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ARTICLE

Life history effects on hatchery contributions to ocean harvest and natural-area spawning

Raziel J. Davison and William H. Satterthwaite

Abstract: Hatcheries can support salmon fisheries but also impact natural populations. We model the proportional hatchery contributions to ocean catch, natural-area spawning, and egg production based on hatchery production, maturation, fecundity, and straying. We develop indices of hatchery-origin catch per stray spawner measuring the trade-off between supplementing harvest and limiting natural-area impacts; higher values indicate success in increasing hatchery ocean harvest contributions relative to strays spawning in natural areas. Hatchery fish maturing early lowers catch per stray (and proportion hatchery-origin catch) by shifting the age distributions of both catch and spawners toward younger ages. Age-dependent fecundity may complicate predicted effects of changing maturation schedules. Increased straying does not affect catch but increases hatchery-origin spawning and decreases catch per stray. Differences in hatchery production affect hatchery contributions to both catch and spawning, exacerbating the trade-off between these conflicting goals but with no net effect on catch per stray. Fishery intensity magnifies the effects of accelerated hatchery fish maturation by reducing spawning contributions of older fish, with contrasting effects depending on whether hatchery fish mature early versus late.

Résumé : Les alevinières peuvent supporter les pêches au saumon, mais ont également des impacts sur les populations naturelles. Nous modélisons les contributions proportionnelles des alevinières aux prises océaniques, au frai en milieu naturel et à la production d'œufs à la lumière de la production, de la maturation, de la fécondité et de l'égarement en alevinières. Nous élaborons des indices des prises issues d'alevinières par géniteur égaré qui mesurent le compromis entre la supplémentation des pêches et la limitation des impacts sur les milieux naturels; des valeurs plus élevées indiquent le succès de l'accroissement des contributions des alevinières aux prises océaniques par rapport au frai en milieu naturel de géniteurs égarés. Les poissons issus d'alevinières à maturité précoce réduisent les prises par individu égaré (et la proportion des prises issues d'alevinières) en déplaçant la répartition des âges tant des prises que des géniteurs vers des âges plus faibles. La fécondité dépendant de l'âge pourrait compliquer les effets prévus des modifications du moment de la maturité. L'augmentation de l'égarement n'a pas d'incidence sur les prises, mais accroît le frai de géniteurs issus d'alevinière et réduit les prises par individu égaré. Les variations de la production d'alevinières a une incidence sur les contributions des alevinières tant aux prises qu'au frai, exacerbant le compromis entre ces objectifs contradictoires, mais sans effet sur les prises par individu égaré. L'intensité des pêches amplifie les effets de la maturation accélérée des poissons issus d'alevinières en réduisant les contributions au frai de poissons plus âgés, entraînant des effets variables selon que les poissons issus d'alevinières atteignent la maturité précocement ou tardivement. [Traduit par la Rédaction]

Introduction

Given current freshwater habitat conditions in much of their range, an economically viable Pacific salmon (*Oncorhynchus* spp.) fishery likely depends on supplementation via hatchery production (Brannon et al. 2004), but the net effect of hatcheries coastwide is difficult to ascertain (e.g., Hilborn 1998; Ruckelshaus et al. 2002; Morita et al. 2006) due to the complex interactions between hatchery and wild fish (Waples 1991; Naish et al. 2008). In addition, serious concerns have been raised about the effects that hatchery-origin fish have on naturally spawning populations through competition for limited resources (e.g., Hilborn and Hare 1992; Kostow et al. 2003) and genetic introgression (e.g., Waples 1991; Utter 1998; Araki et al. 2008). Therefore, large production hatcheries are generally managed for multiple, sometimes conflicting goals: to boost overall fish production, and thus fishery harvest opportunity, while also controlling the impacts of straying fish on natural-area spawners and wild fish population dynamics. Ideally, hatchery-origin fish from large production hatcheries would make a large contribution to harvest and a small contribution to natural-area spawning, although hatchery fish spawning in natural areas adjacent to hatcheries are compatible with the goals of "integrated" hatchery programs (HSRG 2009).

Hatchery contributions to fishery harvest opportunity are obviously increased when hatcheries release more fish or when fish are released in a way that increases survival from the juvenile phase until recruitment to the fishery. Therefore, all else being

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R.J. Davison.* Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, USA; Southwest Fisheries Science Center, Fisheries Ecology Division, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 Shaffer Rd., Santa Cruz, CA 95060, USA.
W.H. Satterthwaite. Fisheries Ecology Division, Southwest Fisheries Science Center, Fisheries Ecology Division, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 110 Shaffer Rd., Santa Cruz, CA 95060, USA.

Corresponding author: William H. Satterthwaite (email: Will.Satterthwaite@noaa.gov).

*Present address: Department of Anthropology, Institute for Social, Behavioral and Economic Research, University of California Santa Barbara, Santa Barbara, CA 93106-2150, USA.

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equal, harvest opportunity is increased by hatchery practices that increase juvenile survival (Johnson et al. 1990; Solazzi et al. 1991; Satterthwaite et al. 2014*a*) and (or) the rate at which hatchery fish grow to harvestable size. Although the effects of life history schedules may be less immediately obvious than the size and survival of hatchery releases, maturation rates of hatchery-origin fish also affect the degree to which they increase ocean harvest opportunity, since later-maturing fish experience more cumulative exposure to the fishery before returning to spawn (Hankin and Healey 1986). For example, the proportion of Chinook salmon (*Oncorhynchus tshawytscha*) catch in Lake Michigan made up by natural-origin fish was found to increase with age due to earlier maturation of hatchery fish (Williams 2012). If this pattern holds in the ocean as well, that would reduce hatchery contributions to ocean harvest, but potentially increase hatchery contributions to instream harvest as well as natural-area spawning, since more hatchery-origin fish would escape ocean harvest.

Similarly, the most obvious drivers of the impact of hatchery-origin fish on natural-area spawning grounds are the number of juveniles released and their survival, as well as the stray rates of adult fish returning to spawn. There is also concern about loss of local adaptation due to introgression from hatcheries (e.g., Hard et al. 1992; Quinn 1993), and such impacts are of course higher when hatchery and natural populations are less similar. The impact of straying depends on the proportion of natural-area spawners that originated in hatcheries (Naish et al. 2008), which depends not just on the proportion of hatchery production straying but also on the magnitude of hatchery production. Thus, low stray rates from very large hatcheries can have a larger impact than high stray rates from small hatcheries (Grant 1997). In addition, offsite releases increase juvenile survival (Johnson et al. 1990; Solazzi et al. 1991) but may also increase stray rates (e.g., Vreeland et al. 1975; Johnson et al. 1990; Lasko et al. 2014), amplifying the resultant impacts of hatchery-origin fish on natural-area spawning. As with contributions to harvest, life history schedules may also have important, if less widely appreciated, effects on the impacts of hatchery-origin fish on natural spawning areas. As noted previously, earlier maturation of hatchery fish could increase the proportion of hatchery-origin fish escaping the ocean fishery and potentially returning to natural spawning areas.

There are documented life history differences between hatchery- and natural-origin fish, including size and age distributions (e.g., Swain et al. 1991; Knudsen et al. 2006; Vainikka et al. 2010), reproductive traits (e.g., Fleming and Gross 1993; Quinn 1993), survival and growth (e.g., Jonsson et al. 2003; see Naish et al. (2008) for a review of hatchery life history effects). Many studies track hatchery-origin proportions in fisheries harvest (e.g., Zaugg et al. 1983; Hilborn and Eggers 2000; Barnett-Johnson et al. 2007) and among natural-area spawners (e.g., Seelbach and Whelan 1988; Kostow et al. 2003; Nickelson 2003). Stray rates vary widely among natural and hatchery populations (Quinn 1993), and straying of hatchery fish has been implicated in wild salmon declines (e.g., Hilborn and Eggers 2000), but much remains to be learned about the interactive effects of hatchery practices and their relative influences on total production, on the proportions of hatchery-origin fish in ocean and instream harvests, and on the contribution of hatchery-origin fish to natural-area reproduction.

To better understand the integrated effects of hatchery practices on harvest opportunity and natural-area impacts, we developed a series of population models integrating the effects of hatchery production, survival, maturation and fecundity schedules, ocean harvest rates, and stray rates. We used these models to explore how life history differences across the life cycle influence harvest opportunity and natural-area population dynamics through hatchery contributions to natural-area spawning, both in terms of spawning adults competing for redd sites and mating access and in terms of hatchery contributions to eggs laid in natural areas. Hatchery contributions to natural-area spawning depend on production, survivorship, maturation schedules, and straying, whereas contributions to birth cohorts also depend on fecundity. We are particularly interested in effects of maturation schedules because hatchery practices can alter maturation schedules (e.g., Knudsen et al. 2006; Hankin et al. 2009; Vainikka et al. 2010), and changes in maturation rates feed through age- and size-dependent differences in survival and reproductive success (e.g., Healey and Heard 1984; Kaufman et al. 2009). Since early-maturing fish are more likely to survive to spawn but are often smaller and less fecund at maturity, we are interested in how hatchery differences in life history traits like survival, maturation, and fecundity trade off against one another and interact with the intensity of ocean fisheries to amplify or to dampen hatchery contributions to both ocean fishery catch and spawning in natural areas.

We use six metrics to interpret hatchery effects under scenarios in which hatchery life histories differ from wild populations in production and survival, maturation rates, fecundity, and stray rates. We predict how each of these life history differences would affect (*i*) the proportion hatchery-origin among natural-area spawners (pHOS), (*ii*) the proportion hatchery-origin among natural-area eggs produced (pHOG), (*iii*) the proportion hatchery-origin among ocean-harvested fish (pHOC), (*iv*) the proportion of surviving hatchery-origin fish that end up in ocean harvest rather than returning to spawn (pC), (*v*) the proportion of hatchery-origin fish that end up spawning in natural areas rather than ocean harvest or returning to the hatchery (pS), and (*vi*) the ratio between number of hatchery-origin fish caught in the ocean harvest and the number spawning in natural areas (CPS).

The first three metrics describe system-wide effects of hatchery fish on a system containing both hatchery- and natural-origin fish (and so are sensitive to the size of hatchery programs relative to natural production), while the last three metrics compare the per-capita fates of hatchery fish (and so do not depend on relative population sizes). CPS directly captures the trade-off, at an individual-hatchery level, between contributing to ocean harvest versus contributing to strays spawning in natural areas. All acronyms are defined in Table 1.

Methods

Population model

We developed a model of a hypothetical fall run Chinook salmon stock with both natural-origin (denoted by a subscript w when needed) and hatchery-origin (subscript h) components (see Table 1 for a complete list of variable definitions). We assume a discrete sequence of events each year: maturing spawners from each cohort (age a) leave the ocean in the fall (with age-specific maturation probabilities b_a), followed by a period of overwinter survival (with probability p_a of surviving from age a to age $a + 1$), then followed by a pulse of ocean harvest (with age-specific fishing mortality f_a), cycling back to another opportunity for maturing spawners to leave the ocean (see Fig. 1).

Following management convention for California stocks (O'Farrell et al. 2010), we advance ocean fish by one age class after spawners return each fall, with the assigned ocean age corresponding to the age ocean-caught fish would be assigned if they had instead spawned at their next opportunity. We do not model an instream fishery, but we do separately track the fraction of hatchery-origin fish that stray to natural areas with probability y, which we assume is independent of age. Ocean fishing mortality (f_a) is the product of a fully vulnerable exploitation rate (e, the intensity of the fishery, roughly corresponding to fishing effort) and age-specific vulnerability q_a, yielding $f_a = e\, q_a$, with the oldest ages assumed to be fully vulnerable ($q_4 = q_5 = 1.0$) and assuming no exposure to the fishery prior to age 2 ($q_1 = 0$).

Given an initial cohort size of N_1 (corresponding to the number of juveniles released from the hatchery or resulting from natural-

Table 1. Variable definitions and symbols with baseline value(s) or range.

Symbol	Variable	Definition or example	Baseline value(s) or range
A	Maximum age (subscript)	Oldest age of surviving individuals	5
a	Age (subscript)	Age class	$\{1, 2, 3, 4, 5\}^a$
b_a	Maturation probability	Probability of spawning if alive at age a	$\{0, 0.03, 0.5, 0.9, 1\}^a$
c_a	Catch	Ocean harvest of age a fish	Eq. 2^b
CPS	Catch per stray spawner	Ratio $C_{T,h}$:$S_{T,h}$	Eq. 12^b
e	Fishing intensity (effort)	Scalar applied to fishing vulnerability	0.5 (0.1, 0.8)^c
f_a	Fishing mortality	Probability of ocean harvest if alive at age a	$f_a = e\, q_a{}^b$
h	Hatchery origin (subscript)	Captive-reared with hatchery life history effect	NA
g_a	Egg production	Eggs produced in natural areas at age a	Eqs. 5, 6^b
g_a	Fecundity	Female eggs per age a spawner	$\{0, 2100, 2900, 3000, 3700\}^a$
N_a	Cohort size	Number of individuals alive at age a	Eq. 1^b
p_a	Survival	Age-specific survival probability (age a to age $a + 1$)	$\{0.01, 0.5, 0.8, 0.8, 0\}^a$
pC	Proportion caught	Proportion of hatchery-origin fish caught in ocean harvest	Eq. 10^b
pS	Proportion spawning	Proportion of hatchery-origin fish that spawn in natural areas	Eq. 11^b
pHOC	Ocean harvest composition	Proportion hatchery-origin among ocean catch	Eq. 9^b
pHOG	Egg composition	Proportion hatchery-origin within natural-area egg production	Eq. 8^b
pHOS	Spawner composition	Proportion hatchery-origin among natural-area spawners	Eq. 7^b
q_a	Fishing vulnerability	Probability of ocean harvest relative to "highest vulnerability"	$\{0, 0.05, 0.5, 1, 1\}^a$
R_a	Returns	Number of age a fish returning to spawn	Eq. 3^b
S_a	Spawners	Number of age a fish spawning in natural areas	Eq. 4^b
T	Total (subscript)	Sum across ages $a = \{2, 3, 4, 5\}$	NA
w	"Wild" (subscript)	Naturally spawning fish with "wild" life history	NA
y	Stray rate	Probability of straying to spawn in natural area	0.3 (0, 1)^c
ϕ_b	Maturation ratio	$b_{a,h}$:$b_{a,w} = \min\{(\phi_b\, b_{a,w}), 1\}$:$b_{a,w}$	1 (0.1, 8)^c
ϕ_g	Fecundity ratio	$g_{a,h}$:$g_{a,w} = \phi_g g_{a,w}$:$g_{a,w}$	1 (0.1, 8)^c
ϕ_N	Cohort ratio	$N_{1,h}$:$N_{1,w} = \phi_N N_{1,w}$:$N_{1,w}$	1 (0.1, 8)^c

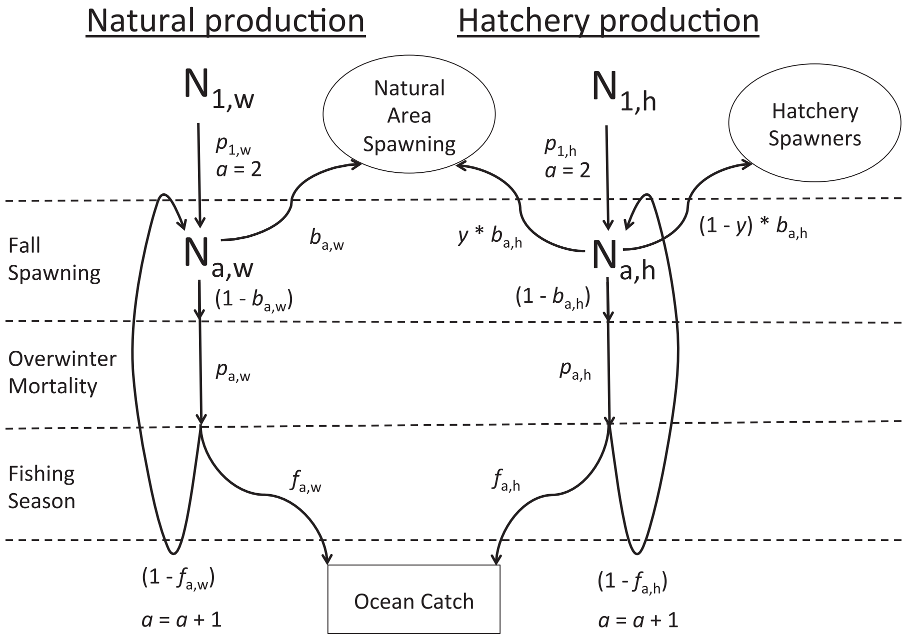
Note: NA indicates a non-numeric entry.

[a] Age schedule of vital rates for ages $a = \{1, 2, 3, 4, 5\}$ (e.g., $b_a = \{0, 0.03, 0.5, 0.9, 1\}$).

[b] Equation determining endogenous (output) variable.

[c] Baseline value for perturbed parameters (ϕ_N, ϕ_b, ϕ_g, e, y) along with (min., max.) of perturbation.

Fig. 1. Population model schematic. Lines denote transitions between stages, labeled with rates as defined in Table 1. N = number, a = age, b = maturation rate, p = survival, f = fishing mortality, y = stray rate, h = hatchery origin, w = natural origin. Egg production not shown.



area production, we note that this life stage may not be referred to as age 1 in other studies), juvenile survival p_1 from release or ocean entry until the start of ocean age 2, annual overwinter survival p_a (from ages $a = 2$ to the start of each next age $a + 1$), and age-specific maturation probabilities (b_a) and ocean fishery mortality (f_a), we calculate the preseason ocean abundance (N_a) at each age:

$$N_a = p_{a-1}(1 - b_{a-1})(1 - f_{a-1})N_{a-1} \tag{1}$$

We also calculate the ocean catch (C_a) of age a fish, as well as the number of fish returning to spawn in fresh water (R_a) at each age by applying the age-specific maturation rate (b_a) to the fraction $(1 - f_{a-1})$ not removed by the fishery:

$$C_a = f_a N_a \tag{2}$$

$$R_a = b_a(1 - f_a)N_a \tag{3}$$

We calculate all of the above for hatchery-origin and for natural-origin fish separately. In addition, for hatchery-origin fish, we calculate the number of hatchery strays (S) to natural areas as the product of hatchery returns (R) and hatchery stray rate (y):

$$(4) \qquad S_{a,h} = R_{a,h}y; \quad S_{T,h} = \sum_{a=2}^{5} R_{a,h}y$$

Age-specific natural-area egg production (G) contributed by natural-origin (w) and hatchery-origin (h) fish is calculated as the product of the number of spawners at each age in natural areas ($R_{a,w}$ for natural-origin fish and $S_{a,h}$ for hatchery-origin fish) and their age-specific fecundities (g_a):

$$(5) \qquad G_{a,w} = R_{a,w}g_{a,w}$$

$$(6) \qquad G_{a,h} = S_{a,h}g_{a,h}$$

Because salmon population dynamics are highly variable and to allow use of cohort ratio as a model input rather than a dynamic model output, we do not run the model for multiple generations or until it reaches an equilibrium solution. Rather, we project the short-term, deterministic dynamics of a single cohort. If juvenile production (N_1), vital rates (p_a, b_a, g_a), fishing intensity (e), and stray rates (y) are constant across years, the sum across cohorts within a year is equal to the sum across ages within a cohort's life cycle. Therefore, we define the subscript T to indicate the sum across all ages 2 to A, where A is the maximum achievable age (assumed to have $b_A = 1.0$, rendering p_A irrelevant, but we set $p_A = 0$ to emphasize that this is the terminal age class). Our model does not separate fish by sex, and so it implicitly assumes a 50:50 sex ratio, that maturation schedules and fishery exposure are the same for both sexes, and g_a is discounted to one-half the egg production of a female fish (equivalent to the production of female eggs, assuming a 50:50 sex ratio). Alternatively, the model could be applied to each sex separately, with g_a reformulated to represent male mating success.

Baseline parameterization

Our model is intended to reflect a realistic set of vital rates for a Chinook salmon population but not provide quantitative advice for any specific system. However, to establish plausible values and ranges for parameters, we loosely based most of our parameterization on data from Klamath River Fall Chinook, a hatchery-supplemented stock harvested subject to ocean harvest off the coasts of northern California and southern Oregon (PFMC 2016). We initially set all parameters equal between hatchery- and natural-origin populations, with maximum age $A = 5$ and set $N_0 = 1.0$ as an arbitrary scaling constant. Based loosely on natural mortality and maturation rate estimates for Iron Gate Hatchery fall run fingerling releases (Hankin and Logan 2010), we set survival probabilities $p_1 = 0.01$, $p_2 = 0.5$, and $p_3 = p_4 = 0.8$, along with maturation probabilities $b_2 = 0.03$, $b_3 = 0.5$, $b_4 = 0.9$, and $b_5 = 1.0$. We assumed that ocean age 4 and age 5 fish were fully vulnerable to the fishery (vulnerability $q_4 = q_5 = 1.0$) and set $q_3 = 0.5$ based on the approximate ratio between age 3 and age 4 exploitation rates calculated by Hankin and Logan (2010). We set $q_2 = 0.05$ based on the knowledge that ocean age 2 fish from some stocks are caught in recreational ocean fisheries (Satterthwaite et al. 2013), while setting $q_1 = 0$. We set fishing intensity $e = 0.5$, approximately midway between the limit for age 4 Klamath River Fall Chinook of 0.16 (strongly constrained by the co-occurring threatened California Coastal Chinook stock; O'Farrell et al. 2012*a*) and the Pacific Fishery Management Council's default fishing mortality rate (0.78) corresponding to maximum yield (F_{MSY}) for Chinook salmon (Pacific Fishery Management Council 2016). The baseline value of $e = 0.5$ appears roughly consistent with the mean fraction of adults removed from Sacramento River Fall Chinook (O'Farrell et al. 2012*b*), a hatchery-supplemented stock that is heavily targeted by fisheries that are usually constrained by co-occurring stocks. For comparative purposes, we assume no straying of natural-origin fish and specify stray rate $y = 0.3$ for hatchery-origin fish. Stray rates reported in the literature vary widely (e.g., Pascual et al. 1995; Westley et al. 2013), as does the very definition of a stray when it involves natural areas near the source hatchery (e.g., Keefer and Caudill 2012; Kormos et al. 2012), but we picked this value for use in displaying the effects of changes in other parameters when y is held constant, because it is well within the range reported for hatchery releases (Pascual et al. 1995). Baseline age-specific fecundity was modeled after Mokelumne River fall run Chinook salmon from California's Central Valley (Kaufman et al. 2009).

Perturbation analyses

To understand the impacts of variation in life history parameters potentially affected by hatchery practices, we varied parameters individually with respect to the baseline and also explored interactive effects of sets of variables that could mediate a trade-off between the conflicting hatchery goals of supplementing harvest while avoiding strays spawning in natural areas, as shown in analysis of our metrics below. We held natural-origin parameters constant in all projections. We varied stray rate (y) over the range 0.01 to 0.90 to encompass the wide range of values reported in the literature (e.g., Pascual et al. 1995; Westley et al. 2013) and varied the fully vulnerable fishing mortality (e) from 0.1 to 0.8 based loosely on O'Farrell et al. (2012*a*) and PFMC (2016), respectively, as described in deriving the baseline e.

Remaining life history parameters were perturbed from their baseline values by applying a range of multipliers denoted by ϕ_x, with the subscript x representing the parameter being multiplied. Because initial cohort size (N_1) and juvenile survival (p_1) only appear in our model as a product, we varied their joint outcome N_2 by applying a cohort ratio ($f_N = N_{2,h}{:}N_{2,w}$) varying from 0.1 to 8 to allow for a range of scenarios between a small hatchery program in conjunction with a small stock to a hatchery-dominated system where over 90% of fish are of hatchery origin (e.g., Barnett-Johnson et al. 2007). We assumed that the maturation multiplier ϕ_b applied equally to all ages, with the exception that no value of b_a could exceed 1.0 (since maturation rates cannot exceed 100%) and b_5 was fixed at 1.0 ($b_{x,h} = \min\{b_{x,w}, 1\}$). We set a lower bound of 0.1 on ϕ_b loosely based on the reported minimum age 3 maturation rates for Cole Rivers Hatchery (on the nearby Rogue River) spring run Chinook of 0.06 (Hankin and Logan 2010), and an upper bound of 8.0 was loosely based the reported maximum age 2 maturation rate of 0.16 for Sacramento River Winter Chinook (O'Farrell et al. 2012*b*). Of particular relevance, $\phi_b = 2.0$ yields an age 3 maturation rate of 100%, while $\phi_b = 0.5$ roughly corresponds to the approximate ratio between mean age 3 maturation rates estimated for Iron Gate Hatchery fall fingerling (0.48) versus yearling (0.24) releases (Hankin and Logan 2010).

We also examined the effects of fecundity differences between hatchery- and natural-origin fish. Because selection for large egg size is relaxed in hatchery fish, fecundity selection may favor large broods of small eggs (Heath et al. 2003; Fleming et al. 2003). However, fecundity has declined substantially at some hatcheries (e.g., Williams 2006), and obtaining accurate estimates of fecundity is difficult and empirical estimates must be interpreted with caution (Beacham 2003, 2010; Fleming et al. 2003). We model hatchery fish fecundity by applying the scalar multiplier ($\phi_g = g_{x,h}{:}g_{x,w}$ ranging from 0.1 to 8, hereinafter "fecundity ratios") to baseline age-specific fecundity rates (g_a) just as we did for maturation probabilities (b_a), with the exception that there is no upper bound on hatchery fecundity.

Metrics

Our model allows straightforward prediction of commonly measured quantities such as the proportion hatchery-origin spawners (strays) in natural areas (pHOS), which depends on the number of strays ($S_{T,h}$) and returning natural-origin fish ($R_{T,w}$); the proportion hatchery-origin among eggs laid in natural areas (pHOG),which depends on egg production of hatchery-origin fish ($G_{T,h}$) and natural-origin fish ($G_{T,w}$); and the proportion hatchery-origin fish in the ocean catch (pHOC), which depends on total catch of hatchery- ($C_{T,h}$) and natural-origin fish ($C_{T,w}$):

$$\text{(7)} \qquad \text{pHOS} = \frac{S_{T,h}}{R_{T,w}+S_{T,h}}$$

$$\text{(8)} \qquad \text{pHOG} = \frac{G_{T,h}}{G_{T,w}+G_{T,h}}$$

and

$$\text{(9)} \qquad \text{pHOC} = \frac{C_{T,h}}{C_{T,h}+C_{T,w}}$$

While these metrics are commonly measured in the field, so many parameters influence them that it can be difficult to gain general insights by looking at their responses to only one or two parameters at a time. We therefore developed additional metrics of hatchery performance that are independent of natural-origin numbers and thus provide scale-independent information on how hatchery practices influence the trade-off between supplementing harvest and impacting natural-area spawning. Whereas we used pHOC to estimate hatchery-origin proportions in ocean harvest, we calculate the proportion of surviving hatchery production (i.e., not lost to natural mortality except through spawning) contributing to the ocean catch (pC) to predict the likely distribution of outcomes for hatchery fish:

$$\text{(10)} \qquad \text{pC} = \frac{C_{T,h}}{R_{T,h}+C_{T,h}}$$

Note that pC describes the chance of a hatchery fish being caught (a trait of hatchery fish in particular), while pHOC describes the chance of finding a hatchery fish among ocean harvest (a trait of the mixed fishery). Likewise, in addition to the proportion hatchery-origin fish in natural-area spawning (pHOS), we also calculate the proportion of hatchery fish ending up as strays spawning in natural areas (pS) as follows:

$$\text{(11)} \qquad \text{pS} = \frac{S_{T,h}}{R_{T,h}+C_{T,h}}$$

Note that because hatchery-origin fish returning to the hatchery ($R_{T,h} - S_{T,h}$) are not included in the numerator of either pC or pS, these two metrics do not sum to 1.0 unless the stray rate $y = 1.0$.

The trade-off between harvest contribution and straying is reflected in the ratio of hatchery-origin ocean catch per stray spawner (CPS):

$$\text{(12)} \qquad \text{CPS} = \frac{C_{T,h}}{S_{T,h}}$$

If CPS is high then it is likely that an individual hatchery fish will be caught in the ocean harvest instead of spawning in natural areas, reflecting success in balancing the dual goals of contributing to ocean harvest while avoiding impacts associated with strays spawning in natural areas.

Note that none of these metrics explicitly account for fish dying of natural mortality in the ocean (or during downstream migration of juveniles). Metrics accounting for fish "lost" to natural mortality might be of interest in future studies examining the ecosystem role of hatchery salmon as food sources for predators.

Results

Individual rate effects

Higher cohort ratios (i.e., the ratio of hatchery- to natural-origin cohort size, ϕ_N) increase the proportion hatchery-origin fish among natural-area spawners (pHOS) and among ocean catch (pHOC), but do not alter the proportion of hatchery fish ending up in ocean catch (pC) or spawning in the wild (pS) because both of these measures are standardized to the size of hatchery cohorts (see Fig. 2*a*). Maturation ratios (ϕ_b) affect all four metrics (pHOS, pHOC, pC, pS), but there are diminishing returns to increasing maturation ratios beyond ϕ_b^*, the critical threshold where all fish mature by age 3 ($\phi_b^* = 2.0$ in this case; see Fig. 2*b*). Earlier maturation (higher ϕ_b) decreases pHOC and pC as more hatchery fish leave the ocean earlier and are therefore exposed to less fishing hazard, but earlier maturation increases pHOS and pS since early-maturing hatchery fish are more likely to survive and contribute to natural-area spawning (see Fig. 2*b*). Higher fishing intensity (*e*) increases pC and reduces pS as more hatchery fish are caught before they return to spawn, but pHOS and pHOC are unaltered because fishing intensity affects hatchery- and natural-origin fish equally (see Fig. 2*c*). Higher stray rates (*y*) directly increase pS and pHOS) (see Fig. 2*d*). If hatchery cohorts are equal in size to natural-origin cohorts ($\phi_N = 1$) and mature at the same rates ($\phi_b = 1$), then 100% straying would predict pHOS saturation at 50% of natural-area spawners (see Fig. 2*d*). Neither pC nor pHOC respond to stray rates of fish that have already left the ocean to spawn (see Fig. 2*d*).

Hatchery contributions to natural-area spawning

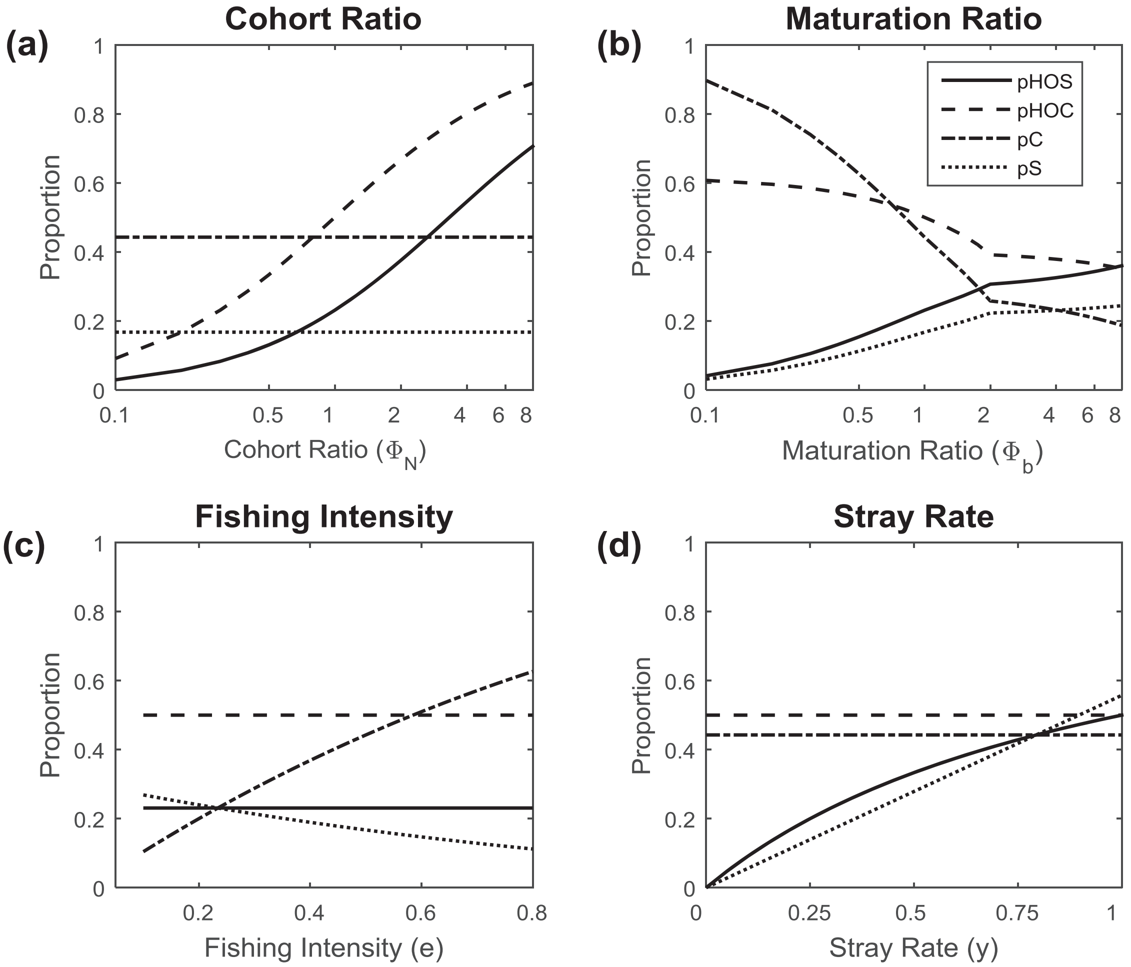
The proportion of hatchery-origin strays among natural-area spawners (pHOS) increases with higher stray rates (*y*; Figs. 3*a*, 3*d*, 3*e*), higher maturation ratios (ϕ_b; Figs. 3*a*, 3*b*, 3*c*), and higher cohort ratios (ϕ_N; Figs. 3*c*, 3*d*, 3*f*), but pHOS does not respond to fishing intensity (*e*) when hatchery fish mature at the same ages as natural-origin fish (Figs. 3*e*, 3*f*). When hatchery fish mature before natural-origin fish ($\phi_b < 1$), increasing *e* reduces pHOS, but if hatchery fish mature late ($\phi_b > 1$), then increasing *e* increases pHOS (see Fig. 3*b*).

pHOS responds more to increasing stray rates when stray rates are initially low (Figs. 3*a*, 3*d*, 3*e*) but responds more to higher cohort ratios when cohort ratios are large (Figs. 3*c*, 3*d*, 3*f*). pHOS responds less to higher maturation ratios (ϕ_b) when hatchery fish mature very late or very early and respond much less to earlier maturity when maturation ratios are above the critical maturation threshold ($\phi_b^* = 2.0$ in this parameterization), where all hatchery fish mature by age 3.

Hatchery contributions to natural-area egg production

Higher fecundity ratios (i.e., the ratio of hatchery-origin to natural-origin fecundity, ϕ_g) increase the proportion of natural-area egg production derived from hatchery-origin fish (pHOG) but do not alter the age structure of spawners. Higher ϕ_g act in conjunction with higher stray rates (*y*) to increase pHOG (Fig. 4*a*) in exactly the same manner they interact with hatchery cohort ratios (ϕ_N; Fig. 4*b*). The two scalar multipliers ϕ_g and ϕ_N compound their effects on pHOG (Fig. 4*c*). Like spawner proportions (pHOS; Fig. 3), egg proportions (pHOG) respond more to increasing maturation ratios (ϕ_b) when maturity is late (low ϕ_b; Figs. 4*d*–4*g*) and respond more to increasing ϕ_N when hatchery cohorts are large (high ϕ_N; Figs. 4*b*, 4*c*, and 4*e*), and pHOG responds identically to changes in ϕ_N or ϕ_g (compare Figs. 4*e* and 4*f*). Also like spawner proportions, egg proportions show little response to increasing ϕ_b beyond ϕ_b^* (Figs. 4*d*–4*g*). Higher fishing intensity (*e*) increases pHOG when hatch-

Fig. 2. Different lines predict individual rate effects on the proportion hatchery-origin among spawners (pHOS), the proportion hatchery-origin among ocean fishery catch (pHOC), the proportion of hatchery fish ending up in ocean catch (pC), and the proportion of hatchery fish that end up spawning in natural areas (pS). Panels show the effects of varying one the following rates (ϕ_N, ϕ_b, e, y) when the other four are held constant at baseline values ($\phi_N = 1$, $\phi_b = 1$, $e = 0.5$, $y = 0.3$): (*a*) cohort ratios (ϕ_N), (*b*) maturation ratios (ϕ_b), (*c*) fishing intensity (e), and (*d*) stray rates (y) of hatchery fish.



ery fish mature late ($\phi_b < 1$), and higher fishing intensity decreases pHOG when hatchery fish mature early ($\phi_b > 1$; Fig. 4*g*).

Hatchery contributions to ocean harvest

The proportion of ocean catch comprising hatchery-origin fish (pHOC) goes up with larger ϕ_N, with the largest effect from a given change in cohort ratios occurring when hatchery- and natural-origin cohorts have similar initial abundance ($\phi_N \approx 1$; Figs. 5*a*, 5*c*). Differences in maturation ratios also have the largest effect on pHOC when hatchery- and natural-origin fish mature at close to the same rates ($\phi_b \approx 1$), and there is little effect of increasing maturation ratios beyond the threshold ϕ_b (Figs. 5*b*, 5*c*). When hatchery fish mature late ($\phi_b < 1$), increasing e reduces pHOC, but when hatchery fish mature early ($\phi_b > 1$), increasing fishing intensity increases pHOC (Fig. 5*b*).

Catch per stray spawner (CPS) increases with e (Figs. 5*d*, 5*e*) and decreases with both y (Figs. 5*d*, 5*f*) and ϕ_b (Figs. 5*e*, 5*f*), but does not respond much to increases in maturation ratios beyond ϕ_b^*.

Discussion

Our model indicates that hatchery contributions to ocean harvest (generally regarded as desirable) could be increased by larger numbers of hatchery fish released, by higher survival of hatchery releases, or by later maturation of hatchery fish, while proportional contributions of hatchery- versus natural-origin fish to ocean harvest are insensitive to stray rates. At the same time, hatchery contributions to natural-area spawning (generally regarded as undesirable, at least for large production hatcheries) are decreased by smaller numbers of hatchery fish released, lower survival of hatchery fish, lower stray rates, or later maturation of hatchery fish. Thus the total size and survival of hatchery releases have opposite effects on the dual goals of maximizing hatchery contribution to harvest and minimizing straying of hatchery fish to natural spawning areas, while the remaining factors have some potential to at least partially mediate a trade-off.

By exploring the effects of multiple parameters individually or in concert, we also explored the sensitivity of model results to most input parameters. Although we used only a single set of age-specific fishing vulnerability and age-specific fecundity, further simulations show that the modeled effects of changes in stray rates and maturation schedules on catch per stray egg are qualitatively robust and show minimal quantitative changes unless fecundity decreases strongly with age (see online supplement, Fig. S1[1]). Effects of straying and maturation rates on catch per stray spawner

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0457.

Fig. 3. Contours predict the proportion of natural-area spawners that are of hatchery origin (pHOS) under different pairwise combinations of varying cohort ratios (ϕ_N), maturation ratios (ϕ_b), fishing intensity (e), and stray rates (y), with the other two of these four parameters held at baseline rates ($\phi_N = 1$, $\phi_b = 1$, $e = 0.5$, $y = 0.3$).

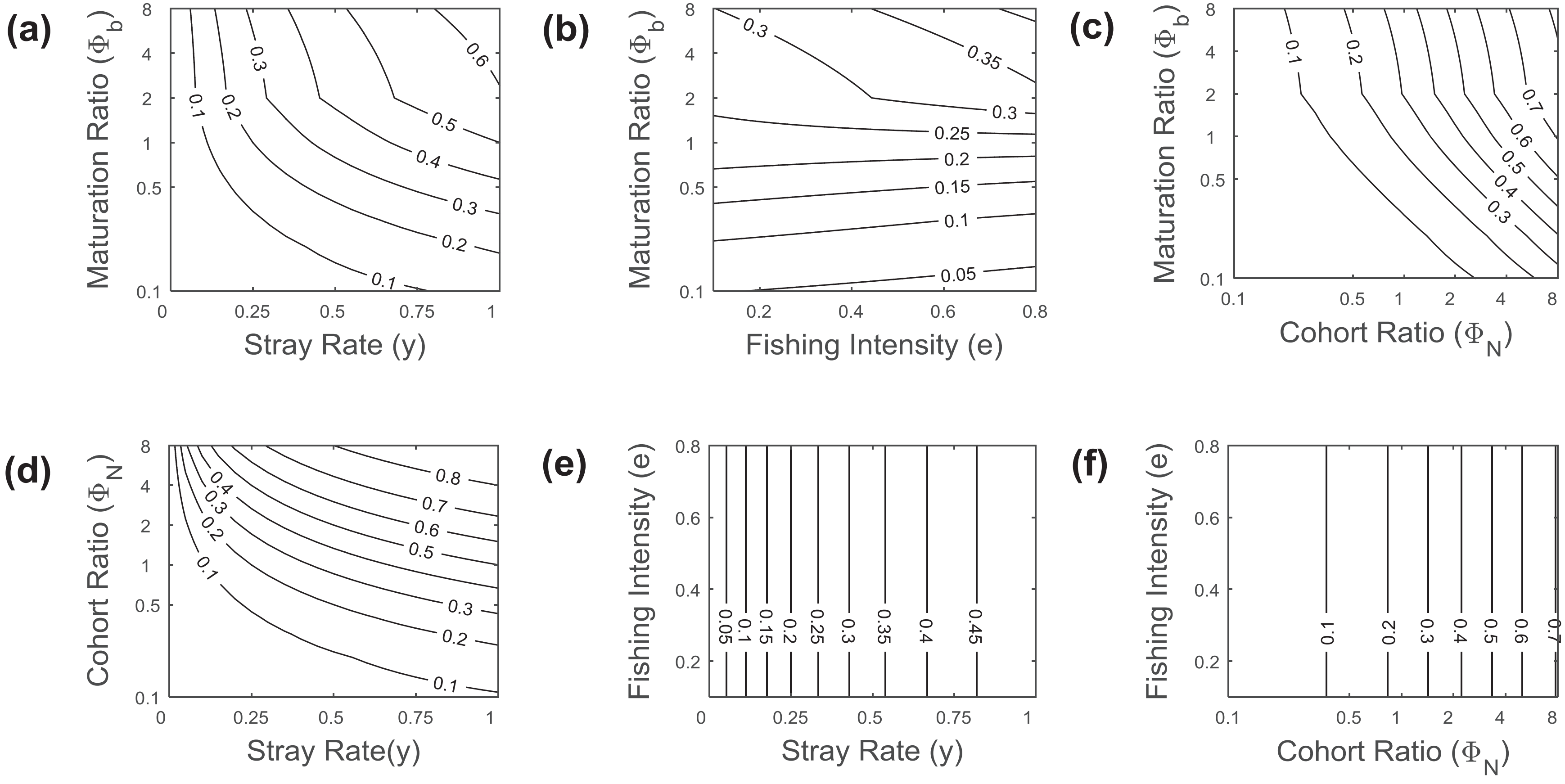


Fig. 4. Contours predict the proportions of natural-area egg production made by hatchery-origin fish (pHOG) under different pairwise combinations of varying cohort ratios (ϕ_N), maturation ratios (ϕ_b), fecundity ratios (ϕ_g), fishing intensity (e), and stray rates (y), with the other two of these four parameters held at baseline rates ($\phi_N = 1$, $\phi_b = 1$, $\phi_g = 1$, $e = 0.5$, $y = 0.3$). Note that pairwise combinations without changes along both axes have been omitted.

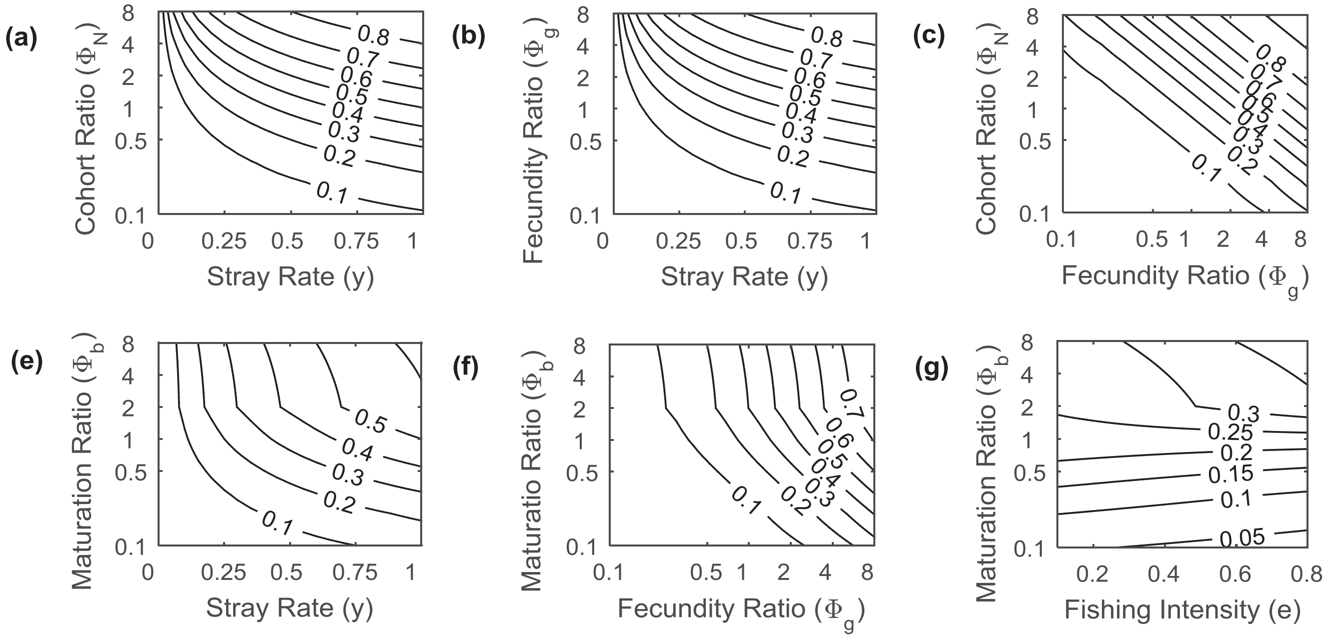
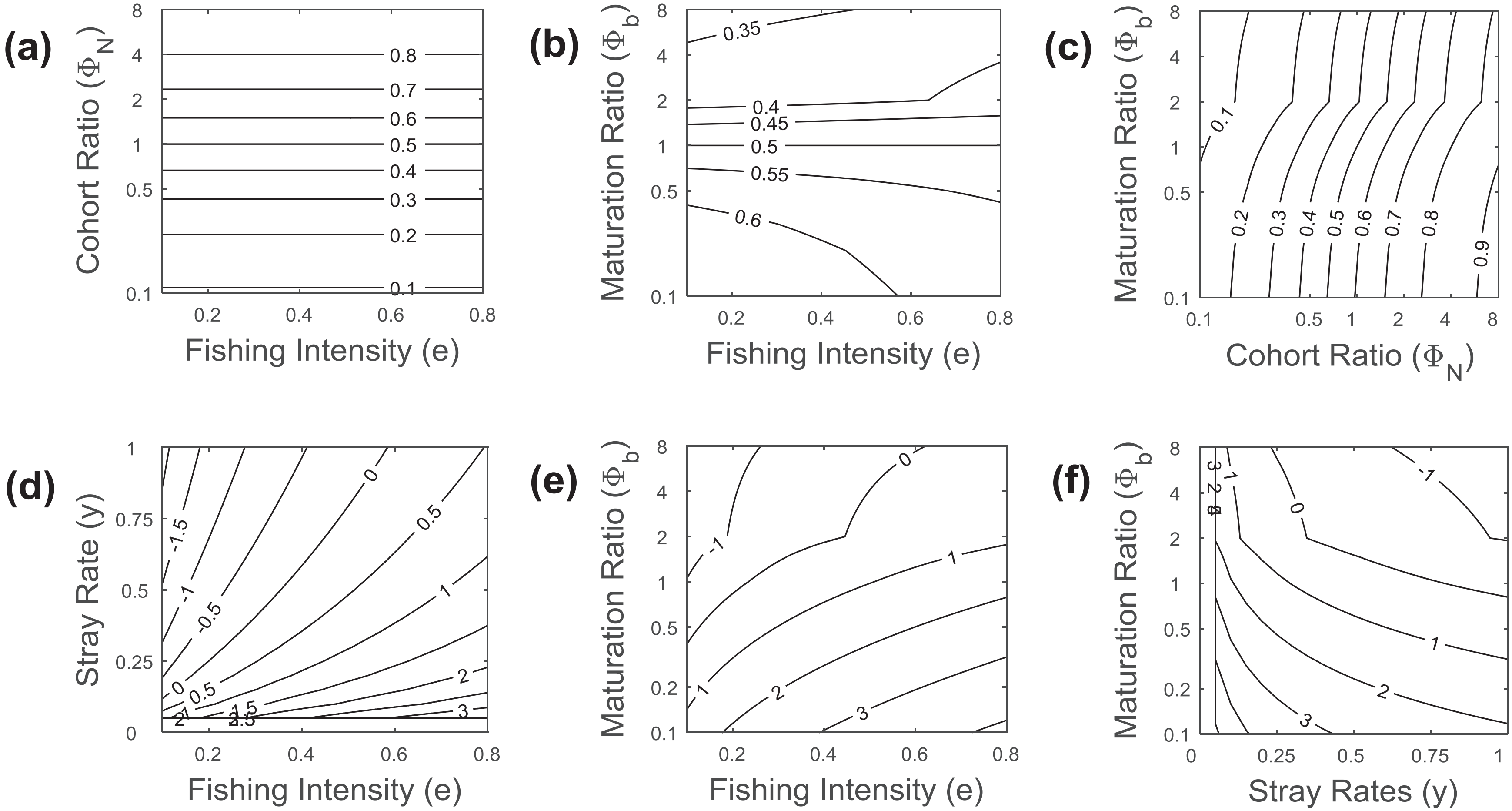


Fig. 5. (*a*–*c*) Prediction of the proportion of ocean harvest that would be of hatchery origin (pHOC) under different pairwise combinations of varying cohort ratios (ϕ_N), maturation ratios (ϕ_b), fishing intensity (*e*), and stray rates (*y*), with the other two of these four parameters held at baseline rates ($\phi_N = 1$, $\phi_b = 1$, $e = 0.5$, $y = 0.3$). (*d*–*f*) Prediction of catch per stray spawner ratios (CPS contours on a natural logarithmic scale) under different parameter combinations (again with all but two fixed at baseline rates). Note that no panels are required to show effects of *y* on pHOC because straying occurs after fish have left the ocean, and there is no effect of ϕ_N on CPS because hatchery cohort scaling applies equally to catch (*C*) and spawner cohorts (*S*).



weaken but are not reversed if fishing vulnerability decreases with age (online supplement, Fig. S2[1]), since cumulative exposure to fisheries always increases with age. Neither of those scenarios is plausible. It is well established that fecundity in salmon increases with age (e.g., Mangel 1994), and the same is almost certainly true of fishing vulnerability. There may be small age-specific differences in ocean spatial distribution and thus exposure to fisheries (Satterthwaite et al. 2013, 2014*b*), but for ages recruited to the fishery these differences are small, and fishing vulnerability primarily reflects the effects of minimum size limits (Satterthwaite et al. 2012; McHugh et al. 2015), with older fish being larger and thus more often legal to retain.

Although a simplified theoretical model such as this one is difficult to fully validate with empirical data, we note that consistent with generally earlier maturation of hatchery-origin fish, empirical studies have observed decreasing proportions hatchery-origin catch for older age classes in Lake Michigan Chinook (Williams 2012). The spawning escapement of Central Valley fall Chinook appears to have a higher proportion hatchery origin than the ocean harvest off Central California (Rachel Johnson, National Marine Fisheries Service, Santa Cruz, California, personal communication, based on calculations performed using data reported in Kormos et al. 2012 and Palmer-Zwahlen and Kormos 2013 and 2015), although natural-origin fish from northern stocks may make small contributions to harvest off Central California (Bellinger et al. 2015; Satterthwaite et al. 2015). Future work could investigate the effects of stronger or weaker differences in the fecundity of young versus old fish, variation in how rapidly fishery vulnerability increases with age, density-dependence, or stochastic effects.

Hatchery cohort size

It should not be surprising that increased recruitment of hatchery fish (through larger releases or increased juvenile survival) increases both the number of hatchery fish harvested and the number of hatchery fish escaping to natural spawning areas, exacerbating the trade-off between the dual management goals of increasing hatchery harvest contributions but reducing hatchery inputs to natural-area spawning. Thus, hatchery cohort size has no potential to mediate between these opposing goals but scales the magnitude of this trade-off. This is made readily apparent by comparisons of different metrics — the proportion hatchery origin among ocean catch (pHOC) and among natural-area spawners (pHOS) show opposite responses to hatchery cohort size, whereas measures of individual fish fates (the proportion straying (pS) or caught (pC)) and metrics of hatchery performance that are independent of the relative sizes of hatchery and natural populations such as catch per stray spawner (CPS) show no response. It seems important to note here that empirical measures of pHOC (e.g., Barnett-Johnson et al. 2007; Kormos et al. 2012) and pHOS (e.g., Johnson et al. 2012; Kormos et al. 2012; Hinrichsen et al. 2016) are common in the literature, but we are not aware of estimates of the latter quantities (i.e., pS, pC, CPS). This suggests that consideration of empirical measures of the latter metrics may be helpful in informing hatchery managers on their success in trading off between competing goals, given the overall size of the hatchery program.

Stray rate

Lowering stray rates would reduce impacts of straying spawners without altering ocean harvest in terms of either numbers or composition, and thus, in isolation, reductions in stray rates present no conflict for the dual goals of fisheries supplementation and natural-area conservation. However, hatchery fish are often released offsite to increase their survival and thus increase their contribution to ocean fisheries (Johnson et al. 1990; Solazzi et al. 1991), but such offsite releases may increase stray rates (Vreeland et al. 1975; Johnson et al. 1990; Lasko et al. 2014). It is possible that the survival advantage might be lost if hatchery practices were altered to reduce straying, sacrificing harvest opportunity. In addition, onsite releases may lead to increased instream competition with naturally produced juveniles.

Fecundity

Similar to stray rates, reducing the fecundity of hatchery fish has no effect on contributions to harvest but reduces the number of hatchery-origin juveniles present in the next generation of natural-area fish and thus reduces the genetic impact of strays. Therefore, releasing hatchery fish with lower fecundity (or zero fecundity in the case of triploids) might reduce the production of hatchery-origin juveniles in natural areas and so reduce the population genetic impacts of straying, but lower fecundity hatchery fish would still compete for redd sites and mates and might introduce genes or gene combinations leading to low fecundity into natural populations.

Maturation schedule

Our model suggests that alterations in hatchery maturation schedules could contribute to achieving both goals of hatchery production by inducing delayed maturation, which would both increase hatchery contributions to harvest and decrease hatchery impacts through natural-area spawning. Although delayed maturity of hatchery fish always reduces the contribution of hatchery spawners to natural-area spawning, the effects on egg production are harder to predict and may be reversed, because older spawners have higher fecundity. The net effect of changes in age structure on age production reflect a complicated trade-off among multiple age classes and so will depend on the specific mortality and fecundity schedule for a particular system. In our particular parameterization, the increase in fecundity with greater age was not large enough to compensate for intervening mortality, so delayed maturation never increased the proportional contribution of hatchery-origin eggs. However, a different pattern might arise if the increase in fecundity with age were stronger. In addition, larger fish tend to have larger eggs (Kinnison et al. 2001) that are more likely to produce surviving offspring (e.g., Williams 2006; Heath et al. 1999), but this effect of delayed maturation is not accounted for in our model. Because increased fishing intensity dampens the effects of changes in maturation schedules on the composition of catch and returning spawners, higher fishing intensity may reduce the observed impacts of early maturation in terms of spawner composition, but it may reduce the observed benefits of delayed maturation in terms of harvest composition.

Although there is extensive literature on the effect of hatchery practices on maturation schedules (e.g., Knudsen et al. 2006; Hankin et al. 2009; Vainikka et al. 2010), the potential for changes in maturation schedules to contribute to achieving these management goals does not seem to be widely appreciated (but see Hankin and Healey 1986 for hatchery contributions to harvest). For example, despite extensive attention to the tension between supplementing harvest and avoiding natural-area impacts, the Hatchery Scientific Review Group (HSRG 2014) did not discuss the effects of hatchery practices on maturation schedules. The California Hatchery Scientific Review Group (California HSRG 2012) did discuss the effects of hatchery practices on maturation schedules and the implications of altered maturation schedules for equivalence to natural populations in "integrated" hatchery programs, but they did not consider maturation schedules with respect to the goals of supplementing harvest or limiting stray spawners.

In many cases, existing hatchery practices tend to favor earlier maturation (e.g., Knudsen et al. 2006; Hankin et al. 2009; Vainikka et al. 2010), conflicting with both harvest and spawner goals, but this need not universally be the case. For example, since much of the variation in age at maturity is heritable (Hankin et al. 1993), careful broodstock selection could reverse the tendency toward early maturation in hatchery fish (California HSRG 2012). Additionally, fall run Chinook salmon held for extended rearing periods and released the following fall, as "yearlings" tend to mature later than earlier releases (Hankin 1990). Among wild salmon, however, size at ocean entry is negatively correlated with age at maturity (e.g., Vøllestad et al. 2004), and so yearling releases (of larger fish) may not delay maturity in all cases, although timing effects may predominate over the effects of size at release.

However, attempts to induce later maturation in hatchery fish would not be without complications. Although random or haphazard broodstock selection likely leads to unnaturally early maturation in hatchery salmon (Hankin et al. 2009), deliberately swinging the pendulum too far in the opposite direction and selecting for later maturation than natural fish could pose problems for "integrated" hatchery programs intended to match the life histories of natural-origin fish (California HSRG 2012). Yearling releases may be exposed to increased domestication selection due to their extended rearing in the hatchery and thus may introduce undesirable traits if spawning in natural areas or if used as broodstock upon their return (California HSRG 2012). In addition, later maturity may allow hatchery fish to grow larger, making them more effective competitors for spawning sites and having higher fecundity. Yearling releases could also increase the expense of hatchery operations due to their extended rearing, although due to higher survival of yearling releases and their increased exposure to the fishery (Hankin 1990), this may be partially compensated by the smaller number of yearling fish needed to yield the same fishery benefit as earlier releases. Also, because yearlings are released in the fall after naturally spawned juveniles have migrated to the ocean, this would likely decrease competition for instream resources (California HSRG 2012).

This higher survival of yearling releases would also, if all else is held constant, partially counter the benefit of later maturation in reducing hatchery impacts on natural-area spawning due to increases in the total number of surviving hatchery fish. Additionally, there is a trade-off between maturity and fecundity in which the lower fecundity of early-maturing fish reduces hatchery contributions to natural-area egg production and the potentially lower offspring survival from smaller eggs further reduces hatchery contributions to future generations (e.g., Kostow et al. 2003), whereas the higher fecundity and larger eggs of later-maturing hatchery fish could increase their genetic impacts. Finally, there is some evidence that older fish are more likely to stray (e.g., Quinn and Fresh 1984; Pascual et al. 1995), again potentially countering some of the benefit of later maturation of hatchery fish for natural-area spawning impacts.

Synthesis

Taken together, our results suggest that consideration of life history can help mediate between the conflicting hatchery goals of contributing to ocean harvest while reducing the impacts of hatchery spawners straying into natural areas. The roles of hatchery size and stray rates are already well appreciated (e.g., Grant 1997). It is also intuitively obvious that reduced fecundity of hatchery fish will reduce their contribution to juvenile production in natural areas, although the competitive and genetic consequences of low-fecundity spawners intermingling with natural-origin fish need to be carefully considered, especially in the context of "integrated hatcheries". Our model also quantifies the effects of maturation schedule and its interaction with fecundity effects, with delayed maturation increasing the contribution of hatchery fish to the harvest and decreasing the impacts of stray spawners in natural areas. In contrast, however, hatchery contributions to natural-area egg or juvenile production may sometimes increase with later maturity because older spawners have higher fecundity or higher survival from egg to fry. Thus, with the possible exception of egg–fry production, it appears hatcheries can best meet their conflicting goals by working to reduce stray rates and not foster early maturation. Which of these options is likely to provide greater returns is likely to be context-dependent. If stray rates are high (e.g., 80% or higher in some cases; Pascual et al. 1995), there is great scope to achieve benefits by reducing them, but if stray rates are minimal, reducing them further would yield diminishing returns. At least in some cases, there may be substantial scope for reducing early maturation rates (e.g., Hankin and Logan 2010 report as great as a 50% reduction in the age-3 maturation rate). Reducing the early maturation of hatchery fish may be especially helpful when the ocean fishery exploitation rate is high, skewing the spawner age composition toward younger fish. This suggests that steps to delay maturation in hatchery fish, or at least avoid unnaturally early maturation, may be an important alternative to consider in attempts to minimize hatchery impacts on natural areas while contributing to ocean harvest.

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References

Araki, H., Cooper, B., and Blouin, M.S. 2008. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science, **318**: 100–103. doi:10.1126/science.1145621. PMID:17916734.

Barnett-Johnson, R., Grimes, C.B., Royer, C.F., and Donohoe, C.J. 2007. Identifying the contribution of wild and hatchery Chinook salmon (*Oncorhynchus tshawytscha*) to the ocean fishery using otolith microstructure as natural tags. Can. J. Fish. Aquat. Sci. **64**(12): 1683–1692. doi:10.1139/f07-129.

Beacham, T.D. 2003. Comment on "Rapid evolution of egg size in captive salmon" (II). Science, **302**(5642): 59–59. PMID:14526063.

Beacham, T.D. 2010. Revisiting trends in the evolution of egg size in hatchery-enhanced populations of Chinook salmon from British Columbia. Trans. Am. Fish. Soc. **139**(2): 579–585. doi:10.1577/T09-093.1.

Bellinger, M.R., Banks, M.A., Bates, S.J., Crandall, E.D., Garza, J.C., Sylvia, G., and Lawson, P.W. 2015. Geo-referenced, abundance calibrated ocean distribution of Chinook salmon (*Oncorhynchus tshawytscha*) stocks across the West coast of North America. PLoS ONE, **10**: e0131276-25. doi:10.1371/journal.pone.0131276.

Brannon, E.L., Amend, D.F., Cronin, M.A., Lannan, J.E., LaPatra, S., McNeil, W.J., Noble, R.E., Smith, C.E., Talbot, A.J., Wedemeyer, G.A., and Westers, H. 2004. The controversy about salmon hatcheries. Fisheries, **29**(9): 12–31. doi:10.1577/1548-8446(2004)29[12:TCASH]2.0.CO;2.

California HSRG. 2012. California Hatchery Review Report [online]. California Hatchery Scientific Review Group. Prepared for the US Fish and Wildlife Service and Pacific States Marine Fisheries Commission. Available from http://cahatcheryreview.com/reports/.

Fleming, I.A., and Gross, M.R. 1993. Breeding success of hatchery and wild coho salmon (*Oncorhynchus kisutch*) in competition. Ecol. Appl. **3**(2): 230–245. doi:10.2307/1941826. PMID:27759325.

Fleming, I.A., Einum, S., Jonsson, B., and Jonsson, N. 2003. Comment on "Rapid evolution of egg size in captive salmon" (I). Science, **302**(5642): 59. PMID:14526064.

Grant, W.S. 1997. Genetic effects of straying of non-native hatchery fish into natural populations: proceedings of the workshop. NOAA Tech. Memo. NOAA-TM-NMFS-NWFSC-30.

Hankin, D.G. 1990. Effects of month of release of hatchery-reared Chinook salmon on size at age, maturation schedule and fishery contribution [online]. Oregon Dept. of Fish and Wildlife. Information Report 90-4. Available from http://docs.streamnetlibrary.org/Oregon/DFW/inforept90-4.pdf.

Hankin, D.G., and Healey, M.C. 1986. Dependence of exploitation rates for maximum yield and stock collapse on age and sex structure of chinook salmon (*Oncorhynchus tshawytscha*) stocks. Can. J. Fish. Aquat. Sci. **43**(9): 1746–1759. doi:10.1139/f86-219.

Hankin, D.G., and Logan, E. 2010. A preliminary analysis of Chinook salmon coded-wire tag recovery data from Iron Gate, Trinity River and Cole Rivers Hatcheries, brood years 1978–2004 [online]. Prepared for The Hoopa Valley Tribal Council and the Arcata Office, US Fish and Wildlife Service. Available from https://www.fws.gov/arcata/fisheries/reports/technical/IGHTRH.CWTanalysis2009%20Hankin%20Rpt.pdf.

Hankin, D.G., Nicholas, J.W., and Downey, T.W. 1993. Evidence for inheritance of age of maturity in chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **50**(2): 347–358. doi:10.1139/f93-040.

Hankin, D.G., Fitzgibbons, J., and Chen, Y. 2009. Unnatural random mating policies select for younger age at maturity in hatchery Chinook salmon (*Oncorhynchus tshawytscha*) populations. Can. J. Fish. Aquat. Sci. **66**(9): 1505–1521. doi:10.1139/F09-085.

Hard, J.J., Jones, R.P., Jr., Delarm, M.R., and Waples, R.S. 1992. Pacific salmon and artificial propagation under the Endangered Species Act. NOAA Tech. Memo. NMFS-NWFSC-2.

Healey, M.C., and Heard, W.R. 1984. Inter- and intra-population variation in the fecundity of chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. Can. J. Fish. Aquat. Sci. **41**(3): 476–483. doi:10.1139/f84-057.

Heath, D.D., Fox, C.W., and Heath, J.W. 1999. Maternal effects on offspring size: variation through early development of Chinook salmon. Evolution, **53**(5): 1605–1611. doi:10.2307/2640906.

Heath, D.D., Heath, J.W., Bryden, C.A., Johnson, R.M., and Fox, C.W. 2003. Rapid evolution of egg size in captive salmon. Science, **299**(5613): 1738–1740. doi:10.1126/science.1079707. PMID:12637746.

Hilborn, R. 1998. The economic performance of marine stock enhancement projects. Bull. Mar. Sci. **62**(2): 661–674.

Hilborn, R., and Eggers, D. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Trans. Am. Fish. Soc. **129**(2): 333–350. doi:10.1577/1548-8659(2000)129<0333:AROTHP>2.0.CO;2.

Hilborn, R., and Hare, S.R. 1992. Hatchery and wild fish production of anadromous salmon in the Columbia River basin [online]. Fisheries Research Institute Tech. Rep. FRI-UW-9207. Available from https://digital.lib.washington.edu/researchworks/bitstream/handle/1773/4173/9207.pdf?sequence.

Hinrichsen, R.A., Steele, C.A., Ackerman, M.W., Campbell, M.R., Narum, S.R., Hess, M.A., Young, W.P., Shields, B.A., Nez Perce Tribe, and Maschhoff, B.L. 2016. Maximum likelihood estimation of the proportion of hatchery-origin fish on spawning grounds using coded wire tagging and parentage-based tagging. Trans. Am. Fish. Soc. **145**(3): 671–686. doi:10.1080/00028487.2016.1146163.

HSRG. 2009. Columbia River hatchery reform system-wide report [online]. Hatchery Scientific Review Group. Bonneville Power Administration and NOAA Fisheries. Available from http://hatcheryreform.us/hrp/uploads/C1EKAOMVHURK/01_HSRG%20Final%20Systemwide%20R eport.pdf.

HSRG. 2014. On the science of hatcheries: an updated perspective on the role of hatcheries in salmon and steelhead management in the Pacific Northwest [online]. Hatchery Scientific Review Group. Available from http://hatcheryreform.us/reports/columbia-river/system-wide-report/.

Johnson, R.C., Weber, P.K., Wikert, J.D., Workman, M.L., MacFarlane, R.B., Grove, M.J., and Schmitt, A.K. 2012. Managed metapopulations: Do salmon hatchery 'sources' lead to in-river 'sinks' in conservation? PLoS ONE, **7**(2): e28880. doi:10.1371/journal.pone.0028880. PMID:22347362.

Johnson, S.L., Solazzi, M.F., and Nickelson, T.E. 1990. Effects on survival and homing of trucking hatchery yearling coho salmon to release sites. N. Am. J. Fish. Manage. **10**(4): 427–433. doi:10.1577/1548-8675(1990)010<0427:EOSAHO>2.3.CO;2.

Jonsson, N., Jonsson, B., and Hansen, L.P. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. J. Appl. Ecol. **40**(5): 900–911. doi:10.1046/j.1365-2664.2003.00851.x.

Kaufman, R.C., Houck, A.G., Workman, M., and Cech, J.J., Jr. 2009. Chinook salmon length/fecundity: a regression model for the Mokelumne River, California. Calif. Fish Game, **95**(2): 88–105.

Keefer, M.L., and Caudill, C.C. 2012. A review of adult salmon and steelhead straying with an emphasis on Columbia River populations [online]. Technical Report 2012-6. Department of Fish and Wildlife Resources, College of Natural Resources, University of Idaho. Available from http://www.dfw.state.or.us/fish/OHRC/docs/2013/pubs/steelhead_and_salmon_straying.pdf.

Kinnison, M.T., Unwin, M.J., Hendry, A.P., and Quinn, T.P. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. Evolution, **55**(8): 1656–1667. doi:10.1111/j.0014-3820.2001.tb00685.x. PMID:11580025.

Knudsen, C.M., Schroder, S.L., Busack, C.A., Johnston, M.V., Pearsons, T.N., Bosch, W.J., and Fast, D.E. 2006. Comparison of life history traits between first-generation hatchery and wild upper Yakima River spring Chinook salmon. Trans. Am. Fish. Soc. **135**(4): 1130–1144. doi:10.1577/T05-121.1.

Kormos, B., Palmer-Zwahlen, M., and Low, A. 2012. Recovery of coded-wire tags from Chinook salmon in California's Central Valley escapement and ocean harvest in 2010. Technical report, California Department of Fish and Game Fisheries Branch Administrative Report 2012-02.

Kostow, K.E., Marshall, A.R., and Phelps, S.R. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. Trans. Am. Fish. Soc. **132**(4): 780–790. doi:10.1577/T02-051.

Lasko, G.R., Titus, R.G., Ferreira, J.R., and Coleman, R.M. 2014. Straying of late-fall run Chinook salmon from the Coleman National Fish Hatchery into the lower American River, California. Calif. Fish Game, **100**(4): 665–682.

Mangel, M. 1994. Climate change and salmonid life-history variation. Deep-Sea Res. II Top. Studies Oceanogr. **41**: 75–106. doi:10.1016/0967-0645(94)90063-9.

McHugh, P., Johnson, G., and Schaffler, J. 2015. Chinook FRAM Base Period Documentation: Growth functions [online]. Report to Pacific Fishery Management Council. Available from http://www.pcouncil.org/wp-content/uploads/2015/10/D2_Att2_FRAM_Growth_Meth_Nov2015BB.pdf.

Morita, K., Saito, T., Miyakoshi, Y., Fukuwaka, M.A., Nagasawa, T., and Kaeriyama, M. 2006. A review of Pacific salmon hatchery programmes on Hokkaido Island, Japan. ICES J. Mar. Sci. **63**(7): 1353–1363. doi:10.1016/j.icesjms.2006.03.024.

Naish, K.A., Taylor, J.E., Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, D., and Hilborn, R. 2008. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. Adv. Mar. Biol. **53**: 61–194. doi:10.1016/S0065-2881(07)53002-6. PMID:17936136.

Nickelson, T. 2003. The influence of hatchery coho salmon (*Oncorhynchus kisutch*) on the productivity of wild coho salmon populations in Oregon coastal basins. Can. J. Fish. Aquat. Sci. **60**(9): 1050–1056. doi:10.1139/f03-091.

O'Farrell, M.R., Palmer-Zwahlen, M.L., and Simon, J. 2010. Is the September 1 river return date approximation appropriate for Klamath River fall Chinook? NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-468.

O'Farrell, M.R., Satterthwaite, W.H., and Spence, B.C. 2012*a*. California Coastal Chinook salmon: status, data, and feasibility of alternative fishery management strategies. NOAA Tech. Memo. NMFS-SWFSC-494.

O'Farrell, M.R., Mohr, M.S., Grover, A.M., and Satterthwaite, W.H. 2012*b*. Sacramento River winter Chinook cohort reconstruction: analysis of ocean fishery impacts. NOAA Tech. Memo. NMFS-SWFSC-491.

PFMC. 2016. Pacific Coast salmon fishery management plan for commercial and recreational salmon fisheries off the coasts of Washington, Oregon, and California as revised through amendment 19. Pacific Fishery Management Council, 7700 NE Ambassador Place, Suite 101, Portland, OR 97220-1384, USA.

Palmer-Zwahlen, M., and Kormos, B. 2013. Recovery of coded-wire tags from Chinook salmon in California's Central Valley escapement and ocean harvest in 2011. Technical report, California Department of Fish and Game Fisheries Branch Administrative Report 2013-02.

Palmer-Zwahlen, M., and Kormos, B. 2015. Recovery of coded-wire tags from Chinook salmon in California's Central Valley escapement and ocean harvest in 2012. Technical report, California Department of Fish and Game Fisheries Branch Administrative Report 2015-04.

Pascual, M.A., Quinn, T.P., and Fuss, H. 1995. Factors affecting the homing of fall Chinook salmon from Columbia River hatcheries. Trans. Am. Fish. Soc. **124**(3): 308–320. doi:10.1577/1548-8659(1995)124<0308:FATHOF>2.3.CO;2.

Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fish. Res. **18**(1–2): 29–44. doi:10.1016/0165-7836(93)90038-9.

Quinn, T.P., and Fresh, K. 1984. Homing and straying in chinook salmon (*Oncorhynchus tshawytscha*) from Cowlitz River Hatchery, Washington. Can. J. Fish. Aquat. Sci. **41**(7): 1078–1082. doi:10.1139/f84-126.

Ruckelshaus, M.H., Levin, P., Johnson, J.B., and Kareiva, P.M. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annu. Rev. Ecol. Syst. **33**(Jan. 1): 665–706. doi:10.1146/annurev.ecolsys.33.010802.150504.

Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., and Wells, B.K. 2012. A Bayesian hierarchical model of size-at-age in ocean-harvested stocks — quantifying effects of climate and temporal variability. Can. J. Fish. Aquat. Sci. **69**(5): 942–954. doi:10.1139/f2012-036.

Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., and Wells, B.K. 2013. A comparison of temporal patterns in the ocean spatial distribution of California's Central Valley Chinook salmon runs. Can. J. Fish. Aquat. Sci. **70**(4): 574–584. doi:10.1139/cjfas-2012-0395.

Satterthwaite, W.H., Carlson, S.M., Allen-Moran, S.D., Vincenzi, S., Bograd, S.J., and Wells, B.K. 2014*a*. Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of Central Valley fall run Chinook salmon. Mar. Ecol. Prog. Ser. **511**: 237–248. doi:10.3354/meps10934.

Satterthwaite, W.H., Mohr, M.S., O'Farrell, M.R., Anderson, E.C., Banks, M.A., Bates, S.J., Bellinger, M.R., Borgerson, L.A., Crandall, E.D., Garza, J.C., Kormos, B.J., Lawson, P.W., and Palmer-Zwahlen, M.L. 2014*b*. Use of genetic stock identification data for comparison of the ocean spatial distribution, size at age, and fishery exposure of an untagged stock and its indicator: California Coastal versus Klamath River Chinook salmon. Trans. Am. Fish. Soc. **143**(1): 117–133. doi:10.1080/00028487.2013.837096.

Satterthwaite, W.H., Ciancio, K., Crandal, E., Palmer-Zwahlen, M.L., Grover, A.M., O'Farrell, M.R., Anderson, E.C., Mohr, M.S., and Garza, J.C. 2015. Stock composition and ocean spatial distribution inference from California recreational Chinook salmon fisheries using genetic stock identifications. Fish. Res. **170**: 166–178. doi:10.1016/j.fishres.2015.06.001.

Seelbach, P., and Whelan, G. 1988. Identification and contribution of wild and hatchery steelhead stocks in Lake Michigan tributaries. Trans. Am. Fish. Soc. **117**(5): 444–451. doi:10.1577/1548-8659(1988)117<0444:IACOWA>2.3.CO;2.

Solazzi, M.F., Nickelson, T.E., and Johnson, S.L. 1991. Survival, contribution, and return of hatchery coho salmon (*Oncsrhynchus kisutch*) released into freshwater, estuarine, and marine environments. Can. J. Fish. Aquat. Sci. **48**(2): 248–253. doi:10.1139/f91-034.

Swain, D.P., Riddell, B.E., and Murray, C.B. 1991. Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. Can. J. Fish. Aquat. Sci. **48**(9): 1783–1791. doi:10.1139/f91-210.

Utter, F. 1998. Genetic problems of hatchery-reared progeny released into the wild, and how to deal with them. Bull. Mar. Sci. **62**(2): 623–640.

Vainikka, A., Kallio-Nyberg, I., Heino, M., and Koljonen, M.L. 2010. Divergent trends in life-history traits between Atlantic salmon *Salmo salar* of wild and hatchery origin in the Baltic Sea. J. Fish Biol. **76**(3): 622–640. doi:10.1111/j.1095-8649.2009.02520.x. PMID:20666901.

Vøllestad, L.A., Peterson, J., and Quinn, T.P. 2004. Effects of freshwater and marine growth rates on early maturity in male coho and Chinook salmon. Trans. Am. Fish. Soc. **133**(3): 495–503. doi:10.1577/T03-033.1.

Vreeland, R.R., Wahle, R.J., and Arp, A.H. 1975. Homing behavior and contribution to Columbia River fisheries of marked coho salmon released at two locations. Fish. Bull. **73**: 717–725.

Waples, R.S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. Can. J. Fish. Aquat. Sci. **48**(S1): 124–133. doi:10.1139/f91-311.

Westley, P.A.H., Quinn, T.P., and Dittman, A.H. 2013. Rates of straying by hatchery-produced Pacific salmon (*Oncorhynchus* spp.) and steelhead (*Oncorhynchus mykiss*) differ among species, life history types, and populations. Can. J. Fish. Aquat. Sci. **70**(5): 735–746. doi:10.1139/cjfas-2012-0536.

Williams, J.G. 2006. Central Valley salmon: a perspective on Chinook and steelhead in the Central Valley of California. San Francisco Estuary and Watershed Science, **4**(3): Art. 2.

Williams, M.C. 2012. Spatial, temporal, and cohort-related patterns in the contribution of wild Chinook salmon (*Oncorhynchus tshawytscha*) to total Chinook harvest in Lake Michigan [online]. Ph.D. thesis, Michigan State University, East Lansing, Michigan. Available from http://qfc.fw.msu.edu/Publications/Theses_Dissertations/2012/MWilliams_thesis.pdf.

Zaugg, W.S., Roley, D.D., Prentice, E.F., Gores, K.X., and Waknitz, F.W. 1983. Increased seawater survival and contribution to the fishery of chinook salmon (*Oncorhynchus tshawytscha*) by supplemental dietary salt. Aquaculture, **32**(1): 183–188. doi:10.1016/0044-8486(83)90280-6.