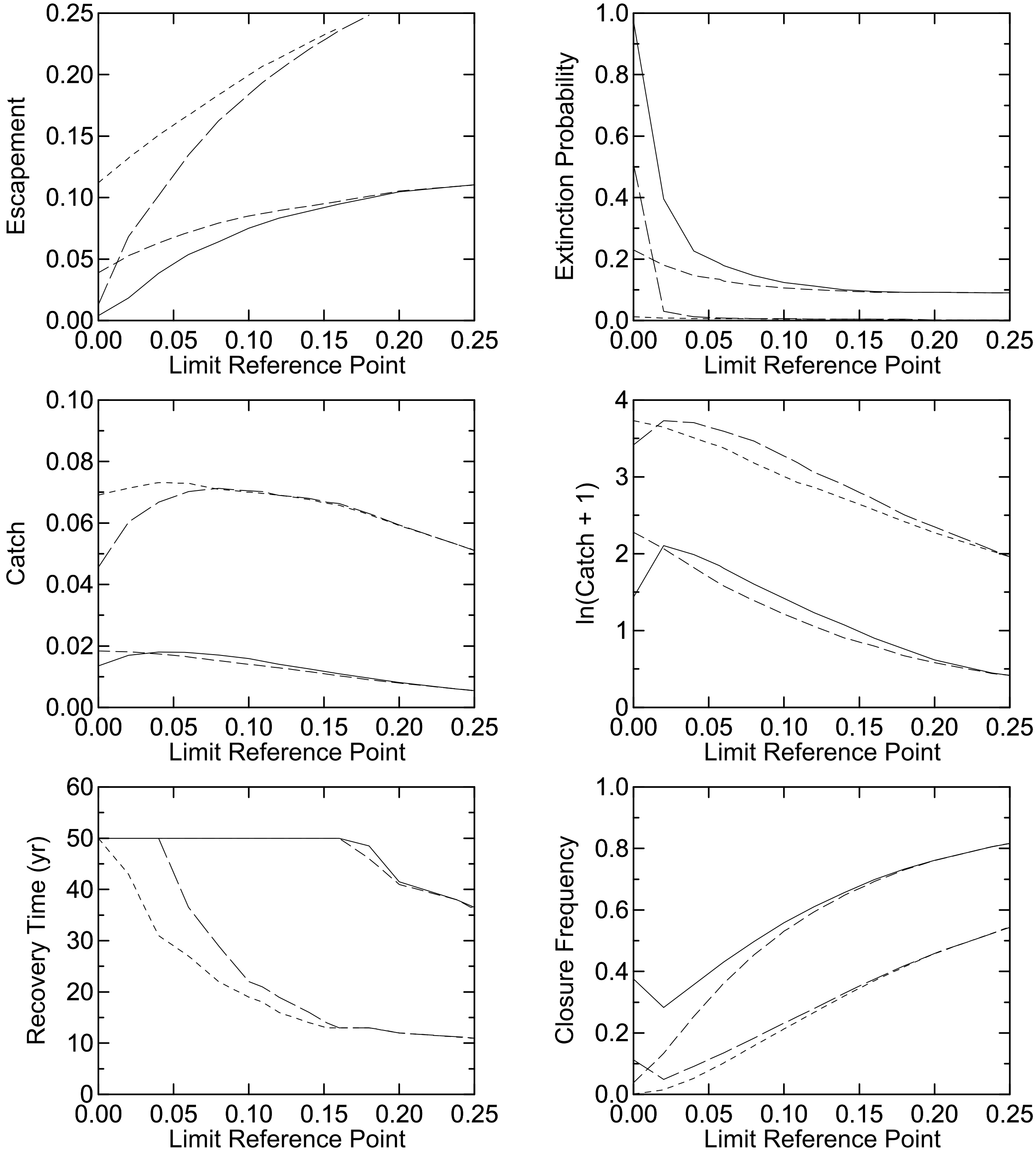

Fig. 13. The effects of limit reference point definitions and stock productivity on performance indicators under a proportional threshold harvesting rule with either: a single abundance threshold (limit reference point, LRP) below which forecast abundance the harvesting ceases (—— and — — —), or a limit reference point and a precautionary reference point at 0.25B (– – – and - - -) below which forecast abundance the

nominal harvest rate declines linearly to zero at the LRP. Data are shown for low stock productivity (1.4 recruits·spawner^{-1}, —— and – – –) and for moderate stock productivity (2.2 recruits·spawner^{-1}, — — — and - - -). Limit reference points, escapement, and catch are in units of B, the asymptotic maximum adult recruitment. The nominal harvest fraction for surplus fish above the threshold is 0.5, the initial population size is N_0 = 0.1B, B = 1 000, the variation in smolt-to-adult survival is $\sigma_{survival}$ = 0.629, and temporal autocorrelation in survival deviations is ρ = 0.7 in this example.

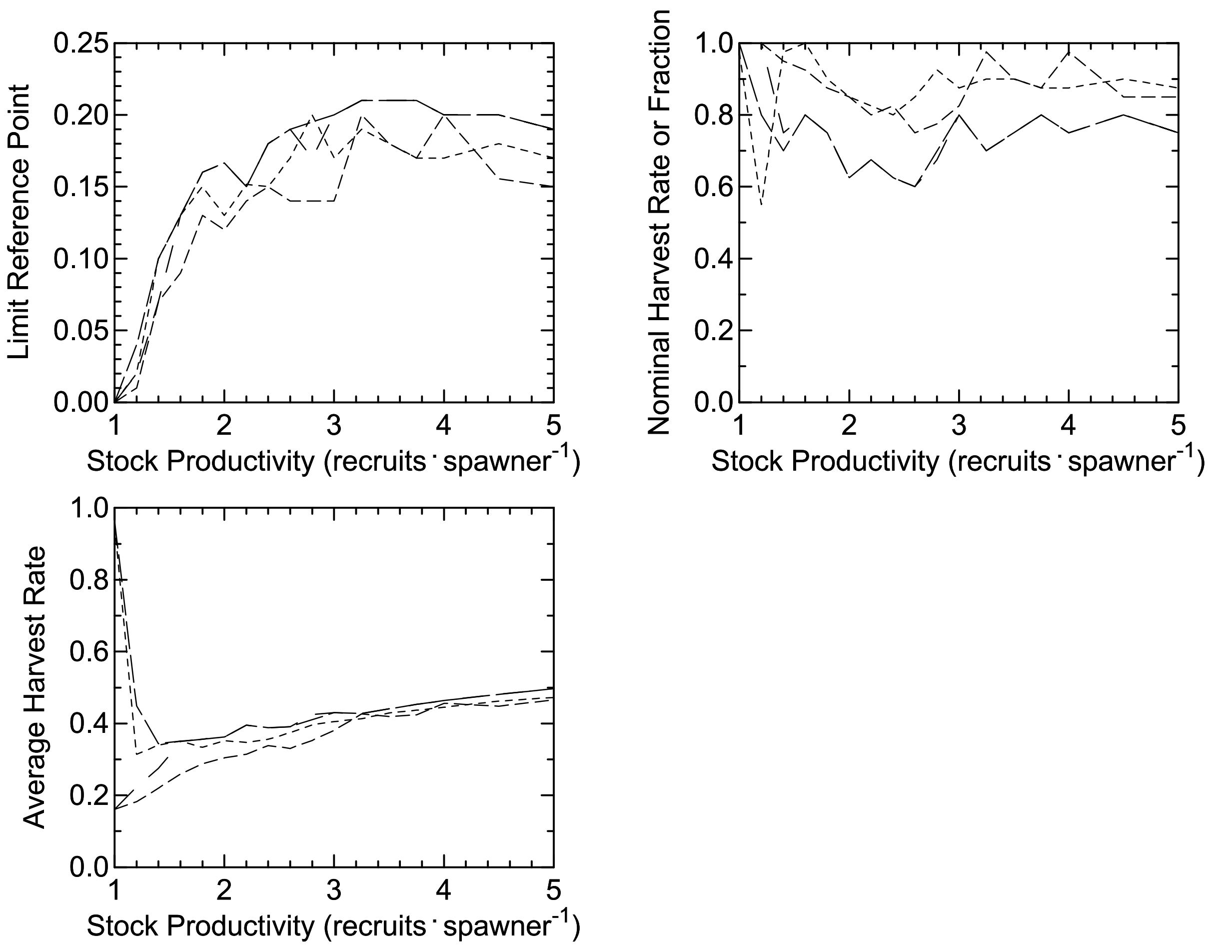

Fig. 14. (upper panel) Limit reference points (left panel) and nominal harvest rates or harvest fractions on surplus fish (right panel) that maximize catch at different values of stock productivity for: constant exploitation rate harvest policies with either a single limit reference point (LRP) below which forecast abundance harvesting ceases (———) or a precautionary threshold at 0.25B below which forecast abundance the harvest rate decreases linearly to zero at the LRP (— — —), or for proportional threshold harvesting policies with either a single LRP below which forecast abundance harvesting ceases (- - -) or a precautionary threshold at 0.25B below which forecast abundance the nominal harvest fraction on surplus fish decreases linearly to zero at the LRP (− − −).

(lower panel) Average harvest rates applied during periods of fishing for the LRPs and nominal harvest rates or harvest fractions that maximize catch at different values of stock productivity. Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

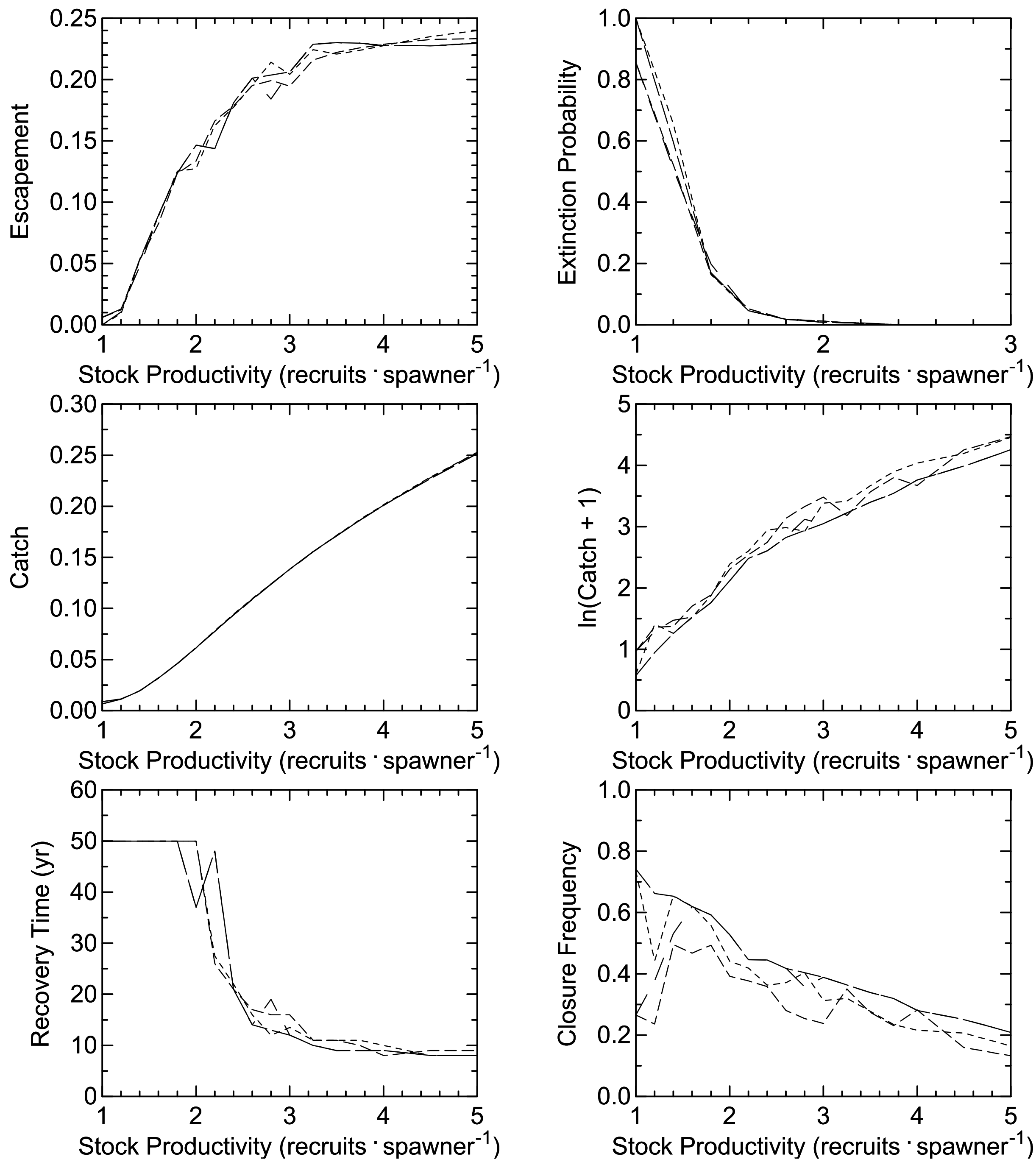

Fig. 15. Performance indicators for the catch-maximizing values of limit reference points and nominal harvest rates or harvest fractions on surplus fish at different stock productivity values for: constant exploitation rate harvest policies with either a single limit reference point (LRP) below which forecast abundance harvesting ceases (———) or a precautionary threshold at 0.25B below which forecast abundance the harvest rate decreases linearly to zero at the LRP (— — —), or for proportional threshold

harvesting policies with either a single LRP below which forecast abundance harvesting ceases (- - -) or a precautionary threshold at 0.25B below which forecast abundance the nominal harvest fraction on surplus fish decreases linearly to zero at the LRP (− − −). Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

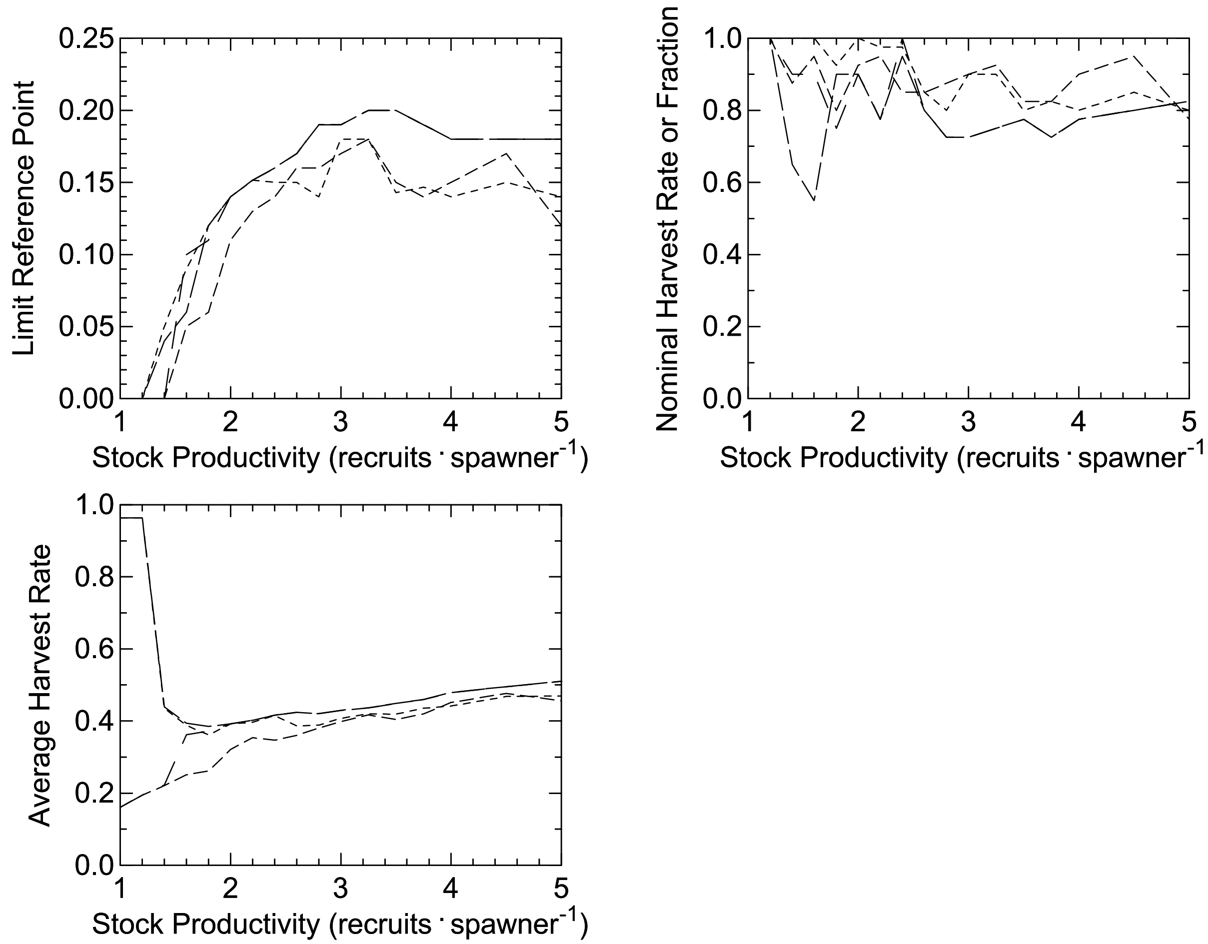

Fig. 16. (upper panel) Limit reference points (left panel) and nominal harvest rates or harvest fractions on surplus fish (right panel) that maximize discounted catch (3% annual rate) at different values of stock productivity for: constant exploitation rate harvest policies with either a single limit reference point (LRP) below which forecast abundance harvesting ceases (———) or a precautionary threshold at 0.25B below which forecast abundance the harvest rate decreases linearly to zero at the LRP (— — —), or for proportional threshold harvesting policies with either a single LRP below which forecast abundance harvesting ceases (- - -) or a precautionary threshold at 0.25B below which forecast abundance the nominal harvest fraction on surplus fish decreases linearly to zero at the LRP (− − −).

(lower panel) Average harvest rates applied during periods of fishing for the LRPs and nominal harvest rates or harvest fractions that maximize discounted catch at different values of stock productivity. Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

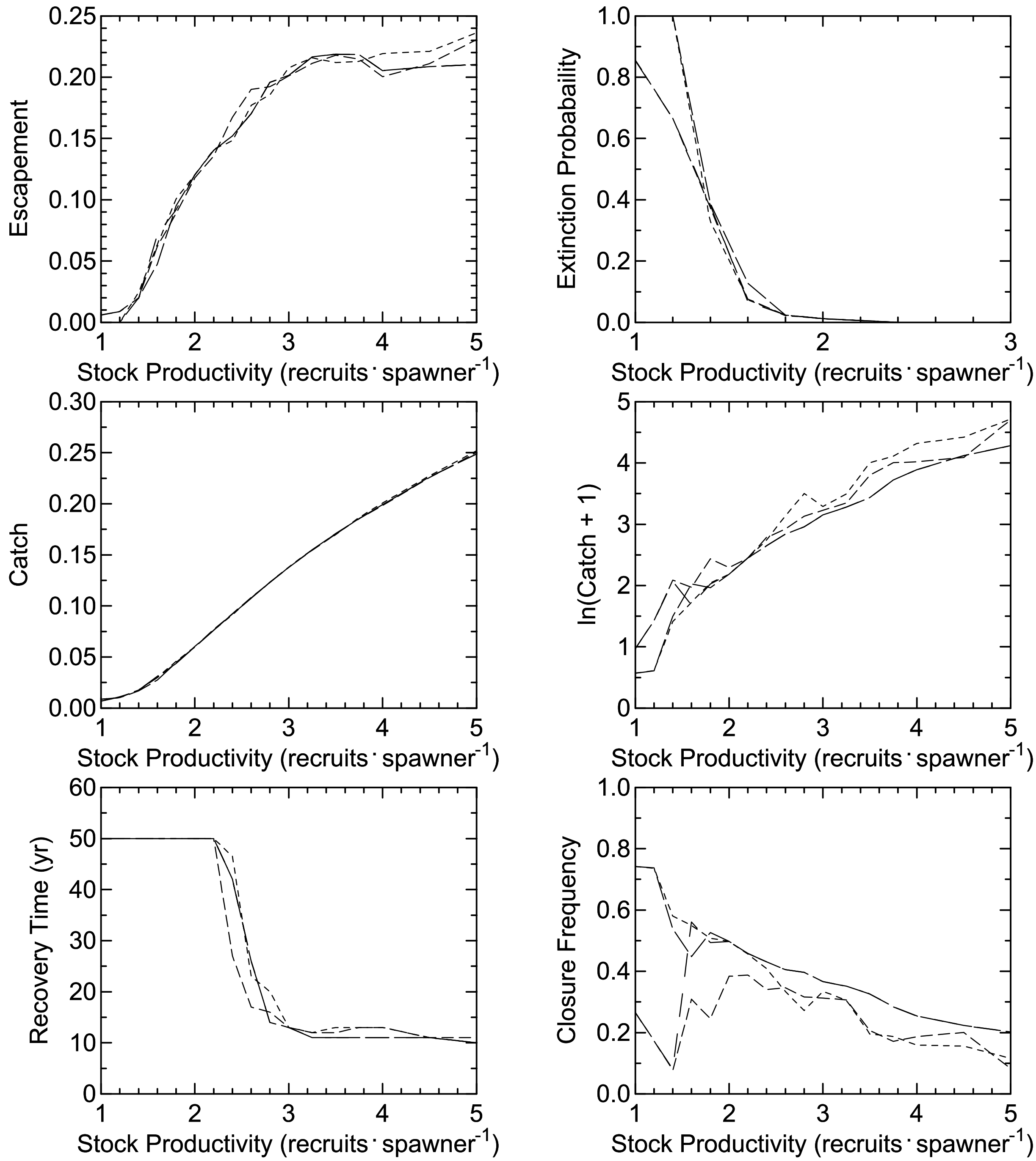

Fig. 17. Performance indicators at the limit reference points and nominal harvest rates or harvest fractions on surplus fish that maximize discounted catch (3% annual rate) at different stock productivity values for: constant exploitation rate harvest policies with either a single limit reference point (LRP) below which forecast abundance harvesting ceases (— — —) or a precautionary threshold at 0.25B below which forecast

abundance the harvest rate decreases linearly to zero at the LRP (— — —), or for proportional threshold harvesting policies with either a single LRP below which forecast abundance harvesting ceases (- - -) or a precautionary threshold at 0.25B below which forecast abundance the nominal harvest fraction on surplus fish decreases linearly to zero at the LRP (− − −). Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

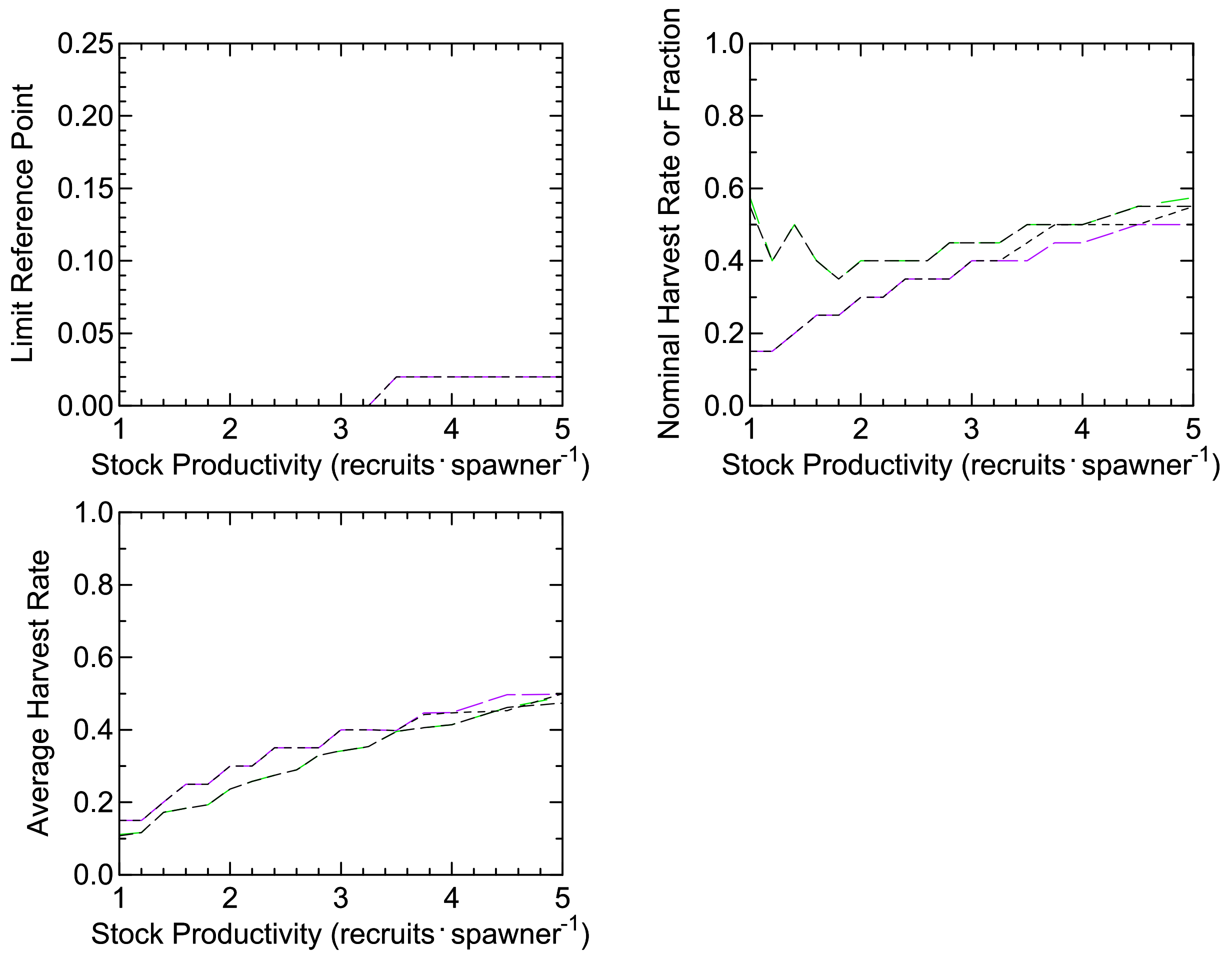

Fig. 18. (upper panel) Limit reference points and nominal harvest rates or harvest fractions on surplus fish that maximize ln(catch) at different stock productivity values for: constant exploitation rate harvest policies with either a single limit reference point (LRP) below which forecast abundance harvesting ceases (———) or a precautionary threshold at 0.25B below which forecast abundance the harvest rate decreases linearly to zero at the LRP (— — —), or for proportional threshold harvesting policies with either a single LRP below which forecast abundance harvesting ceases (- - -) or a precautionary threshold at 0.25B below which forecast abundance the nominal harvest fraction on surplus fish decreases linearly to zero at the LRP (− − −). Note that constant exploitation rate and proportional threshold policies with corresponding thresholds coincide. Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

(lower panel) Average harvest rates during periods of fishing at the LRP and nominal harvest rate or nominal harvest fraction on surplus fish that maximize ln(catch).

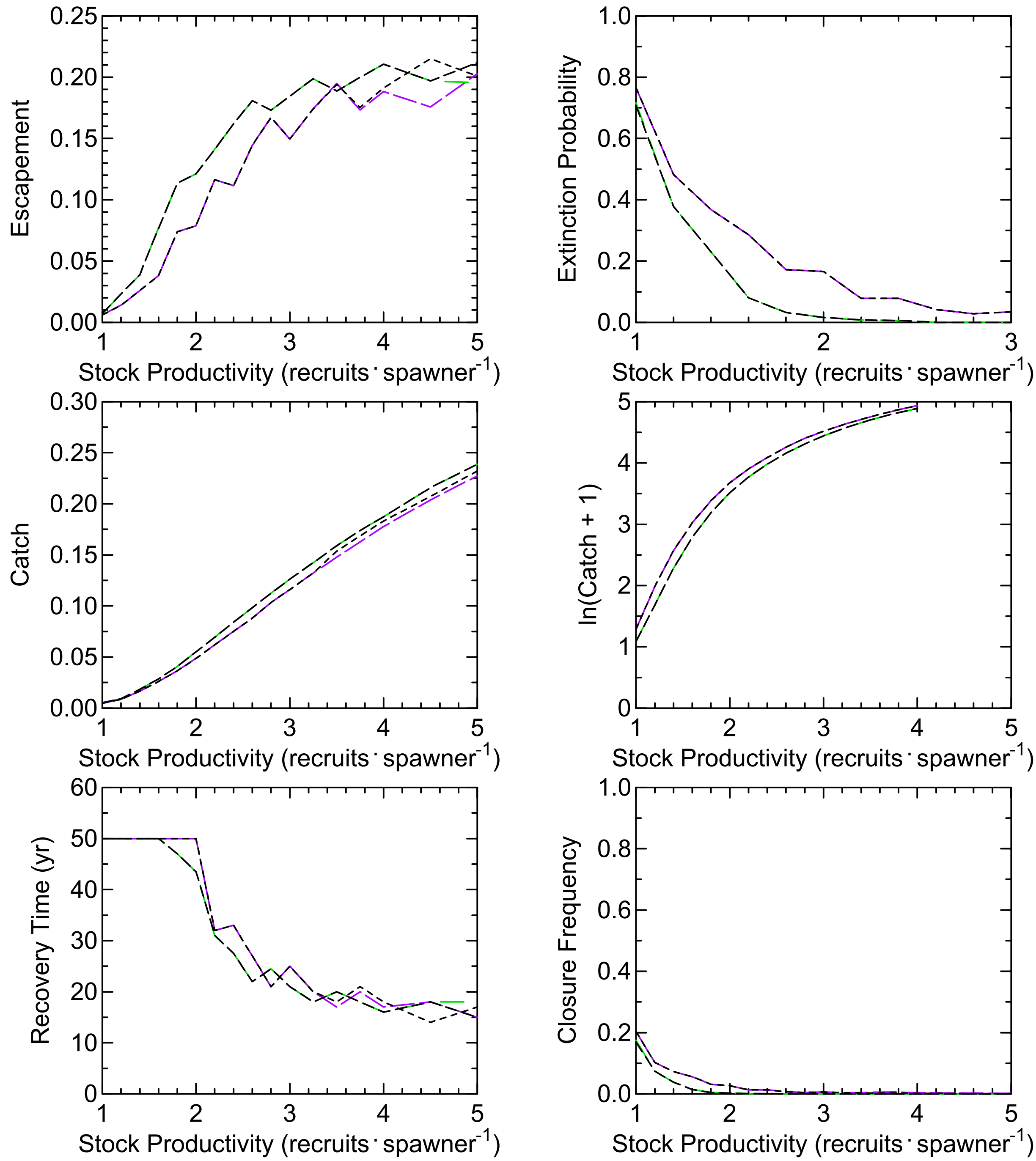

Fig. 19. Performance indicators at the limit reference points and nominal harvest rates or harvest fractions on surplus fish that maximize ln(catch) at different stock productivity values for: constant exploitation rate harvest policies with either a single limit reference point (LRP) below which forecast abundance harvesting ceases (— — —) or a precautionary threshold at 0.25B below which forecast abundance the harvest rate

decreases linearly to zero at the LRP (— — —), or for proportional threshold harvesting policies with either a single LRP below which forecast abundance harvesting ceases (- - -) or a precautionary threshold at 0.25B below which forecast abundance the nominal harvest fraction on surplus fish decreases linearly to zero at the LRP (− − −). Note that corresponding “optimal” constant exploitation rate and proportional threshold harvesting policies coincide. Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

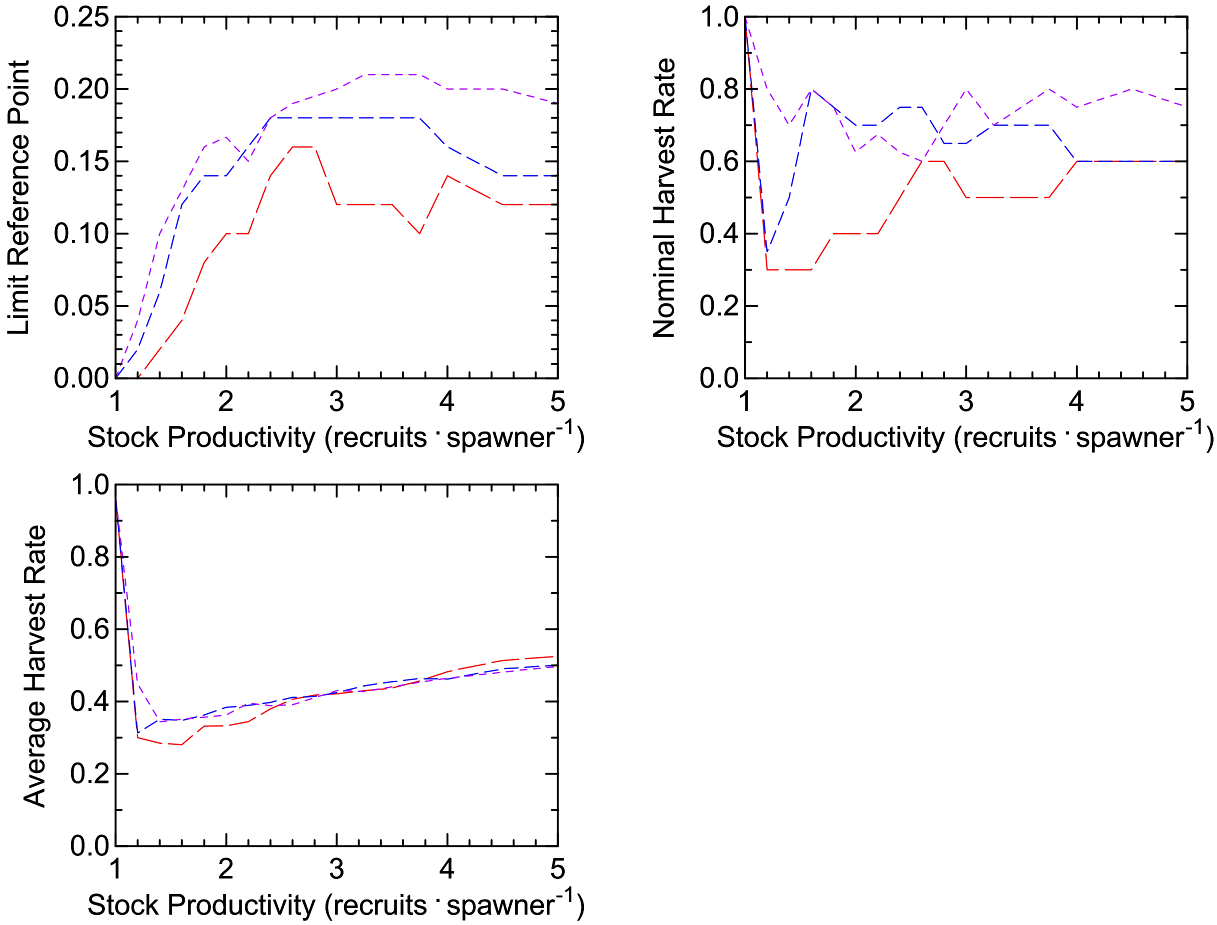

Fig. 20. (upper panel) The effects of temporal autocorrelation in survival deviations on the limit reference points (left panel) and nominal harvest rates (right panel) that maximize catch at different values of stock productivity for a constant exploitation rate harvest policy with a single limit reference point (LRP) below which forecast abundance harvesting ceases. Autocorrelations are: ρ = 0.0 (— — —), ρ = 0.4 (− − −), and ρ = 0.7(- - -).

(lower panel) Average harvest rates applied during periods of fishing for the values of LRPs and nominal harvest rates that maximize catch. Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629.

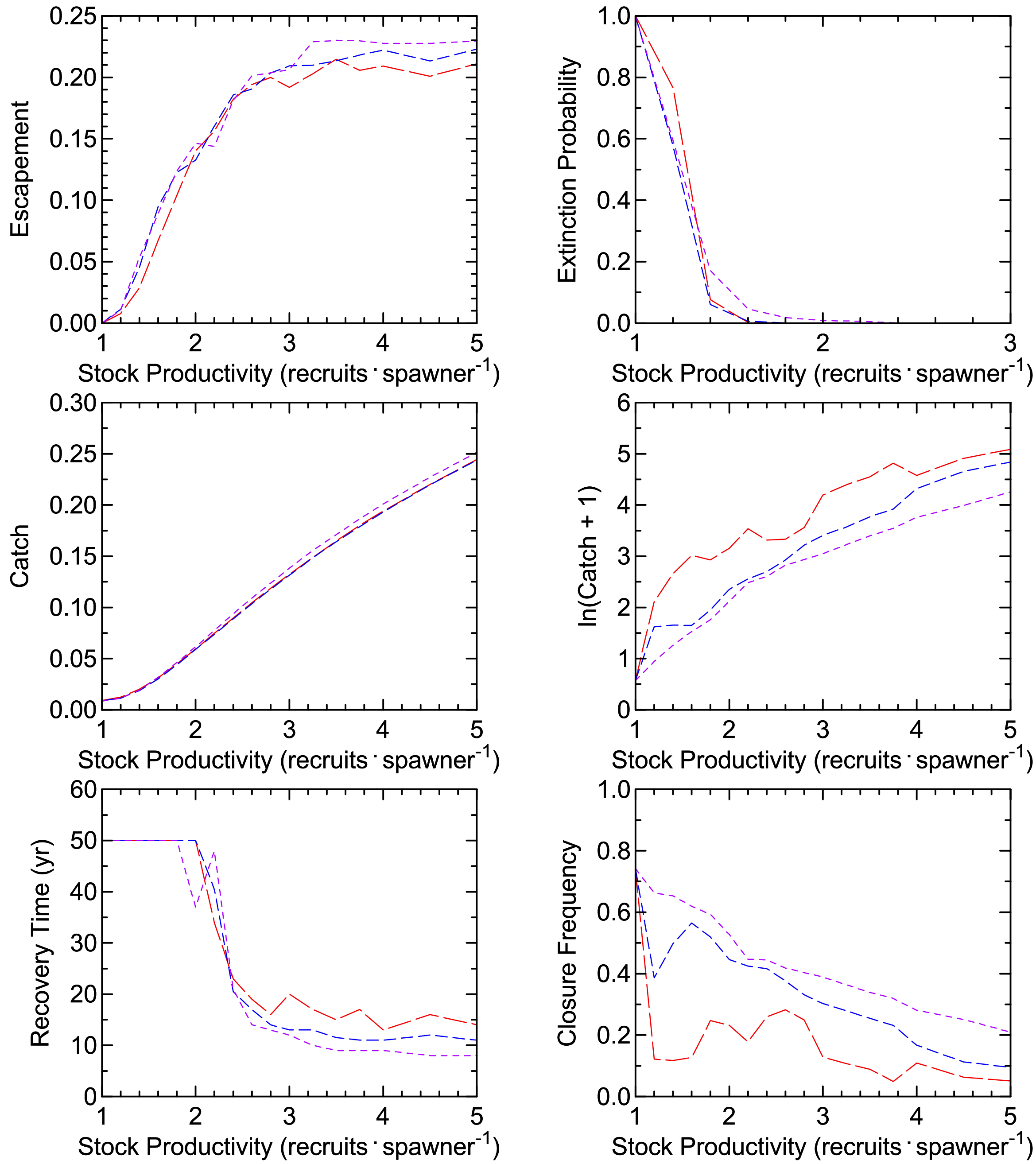

Fig. 21. The effects of temporal autocorrelation in survival deviations on performance indicators at the catch-maximizing limit reference points and nominal harvest rates at different stock productivity values for a constant exploitation rate harvest policy with a single limit reference point (LRP) below which forecast abundance harvesting ceases. Autocorrelations are: ρ = 0.0 (— — —), ρ = 0.4 (− − −), and ρ = 0.7(- - -). Abundance is in units of B, the asymptotic maximum adult recruitment. The initial population size was 0.1B, B = 1 000, and $\sigma_{survival}$ = 0.629.

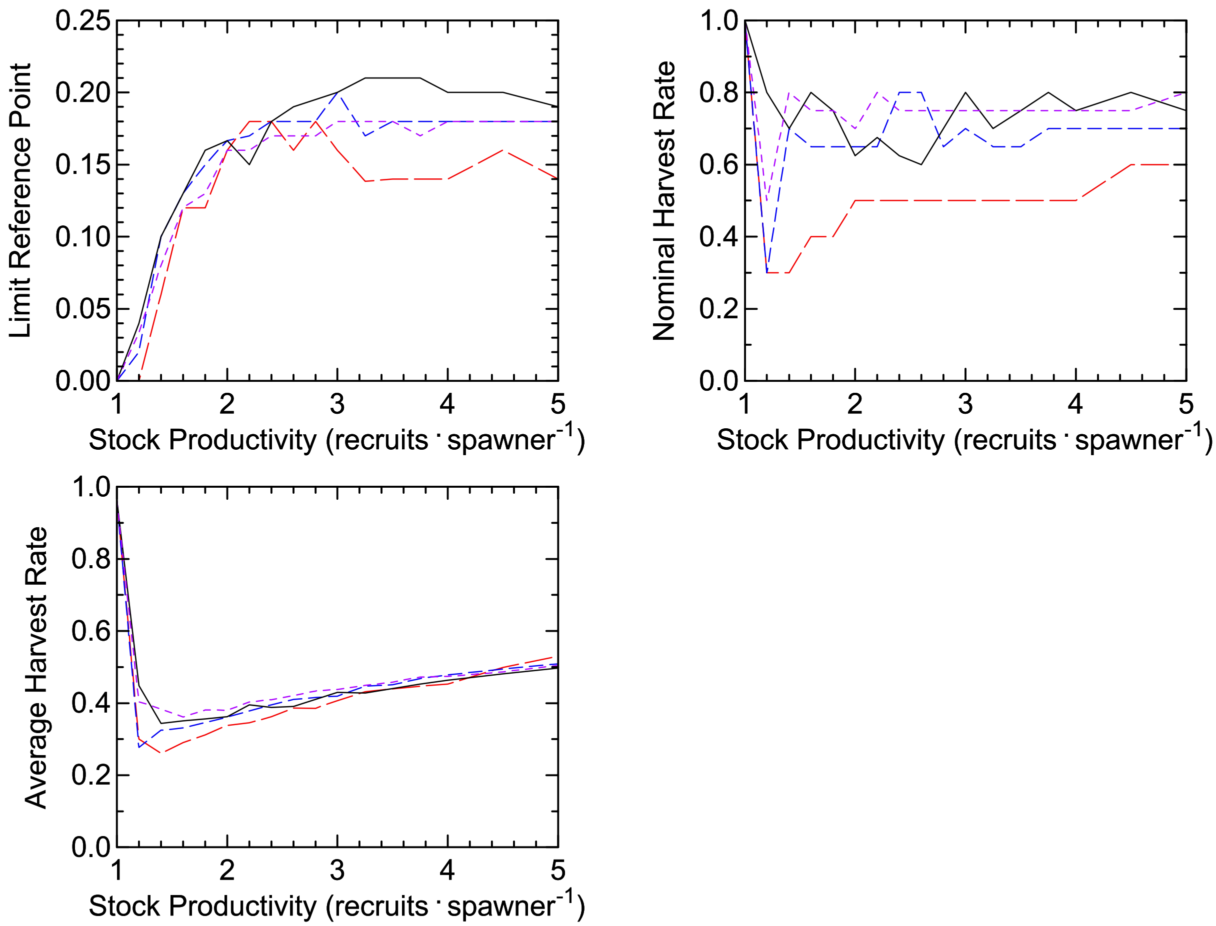

Fig. 22. (upper panel) The effects of variation in smolt-to-adult survival on the limit reference points (left panel) and nominal harvest rates (right panel) that maximize catch at different values of stock productivity for a constant exploitation rate harvest policy with a single limit reference point (LRP) below which forecast abundance harvesting ceases. Standard deviations in survival are: σ = 0.2 (— — —), σ = 0.4 (− − −), σ = 0.629 (——), and σ = 0.8 (- - -).

(lower panel) Average harvest rates applied during periods of fishing for the values of LRPs and nominal harvest rates that maximize catch.

Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, ρ = 0.7.

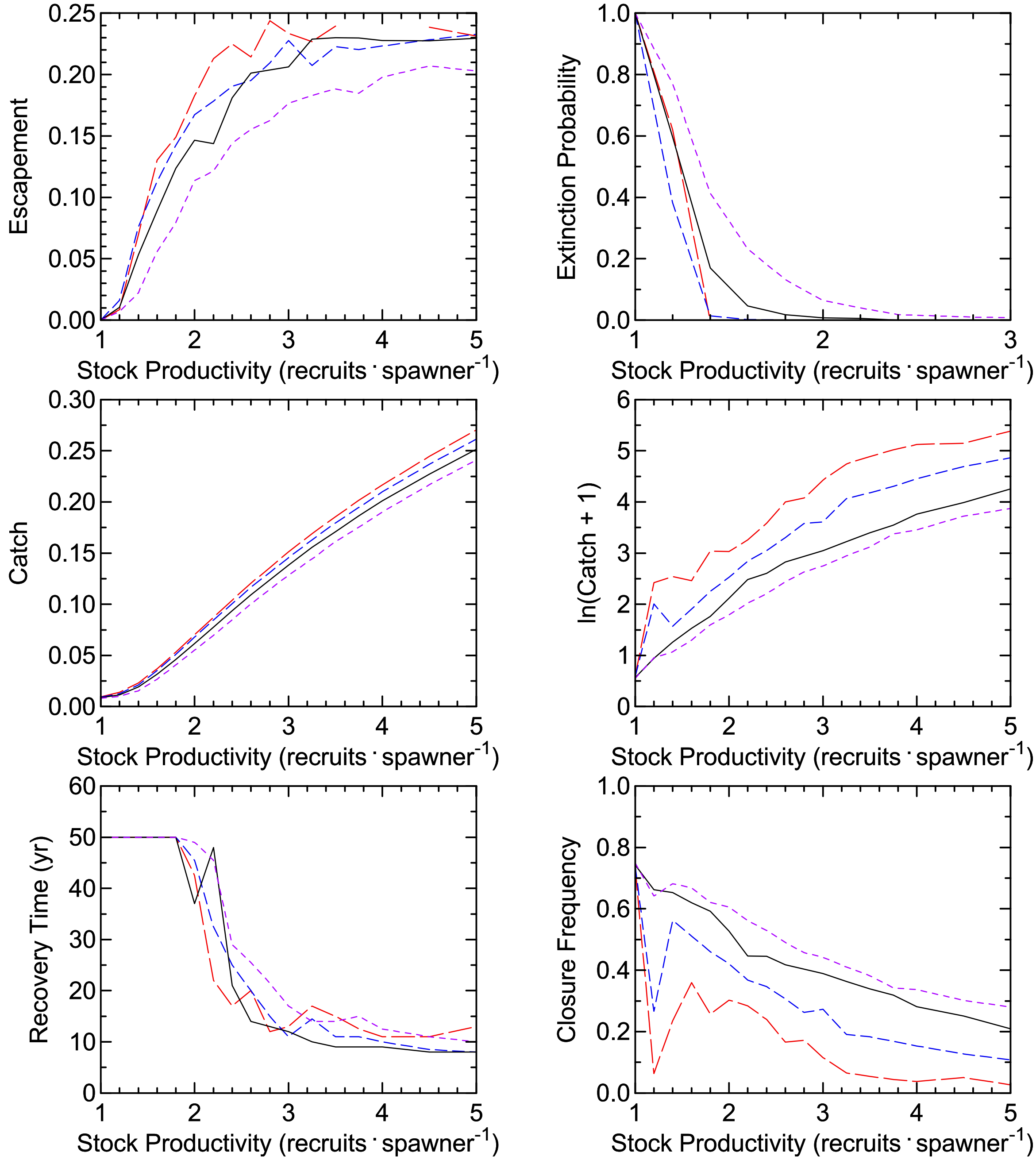

Fig. 23. The effects of variation in smolt-to-adult survival on performance indicators at the catch-maximizing limit reference points and nominal harvest rates at different stock productivity values for a constant exploitation rate harvest policy with a single limit reference point (LRP) below which forecast abundance harvesting ceases. Standard deviations in survival are: $\sigma = 0.2$ (— — —), $\sigma = 0.4$ (− − −), $\sigma = 0.629$ (——), and $\sigma = 0.8$ (- - -). Abundance is in units of B, the asymptotic maximum adult recruitment. The initial population size was 0.1B, B = 1 000, $\rho = 0.7$.

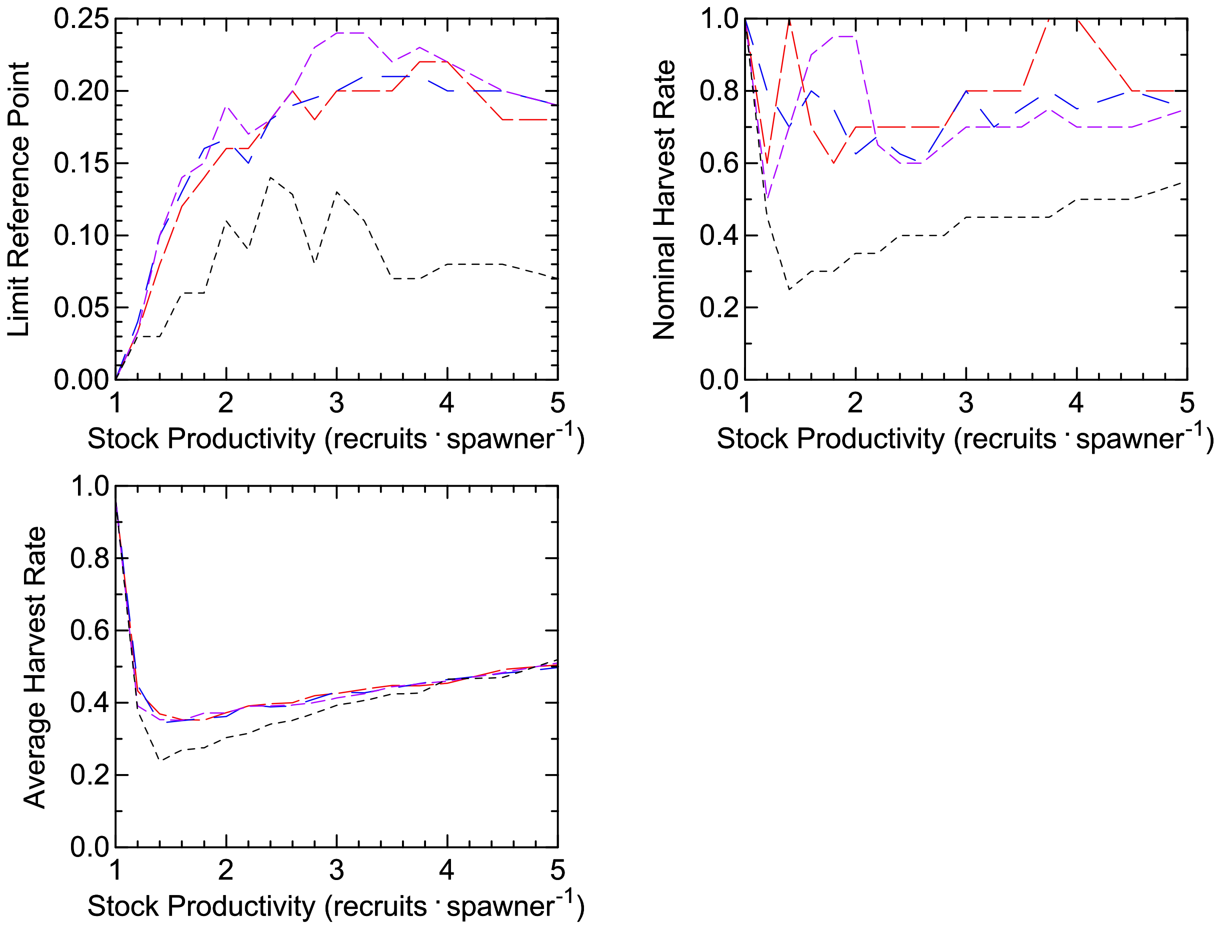

Fig. 24. (upper panel) The effect of uncertainty in the estimate of the asymptotic maximum adult recruitment, B, on the limit reference points (left panel) and nominal harvest rates (right panel) that maximize catch at different values of stock productivity for a constant exploitation rate harvest policy with a single limit reference point (LRP) below which forecast abundance harvesting ceases. Standard deviations in B are: $\sigma_B = 0.122$ (———), $\sigma_B = 0.243$ (— — —), $\sigma_B = 0.486$ (– – –), and $\sigma_B = 0.972$ (- - -).

(lower panel) Average harvest rates applied during periods of fishing for the values of LRPs and nominal harvest rates that maximize catch.

Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival} = 0.629$, and $\rho = 0.7$.

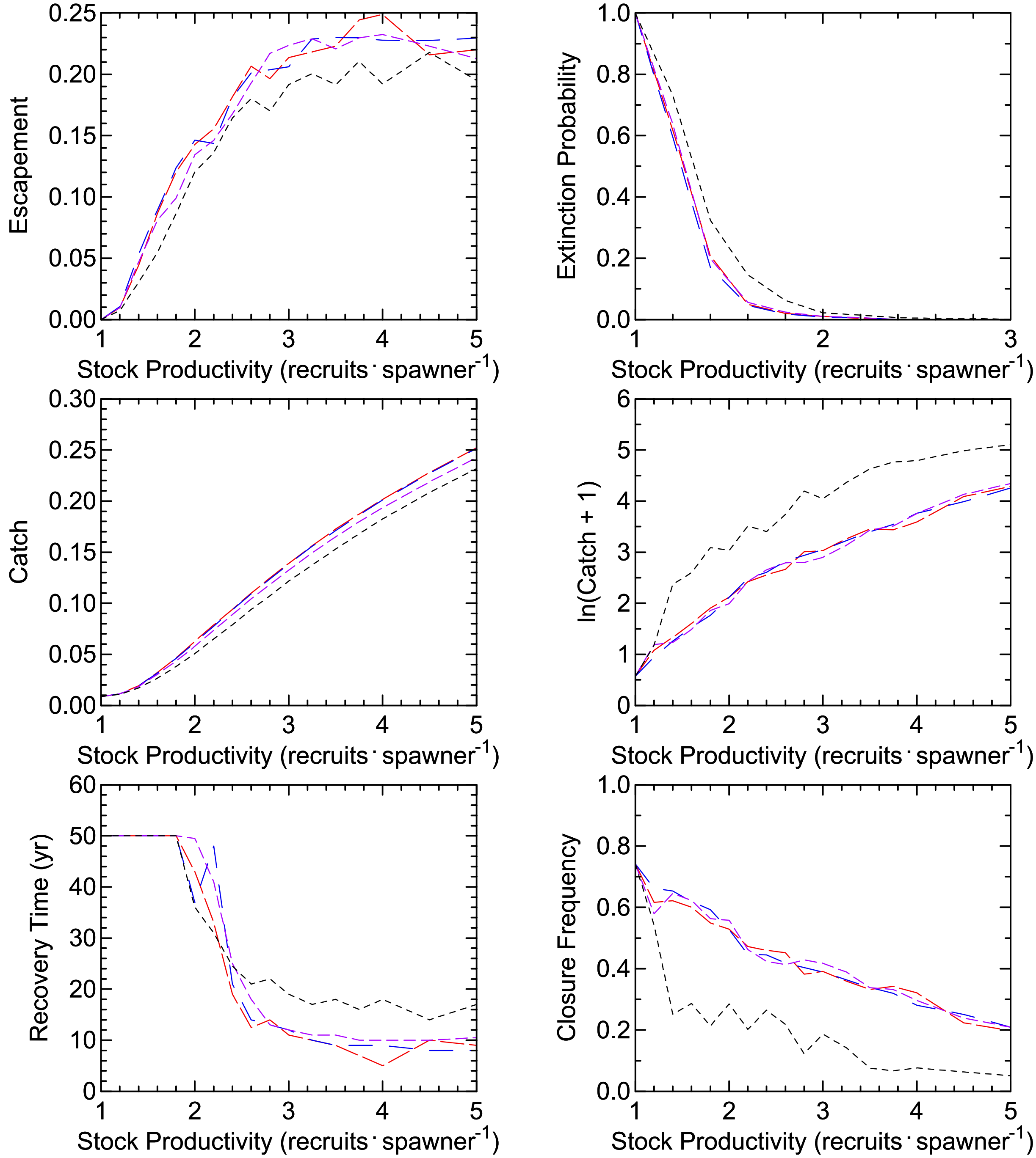

Fig. 25. The effects of uncertainty in the estimate of the asymptotic maximum adult recruitment on performance indicators at the catch-maximizing limit reference points and nominal harvest rates at different stock productivity values for a constant exploitation rate harvest policy with a single limit reference point below which forecast abundance harvesting ceases. Standard deviations in B are: σ_B = 0.122 (— — —), σ_B =

0.243 (— — —), σ_B = 0.486 (− − −), and σ_B = 0.972 (- - -). Abundance is in units of B. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

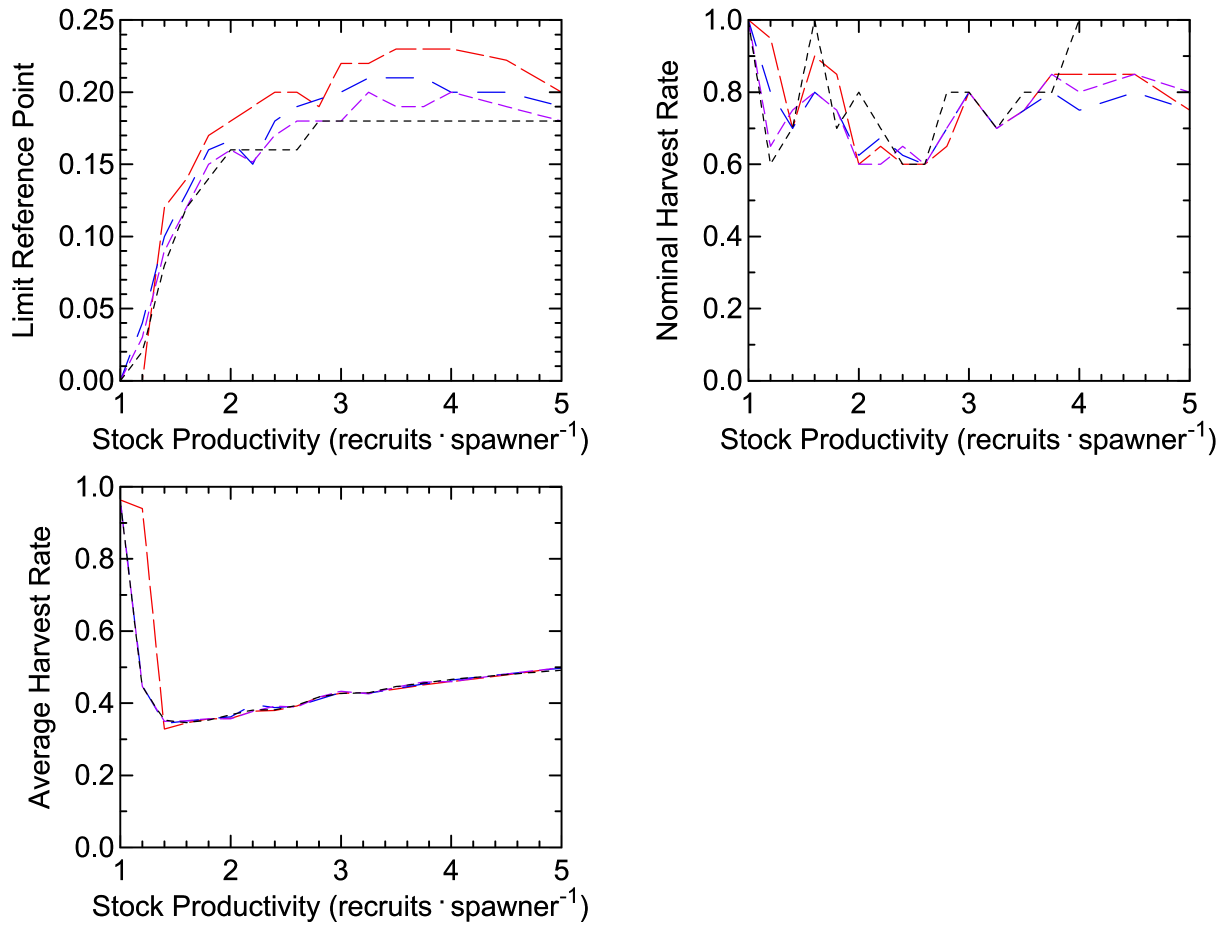

Fig. 26. (upper panel) The effect of asymptotic maximum adult recruitment, B, on the limit reference points (left panel) and nominal harvest rates (right panel) that maximize catch at different values of stock productivity for a constant exploitation rate harvest policy with a single limit reference point (LRP) below which forecast abundance harvesting ceases. B values are: 400 (———), 1 000 (— — —), 2 500 (− − −), and 6 250 (- - -).

(lower panel) Average harvest rates applied during periods of fishing for the values of LRPs and nominal harvest rates that maximize catch.

Abundance is in units of B. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

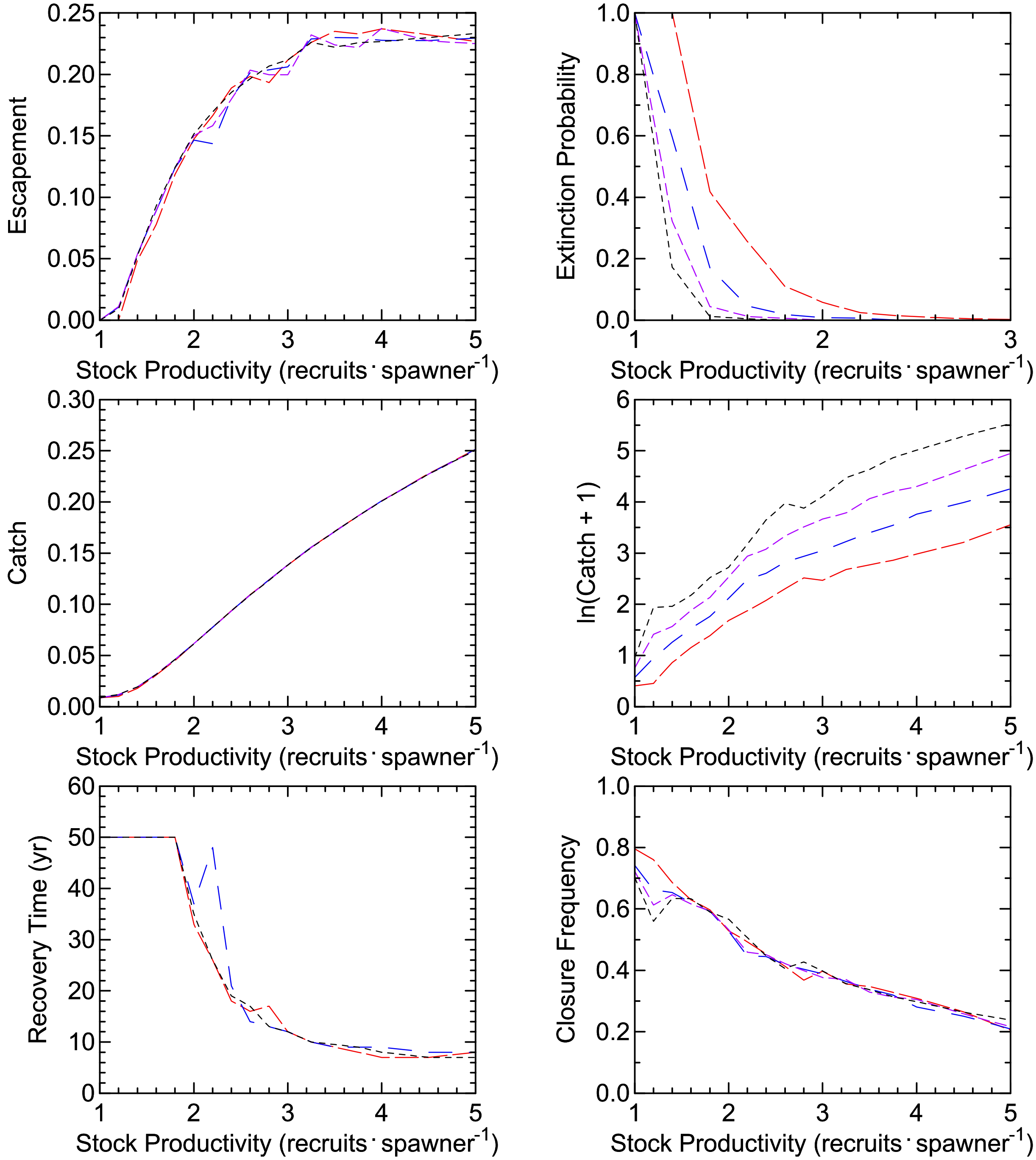

Fig. 27. The effects of the asymptotic maximum adult recruitment on performance indicators at the catch-maximizing limit reference points and nominal harvest rates for different stock productivity values for a constant exploitation rate harvest policy with a single limit reference point below which forecast abundance harvesting ceases. B values are: 400 (———), 1 000 (— — —), 2 500 (– – –), and 6 250 (- - -). Abundance is in units of B. The initial population size was 0.1B, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

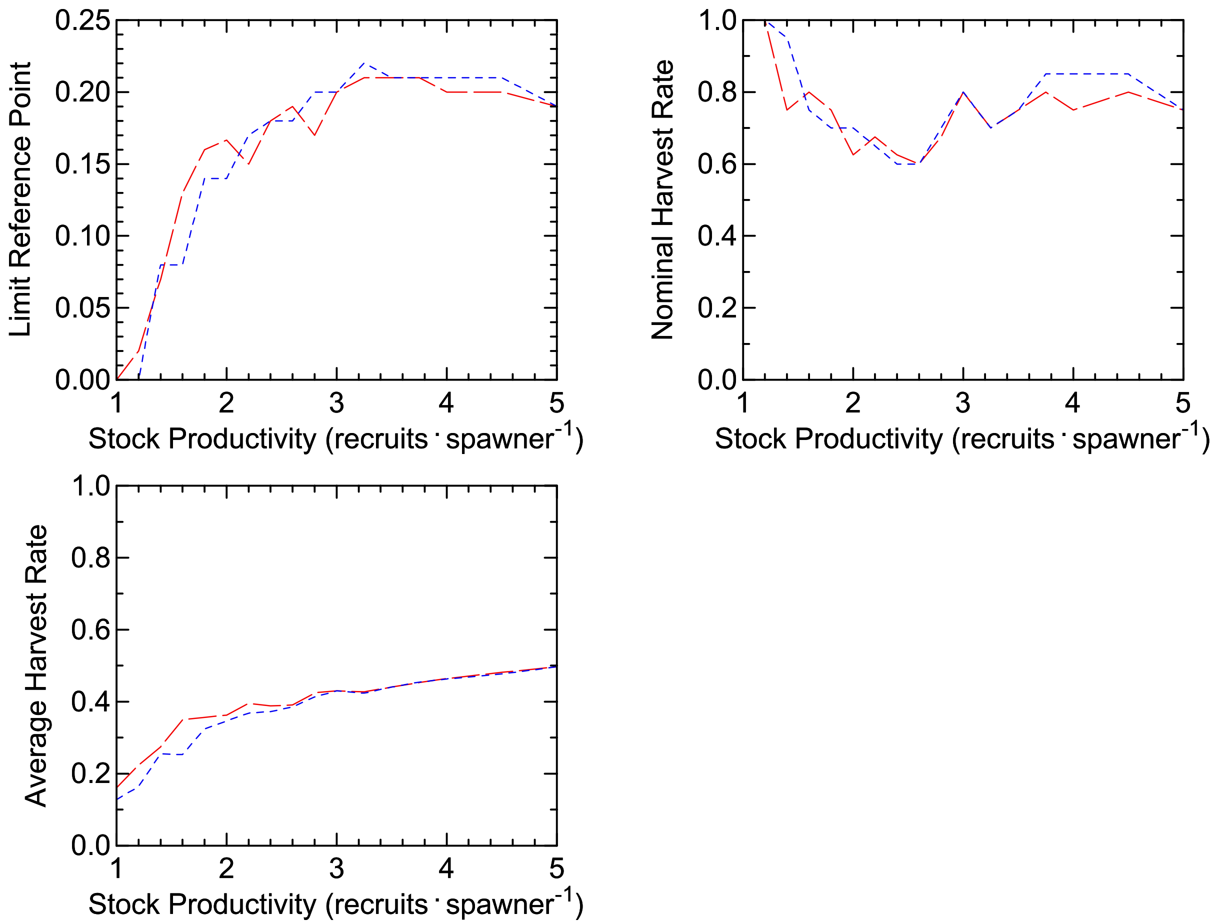

Fig. 28. (upper panel) The effect of the precautionary threshold on the limit reference points (left panel) and nominal harvest rates (right panel) that maximize catch at different values of stock productivity for a constant exploitation rate harvest policy with a precautionary threshold below which forecast abundance the nominal harvest rate declines to zero at the limit reference point (LRP). Precautionary thresholds are: 0.25B (———) and 0.35B (- - -).

(lower panel) Average harvest rates applied during periods of fishing for the values of LRPs and nominal harvest rates that maximize catch.

Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival} = 0.629$, and $\rho = 0.7$.

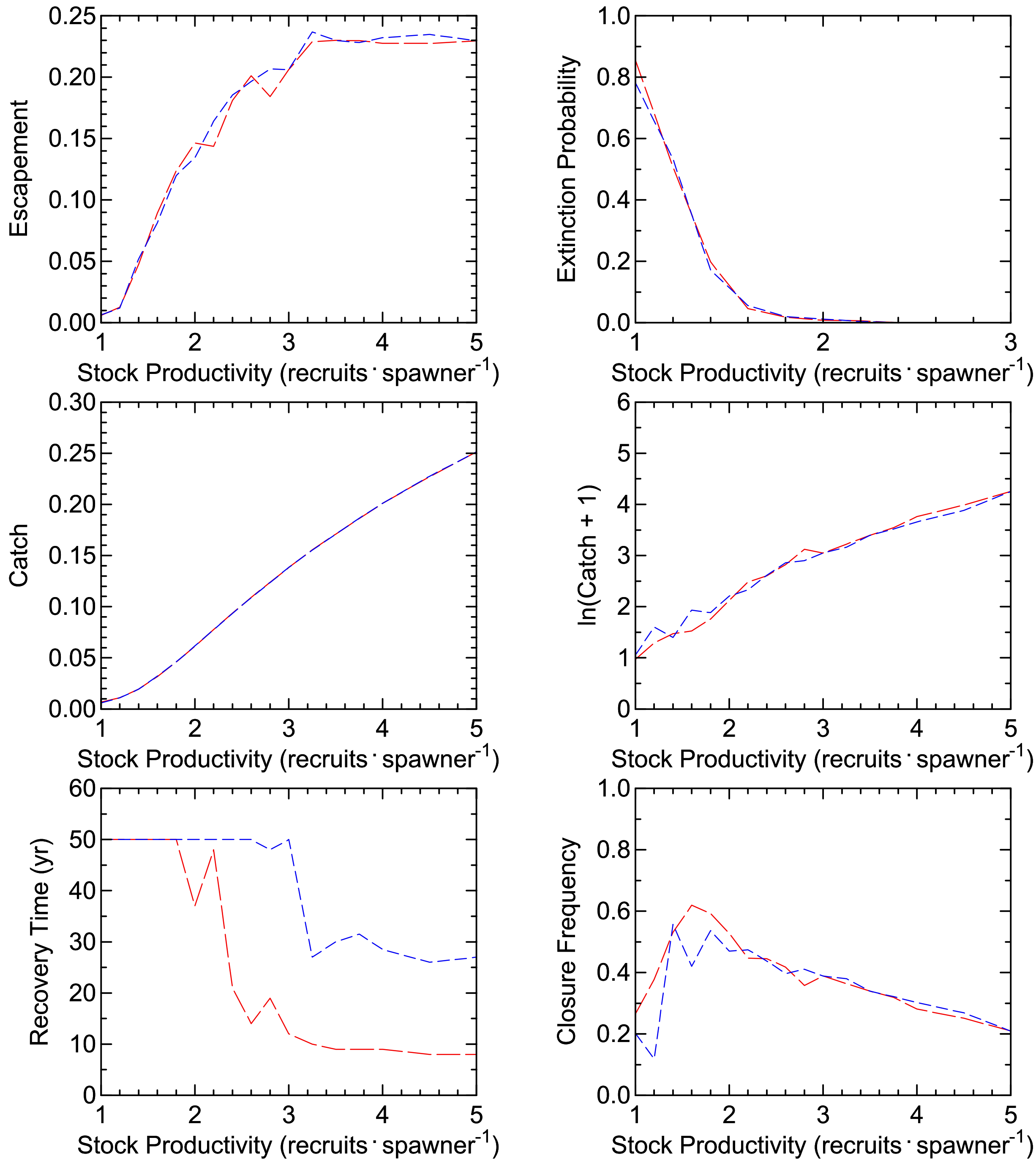

Fig. 29. Effect of the precautionary threshold on performance indicators at the catch-maximizing limit reference points and nominal harvest rates at different stock productivity values for a constant exploitation rate harvest policy with a precautionary threshold below which forecast abundance the harvest rate declines linearly to zero at the limit reference point. Precautionary threshold values are: 0.25B (— — —) and 0.35B

(- - -). Abundance is in units of B, the asymptotic maximum adult recruitment. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

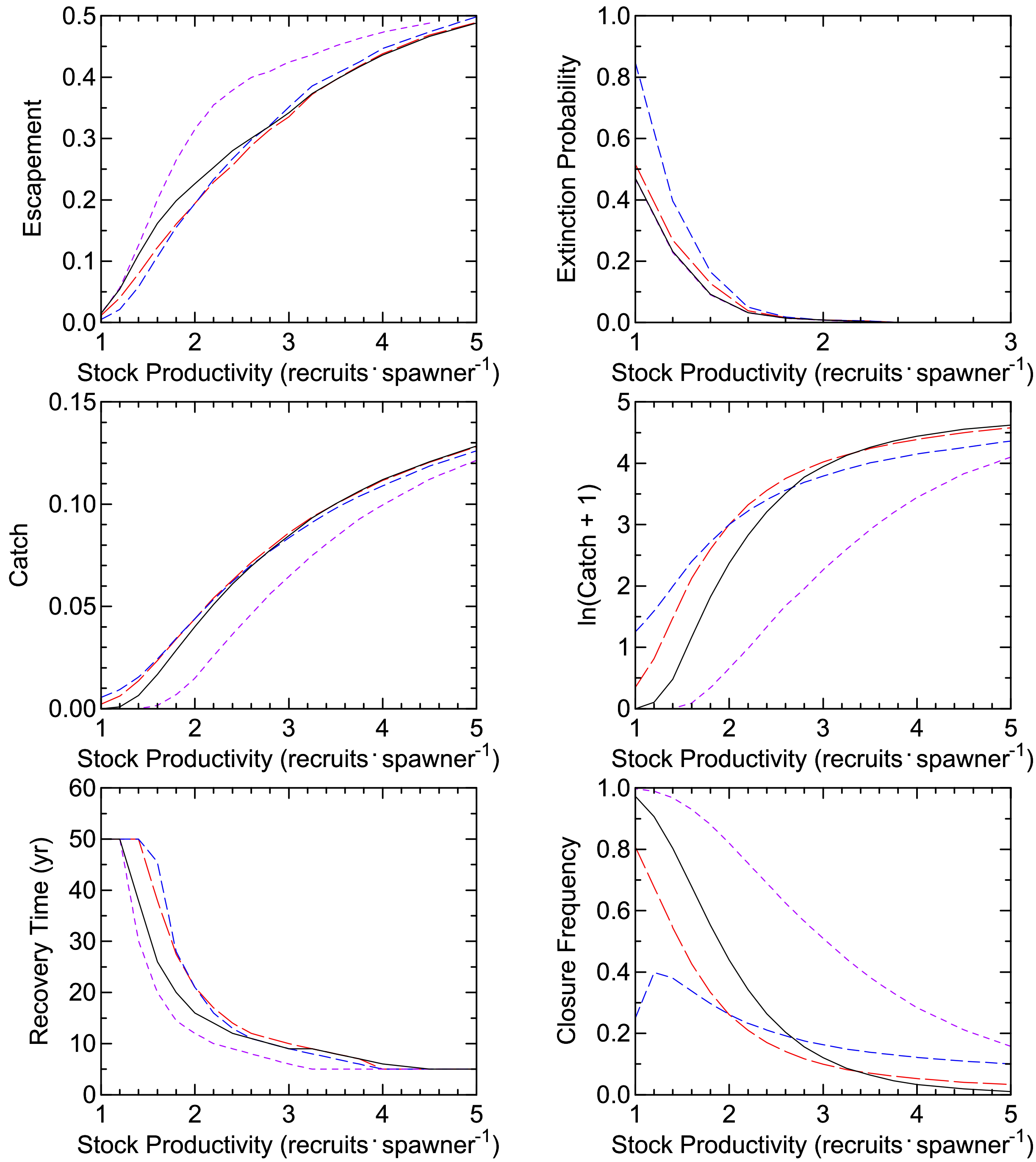

Fig. 30. Effects of limit reference point definition on performance indicators at a low nominal harvest rate (0.2) and different stock productivity values for a constant exploitation rate harvest policy with a limit reference point (LRP) below which forecast abundance the harvesting ceases. LRPs are: 0.1B (— — —), $0.2N_{equil}$ (– – –), $N_{50\%}$ (- - -), and N_{LRP} (——). Abundance is in units of B, the asymptotic maximum adult recruitment. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

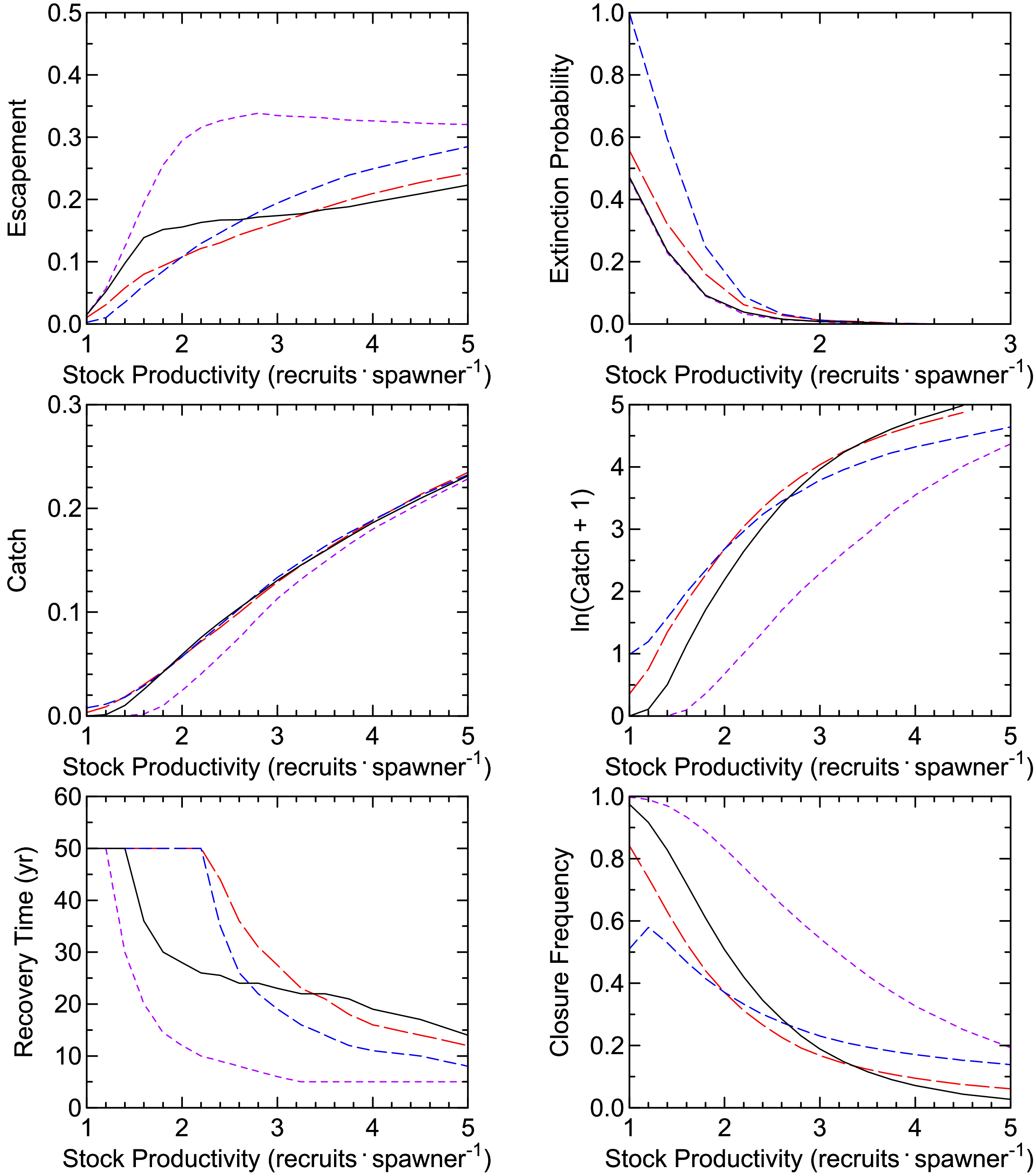

Fig. 31. Effects of limit reference point definition on performance indicators at a high nominal harvest rate (0.5) and different stock productivity values for a constant exploitation rate harvest policy with a limit reference point (LRP) below which forecast abundance the harvesting ceases. LRPs are: 0.1B (— — —), $0.2N_{equil}$ (– – –), $N_{50\%}$ (- - -), and N_{LRP} (——). Abundance is in units of B, the asymptotic maximum adult recruitment. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

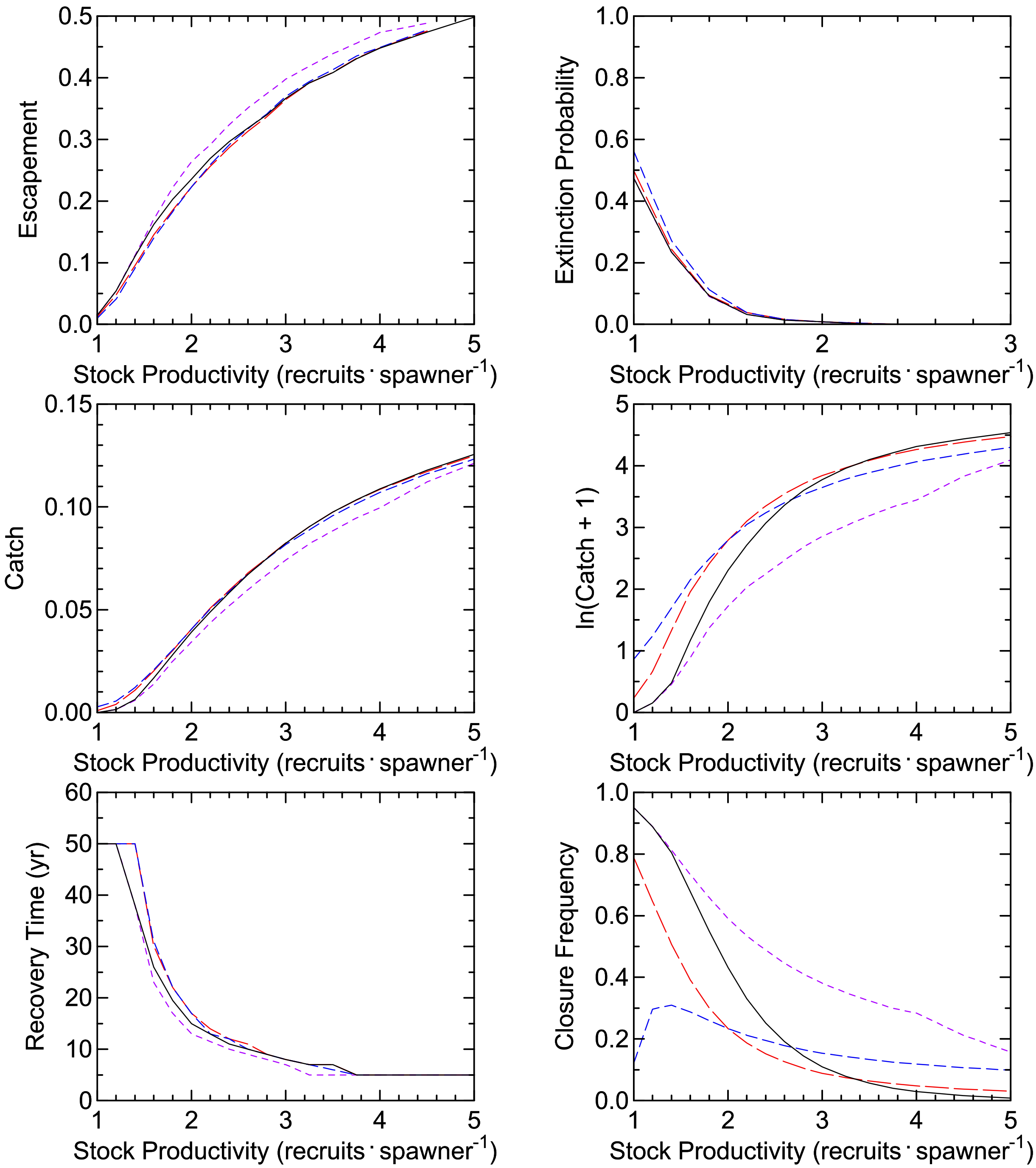

Fig. 32. Effects of limit reference point (LRP) definition on performance indicators at a low nominal harvest rate (0.2) and different stock productivity values for a constant exploitation rate harvest policy with precautionary threshold at 0.25B below which forecast abundance the harvest rate declines linearly to zero at the LRP. LRPs are: 0.1B (— — —), 0.2N_{equil} (– – –), $N_{50\%}$ (- - -), and N_{LRP} (——). Abundance is in units of

B, the asymptotic maximum adult recruitment. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

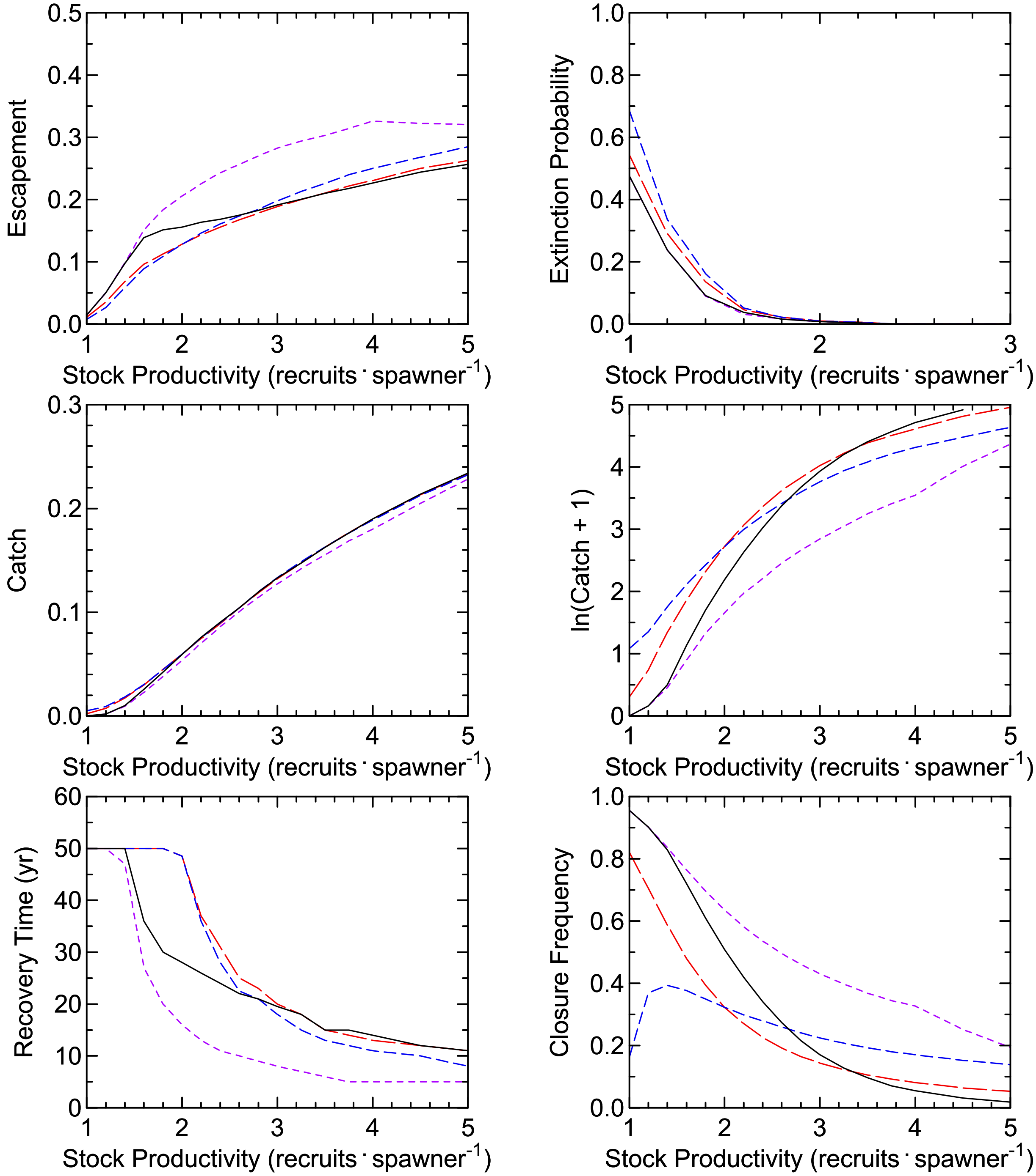

Fig. 33. Effects of limit reference point (LRP) definition on performance indicators at a high nominal harvest rate (0.5) and different stock productivity values for a constant exploitation rate harvest policy with precautionary threshold at 0.25B below which forecast abundance the harvest rate declines linearly to zero at the LRP. LRPs are: 0.1B (— — —), $0.2N_{equil}$ (– – –), $N_{50\%}$ (- - -), and N_{LRP} (——). Abundance is in units of

B, the asymptotic maximum adult recruitment. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

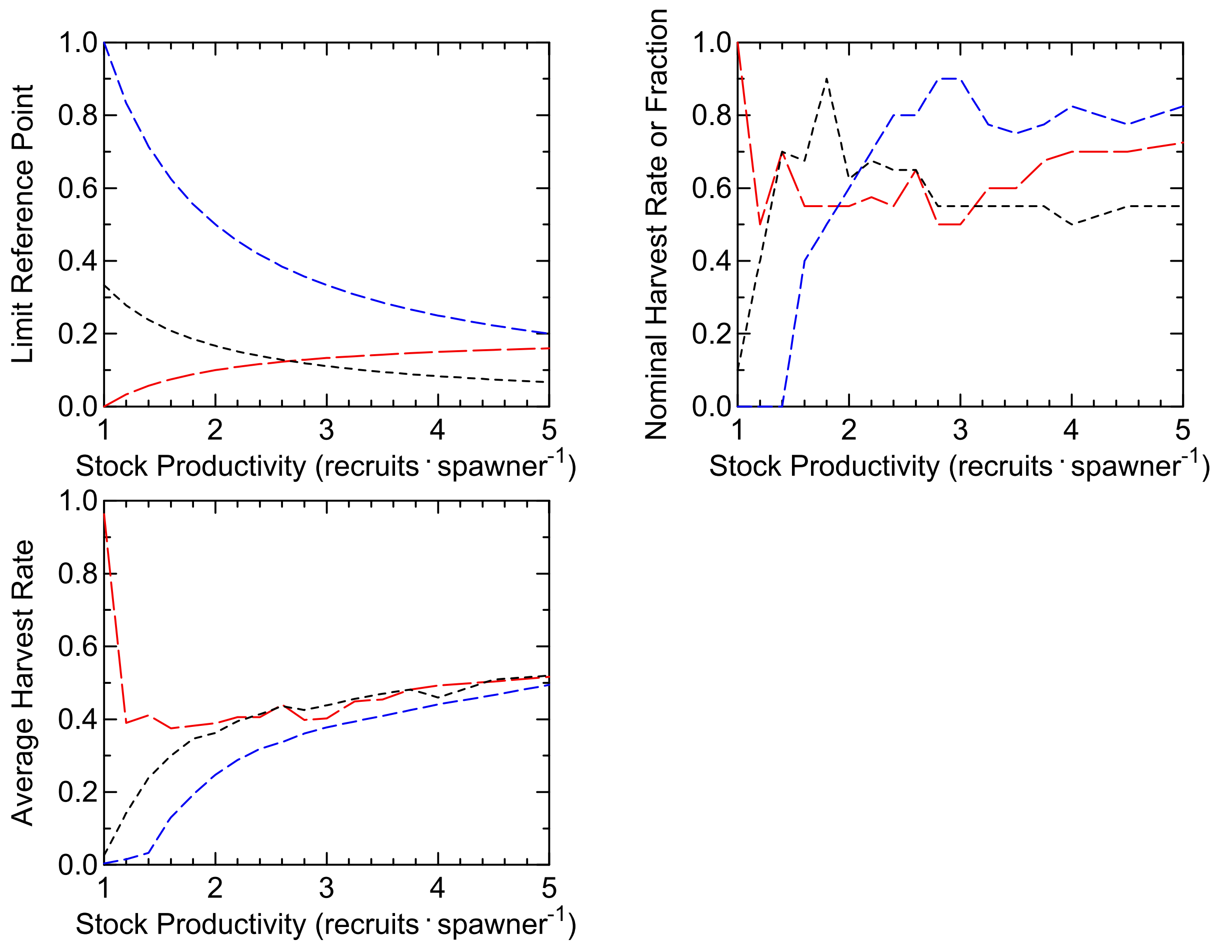

Fig. 34. (upper panel) N_{LRP} (- - -), $N_{50\%}$ (– – –), and $0.2N_{equil}$ (———) as functions of stock productivity (left panel) and the resulting nominal harvest rates (right panel) that maximize catch at different values of stock productivity for a constant exploitation rate harvest with a single limit reference point below which forecast abundance harvesting ceases.

(lower panel) Average harvest rates applied during periods of fishing for the nominal harvest rates that maximize catch for $N_{LRP,}$ $N_{50\%}$, and $0.2N_{equil}$.

Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival} = 0.629$, and $\rho = 0.7$.

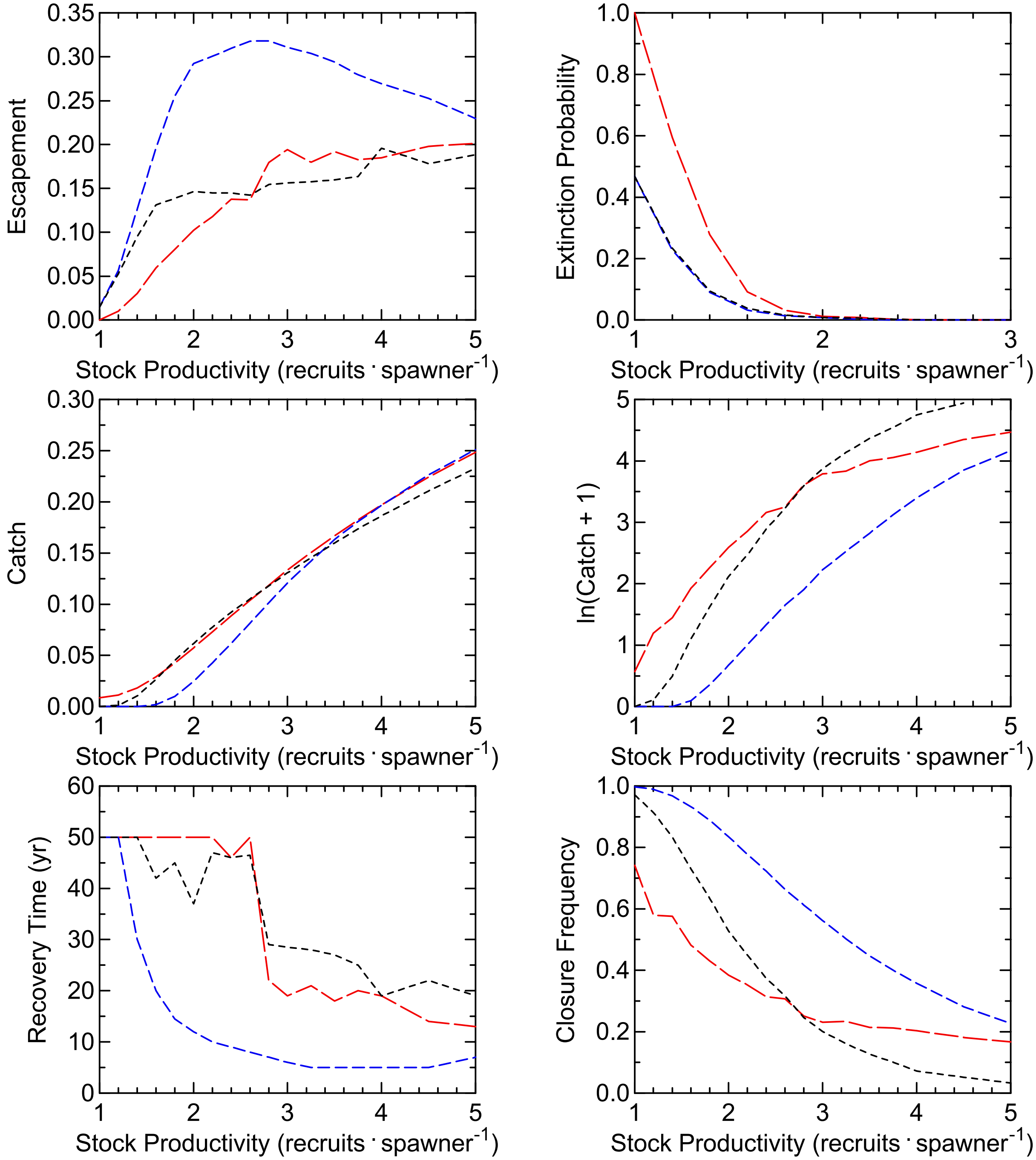

Fig. 35. Performance indicators for the catch-maximizing values of nominal harvest rates at different stock productivity values for N_{LRP} (- - -), $N_{50\%}$ (– – –), and $0.2N_{equil}$ (— — —) for a constant exploitation rate harvest policy with a single limit reference point below which forecast abundance harvesting ceases. Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year

trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

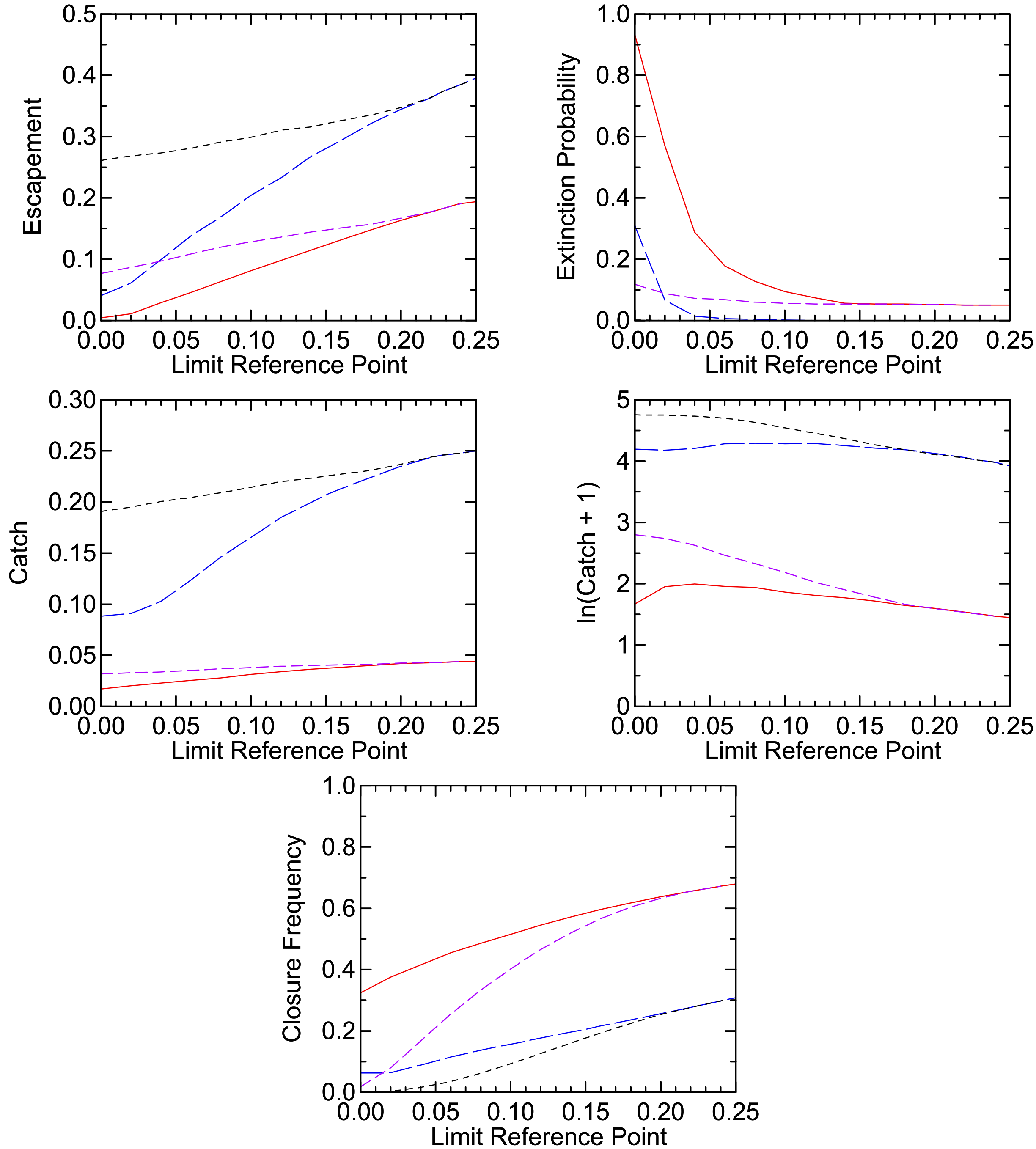

Fig. 36. The performance of different harvest control rules and threshold definitions under a "hockey-stick"-type rectilinear spawner-smolt recruitment relationship. The effects of limit reference point definitions and stock productivity on performance indicators under a "constant" exploitation rate harvesting rule with either: a single abundance threshold (limit reference point, LRP) below which forecast abundance the harvesting ceases (—— and — — —), or a limit reference point and a precautionary reference point at 0.25B

(– – – and - - -) below which forecast abundance the nominal harvest rate declines linearly to zero at the LRP. Data are shown for low stock productivity (1.4 recruits·spawner^{-1}, —— and – – –) and for moderate stock productivity (2.2 recruits·spawner^{-1}, — — — and - - -). Limit reference points, escapement, and catch are in units of B, the asymptotic maximum adult recruitment. The nominal harvest rate is 0.5, the initial population size is $N_0 = 0.1B$, B = 1 000, the variation in smolt-to-adult survival is $\sigma_{survival} = 0.629$, and temporal autocorrelation in survival deviations is $\rho = 0.7$ in this example. Note that a LRP of zero is a conventional constant exploitation rate harvesting rule.

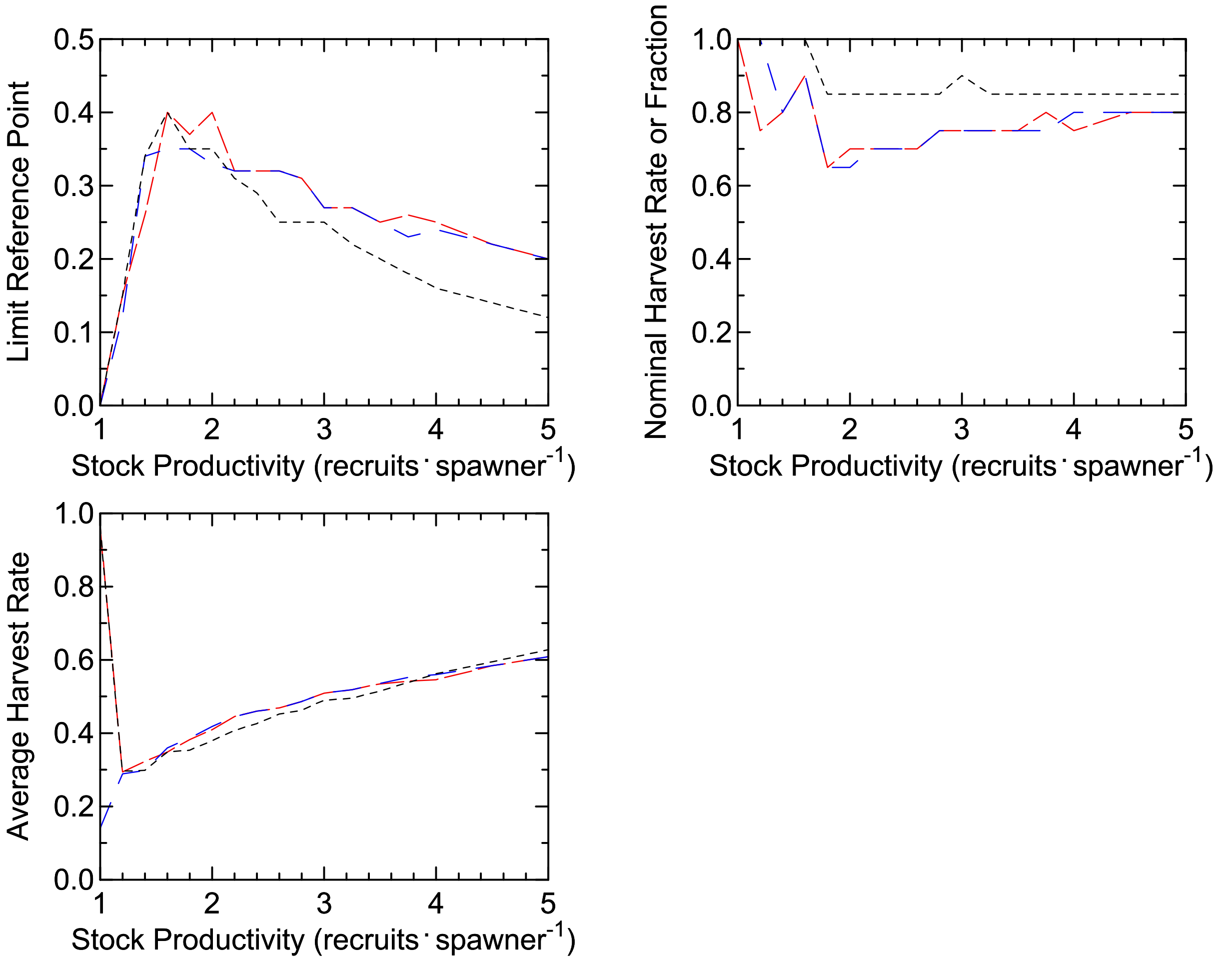

Fig. 37. Catch-maximizing values of limit reference points and harvest rates for a “hockey-stick”-type spawner-smolt recruitment relationship.

(upper panel) Limit reference points (left panel) and nominal harvest rates or harvest fractions on surplus fish (right panel) that maximize catch at different values of stock productivity for: constant exploitation rate harvest policies with either a single limit reference point (LRP) below which forecast abundance harvesting ceases (———) or a precautionary threshold at 0.35B below which forecast abundance the harvest rate decreases linearly to zero at the LRP (— — —), or for proportional threshold harvesting policies with a single LRP below which forecast abundance harvesting ceases (- - -).

(lower panel) Average harvest rates applied during periods of fishing for the LRPs and nominal harvest rates or harvest fractions that maximize catch at different values of stock productivity. Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

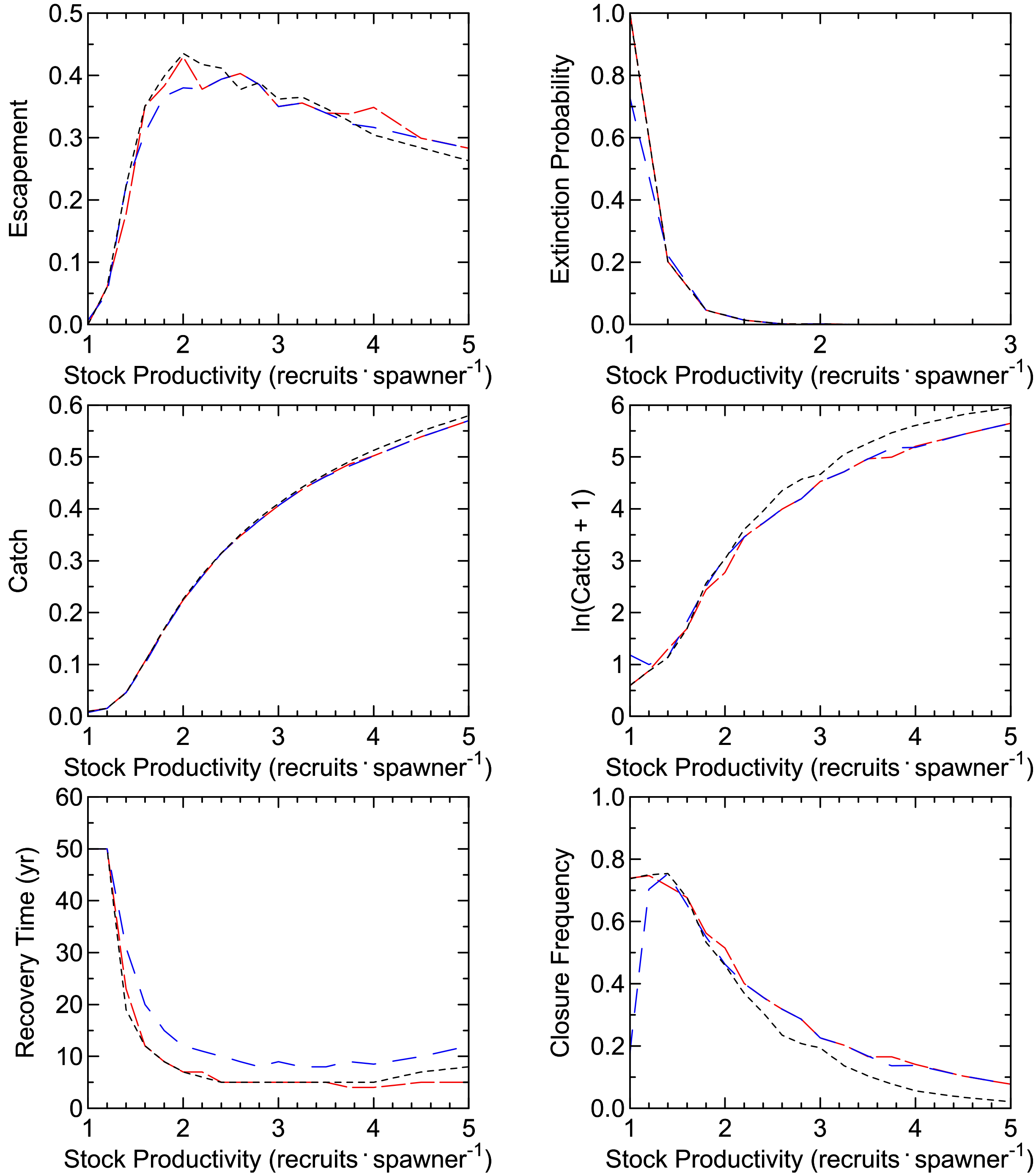

Fig. 38. Performance indicators for the catch-maximizing values of limit reference points and nominal harvest rates or harvest fractions on surplus fish at different stock productivity values for a "hockey-stick"-type rectilinear spawner-smolt recruitment function for different harvest control rules: constant exploitation rate harvest policies with either a single limit reference point (LRP) below which forecast abundance

harvesting ceases (— — —) or a precautionary threshold at 0.35B below which forecast abundance the harvest rate decreases linearly to zero at the LRP (—   —   —), or for proportional threshold harvesting policies with either a single LRP below which forecast abundance harvesting ceases (- - -). Abundance is in units of B, the asymptotic maximum adult recruitment. Results are based on 500 50-year trials using the stochastic age-structured steelhead population model described in the text. The initial population size was 0.1B, B = 1 000, $\sigma_{survival}$ = 0.629, and ρ = 0.7.

Appendix 1. Empirical Data Used to Parameterize the Steelhead Population Dynamics Model

We summarize here important empirical data and relationships that were used to construct and parameterize the steelhead population dynamics model. The empirical data describe the Keogh River steelhead population, and are derived from published (Ward and Slaney 1988) and unpublished (B.R. Ward, BC Fisheries, 2204 Main Mall, Vancouver, B.C., V6T 1Z4, *pers. comm.*) sources.

The model assumes a Beverton-Holt type relationship between the potential egg deposition and the smolt output from the spawners in a given brood year (Fig. A1). We used a Bayesian analysis similar to that described above to calculate the posterior marginal probabilities of Beverton-Holt, Ricker, and rectilinear ("hockey stick") stock-recruit models, given the observed data (Table A1). The analysis computed likelihood values over a grid of smolt productivity values, maximum smolt recruitment values, and stock-recruitment relationships. Posterior marginal probabilities for the SRRs were obtained by summing and normalizing likelihood over the grid of productivity and maximum smolt production. The posterior marginal probabilities were 0.63 for the Beverton-Holt model, 0.15 for the Ricker model, and 0.22 for the hockey stick model. The maximum likelihood estimates of α and β for the Beverton-Holt SRR were: $\alpha = 77.5$ smolts$\cdot 10^4$ eggs and $\beta =$ 6 850 smolts. We did not fit 3-parameter stock-recruitment models (Shepherd 1982, Barrowman and Myers 2000) because none encompasses the full range of plausible models (e.g., Beverton-Holt, Ricker, and "hockey stick" models).

Egg deposition in brood year *t* was estimated as:

$$Eggs_t = \sum_{i=1}^{3} fecundity_i \cdot Nfemales_{i,t}$$

where $fecundity_i$ is the average fecundity of females of ocean age *i* and $Nfemales_{i,t}$ is the number of females of ocean age *i* enumerated in year *t*. The average fecundity of ocean age 1,2, and 3 females was estimated from the size distribution of females of a given ocean age and the size-fecundity relationship. The best fit to the size-fecundity data for Keogh River fish was a linear relation:

$$fecundity = 146.7 \cdot Fork\ Length\ (cm) - 6599 \qquad r^2 = 0.54,\ N = 38.$$

We used lognormal distributions of female size at age with the observed mean and variances (Ward and Slaney 1988, Table 4. II.) to estimate average fecundity. Mean fecundity was estimated as 296 for 1-ocean females, 3 274 for 2-ocean females, and 4 800 for 3-ocean females. We assumed that 4-ocean females (which were very rare) had the same fecundity as 3-ocean fish. The number of female spawners by age was obtained by direct enumeration of the large late-run component and mark-recapture estimates of the small early-run component, as described in Ward and Slaney (1988).

The mean number of eggs per spawner (Table A1) for a brood year was calculated from counts and age distributions of female and male spawners. The average spawner sex ratio was 1.05 females per male.

The smolts produced from a given brood year emigrate at freshwater ages 1 to 5 years. The proportions of smolts emigrating at ages 1 to 5 are given in Table A1. The proportions by age for brood years that were not affected by stream fertilization were used to initialize the age distribution in our simulations.

Ward (2000) gives smolt-to-adult survival data for the Keogh River steelhead population, which are reproduced in Table A2. The mean survival is 0.110 (SD = 0.079, N = 21). The SD of ln(survival) is 0.808 over the 1977-1997 period.

Table A1. Spawner numbers, subsequent smolt production, and proportion of smolt production by age at emigration for steelhead in the Keogh River, 1976 to 1998. Note that smolt production from the 1982 to 1986 brood years was affected by experimental nutrient additions to the river, and is omitted from our analysis.

Brood Year	Spawners	Spawner F:M ratio	Mean eggs per spawner	Smolt production	Age-1 smolts	Age-2 smolts	Age-3 smolts	Age-4 smolts	Age-5 smolts
1976	859	2.198	2 892	6 688	0.000	0.167	0.731	0.084	0.018
1977	625	1.061	1 768	6 914	0.000	0.121	0.485	0.392	0.002
1978	706	0.867	1 971	7 242	0.000	0.213	0.772	0.014	0.000
1979	299	1.147	1 871	6 251	0.000	0.556	0.380	0.064	0.000
1980	209	1.250	2 297	6 071	0.000	0.248	0.610	0.143	0.000
1981	652	0.767	1 492	5 725	0.000	0.533	0.189	0.278	0.000
1982	1 494	0.834	1 966	7 834	0.000	0.675	0.320	0.005	0.000
1983	3 469	0.623	1 336	8 024	0.000	0.823	0.157	0.021	0.000
1984	4 248	0.969	2 016	10 750	0.000	0.772	0.227	0.001	0.000
1985	1 161	1.984	2 653	10 407	0.022	0.940	0.028	0.010	0.000
1986	3 984	1.049	2 114	6 528	0.227	0.464	0.302	0.007	0.000
1987	3 533	1.644	2 534	4 027	0.000	0.533	0.189	0.278	0.000
1988	2 061	0.981	2 151	6 687	0.003	0.348	0.607	0.042	0.000
1989	2 115	0.708	1 601	5 418	0.003	0.154	0.697	0.146	0.000
1990	1 916	1.184	2 410	6 346	0.000	0.486	0.507	0.007	0.000
1991	327	0.473	1 208	2 330	0.000	0.661	0.198	0.141	0.000
1992	755	1.179	2 492	2 032	0.000	0.476	0.490	0.034	0.000
1993	240	0.886	2 031	994	0.000	0.143	0.721	0.135	0.000
1994	227	0.895	2 146	1 877	0.000	0.405	0.576	0.019	0.000

Table A1. (cont'd.)

Brood Year	Spawners	Spawner F:M ratio	Mean eggs per spawner	Smolt production	Age-1 smolts	Age-2 smolts	Age-3 smolts	Age-4 smolts	Age-5 smolts
1995	332	0.791	1 953	567	0.000	0.166	0.515	0.319	0.000
1996	106	1.053	2 149	> 1 438					
1997	62	0.923							
1998	31	0.550							

Table A2. Overall smolt-to-adult survival for Keogh River steelhead, by year of smolt emigration.

Emigration year	Smolt-to-adult survival
1977	0.152
1978	0.074
1979	0.152
1980	0.084
1981	0.254
1982	0.261
1983	0.155
1984	0.183
1985	0.253
1986	0.100
1987	0.133
1988	0.067
1989	0.154
1990	0.063
1991	0.036
1992	0.030
1993	0.033
1994	0.026
1995	0.400
1996	0.024
1997	> 0.036

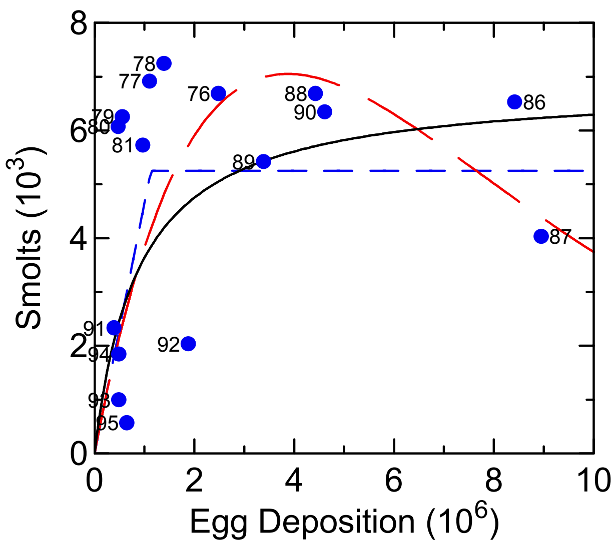

Fig. A1. Egg deposition and smolt output for steelhead in the Keogh River for the 1976-1995 brood years. Data (●) are labeled by year of spawning; smolts emigrate 1 to 5 years later. Data for the 1982 to 1985 brood years were affected by experimental nutrient additions and are omitted. Lines are maximum likelihood estimates of Beverton-Holt (—), Ricker (— —), and "hockey stick" (—— ——) stock-recruitment relationships.