Consequences of potential density-dependent mechanisms on recovery of ocean-type chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: Restoring salmon populations depends on our ability to predict the consequences of improving aquatic habitats used by salmon. Using a Leslie matrix model for chinook salmon (*Oncorhynchus tshawytscha*) that specifies transitions among spawning nests (redds), streams, tidal deltas, nearshore habitats, and the ocean, we compared the relative importance of different habitats under three density-dependent scenarios: juvenile density independence, density-dependent mortality within streams, delta, and nearshore, and density-dependent migration among streams, delta, and nearshore. Each scenario assumed density dependence during spawning. We examined how these scenarios influenced priorities for habitat restoration using a set of hypothetical watersheds whose habitat areas could be systematically varied, as well as the Duwamish and Skagit rivers. In all watersheds, the three scenarios shared high sensitivity to changes in in nearshore and ocean mortality and produced similar responses to changes in other parameters controlling mortality (i.e., habitat quality). However, the three scenarios exhibited striking variation in population response to changes in habitat area (i.e., capacity). These findings indicate that nearshore habitat relationships may play significant roles for salmon populations and that the relative importance of restoring habitat area will depend on the mechanism of density dependence influencing salmon stocks.

Résumé : La restauration des populations de saumons est conditionnée par la possibilité de prédire les conséquences de l'amélioration des habitats aquatiques utilisés par les saumons. Un modèle comportant une matrice de Leslie qui quantifie les transitions entre les nids de fraye, les cours d'eau, les deltas de marée, les habitats côtiers et l'océan chez le saumon quinnat (*Oncorhynchus tshawytscha*) nous a permis de comparer l'importance relative de différents habitats selon trois scénarios de densité-dépendance : indépendance de la densité chez les jeunes, mortalité dépendante de la densité dans les cours d'eau, le delta et la côte et migration dépendante de la densité entre le cours d'eau, le delta et la côte. Tous les scénarios présupposent une dépendance de la densité durant la fraye. Nous avons examiné comment ces scénarios influencent les priorités de restauration des habitats en utilisant une série de bassins versants hypothétiques dont les surfaces d'habitats pouvaient être modifiées systématiquement, d'une part, et les rivières Duwamish et Skagit, d'autre part. Dans tous les bassins versants, les trois scénarios ont une forte sensibilité aux changements de mortalité sur la côte et dans l'océan et ils génèrent des réponses semblables aux changements des autres variables (i.e., la qualité de l'habitat) qui contrôlent la mortalité. Toutefois, les trois scénarios génèrent de remarquables variations dans les réactions de la population aux changements de surface (i.e., la capacité) des habitats. Ces résultats indiquent que les interactions au niveau de l'habitat côtier jouent un rôle significatif chez les populations de saumons. De plus, l'importance relative de la restauration des surfaces d'habitat dépendra des mécanismes de densité-dépendance qui influencent les stocks de saumons.

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Introduction

Habitat degradation and loss have been listed as major causes of population declines in Pacific salmon (*Oncorhynchus* spp.) (Nehlson et al. 1991). However, it has been difficult to compare the relative effect of freshwater habitat degradation with other factors such as changes in marine survival (Coronado and Hilborn 1998) or harvest (Cass and Riddell 1999), in p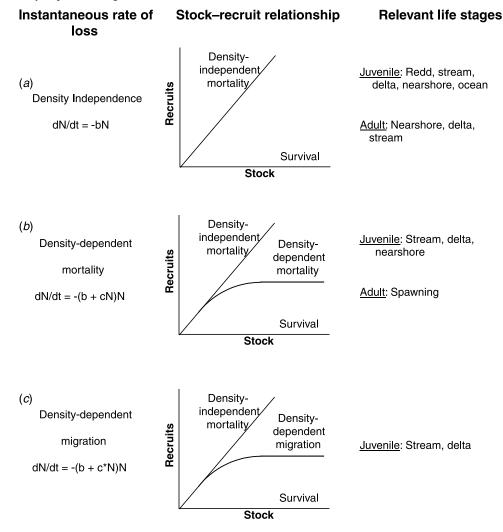art because anadromous salmonids use multiple habitats during their life cycle. Attempts to address recovery issues like these typically employ life cycle models because such models integrate survival changes at multiple life stages (Crowder et al. 1994; Caswell 2001). Such models often assume that population dynamics are density independent (Kareiva et al. 2000; Wilson 2003) (Fig. 1*a*), especially when applied to threatened species whose populations are small and for which compensatory interactions are presumed to be negligible. However, where habitat has been

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Fig. 1. Three potential scenarios of density dependence, their mathematical formulation, graphical depiction, and relevant possible life stages in this model. In the first two scenarios (density independence and density-dependent mortality), the instantaneous rate of loss refers to instantaneous mortality, where b is the density-independent mortality rate, c is the density-dependent mortality rate, and N is the population size. In the density-dependent migration scenario, the rate of loss is a combination of instantaneous density-independent mortality (b) and density-dependent migration rate (c^*).

Instantaneous rate of loss	Stock–recruit relationship	Relevant life stages

(a)
Density Independence

$$dN/dt = -bN$$

Density-independent mortality

Recruits / Stock / Survival

Juvenile: Redd, stream, delta, nearshore, ocean

Adult: Nearshore, delta, stream

(b)
Density-dependent mortality

$$dN/dt = -(b + cN)N$$

Density-independent mortality / Density-dependent mortality

Recruits / Stock / Survival

Juvenile: Stream, delta, nearshore

Adult: Spawning

(c)
Density-dependent migration

$$dN/dt = -(b + c^*N)N$$

Density-independent mortality / Density-dependent migration

Recruits / Stock / Survival

Juvenile: Stream, delta

severely degraded or eliminated, concentration of organisms into remaining suitable habitat may result in compensatory interactions and limit the population at a reduced capacity (Achord et al. 2003). Thus, an incorrect assumption of density independence may erroneously suggest to managers that recovery of habitat area will not benefit populations because improvements can be made only to a population's productivity (habitat quality) and not to capacity (habitat quantity).

Some researchers have integrated density dependence into population viability models to examine how changes in both productivity and capacity affect population response (e.g., Ginzburg et al. 1990; Nickelson and Lawson 1998). Most such models assume that compensation operates directly on survival during a population's residency in a habitat and that instantaneous mortality rate is a second-order function of population size (Fig. 1b). This assumption is valid for species that are unable to emigrate from a particular habitat (e.g., Connell 1961) but not necessarily for mobile species such as anadromous salmon for which density dependence may manifest itself in altered migration rates (Reimers 1973;

Bradford and Taylor 1997). As they migrate from headwaters to oceans, salmon use multiple habitats, and the existence and form of density dependence may vary depending upon life history and habitat availability. For example, sockeye salmon (*Oncorhynchus nerka*) rear at least 1 year in lakes and, not surprisingly, show some of the most striking patterns of density-dependent mortality (Burgner 1991). In contrast, some stocks of ocean-type chinook salmon (*Oncorhynchus tshawytscha*) appear to respond to increases in density by modifying residency in freshwater and estuarine habitats (Reimers 1973), thereby supporting the existence of density-dependent migration.

Many salmon populations are depressed, and managers are faced with multiple recovery options and the need to understand which habitat restoration actions might yield the greatest population responses. These circumstances motivate the need to carefully examine how different possible mechanisms of density dependence may influence the response of populations to restoration actions. The goals of this paper are to examine the contribution of various aquatic habitats to

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population dynamics of wild chinook salmon in the Puget Sound region and evaluate how different types of density dependence might change the importance of these habitat-specific effects. We first formulate a modified age-structured Leslie matrix model that specifies redd, stream, tidal delta, nearshore, and ocean transitions. We parameterize the model to represent ocean-type chinook salmon in Puget Sound, which is the dominant life history type in the basin (Healey 1991). With this model, we evaluate how varying assumptions of density dependence alter the estimated importance of different habitats to a population. We examine three possible forms of density dependence: juvenile density independence with a spawning habitat capacity, density-dependent mortality in various juvenile rearing habitats, and density-dependent migration between rearing habitats. We model ocean-type chinook salmon populations from four hypothetical watersheds with differing habitat configurations as well as two real-world examples: the Duwamish and Skagit rivers. For each watershed, we systematically alter survival parameters at each life stage to examine how populations might respond to changes in quality of various habitats. We then systematically vary habitat area for spawning, stream rearing, delta rearing, and nearshore rearing to examine how assumptions of density dependence might alter predictions of population response to habitat restoration actions that increase habitat area. Our purpose is not to recommend specific restoration strategies for particular populations but rather to examine how assumptions of density dependence in different habitats might alter our conclusions about effects of habitat change on a population.

Methods

Puget Sound ocean-type chinook life history

Ocean-type chinook salmon enter Puget Sound rivers between June and September and typically spawn in September and October (Williams et al. 1975; Healey 1991). Eggs develop in the gravel for up to 150 days, remaining in redds even after emergence. After leaving redds, fry migrate downstream over a period of 1–3 months, with most fish reaching the tidal delta (tidally influenced habitats near the river mouth) between February and June. Juveniles reside in the tidal delta for up to 2 months. Juveniles then migrate to nearshore marine habitats such as beaches and eelgrass beds that are subject to freshwater influence, where they remain for approximately 4 months. The vast majority of adults then rear at sea for 3–5 years before returning to spawn, but some individuals spawn at 2 and 6 years of age (Myers et al. 1997; Coronado and Hilborn 1998).

The generalized matrix model

To examine the response of the population to changes in habitat-specific survival rates, we used a modified Leslie matrix model (cf. Sabaton et al. 1998; Kareiva et al. 2000; Gouraud et al. 2001) to track survival of females in the population. This approach specifies age-specific transition probabilities to calculate changes in population size following

$$(1) \qquad N_{t+1} = \mathbf{A}N_t$$

where N_t and N_{t+1} are vectors of population size in year t and $t + 1$ (specific cells in each vector at a particular t are

represented as $N_{x,t}$) and $\mathbf{A}$ is a Leslie matrix that incorporates both habitat- and age-specific survival (Table 1).

Leslie matrices usually specify a single survival rate to indicate the transition probability from one age to the next. To incorporate the effects of multiple habitats used within a particular age transition, we subdivided the life cycle into finer intervals based on the residence time (in weeks) in specific habitats. Habitat-specific survival rates are determined by instantaneous (weekly) mortality rates through redds (b_r), streams (b_{sj}), tidal delta (b_{dj}), and nearshore habitat (b_{nj}), where the subscript "j" denotes the juvenile life stage. If residency (in weeks) in these habitats is τ_r, τ_{sj}, τ_{dj}, and τ_{nj}, respectively, survival of juveniles through each habitat is $r = e^{-b_r \tau_r}$ for redds, $s_j = e^{-b_{sj} \tau_{sj}}$ for the stream, $d_j = e^{-b_{dj} \tau_{dj}}$ for the tidal delta, and $n_j = e^{-b_{nj} \tau_{nj}}$ for the nearshore. Total survival for the transition from the first year to the second year is therefore $r s_j d_j n_j$. After the first year, smolts must survive at least 1 year in the ocean (o_x = ocean survival at age x), during which time the population incurs incidental harvest (h, assumed to be constant and not age specific). Each year, a proportion (a_x) of adults mature and return to spawn, with the remainder ($1 - a_x$) staying in the ocean. Spawners must survive terminal harvest (μ, also assumed to be constant and not age specific) and migration through the nearshore (n_a), delta (d_a), and stream (s_a) to reproduce. Like juvenile habitat-specific parameters, survival of adults returning through habitats to spawn is $s_a = e^{-b_{sa} \tau_{sa}}$ for the stream, $d_a = e^{-b_{da} \tau_{da}}$ for the tidal delta, and $n_a = e^{-b_{na} \tau_{na}}$ for the nearshore. These parameters as well as age-specific fecundity (m_x) and the female natal sex ratio (f) determine spawners' contribution to the next generation.

Habitat-specific density dependence

The generalized matrix model assumes density independence at all stages in the life cycle. In addition to a scenario assuming density independence in all juvenile life stages, we examined two additional scenarios: density-dependent mortality and density-dependent migration. All scenarios also assumed density-dependent interactions during adult spawning (see below).

In the density-dependent mortality scenario, the instantaneous mortality rate within a particular habitat increases as a function of density following a Beverton–Holt relationship (Fig. 1b) (also see Moussalli and Hilborn 1986). Beverton and Holt (1957) devised their classic relationship by incorporating residency in particular life stages. The instantaneous density-independent mortality rate b and the density-dependent mortality rate c (per hectare) are used to calculate R, the number of fish surviving a particular life stage. We modified Beverton and Holt's (1957) formulation to separate c from A, the habitat area:

$$(2) \qquad R = \frac{1}{\dfrac{c}{Ab}(e^{b\tau} - 1) + \dfrac{e^{b\tau}}{S}}$$

where τ is length of residency in the life stage and S is the initial population size. In this equation, the units of c (hectares per week per fish) are analogous to the amount of area required by an individual per week of residency. A more intuitive and easily measured quantity is the inverse of c (fish

Table 1. Leslie matrix for ocean-type chinook salmon.

Year	1	2	3	4	5	6
1		$o_2 a_2 n_a d_a s_a fm_2$ $e^{-(\mu+h)}$	$o_3 a_3 n_a d_a s_a fm_3$ $e^{-(\mu+h)}$	$o_4 a_4 n_a d_a s_a fm_4$ $e^{-(\mu+h)}$	$o_5 a_5 n_a d_a s_a fm_5$ $e^{-(\mu+h)}$	$o_6 a_6 n_a d_a s_a fm_6$ $e^{-(\mu+h)}$
2	$rs_j d_j n_j$					
3		$o_2(1 - a_2)e^{-h}$				
4			$o_3(1 - a_3)e^{-h}$			
5				$o_4(1 - a_4)e^{-h}$		
6					$o_5(1 - a_5)e^{-h}$	

Note: The matrix shows transition rates from cohorts in their xth year (columns) to cohorts in their yth year (rows). Total survival in the first year is determined by survival within each habitat (r, redd survival; s_j, juvenile stream survival; d_j, tidal delta survival; n_j, nearshore survival) based on instantaneous (weekly) mortality estimates, as are adult survival rates during return through nearshore (n_a), tidal delta (d_a), and stream (s_a). Mean survival (o_x) and terminal (μ) and nonterminal harvest (h) are based on annual rates. a_x, age-specific breeding propensity; f, female natal sex ratio; m_x, age-specific fecundity.

per week per hectare), the instantaneous capacity per unit of habitat. Therefore, if we define $C = 1/c$ and rearrange terms, eq. 2 can be rewritten as

$$(2a) \quad R = \frac{SAbC}{S(e^{b\tau} - 1) + AbC\,e^{b\tau}}$$

Equation 2a can readily be applied to any of the habitats specified in the generalized matrix model by transforming eq. 2 into a survival rate (R/S). For example, if we assumed that density-independent mortality occurred in redds, then $S = rN_{1,t}$ and

$$(3) \quad s_j = \frac{rN_{1,t}A_s b_s C_s}{rN_{1,t}(e^{b_s \tau_s}-1) + A_s b_s C_s e^{b_s \tau_s}} \bigg/ rN_{1,t}$$
$$= \frac{A_s b_s C_s}{rN_{1,t}(e^{b_s \tau_s} - 1) + A_s b_s C_s e^{b_s \tau_s}}$$

The equations for each life stage are summarized in Appendix A.

Equation 2 can also be used to model density-dependent migration by assuming that c specifies the rate of individuals migrating from the habitat prematurely (Fig. 1c). In this scenario, the number of surviving recruits can be classified into those individuals that remain in the habitat (R_h) and early migrants (R_m). Hence, for any transition through a particular habitat:

$$(4a) \quad R_h = \frac{SAbC}{S(e^{b\tau} - 1) + AbC\,e^{b\tau}}$$

and

$$(4b) \quad R_m = S\sigma - R_h$$

where σ is the total survival in that habitat (in our analysis, s_j or d_j). The proportion p_h of fish that remain in the habitat for an extended residency is therefore

$$(5) \quad p_h = \frac{R_h}{R_h + R_m} = \frac{R_h}{S\sigma}$$

and the proportion p_m of early migrants is $\sigma - p_h$ (Fig. 1c). The equations for each life stage are summarized in Appendix A.

Applying eq. 5 to the generalized matrix model requires assumptions about the residency time of fish that prematurely move downstream and about the expected survival of different subgroups of migrants. We modeled the residency patterns of these subgroups based on known variation in ocean-type life history. Subyearling juvenile chinook salmon exhibit variation in the extent to which they use stream, delta, and nearshore habitats (Reimers 1973). Reimers (1973) posited the existence of four different subyearling variants utilizing habitats in the Sixes River, and other researchers (e.g., Healey 1991) have observed subsets of these combinations in other watersheds. In the Puget Sound region, three life history subtypes have been observed. These include (i) parr migrants, which rear in streams for 3 months before migrating to the nearshore, (ii) delta users, which migrate downstream for 1 month, reside in the delta for 1–2 months, and then migrate to the nearshore, and (iii) fry migrants, which migrate downstream within 1 month, bypass the tidal delta, and rear in the nearshore (E. Beamer, Skagit System Cooperative, P.O. Box 268, La Connor, WA 98257, U.S.A., unpublished data).

For the purposes of our simulation, we assumed that these three behavioral variants are the result of two stages of migration among habitats following eq. 5. The first stage assumes density-dependent migration in the stream, and the second stage assumes density-dependent migration in the delta. A proportion of fish (p_s, parr migrants) rear in the stream, while the remaining proportion ($s_j - p_s$) migrates downstream. Of those migrants, a proportion of fish (p_d, delta users) rear in the delta, while the remaining fish ($d_j - p_d$, fry migrants) migrate directly to the nearshore.

Because residency in different habitats differs among the life history variants, survival of certain variants must be adjusted for residency. Delta users are the typical life history type, and their transition probability through life history stages is $rs_j(s_j - p_s)p_d n_j$. Survival for parr migrants, which we assume spend an additional 4 weeks in the stream before migrating, is reduced by $e^{-4b_{sj}}$. The transition probability of parr migrants through juvenile life history stages is therefore $rs_j p_s n_j e^{-4b_{sj}}$. Fry migrants spend 4 weeks less in the stream and in the delta compared with delta users and rear instead in the nearshore for 8 weeks. An apparent consequence of reduced stream and delta rearing is higher mortality (following Levings et al. 1989). Based on these assumptions, total sur-

vival for fry migrants is $rs_j(s_j - p_s)(d_j - p_d)n_j e^{-8\delta b_{nj} + 4(b_{sj} + b_{dj})}$, where δ is the additional nearshore mortality upon fry migrants. The term $e^{-8\delta b_{nj} + 4(b_{sj} + b_{dj})}$ adjusts survival resulting from both increased mortality of fry migrants in the nearshore and decreased mortality due to reduced residency in streams and delta. We assume the existence of density-dependent mortality during weeks in which all variants reside in the nearshore but density independence during the initial weeks when only fry migrants are present. The combined transition probability from the first to the second year of the entire population is therefore

$$(6) \qquad N_{2,t} = N_{1,t} rs_j n_j [(p_s e^{-4b_{sj}})$$
$$+ (s_j - p_s)(p_d + (d_j - p_d)e^{-8\delta b_{nj} + 4(b_{sj} + b_{dj})})]$$

Density dependence during spawning

In years during which a large number of spawners return, populations can be limited by the amount of spawning habitat available (Fukushima et al. 1998), which would violate the matrix model's assumption of density independence during adult life stages. We investigated the possibility of density dependence using a Beverton–Holt model that combines the contribution of different age classes to reproduction by assuming that the contribution to fecundity of adult fish that spawn from each age class is proportional to their representation in the total run. The total spawning run in a given year is

$$(7) \qquad T = (1 - \mu)n_a d_a s_a \sum_{x=2}^{6} a_x o_x N_{x,t}$$

The proportion P_x of the total spawning run represented by spawners of a particular age class is therefore

$$(8) \qquad P_x = \frac{a_x o_x N_{x,t}}{T}$$

The Beverton–Holt relationship describing the number of female eggs produced by multiple age-classes is

$$(9) \qquad N_1 = \frac{fT \sum_{x=2}^{6} m_x P_x}{1 + \dfrac{c_r}{A_r}T}$$

where c_r is the redd capacity (expressed in terms of redds per hectare), A_r is the spawning area (hectares), and $\sum_{x=2}^{6} m_x P_x$ is the age-specific fecundity weighted by P_x. Because this weighting is based solely on the representation of an age class in the spawning run, eq. 9 assumes no competitive differences among age classes. We tested an alternate version of the model that included competitive differences, but the results were not qualitatively different from those produced by eq. 9.

Parameterization

We parameterized the model using published estimates of habitat-specific survival, age-specific maturity and fecundity, and other demographic rates (Table 2). Where possible, we used estimates obtained from Puget Sound populations, but other published estimates were used in their absence. Habitat-

specific survival parameters were particularly difficult to obtain. We know of no published studies of survival in redds (r) in the Puget Sound region, so we used median estimates of survival obtained from redd-capping studies of chinook salmon on the upper reaches of the Yakima River (Wasserman et al. 1984; Fast et al. 1985, 1986), scaled to the 5-month residency typical of Puget Sound populations. We used the median stream survival (s_j) estimate obtained from a 3-year mark–recapture study of chinook salmon in the Green River that factored in random variability of downstream migration rates (Wetherall 1971). These estimates produced a total freshwater survival of 13.4%, in line with published estimates of freshwater survival (Healey 1991; Bradford 1995) and unpublished estimates of egg–fry survival in the Skagit River during years of moderate incubation floods (C. Greene, unpublished data). Age-specific ocean survival (o_x) was based on current projections of index populations (Chinook Technical Committee 2001), and sensitivity analyses followed baseline projections such that o_3, o_4, o_5, and o_6 were 1.167, 1.33, 1.5, and 1.5 times o_2, respectively. We based terminal (μ) and nonterminal (h) harvest rates on the current projections of 40% and 10% (Chinook Technical Committee 2001). To obtain tidal delta (d_j) and nearshore (n_j) survival, we first calculated estuarine survival by factoring out stream and natural ocean survival of 3-year-olds from published median estimates of survival for coded-wire tagged Puget Sound stocks (Coronado 1995; Coronado and Hilborn 1998) from 1972 to 1988. Estuarine survival was divided into tidal delta and nearshore survival by assuming that (*i*) monthly survival in the tidal delta is 40% greater than nearshore survival (consistent with Healey 1980; Levings et al. 1989) and (*ii*) residency in estuary and nearshore habitats is 1 month greater for wild fish than for hatchery fish (Levings et al. 1986), upon which total marine survival is estimated (Coronado and Hilborn 1998). Total juvenile redd, stream, delta, and nearshore survival were converted to weekly mortality rates using natural log transformations based on published estimates of residency (Table 2). For adult habitat-specific survival, we assumed a 1-week residency in nearshore (Williams et al. 1975) and delta (Simenstad et al. 1982) and a 2-week residency in stream habitats (Williams et al. 1975). Mortality in these habitats was assumed to be low (Ratner et al. 1997) but higher in the nearshore compared with the delta and stream.

Although density dependence can play an important role in the population dynamics of chinook salmon, no habitat-specific estimates of density-dependent parameters exist in the literature to our knowledge. Therefore, we explored the consequences of potential density dependence in different habitats using a heuristic approach. We assumed that capacity increased from stream to delta to nearshore habitat, consistent with differences in individual growth rates in these habitats (Reimers 1973) and life history information indicating that chinook exhibit schooling behaviors during tidal delta and nearshore residence (Reimers 1968; Healey 1991).

Watershed simulations

To better understand how restoration options differ in these watersheds among density-dependent scenarios, we examined a set of simulations in which we systematically varied

Table 2. Model parameters, their estimates, and references for these estimates.

Parameter	Description	Value	Reference(s)
b_r	Weekly redd mortality	0.038	Wasserman et al. 1984; Fast et al. 1985, 1986
b_{si}	Weekly juvenile stream mortality	0.138	Wetherall 1971
b_{dj}	Weekly juvenile tidal delta mortality	0.113	See text
b_{nj}	Weekly juvenile nearshore mortality	0.185	See text
b_{sa}	Weekly adult stream mortality	0.025	See text
b_{da}	Weekly adult tidal delta mortality	0.02	See text
b_{na}	Weekly adult nearshore mortality	0.1	See text
δ	Fry migrant increase in nearshore mortality	3.333	Levings et al. 1989
$\tau_r, \tau_{sj}, \tau_{dj}, \tau_{nj}$	Juvenile redd, stream, delta, and nearshore residency (weeks)	20, 8, 4, 16	Williams et al. 1975; Alderdice and Velson 1978; Healey 1980
$\tau_{sa}, \tau_{da}, \tau_{na}$	Adult stream, delta, and nearshore residency (weeks)	2, 1, 1	Williams et al. 1975
o_2, o_3, o_4, o_5, o_6	Annual ocean survival	0.6, 0.7, 0.8, 0.9, 0.9	Chinook Technical Committee 2001
a_2, a_3, a_4, a_5	Age-specific breeding propensity	0.005, 0.097, 0.637, 1.0	Puget Sound TRT, personal communication[a]
m_2, m_3, m_4, m_5, m_6	Age-specific fecundity	2500, 4848, 5710, 6664, 7500	E. Beamer, personal communication[b]
μ	Terminal harvest rate	0.6	Puget Sound TRT, personal communication[a]
h	Nonterminal harvest rate	0.1	Chinook Technical Committee 2001
f	Natal female sex ratio	0.5	
C_r, C_s, C_d, C_n	Redd, stream, delta, and nearshore, capacity	7, 100 000, 200 000, 400 000	
A_r, A_s, A_d, A_n	Redd, stream, delta, and nearshore area (ha)	Table 3	

[a]c/o Mary Ruckelshaus, Northwest Fisheries Science Center, Division of Conservation Biology, 2725 Montlake Boulevard East, Seattle, WA 98112-2097, U.S.A.
[b]Skagit System Cooperative, P.O. Box 268, La Connor, WA 98257, U.S.A.

habitat configuration (amount in each of the four juvenile habitats) such that in any simulation, only one habitat (the "restricted habitat") was a smaller size and all the others were constant at 2000 ha (Table 3). These simulations made no assumptions about which habitat is limiting the population (this an outcome of the model) or the extent to which a particular habitat could be restored.

We also applied our model to two real watersheds, the Skagit and Duwamish rivers. The Skagit River is the largest watershed in Puget Sound and has sustained impacts to some of the headwaters (A_r) as a result of historical logging, mining, and damming, as well as 70–90% loss of rearing habitat in the mainstem (A_s) and delta (A_d) as a result of channelization and diking (Collins et al. 2003). Nearshore habitat area (A_n) may be moderately degraded as a result of shoreline development. However, across the watershed, many of the habitats are still largely intact and functional (Table 3). The Duwamish watershed shares the Skagit's legacy of loss and degradation of headwaters and mainstem habitat but also has undergone recent urbanization resulting in further loss to mainstem rearing habitats, near total loss of the tidal delta, and substantial degradation of nearshore rearing habitats (Table 3) (Simenstad et al. 1982; Collins et al. 2003).

Sensitivity analyses

We evaluated the importance of different habitats on populations by using a simple sensitivity analysis (see Doak et al. 1994). We first established a baseline population trend by simulating dynamics over 300 generations, a more than sufficient amount of time for all runs to equilibrate. We then modified each parameter of interest by 5%, using a decrease in instantaneous mortality for survival parameters and an increase for all other parameters. We then calculated the resulting percent change in the number of spawners resulting from this change. This technique is analogous to the use of elasticity analyses of λ (the dominant eigenvalue of the population matrix) when population dynamics are assumed to be density independent (Doak et al. 1994; Mills et al. 1999; Kareiva et al. 2000).

We evaluated the relative importance of different parameters by comparing population responses with the 5% perturbation. The 5% changes in some demographic parameters could directly correspond to several possible management actions. Increasing redd survival might correspond to better postspawning flow management practices on regulated rivers. Increasing stream survival could correspond to removing rip-rap structures or placing large woody debris as cover, and increasing nearshore survival might result from eelgrass restoration or bulkhead removal. Increases in stream and tidal delta area could result from dam breaching or dike removal, respectively. Changes in other demographic parameters (e.g., ocean survival) make less sense from a management perspective but are useful to gauge ecological or evolutionary responses to environmental changes (e.g.,

Table 3. Habitat areas and the equilibrium spawning population under baseline conditions in six watershed simulations: four model watersheds in which one habitat area is restricted relative to the other three and the Skagit and Duwamish watersheds.

	Model watershed; restricted habitat in				Skagit	Duwamish
	Redd	Stream	Delta	Nearshore		
Parameter						
A_r	500	2 000	2 000	2 000	1 200	375
A_s	2 000	500	2 000	2 000	1 500	570
A_d	2 000	2 000	500	2 000	800	10
A_n	2 000	2 000	2 000	500	8 500	2 000
Baseline equilibrium spawning population						
Juvenile density dependence	349 030	1 396 123	1 396 123	1 396 123	837 674	258 219
Density-dependent mortality	23 620	7 056	19 460	21 799	17 826	1 157
Density-dependent migration	163 519	242 124	171 403	103 494	239 436	10 716

Scavia et al. 2002) relative to changes directly related to management actions.

Results

Baseline population response

In all simulations, the three density-dependent scenarios resulted in markedly different spawning population sizes (Table 3). When density dependence existed solely during spawning, the population increased exponentially until it reached spawning capacity. Not surprisingly, this scenario resulted in the highest equilibrium population size. Under the density-dependent mortality scenario, compensatory processes in stream and delta reduced population growth such that the population size began to level off before it reached spawning capacity. Intriguingly, in the density-dependent migration scenario, the existence of three life history types resulting from density-dependent variation in residency produced between 4 and 34 times the equilibrium population size of the density-dependent mortality scenario, depending upon the habitat configuration (i.e., the distribution of area among habitats). These differences occurred because under the density-dependent migration scenario, the stock–recruit functions specified not mortality but the proportions of the population exhibiting different levels of mortality. This variation enabled a larger total number of fish to exist in different habitats. For example, at high densities, a larger proportion of the population became fry migrants and suffered extremely low survival in the nearshore, but delta residents and stream residents maintained much higher levels. In contrast, in the density-dependent mortality scenario, stock–recruit functions specified mortality on all fish as they migrated through two habitats, resulting in a much lower equilibrium population size.
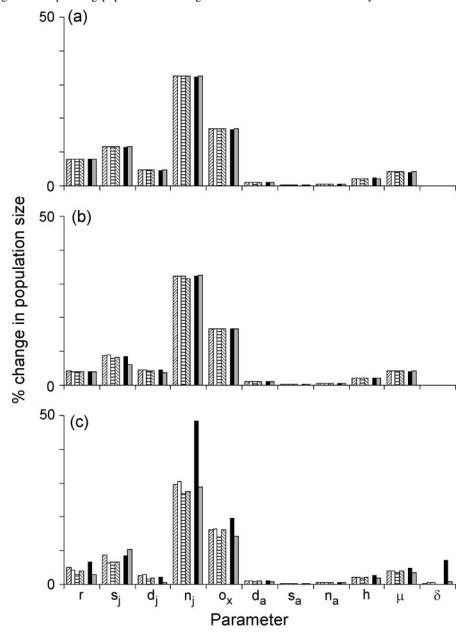
Sensitivity of parameters to perturbation

In the four model watersheds, the contrasting dynamics produced by the three density-dependent scenarios resulted in varied responses to changes in life history parameters. Improvements to survival (Fig. 2) generally had the largest population responses and were qualitatively similar among both scenarios and watersheds. In all scenarios, reducing nearshore (n_j) and ocean mortality (o_x) resulted in the greatest percent change in population size, whereas reducing adult delta (d_a) and stream mortality (s_a) had the smallest effects. Some scenario-specific variation in population sensitivity resulted in slight recovery ranking differences. For example, under the density-dependent mortality scenario (Fig. 2b), reducing juvenile delta mortality (d_j) resulted in greater recovery than reducing redd mortality (r), but rankings for these two measures were reversed for the density-dependent migration scenario (Fig. 2c).

Quantitative differences in sensitivity to changes in survival among habitat configurations existed primarily for the density-dependent migration scenario (Fig. 2c). In habitats subject to the effects of density-dependent migration (stream, delta, and nearshore), sensitivity to changes in habitat-specific survival was lowest when each of those habitats was restricted. This counterintuitive result occurred because density-dependent migration caused fewer individuals to use the restricted habitat, so changes to survival in this habitat benefited a smaller proportion of the population.
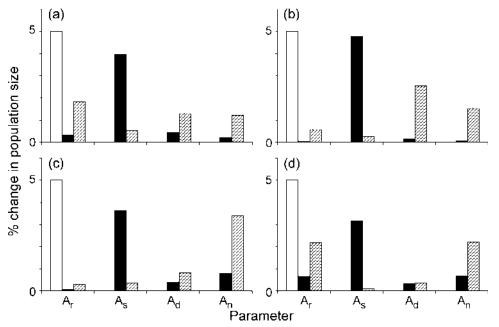
The relatively small differences among density-dependent scenarios and model watersheds to changes in survival contrasted with differences resulting from changes in habitat area (Fig. 3). The most obvious difference was the consistently high sensitivity to changes in redd area (A_r) in the juvenile density independence scenario and in stream habitat area in the density-dependent mortality scenario, in contrast with the variable sensitivities across configurations in the density-dependent movement scenario. Under the density-independent scenario, redd area was the only habitat area parameter that could influence changes in population size, so this change mirrored the 5% habitat area increase. Under the density-dependent mortality scenario, changes in population size most strongly depended upon the habitat with the lowest effective capacity (i.e., the capacity after accounting for mortality in previously used habitats). In the case of these four model watersheds, stream habitat always had the lowest effective capacity regardless of which habitat was restricted; spawning capacity was always very large because of the sheer number of adults that could possibly spawn (Table 3, juvenile density independence scenario), and effective capacity in the delta and nearshore remained relatively large even when these habitats were restricted because many juvenile fish died before entering these habitats. As a conse-

Fig. 2. Sensitivity of population size to changes in survival rates when population dynamics are influenced by juvenile (*a*) density independence, (*b*) density-dependent mortality in the stream, tidal delta, and nearshore, and (*c*) density-dependent migration through the stream and tidal delta. All scenarios incorporate density dependence during spawning. All scenarios are examined in four model watersheds in which redd area (upward-hatched bars), stream area (open bars), delta area (horizontally hatched bars), or nearshore area (downward-hatched bars) is restricted. Also shown are simulations of Skagit (solid bars) and Duwamish (shaded bars). Each bar represents the percent change in the spawning population resulting from a 5% reduction in mortality.

quence, sensitivities to changes in habitat area resulting from the density-dependent mortality scenario showed little variation across habitat configurations. A general conclusion from this finding is that population responses resulting from density-dependent mortality will strongly be influenced by the capacity of single habitats.

Under the density-dependent migration scenario, two habitat configurations caused the restricted habitat to have the highest sensitivity to habitat restoration, while two other configurations caused the habitat "downstream" of the restricted habitat to have the highest sensitivity. Redd and

nearshore habitats (Figs. 3*a* and 3*d*) exhibited the first pattern because all fish in the population were affected by those areas (i.e., there was no density-dependent migration out of those habitats). The second pattern was caused by density-dependent migration from stream and delta habitats. When each of these habitats was restricted (Figs. 3*c* and 3*d*), density-dependent migration resulted in shorter residency for portions of the population using this habitat. As a consequence, the downstream habitat had the highest sensitivity to restoration because more individuals were forced to use this habitat. Hence, population responses resulting from density-

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Fig. 3. Sensitivity of population size to changes in habitat area when population dynamics are influenced by juvenile density independence (open bars), density-dependent mortality in the stream, tidal delta, and nearshore (solid bars), and density-dependent migration through the stream and tidal delta (hatched bars). All scenarios incorporate density dependence during spawning. All scenarios are examined in four model watersheds in which (*a*) redd area, (*b*) stream area, (*c*) delta area, or (*d*) nearshore area is restricted. Each bar represents the percent change in the spawning population resulting from a 5% increase in a habitat's area. Baseline habitat areas are listed in Table 3.

dependent migration are the outcome of both obligate and variable use of different habitats.

The Skagit and Duwamish simulations revealed similar patterns. As in the simulations of model watersheds, sensitivities to changes in survival were qualitatively similar across density-dependent scenarios and between watersheds (Fig. 2). However, under the density-dependent migration scenario, reductions in delta (d_j) and nearshore mortality (n_j and δ) caused larger relative population increases in the Skagit compared with the Duwamish because of the much higher habitat area available in the Skagit. In contrast with changes in survival, changes to habitat area showed great variation among density-dependent scenarios and between watershed simulations (Fig. 4). In the Skagit River (Fig. 4*a*) under the density-dependent mortality scenario, changes in stream area (A_s) resulted in the greatest sensitivity to habitat change, followed to a lesser extent by changes in delta area (A_d). Changes in other habitat areas had minimal effects. In contrast, under the density-dependent migration scenario, the population showed the greatest sensitivity to changes in delta area, followed closely by redd area (A_d). Changes to stream and nearshore area (A_n) had smaller but not insignificant effects. In the Duwamish River (Fig. 4*b*), density-dependent mortality resulted in a much greater sensitivity to changes in delta area and to a lesser extent to changes in stream area. This pattern was reversed for the density-dependent migration scenario. Both scenarios shared minor sensitivities to changes in redd and nearshore habitat area.
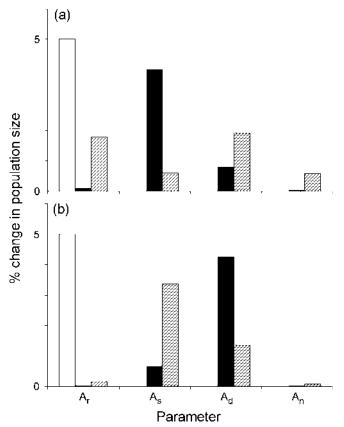
Discussion

Using a population model that disaggregates the chinook life cycle into relevant stages of habitat use, we found that understanding how restoration actions may affect salmon populations depends upon knowledge of density-dependent mechanisms. Assuming density-dependent mortality at all life stages necessarily implies a constant loss of individuals at all life stages (Moussalli and Hilborn 1986). However, if other mechanisms such as density-dependent migration exist, the population may not only equilibrate at a larger size but also respond differently to restoration of habitat.

That different density-dependent mechanisms produce different population responses has long been known in fisheries biology (Ricker 1954; Beverton and Holt 1957). However, its application to population viability analysis and restoration ecology has received much less attention, in part because of the focus on threatened populations, which are often assumed to experience less density dependence. This assumption may actually not be the case if habitat has been lost or degraded, which could result in a resetting of carrying capacity at a lower level (Achord et al. 2003). In such circumstances, alternative density-dependent mechanisms deserve examination to accurately predict population response to restoration.

Our simulations of model watersheds reveal several important generalizations about population responses to restoration. First, the concepts of "habitat limitation" and "limiting factors" are an outcome of both habitat availability and response of the population to habitat availability. For example, density-dependent mortality resulted in a significant population response only to stream habitat restoration, regardless of which habitats might appear in our eyes to be "limited". In contrast, density-dependent migration resulted in increased sensitivity to restoration of habitats downstream of those that we might consider as "limiting" the population. Second, populations may respond very differently to changes in sur-

Fig. 4. Sensitivity of population size to changes in habitat area in the (*a*) Skagit and (*b*) Duwamish rivers when population dynamics are influenced by juvenile density independence (open bars), density-dependent mortality in the stream, tidal delta, and nearshore (solid bars), and density-dependent migration through the stream and tidal delta (hatched bars). All scenarios incorporate density dependence during spawning. Each bar represents the percent change in the spawning population resulting from a 5% increase in a habitat's area. Baseline habitat areas are listed in Table 3.

vival (habitat quality) and habitat area (capacity). For example, all scenarios predicted the highest sensitivity to changes in nearshore survival but often much lower sensitivity to changes in nearshore habitat area relative to that of other habitats. Consequently, recovery plans need to carefully consider how restoration influences demographic parameters. Third, because the distribution of habitats can influence sensitivity of the population to changes in habitat area, recovery options in one watershed may have limited application to other watersheds, even if survival rates in the watersheds are similar.

These issues are highlighted in our real-world simulations of the Skagit and Duwamish watersheds. In both watersheds, delta habitat has undergone much more loss than other habitats. However, the distribution of watershed area differs among spawning, stream, delta, and nearshore habitats. These differences create contrasting responses to changes in habitat area and offer completely opposite predictions of restoration potential under both density-dependent mortality and migration scenarios. These examples point to the critical need for not only empirical assessments of habitat-specific survival

rates but also studies of density dependence in systems of interest.

Our results also indicate that some parameters appear to have particular importance for population dynamics, regardless of the existence and mechanism of density dependence. All model scenarios indicated that habitats used by juveniles were the most important for population dynamics, consistent with other population models of salmon (e.g., Nickelson and Lawson 1998; Kareiva et al. 2000). More specifically, we found that population size was most sensitive to changes in nearshore and ocean survival in all model scenarios. These findings agree with empirical studies of large population responses to changes in marine conditions (Beamish et al. 1995; Coronado and Hilborn 1998; Hollowed et al. 2001). Empirical studies of nearshore survival and residency are notably lacking, but the little that has been documented indicates that the nearshore period is associated with large increases in body size (Levings 1994; Korman et al. 1997) and high risk of predation (Healey 1980; Bravender et al. 1999). The fact that the largest increase in population size resulted from a change in nearshore survival suggests that nearshore conditions may be an important limiting factor in the life cycle of ocean-type chinook salmon.

The finding that survival rates largely do not qualitatively vary among density-dependent scenarios is good news for many population viability analyses that have focused on assessing the consequences of variation in survival and have ignored density dependence (Crowder et al. 1994; Doak et al. 1994; Kareiva et al. 2000). Our results suggest that if the alternative recovery actions being examined target primarily survival, conclusions about the efficacy of particular actions may be robust to the particular mechanism of density dependence. However, as many restoration projects seek to increase the amount of high-quality habitat, population viability assessments of alternative habitat restoration projects need to think carefully about changes in density in response to increases in habitat availability. For example, the ongoing debate on the merits of dam removal for listed stocks in the Columbia River (e.g., Kareiva et al. 2000; Wilson 2003) has largely ignored the huge increases in rearing and spawning habitat capacity that will accompany increases in survival if dams are removed. Listed stocks do exhibit density dependence at various stages of their life cycle (Petrosky et al. 2001; Achord et al. 2003), even at their reduced population size. Hence, the long-term consequences of dam removal for population recovery deserve more careful attention as to how stocks will respond to capacity changes after dam removal.

Our analysis provides one way of examining specific assumptions of density dependence and suggests that regardless of the density-dependent mechanism, improvements to nearshore survival will offer disproportionate benefits to ocean-type chinook salmon populations in Puget Sound. However, the analysis begs the question whether a significant decrease in nearshore mortality is feasible. The extent to which we have modified the conditions of these habitats and how these conditions can be improved is largely unknown. Like other aspects of the marine phase of salmon migration, habitat use and survival in the nearshore remain difficult to quantify. Beaches as well as eelgrass and kelp beds have been cited as important nearshore habitats for chinook and other salmon (Healey 1980; Levings et al. 1991;

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Korman et al. 1997), and their modification via habitat loss (e.g., via dredging and dock building), bulkhead placement, and alteration of the terrestrial margin have been suggested as having potentially significant impacts on juvenile salmon (Korman et al. 1997). Our analysis suggests that efforts to characterize nearshore habitats, their effects on salmon, and the extent to which they have been modified will significantly enhance our understanding of the population dynamics of chinook and other salmon.

Similar arguments can be raised about ocean survival, the second most important parameter in all model scenarios. Here, our knowledge is even murkier, focusing almost solely on climatic effects on survival (e.g., Kope and Botsford 1990; Mueter et al. 2002). As the scales at which we measure changes in ocean mortality can be on the order of decades and of thousands of kilometres, and its variability can be large (Hobday and Boehlert 2001), ocean survival is largely viewed as out of our direct control. If this is true, ocean mortality must be seen as a constraint reducing the realm of possible management actions to more local habitats. Note, however, that if much of the marine mortality occurs in nearshore habitats (as our results suggest), creative habitat restoration attempts may actually be highly successful.

The most commonly suggested habitat restoration attempts concern improvements to freshwater conditions (e.g., rip-rap removal, placement of large woody debris, and removal of barriers to spawners) and to conditions in the tidal delta (e.g., dike removal and riparian revegetation). Our analysis revealed that the extent to which these changes will improve population size might largely depend upon the mechanism of density dependence and whether these restoration efforts improve habitat quality or quantity. Hence, improved understanding of the existence and mechanisms of density dependence should have important implications for the ways in which we manage habitat for juvenile salmon.

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Appendix A

Table A1 appears on the following page.

Table A1. Equations describing life stage transitions through five life stages in the three scenarios of density dependence.

Life stage	Scenarios		
	Juvenile density independence	Density-dependent mortality	Density-dependent migration
Adult spawning	$N_1 = \dfrac{fT\sum\limits_{x=2}^{6} m_x P_x}{1 + \dfrac{c_r}{A_r}T}$	$N_1 = \dfrac{fT\sum\limits_{x=2}^{6} m_x P_x}{1 + \dfrac{c_r}{A_r}T}$	$N_1 = \dfrac{fT\sum\limits_{x=2}^{6} m_x P_x}{1 + \dfrac{c_r}{A_r}T}$
Incubation	$R_r = rN_{1,t}$ $r = e^{-b_r\tau_r}$	$R_r = rN_{1,t}$ $r = e^{-b_r\tau_r}$	$R_r = rN_{1,t}$ $r = e^{-b_r\tau_r}$
Stream residence	$R_s = s_j R_r$ $s_j = e^{-b_{sj}\tau_{sj}}$	$R_s = \dfrac{R_r A_s b_{sj} C_s}{R_r(e^{b_{sj}\tau_{sj}} - 1) + A_s b_{sj} C_s e^{b_{sj}\tau_{sj}}}$ $s_j = R_s/R_r$	$R_s = \dfrac{R_r A_s b_{sj} C_s}{R_r(e^{b_{sj}\tau_{sj}} - 1) + A_s b_{sj} C_s e^{b_{sj}\tau_{sj}}}$ $s_j = e^{-b_{sj}\tau_{sj}}$ $p_s = R_s/R_r s_j$ $p_m = s_j - p_s$
Delta residence	$R_d = d_j R_s$ $d_j = e^{-b_{dj}\tau_{dj}}$	$R_d = \dfrac{R_s A_d b_{dj} C_d}{R_s(e^{b_{dj}\tau_{dj}} - 1) + A_d b_{dj} C_d e^{b_{dj}\tau_{dj}}}$ $d_j = R_d/R_s$	$R_d = \dfrac{R_s A_d b_{dj} C_d}{R_s(e^{b_{dj}\tau_{dj}} - 1) + A_d b_{dj} C_d e^{b_{dj}\tau_{dj}}}$ $d_j = e^{-b_{dj}\tau_{dj}}$ $p_d = R_d/R_s d_j$ $p_m = d_j - p_d$
Nearshore residence	$R_n = n_j R_d$ $n_j = e^{-b_{nj}\tau_{nj}}$	$R_n = \dfrac{R_d A_n b_{nj} C_n}{R_d(e^{b_{nj}\tau_{nj}} - 1) + A_n b_{nj} C_n e^{b_{nj}\tau_{nj}}}$ $n_j = R_n/R_d$	$R_n = \dfrac{R_d A_n b_{nj} C_n}{R_d(e^{b_{nj}\tau_{nj}} - 1) + A_n b_{nj} C_n e^{b_{nj}\tau_{nj}}}$ $n_j = e^{-b_{nj}\tau_{nj}}$ $p_n = R_n/R_d n_j$ $p_m = n_j - p_n$
Total first-year migration	$N_{2,t} = r s_j d_j n_j N_{1,t}$	$N_{2,t} = r s_j d_j n_j N_{1,t}$	$N_{2,t} = N_{1,t}\, r s_j n_j[(p_s e^{-4b_{sj}}) + (s_j - p_s)(p_d + (d_j - p_d)e^{-88b_{nj}+4b_{sj}+b_{dj}})]$