

Implications of spatial contraction for density dependence and conservation in a depressed population of anadromous fish

William I. Atlas, Thomas W. Buehrens, Don J.F. McCubbing, Robert Bison, and Jonathan W. Moore

Abstract: Changes in density-independent mortality can alter the spatial extent of populations through patch extinction and colonization, and spatial contraction may alter population productivity and compensatory capacity. Here, we analyze a time series of steelhead (*Oncorhynchus mykiss*) abundance and examine the hypothesis that spatial contraction can decrease compensatory capacity. Over the last 20 years, steelhead in the Keogh River have declined by an order of magnitude because of a period of poor smolt-to-adult survival. Low abundance has been associated with more depressed production of out-migrating smolts than would be expected based on traditional models of compensatory dynamics. Patterns of juvenile density over time show changes in the spatial distribution of the population. We developed a spatially explicit population model to explore spatial structure and juvenile recruitment under varying marine survival. Results suggest that spatial contraction during a period of poor marine survival can strengthen density-dependent population regulation, reducing smolt production at the watershed scale. Our results highlight that spatial contraction can alter the fundamental density-dependent relationships that define population dynamics, recovery trajectories, and sustainable harvest levels of spatially structured populations.

Résumé : Les variations de la mortalité qui dépendent de la densité peuvent modifier l'étendue spatiale de populations par l'entremise de la disparition et de la colonisation parcellaires, et la contraction spatiale peut modifier la productivité et la capacité de compensation de populations. Nous analysons une série chronologique d'abondances de truites arc-en-ciel (*Oncorhynchus mykiss*) et examinons l'hypothèse voulant que la contraction spatiale puisse réduire la capacité de compensation. Au cours de 20 dernières années, l'abondance des truites arc-en-ciel dans la rivière Keogh a diminué d'un ordre de grandeur en raison d'une période de faibles taux de survie associés à la transition saumoneau-adulte. Cette faible abondance a été associée à une production plus faible de saumoneaux migrant vers la mer que la production prédite par les modèles classiques de dynamique de compensation. Les motifs de densité de juvéniles dans le temps présentent des variations de la répartition spatiale de la population. Nous avons développé un modèle de population spatialement explicite pour examiner la structure spatiale et le recrutement de juvéniles pour différents taux de survie en mer. Les résultats donnent à penser que la contraction spatiale durant une période de faible survie en mer peut renforcer la régulation de la population dépendant de la densité, réduisant ainsi la production de saumoneaux à l'échelle du bassin versant. Nos résultats soulignent le fait que la contraction spatiale peut modifier les relations fondamentales dépendant de la densité qui définissent la dynamique des populations, les trajectoires de rétablissement et les niveaux de prises durables de populations structurées dans l'espace. [Traduit par la Rédaction]

Introduction

Source–sink dynamics are a well-understood phenomenon in natural populations, whereby species occupy a range of habitats that differ in quality, resulting in differences in survival and productivity among patches (Pulliam and Danielson 1991; Caudill 2003; Sulkava et al. 2007, Hickford and Schiel 2011). In some instances, dispersal from highly productive source habitats can sustain large numbers of individuals in recipient sink habitats, which would otherwise fail to support recruitment at a rate that balances local mortality. In these cases, the exchange of individuals among habitat patches within a population may serve to swamp the effects of local scale dynamics (Earn et al. 2000; Liebhold et al. 2006) and can buffer less productive habitat patches from collapse (Järvinen and Väisänen 1984; Brawn and Robinson 1996; Ozgul et al. 2006). Persistent external forcings that depress survival and abundance, such as overexploitation or climate changes, could result in changes in population productivity that alter the balance of source–sink dynamics, with patches that formerly supported population growth becoming sinks. Consequently, populations

may experience contraction of population spatial structure, with a loss of smaller or less productive subpopulations or breeding groups (Smedbol and Wroblewski 2002; Isaak and Thurow 2006). Changes in population structure could have important implications for population productivity and density dependence. For instance, during spatial contraction some patches might be at capacity, while other patches remain unused, limiting the ability of populations to rapidly increase in abundance when depressed to low levels — their compensatory capacity (Rose et al. 2001). Given that compensatory capacity influences sustainable harvest rates and recovery trajectories, understanding this possibility is relevant for management of spatially structured populations.

Anadromous salmonids are an economically and culturally important group of species that can exhibit a high degree of local population structure and patch-level density dependence. Salmon are well known for their fidelity to natal streams (McDowall 2001), fostering local adaptation (e.g., McGlauffin et al. 2011) and fine-scale population structure (Neville et al. 2006b). Within watersheds, habitat patches are linked by the straying of returning adults,

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which may serve to synchronize subpopulations to some degree and provide demographic rescue for less productive or unoccupied habitats (Schlosser and Angermeier 1995; Cooper and Mangel 1999; Anderson et al. 2015). Density dependence during the freshwater portion of the life cycle is a fundamental process limiting population growth in salmonid fishes (Ward and Slaney 1993; Jenkins et al. 1999; Milner et al. 2003; Bailey et al. 2010). As a result, populations should have high per-capita productivity at low abundance (compensatory capacity), providing resilience to perturbations by allowing populations to rebound when reduced to low levels of spawner abundance (Rose et al. 2001) and allowing populations to sustain harvest (Beverton and Holt 1957; Rogers 1980). Typically, stock-recruit relationships measure spawner-to-recruit production at whole-watershed or population scales. However, density-dependent processes exert their effects locally in populations that exhibit a high degree of spatial structure (Ray and Hastings 1996). For stream-rearing salmonids, the relationship between spawner abundance and juvenile recruitment at the whole-watershed scale necessarily integrates density-dependent processes that operate locally at reach or habitat unit scales, for example, limiting the growth and survival of juveniles (Einum and Nislow 2005; Bailey et al. 2010). River systems are characterized by a high degree of spatial heterogeneity in spawning and rearing habitat both at reach and sub-basin scales (Geist and Dauble 1998; Beechie et al. 2008; Thorson et al. 2014). Thus, stream-rearing salmonids represent a relevant system to consider the potential consequences of spatial contraction.

Climate-driven shifts in marine survival may alter the spatial extent of stream-rearing salmon and steelhead, altering their compensatory capacity. Variation in survival during the marine phase of the life cycle is a major driver of population dynamics in anadromous salmonids, and large and persistent shifts in ocean climate regimes may drive variation in marine survival in excess of an order of magnitude (Mantua et al. 1997; Beamish et al. 2000; Ward 2000). While it has been recognized that shifts in marine survival can drive changes in stock-recruit relationships (Moussalli and Hilborn 1986; Walters 1987; Adkinson et al. 1996; Ward et al. 2008; Peterman and Dorner 2012), there has been less appreciation of how marine survival may influence freshwater dynamics. Research on threatened populations of stream-rearing Chinook salmon (*Oncorhynchus tshawytscha*) has demonstrated that population structure is temporally variable, with a contraction of spawning into larger, more productive habitat patches during periods of low abundance (e.g., Isaak and Thurow 2006). Such changes in spatial structure, likely reinforced by strong homing to natal reaches, may result in changes in the realized freshwater productivity at the watershed scale. Specifically, we hypothesize that if reductions in marine survival alter population spatial structure such that juveniles are no longer distributed throughout the available habitats, density dependence may continue to limit the growth and survival of juvenile fish within occupied habitats because of limitations in their dispersal to underutilized habitats (Einum et al. 2008). In such cases, density dependence could continue to limit population growth and realized compensatory capacity even at critically low abundance (Walters et al. 2013). This proposed process should be relevant to setting harvest limits and recovery planning, as it would be associated with lower than predicted recruitment and slower population recovery during periods of spatial contraction.

Here we examine the potential for spatial contraction to influence patterns of density dependence in populations of stream-rearing salmonids. This study is motivated by the observation that despite the compensatory capacity of stream-rearing coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*), many populations from the Salish Sea to Queen Charlotte Sound on the northeastern side of Vancouver Island have declined and remain at critically low abundance following a period of poor marine survival and low marine food web productivity that started in

1990 (Beamish et al. 2000, 2010; Ward 2000; Preikshot et al. 2013). Thus, we sought to understand how reductions in marine survival may interact with population spatial structure to influence patterns of density dependence in fresh water. Using empirical and simulation approaches, we evaluated the relationship between marine survival and population spatial structure and the resultant freshwater smolt production. Analyzing a time series of a steelhead adult and smolt population abundance, as well as steelhead fry densities across space from the Keogh River, British Columbia, we examine the prediction that a prolonged period of poor marine survival has resulted in the spatial contraction of steelhead fry production in the Keogh basin and altered freshwater density dependence. Then to examine the consequences of variation in marine survival on smolt production, we explored the relationship between population spatial structure and freshwater smolt production using a stochastic population dynamics model for a population in a simulated watershed network. We hypothesize that spatial contraction in populations due to persistent external forcing can decrease compensatory capacity, thereby altering recovery trajectories and sustainable harvest levels.

Methods

The Keogh River

The Keogh River drains an area of 130 km² on northeastern Vancouver Island, entering Queen Charlotte Strait just south of Port Hardy, British Columbia, Canada (50°40'43.56"N, 127°20'55.23"W). The Keogh River is a lake-headed tannic stream that supports populations of winter-run steelhead (*O. mykiss*), coho (*O. kisutch*), pink (*Oncorhynchus gorbuscha*), and chum salmon (*Oncorhynchus keta*), as well as coastal cutthroat trout (*Oncorhynchus clarkii clarkii*), Dolly Varden (*Salvelinus malma*), lamprey (*Entosphenus tridentatus*), three-spined stickleback (*Gasterosteus aculeatus*), and coastrange sculpin (*Cottus aleuticus*). Mean annual discharge for the Keogh River is 5.3 m³·s⁻¹.

Adult spawner and juvenile out-migrant data

Life cycle monitoring of steelhead on the Keogh River has been ongoing since 1976 — methods are more fully described in Ward and Slaney (1993) and Ward (2000). Annual estimates of adult spawner abundance are made using mark-recapture methods, wherein fish are captured as they migrate upriver to spawn, marked with an opercular punch hole, and then recaptured and checked for marks as spawned-out kelts in late spring as they migrate back to sea. The number of juvenile smolts leaving the Keogh River each year is counted using a smolt fence, which captures juveniles as they go to sea during the late spring. Information on age structure for both adults and juveniles is determined from scale annuli. Using information on juvenile abundance and age structure, total smolt output is estimated for each brood year, and marine survival is estimated for each out-migrant cohort. Steelhead in the Keogh River typically spend 2 or 3 years rearing in fresh water prior to their seaward migration, and adults spend either two or three summers at sea before returning to spawn. Steelhead are iteroparous, and on average about 10%–20% of returning fish are repeat spawners.

To evaluate whether smolt production was lower than expected during the period of poor marine survival, we compared a series of linear models predicting smolt production per female as a function of spawner abundance, marine survival regime, and combinations of these variables. For this analysis, spawner and smolt abundance data from the Keogh River were partitioned into two marine-survival “regimes”. Based on evidence of a shift in productivity and marine survival in the Salish Sea around 1990 (Beamish et al. 2000; Welch et al. 2000; Smith and Ward 2000; Preikshot et al. 2013), data from 1976 to 1989 were grouped together in the high marine-survival regime and data from 1990 to 2008 were grouped together in the low marine-survival regime. In fitting

spawner-to-recruit relationships, we omitted data from 1982–1985 and 1999–2003 because of the potentially confounding effects of whole-watershed nutrient enrichment, which may have increased smolt capacity during those years (Johnston et al. 1990; Ward 2000; Ward et al. 2008).

We natural log-transformed the number of smolts per female and fit a linear model relating smolts per female to the number of female spawners (eq. 1):

$$(1) \quad \ln(R_t/S_t) = \alpha - \beta S_t + \varepsilon_t$$

This is a linearized Ricker model (Ricker 1954), wherein S_t is the number of spawning females in a given brood year, R_t is the number of smolts produced by fish spawning in time t , and α is the mean productivity in units of $\ln(R/S)$ at near-zero spawner abundance. The effect that female spawner abundance has on productivity is captured by β , indicating the strength of within-brood-year density dependence, and ε_t is the residual. Given the strong negative density dependence experienced by stream-rearing salmonids, the number of smolts per female should decline as female spawner abundance increases.

To explore evidence for changes in the strength of density dependence during low marine survival, we tested four candidate models: (1) the standard Ricker model in which density dependence was assumed not to differ between the two marine survival regimes; (2) a model including regime as a main effect, allowing the intrinsic productivity (i.e., the intercept) to vary between marine survival regimes — support for this model would be indicative of changes in productivity at near-zero abundance (α) between the two regimes; (3) a model including an interaction between female spawners and marine survival regime, which allowed the slope of the relationship between female spawners and smolts per female to vary between marine-survival regimes — a difference in slope between regimes would denote a difference in the strength of within-brood-year density dependence (β); (4) a null model where recruitment was constant (i.e., not related to spawner abundance). We then evaluated the degree of support for candidate models using an information-theoretic approach, fitting models in the statistics program R version 3.0.2 (R Core Team 2013). Akaike's information criterion for small sample sizes (AIC_c) was calculated to compare and rank the various models using the R package `AICcmodavg` (Mazerolle 2014). The lowest AIC_c value denoted the best model, and models with $\Delta AIC_c < 2$ were considered to have substantial support, those with values from 4 to 7 had little support, and those greater than 10 had no support (Burnham and Anderson 2002).

Freshwater juvenile data

Juvenile steelhead densities in the Keogh River were measured over a period of 35 years by the British Columbia Ministry of Environment in four reaches of similar length (W–Z) spanning the entirety of the Keogh River main stem. Reach W is closest to the river mouth, and the reaches proceed alphabetically upstream to reach Z at the top of the mainstem Keogh River. Fry (age 0) and parr (age 1+) densities were estimated using multiple pass electrofishing at several sites within each reach to produce depletion estimates of steelhead fry and parr. These sites, which typically represented a single habitat unit (e.g., pool, riffle, glide), were blocked at both the upstream and downstream ends and electrofished with a minimum of three passes through each pool. Fishing was continued until there was at least a 50% reduction in the number of fish captured between passes. In the latter portion of the time series (1997–2008), steelhead densities were estimated with mark-recapture using multiple-pass electrofishing, rather

than depletion estimates. Mark-recapture has been shown to produce unbiased estimates of density in stream-dwelling salmonids, while multiple-pass depletion estimates may introduce negative bias if sampling efficiency declines between electrofishing passes (Rosenberger and Dunham 2005). We limited our analyses to juvenile densities obtained from riffles, glides, and runs, since these habitat types were the primary habitats occupied by steelhead fry. We tested whether the exclusion deep pools and sloughs influenced our findings and found that our model results did not change when these low-density rearing areas were included in the analysis. Electrofishing was conducted from late July to mid-August, ensuring that fry emergence was complete and fry had not redistributed substantially throughout the watershed. Although the timing and number of sites sampled within each reach varied somewhat among years, this variability was not systematic and was assumed not to have impacted observed fry densities. Juvenile densities were collected in both high (1977, 1979, 1980, and 1981) and low (1997, 1998, 2011, and 2012) marine-survival regimes. All reaches were not sampled in all years, and data for reach W in 1998 was excluded owing to the confounding effects of experimental nutrient addition (see online Supplemental Table 1¹). Nutrient additions generally increased size and abundance of steelhead fry and parr in the Keogh River; however, the benefits of nutrient enrichment for juvenile growth did not continue past the period of active nutrient addition (Johnston et al. 1990).

Temporal changes in the spatial structure of the Keogh River steelhead population were evaluated by testing for differences in densities of steelhead fry and parr among reaches and years. Fry were assumed to closely represent the spatial distribution of spawning by Keogh River steelhead, while the distribution of parr would include 1 or more years of potential movement (e.g., Buehrens et al. 2013). The degree to which temporal patterns of fry and parr density were consistent with a decline in the spatial extent of steelhead spawning between high and low survival regimes was evaluated using linear mixed-effects models in the R package `nlme` (Pinheiro and Bates 2014). In the full model, density was a function of stream reach, marine-survival regime, and the interaction between stream reach and marine-survival regime. This model was compared with models containing either a single or both predictor variables as main effects. Year was modeled as a random effect in all models. Unequal changes in fry abundance among reaches between high and low marine-survival regimes, which would be indicated by a significant interaction term in our model, were assumed to indicate changes in spawner distribution. Density data included many zero values, and the Shapiro–Wilk normality test indicated model residuals were not normally distributed ($P < 0.0001$). We therefore transformed density data using a $\ln(\text{density} + 1)$ procedure to conform to the assumption of normally distributed residuals.

Simulation model

We developed a spatially structured, stochastic, density-dependent population model to explore the sensitivity of watershed-scale salmonid population dynamics to variable marine survival. Specifically, we were interested in whether population responses to changing marine survival varied depending on the strength of reach-scale natal philopatry (homing versus straying) and the magnitude of heterogeneity in habitat quality among patches. We predicted that under low stray rates, population dynamics would predominantly reflect patch-level density dependence and differences in habitat quality, while under high stray rates, population dynamics would be synchronized by high levels of movement between source and sink habitats. We further predicted that during periods of poor marine survival, high patch fidelity and the effect of density dependence at the patch level would buffer pop-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2015-0532>.

ulations from extinction, but would result in lower than expected smolt production and changes in population spatial structure, with the temporary loss of less productive habitat patches.

This spatial population model was based on a hypothetical watershed network with seven discrete spawning and rearing patches occupied by subpopulations that were equally sized and spaced apart. For the purpose of the simulation model, the population was modeled without age structure, and each model step was a generation. Diverse freshwater and adult age classes, overlapping generations, and iteroparity are all characteristics displayed by some stream-rearing salmonids such as steelhead. These aspects of steelhead life histories may support resilience in the face of shorter-term environmental stochasticity (Moore et al. 2014), but should not ultimately change the overall response of population structure to sustained perturbations, and we assumed that simulated population dynamics adequately captured the processes and responses of interest.

Patch-scale density dependence

Smolt production within each habitat patch was governed by a Beverton–Holt stock recruit function (eq. 2), relating the number of smolts produced in a time step (R_{t+1}) to the number of spawning adults in the previous time step (S_t), and reproductive output for a patch was zero when the number of adult spawners dropped below two fish.

$$(2) \quad R_{t+1} = \frac{\alpha \times S_t}{(1 + \beta \times S_t)} + \varepsilon_t$$

Patch productivity and capacity

Each patch was assigned a unique productivity (α_i), which was the number smolts per spawner at near-zero spawner abundance. To simulate differences in habitat quality among patches, α_i varied among the seven patches in the simulated watershed network. To test the sensitivity of model dynamics to the extent of variability in productivity, three productivity scenarios including high, medium, and low variability in smolts per spawner among patches were tested, where each patch was assigned a unique productivity at the beginning of a simulation iteration. An additional scenario with constant productivity among patches was also explored. The juvenile carrying capacity for a patch was the quotient of the productivity at low abundance (α_i) divided by the density-dependence parameter (β), thus producing differences in carrying capacity at the patch scale in all but the constant productivity scenario. In each model scenario, alpha values were drawn from a sequence of values that increased in even increments from low to high, such that none of the patches in the watershed network had the same habitat quality, and each patch was assigned at random at the beginning of the model iteration. Habitat variability scenarios included high variability ($\alpha = 15\text{--}105$), moderate variability ($\alpha = 30\text{--}90$), low variability ($\alpha = 45\text{--}75$), and no variability ($\alpha = 60$). The density-dependence parameter (β) was set to 0.25 and was held constant.

Population connectivity

Subpopulations were linked by straying during the adult phase of the life cycle, in which adults born in one patch spawned in another. While most adult recruits returned to their natal reaches, a small subset of individuals strayed to other adjacent patches. The probability of individuals straying from patch i recruiting to patch j was represented by interpatch stray probabilities p_{ij} , in the interpatch connectivity matrix, \mathbf{P} , where columns were donor patches and rows were receiving patches. Interpatch stray probabilities followed a dispersal kernel that caused the probability of strays arriving at a receiving patch to exponentially decrease with increasing distance from the source patch (see Table S2¹; Schick and Lindley 2007; Fullerton et al. 2011):

$$(3) \quad p_{ij} = \frac{1}{2\sigma} \exp\left(-\left|\frac{d_{ij}}{\sigma}\right|\right)$$

where σ is the maximum distance a fish will stray from a natal patch (equal to the distance between two patches in our model), and d_{ij} is the interpatch distance (the distance between adjacent patches was equidistant and equal to one). We standardized these stray probabilities by summing the off diagonals in \mathbf{P} and dividing them by the column sums so that the probabilities would sum to one for all patches, thus defining the proportion of strays from each patch i that would recruit to patch j . The net number of immigrants (stray arrivals minus departures) to each patch I_t was the product of the donor patch population returning spawner abundance RS_t , the population-wide stray rate SR , and the interpatch stray proportion p_{ij} summed for all donor and recipient patches in our hypothetical watershed network:

$$(4) \quad I_t = \sum_i RS_t \times SR \times p_{ij}$$

where the population-wide stray rate was the proportion of individuals that did not return to their natal patch in each generation, and this quantity was invariant among patches. To examine how stray rates influence dynamics, we compared model scenarios where population-wide stray rates ranged from 0% to 100% in even 5% increments.

Stochasticity

Stochastic survival processes were incorporated into the model during both the freshwater and marine portions of the life cycle. We incorporated two nested levels of stochastic variability in freshwater productivity, allowing us to incorporate processes that may drive variation in freshwater productivity at both the watershed and patch scales. To reflect annual variation in stochastic freshwater survival dynamics, smolt production in each year was the expected value from the Beverton–Holt relationship multiplied by a watershed-scale error term $\varepsilon_w \sim \text{dnorm}(\mu = 1, \text{SD} = 0.2)$ and a patch-scale error term $\varepsilon_r \sim \text{dnorm}(\mu = 1, \text{SD} = 0.1)$. Consistent with the pattern observed in the Keogh River time series, marine survival in our simulation was partitioned into three 20-year regimes and was allowed to vary within each regime: (i) early period where marine survival was high in each year: $MS_H \sim \text{dnorm}(\mu = 10\%, \text{SD} = 2\%)$, (ii) a middle period when marine survival was low: $MS_L \sim \text{dnorm}(\mu = 3.5\%, \text{SD} = 1\%)$, and (iii) a recovery period at the end of the simulated time series when marine survival was distributed identically to the early high period: MS_R .

Full model step

Smolt production in a particular patch and generation was therefore the number of smolts predicted by the density-dependent relationship between spawners and smolts multiplied by both the patch- and watershed-level stochasticity:

$$(5) \quad R_{t+1} = a_i \times \frac{S_t}{(1 + \beta \times S_t)} \times \varepsilon_w \times \varepsilon_r$$

Accordingly, the number of fish returning to spawn in a particular patch and year was the product of the stochastic density-dependent smolt production in their natal patch (R_t) and their stochastic survival at sea (MS_H , MS_L , or MS_R) plus net number of immigrants and emigrants via straying:

$$(6) \quad S_{t+1} = R_t \times MS + I_{t+1}$$

Model duration and iterations

At the outset of each simulation, adult abundance in each of the seven patches was set to 50 fish. Each scenario was run through 100 time steps, with the first 20 time steps corresponding to the early portion of the Keogh River time series, the next 20 time steps corresponding to the more recent period of low marine survival, and a 60 time step period at the end of the simulation wherein marine survival improved and returned to levels observed in the first 20 time steps of the time series. To capture the range of variability in model dynamics, we allowed the 100-year simulations to run 1000 times for each of a range of alpha values ($n = 4$) and stray rates ($n = 21$) for a total of 84 000 model runs.

Response metrics

Simulation results were compared among various combinations of population-wide stray rates and ranges of variability in patch alpha values using six response metrics that described changes in population spatial structure, dynamics, and population persistence. Response metrics included (1) “patch occupancy”, the number of patches occupied in the watershed network during the period of low marine survival; (2) “persistence”, proportion of model iterations in which the population persisted, with at least one habitat patch occupied at the end of the model run; (3) “percent change” in mean annual smolt output between high and low marine-survival regimes; (4) “percent residual”, the percent difference between the realized smolt production for the population during the low marine-survival period and the expected smolt production if density dependence was estimated at the whole-watershed scale based on a Beverton–Holt relationship (only for model iterations where the entire population did not go extinct during the 100-year simulation run); (5) “return time”, the number of generations following the end of the low marine-survival period for patch occupancy to return to full patch occupancy (i.e., seven patches occupied); and (6) number of generations required for smolt output to reach the mean level observed in the first 20 generations of the time series. With the exception of persistence, response metrics were only estimated for model iterations in which the population persisted to the end of the simulation; for model runs in which the population did not return to full patch occupancy or reach the mean level of smolt output from the first 20 generations, the return time was set to 60 generations. Using the model scenario where habitat quality was constant ($\alpha = 60$) among patches, we examined the relationship between a patch’s connectivity with other patches (based on its location within the watershed network) and the proportion of years a given patch was occupied during low marine survival, excluding iterations in which the population went extinct.

Results

Empirical results

Keogh River steelhead abundance and marine survival

Between 1976 and 2010, Keogh River steelhead experienced a marked decline in marine survival. From 1977 to 1990, mean smolt-to-adult survival was 14.9% (SD 6.9%), producing a mean annual return of 1191 (SD 806) wild adult steelhead. From 1991 to 2009, mean marine survival to adulthood for out-migrating smolts was 4.58% (SD 3.08%), producing a mean annual return of 154 (SD 111) wild steelhead. Excluding years where experimental nutrient addition occurred (Johnston et al 1990; Ward 2000), mean smolt production in the Keogh River from the brood years 1976 to 2008 was 3774 smolts (SD 2366). However, the time series of smolt production was characterized by a period of high productivity from 1976 to 1990 when mean brood-year smolt production was 6172 smolts (SD 882) and a later period from 1991 to 2008 characterized by a marked reduction in productivity when mean brood-year smolt production was 1744 smolts (SD 574) (Figs. 1 and 2).

Keogh River steelhead population dynamics

The period of poor marine survival was also associated with decreased per-capita freshwater productivity. An information-theoretic model selection approach comparing alternate Keogh River steelhead adult–juvenile recruitment models found strong support for the model, which included an interaction between density dependence (β) and marine-survival regime. Support for a model including an effect of regime on density dependence is indicative of change in within-brood-year density dependence between regimes, such that strong negative density dependence resulted in lower than expected smolt output during the period of poor marine survival from 1991 to 2008 (Table 1; Fig. 3). Predicted per-capita smolt output for a brood year with 200 female spawners during the period of high marine survival was 28 smolts per female, while during the period of low marine survival and stronger density dependence, per-capita smolt output declined to an estimated seven smolts per female at the same level of spawner abundance. These results were consistent with the observed temporal pattern of smolt productivity in the Keogh River in which the mean number of smolts migrating to sea each year has been on average 72% lower during the recent period of poor marine survival, relative to the 1976 to 1990 period (Fig. 1).

Keogh River steelhead spatial structure over time

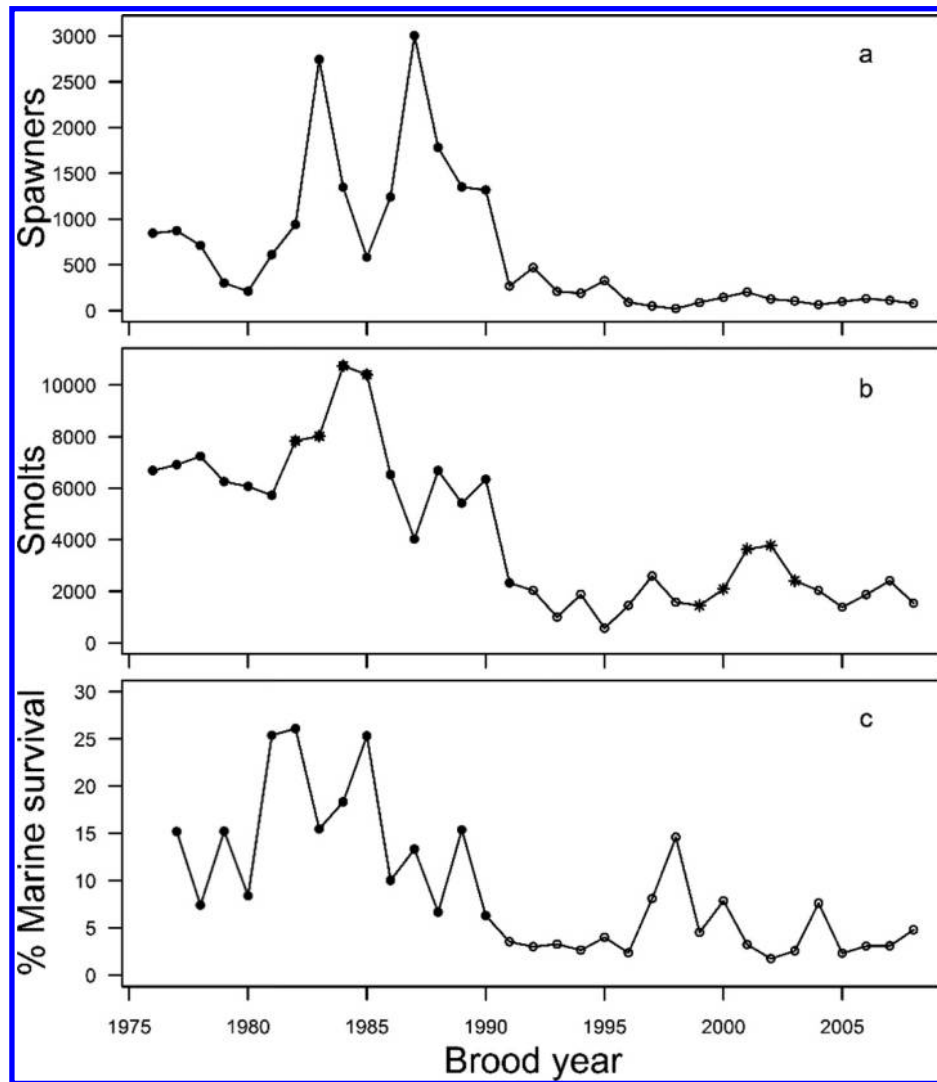
A mixed-effects model including reach, regime, and their interaction and year as a random effect produced strong evidence for an effect of the interaction between reach and regime on mean fry densities ($P = 0.0009$). Estimated mean fry densities were relatively consistent among reaches during the early high marine-survival regime. However, reach Z experienced a marked reduction in fry density during the period of low marine survival from 1990 to 2012, with fry densities falling from a mean of 0.189 fry·m⁻² (95% CI: 0.126–0.259 fry·m⁻²) to a mean of 0.022 fry·m⁻² (95% CI: 0–0.071 fry·m⁻²). In 1997, sampling in six sites found zero fry in reach Z, evidence of the likely absence of steelhead spawning in this reach. There was no evidence of substantial changes in fry densities in reaches W, X, and Y between regimes (Fig. 3). Similarly, temporal patterns of steelhead parr densities showed evidence of an interaction between regime and reach ($P = 0.038$), with reduced parr densities in reach Z during in the years following the 1990 regime change. There was no evidence of a change in parr densities in the other reaches during this period of low marine survival (Table 2).

Simulation model results

Changes in smolt production

Smolt production declined in all model scenarios during the simulated 20-generation period of low marine survival. Mean smolt production during the low survival regime declined by 45%. The model scenario with high variability in habitat quality (α range of 15–105) produced the lowest mean smolt production during the high marine-survival period but showed the smallest change in smolt output when marine survival declined. Scenarios with lower variability in habitat quality did not differ substantially in their mean level of smolt production during the period of high marine survival; however, lower variability in habitat quality produced greater declines in smolt production during the poor marine-survival period. However, the responses among the differing habitat quality scenarios converged as stray rates increased (Fig. 4a). The residual smolt production (observed mean population-wide smolt production relative to that expected with all patches occupied) was on average 7.7% lower during the period of low marine survival for all simulated scenarios, resulting from changes in population spatial extent caused by localized extinction in the model watershed. However, the extent of variation in habitat quality altered the relationship between residual smolt production and stray rate; in simulations where habitat quality was uniform among patches ($\alpha = 60$), residual smolt production was

Fig. 1. Times series of spawner abundance (a) and smolt output (b) for brood years 1976 to 2008, and marine survival for out-migrant smolts 1977 to 2008 (c). Solid points indicate years during a period of high marine survival (1976–1990), and open points indicate years during a period of low marine survival (1991–2008). Asterisks are years effected by whole-watershed fertilization experiments.



consistent across stray rates, whereas simulations with the highest variability in habitat quality ($\alpha = 15-105$) showed increasingly poor smolt output relative to predicted levels as stray rates increased (Fig. 4b).

High levels of natal site fidelity by returning adults (low stray rates) resulted in slower recovery for smolt production compared with the mean for the period before low marine-survival. The mean number of generations required for smolt production to reach the mean prior to the low marine-survival period decreased with increasing stray rate until the stray rate reached 20%. However, even with higher stray rates ($\geq 20\%$), the mean return time for smolt production to reach mean levels observed during the initial period of high marine survival was 3.5 generations (Fig. 4c).

Population persistence

Overall persistence of the population throughout the simulated 100-year period was stable until stray rates surpassed 50%, at which point persistence decreased. Scenarios with high variability ($\alpha = 15-105$) and moderate variability ($\alpha = 30-90$) in habitat quality exhibited the highest levels of persistence in scenarios where stray rates were lower than 50% (means 95.9% and 92.7% persistence, respectively). Scenarios with low habitat variability ($\alpha = 45-75$) showed slightly lower rates of overall persistence

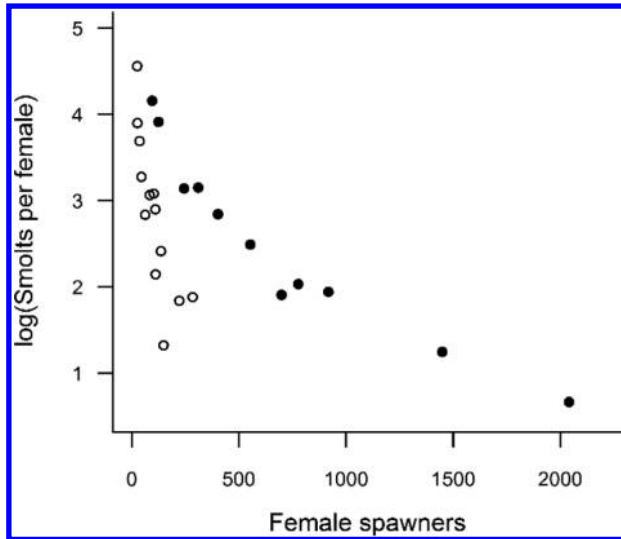
(mean = 85.3% persistence), and no variability in habitat quality ($\alpha = 60$) produced the lowest persistence (mean = 75.5%). When stray rates exceeded 50%, all scenarios exhibited a marked decline in persistence. When stray rates were 100%, high variability in habitat quality produced the lowest level of persistence (25.9%), followed by moderate habitat variability (30.1%), low habitat variability (35.9%), and no habitat variability (40.7%) (Fig. 5a).

Changes in spatial structure

Across the range of scenarios, the simulated population experienced a spatial contraction resulting in fewer than seven patches being occupied during the period of poor marine survival (Fig. 4b). When stray rates were low, simulations with the highest level of variation in habitat quality ($\alpha = 15-105$) exhibited the greatest reduction in patch occupancy, whereas simulations with uniform habitat quality ($\alpha = 60$) maintained the highest levels of patch occupancy. However, as stray rates increased, patch occupancy increased in model runs that did not result in population extinction, regardless of the variability in habitat quality. Scenarios with less variability in habitat quality exhibited greater stability in population spatial extent during low marine survival; however, all levels of habitat variability produced increasing patch occupancy as stray rates increased to 100% (Fig. 4b). Spatial patterns of

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Fig. 2. Per-capita smolt productivity represented by the relationship between female spawner abundance and the number of smolts produced per female. Smolts per spawner were \log_e -transformed to linearize the relationship. Solid points indicate years during a period of high marine survival (1976–1990), and open points indicate years during a period of low marine survival (1991–2008). Years with experimental fertilization were removed.



patch occupancy when habitat quality was uniform demonstrated a relationship between the connectivity of a patch and its propensity for local extinction. Habitat patches at the top of the simulated watershed network (d, e, f, and g) had the lowest connectivity (mean percent immigrants from other patches = 13% per patch), with direct links to only one downstream patch, and were most likely to be unoccupied, whereas patches lower in the watershed (a, b, c) with higher connectivity (mean percent immigrants from other patches = 21% per patch) were more likely to be occupied during the period of poor marine survival (Fig. 6).

Similar to return time for smolt output, return time for full patch occupancy following improved marine survival was lower when stray rates were high. For scenarios with high and moderate variability in habitat quality populations never recovered to seven patches when stray rates were zero, reflecting the fact that patch occupancy was below seven during poor marine survival in all model runs and in the absence of strays from other habitat patches colonization and recovery was impossible. One average, at stray rates of 20% and greater, recovery of full patch occupancy within the simulated watershed network took 1.5 generations following the onset of improved marine survival (Fig. 5c).

Discussion

This study explored the hypothesis that spatial contraction of populations can decrease compensatory capacity by examining a nearly four-decade-long time series of stream-rearing steelhead and simulation modeling. Using data from a population of wild winter-run steelhead trout in the Keogh River, we demonstrate a temporal change in the strength of freshwater density dependence during a period of persistent poor marine survival. Over the last 30 years, the steelhead population in the Keogh River has undergone a pronounced decline in adult returns and marine survival (Ward 2000). Consistent with predictions, we found that this decline in survival has been associated with a spatial contraction of fry production. Furthermore, mean annual smolt output during the period of poor marine survival has been 72% lower than smolt output during the previous period of high marine survival, evidence of decreased compensatory population growth. The simulation model also found that prolonged periods of poor

Table 1. Model selection criteria for models relating female spawner abundance and marine-survival regime to smolt production per female by brood year.

Rank	Model	AIC _c	ΔAIC _c	Likelihood
1	~Female spawners × regime	43.31	0	1
2	~Female spawners + regime	55.19	11.88	0.003
3	~Female spawners	57.13	13.82	0.001
4	~1	70.77	27.46	<0.0001

Note: The best model includes an interaction between female spawner abundance and regime, suggesting that the strength of within-brood-year density dependence (β) differs between two marine-survival regimes.

marine survival and associated spatial contraction can lead to lower than predicted smolt production and highlighted how population connectivity and habitat quality will influence smolt productivity, as well as overall recovery and persistence.

Empirical analyses of steelhead in the Keogh watershed revealed evidence of freshwater spatial contraction and decreased compensatory capacity. Specifically, during periods of extremely poor marine survival and low spawner abundance, there was a marked decline in steelhead fry density in the uppermost reach. This spatial contraction corresponds to a period of much lower than expected smolt output with evidence for a strengthening in watershed-scale density dependence and decreased compensatory capacity. Previous research has demonstrated that persistent changes in survival, such as those driven by environmental change or intensive harvest, can alter stock–recruit relationships (Moussalli and Hilborn 1986), and Walters (1987) demonstrated theoretically that changes in stock–recruit relationships could result if high harvest rates or persistent changes in the environment-altered population structure. In addition, our study adds to the growing body of empirical research on spatial contraction of spawning and rearing in salmon (e.g., Isaak and Thurow 2006). For example, studies of critically depressed Snake River Chinook salmon found evidence of widespread negative density dependence within individual populations despite the fact that the aggregate population is at a fraction of historical abundance (Achor et al. 2003; Walters et al. 2013). Thus, our results and these previous studies suggest that spatial contraction and resultant changes in density dependence may be underappreciated as a process that limits the recovery of depressed stream-rearing salmonids.

In population simulations, smolt output fell below the level predicted by the watershed-scale density dependence regardless of the level of variability in habitat quality. Simulated population responses to persistent changes in marine survival showed evidence for spatial contraction across the range of model scenarios we explored and lower than expected smolt output as a consequence of these changes in habitat occupancy. We had predicted that high patch fidelity (low stray rates) and variation in habitat quality across the simulated watershed network would produce changes in population spatial structure. Further, we predicted that these conditions would produce lower than expected smolt output during low marine survival, with only a subset of the available habitat continuing to sustain recruitment. While variability in habitat quality did result in a greater extent of patch loss when natal site fidelity was high, patch occupancy declined during the period of low marine survival regardless of the level of variability in habitat. These findings suggest that environmental stochasticity alone may be sufficient to produce changes in spatial structure when marine survival or other processes such as overexploitation drive the abundance of spawning adults to extremely low levels.

Our simulations explored how connectivity among patches influences spatial contraction and population dynamics in a simple river network. We observed a trade-off between the effects of straying on population spatial extent and the risks posed to the entire population when this connectivity synchronizes dynamics across heterogeneous habitats. Specifically, we found that while

Fig. 3. Temporal trend in fry densities for four reaches of the Keogh River. Solid points indicate years during a period of high marine survival, open points indicate years during a period of low marine survival, and bars indicate 95% confidence intervals around the mean.

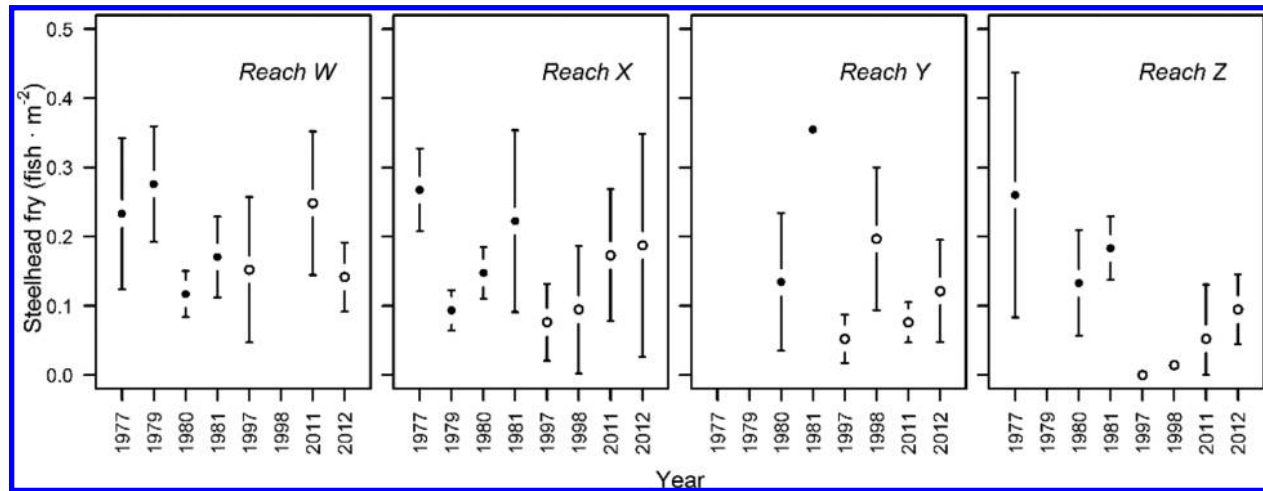


Table 2. Estimated pairwise differences in mean fry and parr densities within each reach of the Keogh River between the high (1976–1990) and low (1991–2008) marine-survival regimes, with *p* values corrected using Tukey’s method for multiple comparisons.

Reach	Estimate	SE	<i>p</i>
Fry			
W	-0.010	0.035	1.000
X	-0.034	0.036	0.982
Y	-0.080	0.045	0.674
Z	-0.163	0.037	0.0009*
Parr			
W	-0.024	0.018	0.863
X	-0.043	0.018	0.263
Y	-0.038	0.022	0.668
Z	-0.077	0.018	0.001*

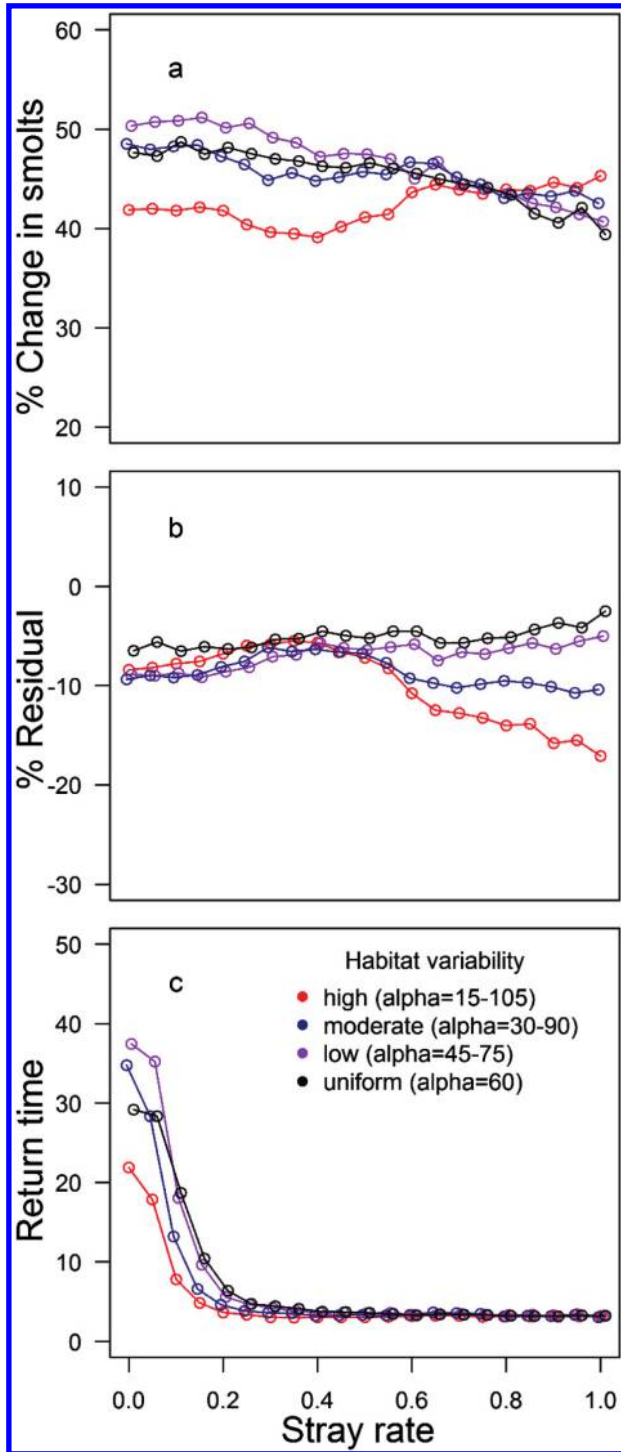
Note: An asterisk (*) indicates significance at *p* ≤ 0.001.

increasing stray rates did maintain the spatial extent of the population during low marine survival and reduce recovery times, stray rates in excess of 60% produced a marked decline in probability of population persistence. Previous work on spatial population dynamics has demonstrated that high connectivity between habitat patches can increase demographic synchrony across populations, increasing risk of extinction (Earn et al. 2000); yet, high fidelity to natal patches limits spatial extent, synchrony, and recovery rates (Fahrig and Merriam 1985; Matthiopoulos et al. 2005; Liebhold et al. 2006). These findings underscore how some degree of fidelity to natal patches, while allowing spatial contraction into more productive patches and delaying recovery, also contributes to population persistence across variable environmental conditions. Stream-rearing salmonids are well known for their propensity to have high site fidelity, with low rates of straying in returning adults (Quinn et al. 2006; Hamann and Kennedy 2012) as well as somewhat limited juvenile dispersal among habitats (Einum et al. 2006). Furthermore, the propensity for dispersal by rearing juvenile salmonids can be mediated by density (Crisp 1993; Bailey et al. 2010), and dispersal of juvenile salmon into unoccupied or underutilized habitats may be an important driver of population spatial expansion (Anderson et al. 2013). However, upstream dispersal is energetically costly and is relatively uncommon in stream-rearing salmonids, and dispersal is thought to occur primarily in the downstream direction (Close and

Anderson 1992; Einum et al. 2008), limiting the dispersal of juveniles into underutilized upstream habitats, such as the uppermost reach of the Keogh River. This directional bias in patterns of dispersal may lead to nonrandom expansion and contraction of populations. More generally, changes in patch fidelity and straying, such as those resulting from hatchery practices that increase rates of straying (CDFG–NOAA 2001; Keefer et al. 2008), could undermine the persistence of populations (Moore et al. 2010).

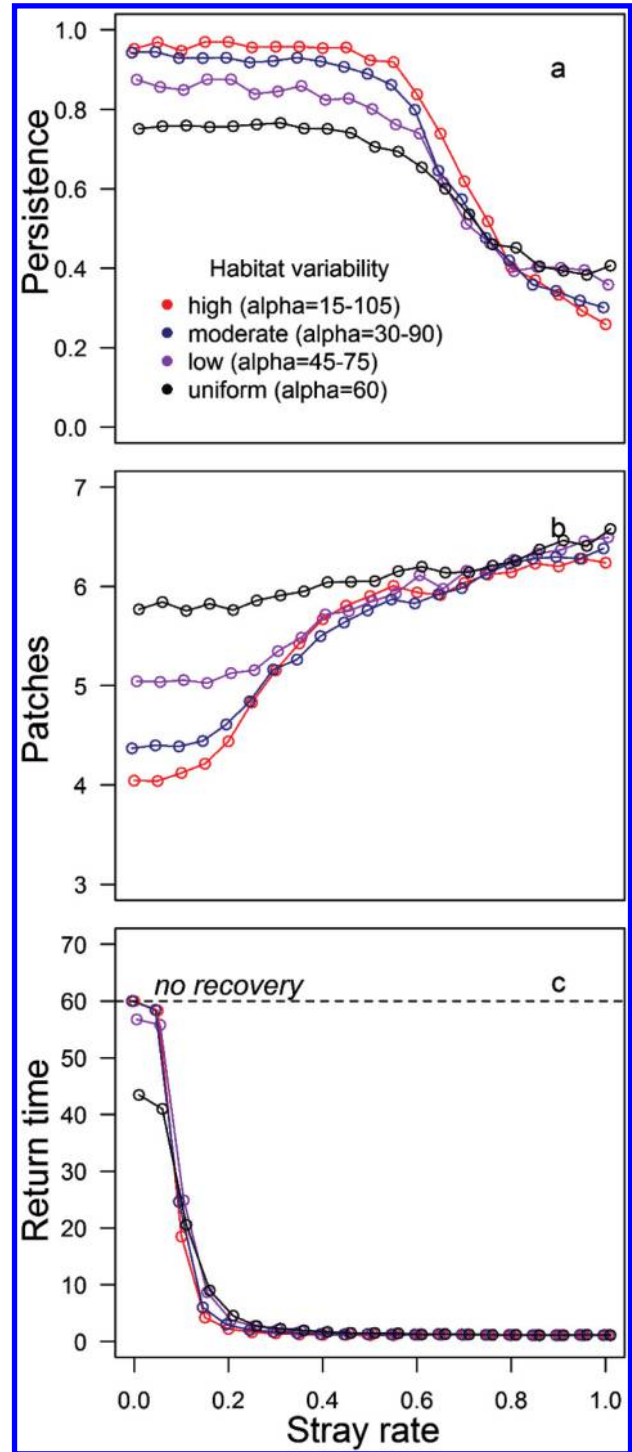
Results from our spatial population model indicate that environmentally driven changes in spatial structure can occur even when all patches within a population are equally productive. In particular, we found that location within the simulated river network predicted patch occupancy at low marine survival, even when habitat quality was uniform. These results match findings from empirical studies of Snake River Chinook, where the authors found that habitat size and connectivity predicted spawning distributions (Isaak et al. 2007), and work by Flitcroft et al. (2012) that found that river network structure and connectivity between habitats better predicted densities of juvenile coho salmon than measures of habitat quality. Similarly, network structure and habitat size has been shown to influence genetic diversity in stream-dwelling salmonids (Neville et al. 2006a), and the processes contributing to low genetic diversity in upstream areas may also be responsible for the lack of population persistence and recovery during periods of poor marine survival. However, the propensity of populations to exhibit spatially asynchronous responses to changes in environmental conditions may be enhanced by variability in the relative quality of spawning and stream rearing habitats, as less productive habitats are less likely to sustain recruitment during periods of poor survival. Heterogeneous habitat quality coupled with low dispersal rates can produce spatially asynchronous responses to variable environmental conditions (Liebhold et al. 2006), and differences in habitat quality may drive patterns of patch occupancy and local extinction (Fryxell 2001; Ozgul et al. 2006). Survival and growth of stream-rearing salmonids are sensitive to density (Einum and Nislow 2005), and the effects of density on growth have been documented at scales as small as 20 m of stream length (Bailey et al. 2010). Spatial variation in density dependence may reduce synchrony in spatially structured populations driving differential responses to environmental forcings among habitat patches (Liebhold et al. 2006). Taken together, fine-scale homing coupled with both density-dependent and -independent processes affecting survival at small spatial scales create the potential for differential responses across space to temporal changes in the environment (Thorson et al. 2014).

Fig. 4. Simulated population responses to a period of poor marine survival for four levels of habitat quality variation across the range of stray rates: (a) overall population persistence (the proportion of simulations in which the population did not go extinct); (b) mean number of patches occupied by adults (out of a possible total of seven) during a 20-year period of low marine survival; (c) the number of generations required for the recovery of full patch occupancy following improvement in marine survival.



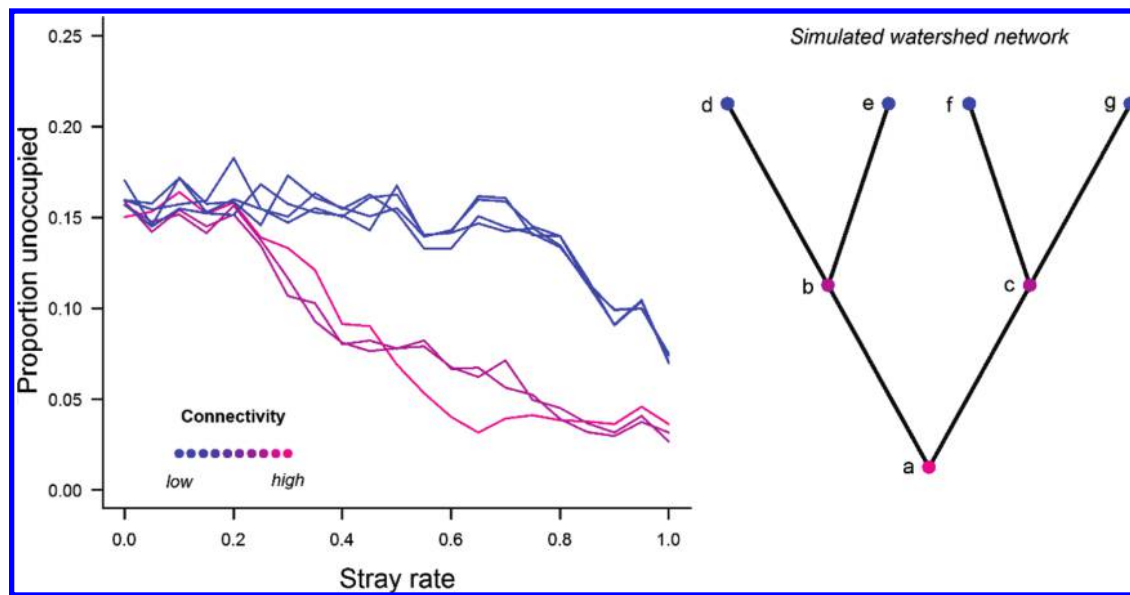
Empirical data are consistent with the hypothesis that spatial contraction may explain stronger than expected density dependence observed in the Keogh River steelhead population during the last 20 years, but it is important to acknowledge alternative

Fig. 5. Simulated response of smolt production to a period of poor marine survival for four levels of habitat quality variation across the range of stray rates: (a) mean percent change in smolt production between high and low marine survival regimes; (b) mean difference between realized and predicted smolt output if all habitats were occupied; (c) the number of generations required for smolt production to reach the mean level of smolt output from an early period following improvement in marine survival.



hypotheses and limitations of the dataset. While information on juvenile densities is not available for all years during both marine-survival regimes, and the sites sampled within each reach do not necessarily represent the entirety of potentially available habitat

Fig. 6. Effect of connectivity on the proportion of years during low marine survival when a patch is unoccupied. The simulated watershed network is depicted on the right, showing the levels of connectivity across all patches in the network.



in the Keogh River, the consistent pattern of dramatic reductions in the number of juveniles in the upstream reach in 4 years spanning a 15-year period during poor marine survival provides evidence of a spatially asynchronous response to reductions in marine survival. During that time, the Keogh River has not experienced major deterioration in habitat conditions that could explain the observed pattern of reduced smolt output and changes in population spatial extent. Indeed, the Keogh River has been subject to extensive habitat restoration during the period in question. One alternative explanation is that large-scale climate conditions simultaneously alter both marine survival as well as freshwater processes affecting both density-dependent and density-independent survival. Evidence is increasingly pointing to the importance of ocean temperatures in mediating the survival of migrant steelhead smolts (Friedland et al. 2014), and freshwater survival may be driven in part by some of the same climatological processes (Clews et al. 2010). However, given the persistent pattern of lower than expected smolt output and the evidence of population spatial contraction within the Keogh watershed, we believe that changes in freshwater rearing conditions alone do not explain the observed pattern of declining freshwater productivity. Alternatively, it is possible that periods of low marine survival were associated with impaired adult fecundity or egg quality, thereby contributing to observed shifts in density-dependent relationships. However, this mechanism would not explain the concurrent shifts in spatial distribution, and data suggests that there were no apparent shifts in the body size of adult female steelhead over the period of the study. Furthermore, juvenile body size may interact with density during freshwater rearing, playing an important role in mediating competitive interactions across differing demographic or environmental conditions (Rincón and Lóbon-Cervía 2002; Imre et al. 2010). While year-to-year variability in juvenile body size and density may have been captured to a certain degree by the inclusion of a random “year” effect in our model, the interaction between body size and density was outside of the scope of the analysis presented here. Future work could examine temporal patterns in body size in relation to density and other environmental factors.

In simulating population dynamics, we made some key simplifications. Most notably, the population did not include diversity in age at smolting or spawning, and unlike the natural population of steelhead in the Keogh River, we did not incorporate iteroparity.

This simplicity likely reduced the resilience of the population to short-term fluctuations in the environment, as life-history diversity in steelhead has been shown to buffer populations from the effects of variability in environmental conditions, stabilizing abundance through time (Moore et al. 2014). However, even after taking the potential buffering effects of life-history diversity into account, poor survival conditions spanning time periods longer than a single generation would overwhelm the benefits conferred by the presence of multiple age classes, producing outcomes very similar to results observed in our simulated population.

Both empirical data from the Keogh River as well as the simulated population responses to variable marine survival have important implications for the management and conservation of Pacific salmon and steelhead. A major assumption of traditional stock–recruit modeling is that the relationship between abundance and recruitment is time-invariant; however, these assumptions are rarely met. Increasing evidence suggests that the relationship between spawner abundance and recruitment can be temporally variable (e.g., Adkinson et al. 1996; Peterman and Dorner 2012). The application of metapopulation theory to salmon for the purposes of management and conservation has often been employed at regional scales incorporating multiple watersheds into evolutionarily significant units or distinct population segments. However, spatial population dynamics and the importance of homing and straying have not often been considered at the watershed scale. This and other studies provide compelling evidence of the temporally dynamic nature of population structure (e.g., Isaak et al. 2007) and suggest the potential for changes in population spatial structure to produce time-variant density dependence at the watershed scale. Data from the Keogh River and evidence from many other depressed and threatened populations of salmon (e.g., Achord et al. 2003; Isaak et al. 2007; Walters et al. 2013) point to an underappreciated linkage between marine survival and freshwater spatial structure and production. Understanding the factors that influence the resilience of population structure and their potential to contribute to temporal variability in freshwater production represents a key frontier in our understanding of the dynamics of spatially structured populations. Our work highlights the importance of monitoring adult-to-smolt recruitment and spatial structure in stream-rearing salmonids for successful management and conservation in the face of climate variability and anthropogenic pressures such as

mixed stock fisheries, habitat alteration, and climate change. While the data and simulation results presented here represent a somewhat simplified view of population responses to a climatic shift, these findings should help shape future work on spatially structured populations and their responses to changes in environmental conditions that influence survival.

Our findings are also broadly relevant to the management and conservation of other spatially structured populations. For example, there is growing appreciation that spatial dynamics influence the sustainable harvest of many fishes ranging from Atlantic cod (*Gadus morhua*) (Smedbol and Wroblewski 2002) to Atlantic herring (*Clupea harengus*) (McQuinn 1997). If external environmental forcings or harvest rates depress survival and lead to unobserved spatial contraction, historical compensatory capacity may be eroded, leading to decreased recovery trajectories or sustainable harvest rates. In instances where strong local density dependence (e.g., Achord et al. 2003) is interpreted as evidence of a population meeting or exceeding the potential for habitats to support larger population sizes, decisions to conduct harvest or relax protections for endangered species may be erroneous and erode the potential for population expansion into areas that are under-seeded or entirely unutilized. We encourage managers to consider contemporary and historic population spatial structure when planning harvest and recovery actions, acknowledging the potential for harvest or other sources of mortality to induce changes in spatial structure and the attendant shifts in large-scale density dependence.

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