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

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

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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 tradeoff 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.

33 Introduction

34 Given current freshwater habitat conditions in much of their range, an economically
35 viable Pacific salmon (*Oncorhynchus* spp.) fishery likely depends on supplementation via
36 hatchery production (Brannon 2004) but the net effect of hatcheries coastwide is difficult to
37 ascertain (e.g., Hilborn et al. 1998; Ruckelshaus 2002; Morita et al. 2006) due to the complex
38 interactions between hatchery and wild fish (Waples 1999; Naish et al. 2008). In addition,
39 serious concerns have been raised about the effects that hatchery-origin fish have on naturally-
40 spawning populations through competition for limited resources (e.g., Hilborn & Hare 1992;
41 Kostow et al. 2003) and genetic introgression (e.g., Waples 1991; Utter 1998; Araki et al. 2008).
42 Therefore, large production hatcheries are generally managed for multiple, sometimes
43 conflicting goals: to boost overall fish production, and thus fishery harvest opportunity, while
44 also controlling the impacts of straying fish on natural-area spawners and wild fish population
45 dynamics. Ideally, hatchery-origin fish from large production hatcheries would make a large
46 contribution to harvest and a small contribution to natural-area spawning, although hatchery
47 fish spawning in natural areas adjacent to hatcheries are compatible with the goals of
48 "integrated" hatchery programs (HSRG 2009).

49 Hatchery contributions to fishery harvest opportunity are obviously increased when
50 hatcheries release more fish, or when fish are released in a way that increases survival from the
51 juvenile phase until recruitment to the fishery. Therefore, all else being equal, harvest
52 opportunity is increased by hatchery practices that increase juvenile survival (Johnson et al.
53 1990; Solazzi et al. 1991; Satterthwaite et al. 2014a) and/or the rate at which hatchery fish
54 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 (*O. 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. 2011) 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 & 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 & Whelan 1998; 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 & Heard 1983; 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: 1. the proportion hatchery-origin among natural-area spawners (p_{HOS}), 2. the proportion hatchery-origin among natural-area eggs produced (p_{HOG}), 3. the proportion hatchery origin among ocean-harvested fish (p_{HOC}), 4. the proportion of surviving hatchery-origin fish that end up in ocean harvest rather than returning to spawn (p_C), 5. the proportion of hatchery-origin fish that end up spawning in natural areas rather than ocean harvest or returning to the hatchery (p_S), and 6. 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 last three metrics compare the per-capita fates of hatchery fish (and so do not depend on relative population sizes). *CPS* directly captures the tradeoff, 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 $a + 1$) 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 which 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 area production, we note that this lifestage may not be referred to as age 1 in other studies), juvenile survival p_1 from release/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:

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

We also calculate the ocean catch (C_a) of age a fish, as well as the number of fish returning to spawn in freshwater (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:

$$(2) \quad C_a = f_a N_a;$$

$$(3) \quad R_a = b_a (1 - f_a) N_a.$$

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):

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

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

162 natural areas ($R_{a,w}$ for natural-origin fish and $S_{a,h}$ for hatchery-origin fish) and their age-specific
 163 fecundities (g_a):

164 (5) $G_{a,w} = R_{a,w} g_{a,w} ;$

165 (6) $G_{a,h} = S_{a,h} g_{a,h} .$

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

179 *Baseline parameterization*

180 Our model is intended to reflect a realistic set of vital rates for a Chinook salmon
 181 population but not provide quantitative advice for any specific system. However, to establish
 182 plausible values and ranges for parameters, we loosely based most of our parameterization on

data from Klamath River Fall Chinook (KRFC), 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 KRFC of 0.16 (strongly constrained by the co-occurring threatened California Coastal Chinook stock, O'Farrell et al. 2012a) and the Pacific Fishery Management Council's default fishing mortality rate corresponding to maximum yield (F_{MSY}) for Chinook salmon, 0.78 (Pacific Fishery Management Council 2016). The baseline value of $e = 0.5$ appears roughly consistent with the average fraction of adults removed from Sacramento River Fall Chinook (O'Farrell et al. 2012b), 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 $\gamma = 0.3$ 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.

205 2012), but we picked this value for use in displaying the effects of changes in other parameters
206 when y is held constant because it is well within the range reported for hatchery releases
207 (Pascual et al. 1995). Baseline age-specific fecundity was modeled after Mokelumne River fall-
208 run Chinook salmon from California's Central Valley (Kaufman et al. 2009).

209 *Perturbation analyses*

210 To understand the impacts of variation in life history parameters potentially affected by
211 hatchery practices, we varied parameters individually with respect to the baseline and also
212 explored interactive effects of sets of variables which analysis of our metrics (below) showed
213 could mediate a tradeoff between the conflicting hatchery goals of supplementing harvest
214 while avoiding strays spawning in natural areas. We held natural-origin parameters constant in
215 all projections. We varied stray rate (y) over the range 0.01 to 0.90 to encompass the wide
216 range of values reported in the literature (e.g., Pascual et al. 1995; Westley et al. 2013) and
217 varied the fully vulnerable fishing mortality (e) from 0.1 to 0.8 based loosely on O'Farrell et al.
218 (2012a) and PPMC (2016), respectively, as described in deriving the baseline e .

219 Remaining life history parameters were perturbed from their baseline values by
220 applying a range of multipliers denoted by ϕ_x , with the subscript x representing the parameter
221 being multiplied. Because initial cohort size (N_1) and juvenile survival (p_1) only appear in our
222 model as a product, we varied their joint outcome N_2 by applying a cohort ratio ($\phi_N = N_{2,h}:N_{2,w}$)
223 varying from 0.1 to 8 to allow for a range of scenarios between a small hatchery program in
224 conjunction with a small stock to a hatchery-dominated system where over 90% of fish are of
225 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. 2012b). 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 significantly at some hatcheries (e.g., Williams 2006), and obtaining accurate estimates of fecundity is difficult and empirical estimates must be interpreted with caution (Beacham et al. 2003; Fleming et al. 2003; Beacham 2010). We model hatchery fish fecundity by applying the scalar multiplier ($\phi_g = g_{x,h} : g_{x,w}$ ranging from 0.1 to 8, hereafter '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 ($C_{T,w}$):

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

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

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

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 tradeoff 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:

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

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 (p_{HOS}) we also calculate the proportion of hatchery fish ending up as strays spawning in natural areas (p_S) as:

$$(11) \quad p_S = \frac{S_{T,h}}{R_{T,h} + C_{T,h}}.$$

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

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

$$(12) \quad CPS = \frac{C_{T,h}}{S_{T,h}}.$$

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 (p_{HOS}) and among ocean catch (p_{HOC}), but do not alter the proportion of hatchery fish ending up in ocean catch (p_C) or spawning in the wild (p_S) because both of these measures are standardized to the size of hatchery cohorts (see Fig. 2a). Maturation ratios (ϕ_b) affect all four metrics (p_{HOS} , p_{HOC} , p_C , p_S) 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. 2b). Earlier maturation (higher ϕ_b) decreases p_{HOC} and p_C as more hatchery fish leave the ocean earlier and are therefore exposed to less fishing hazard, but earlier maturation increases p_{HOS} and p_S since early-maturing hatchery fish are more likely to survive and contribute to natural-area spawning (see Fig. 2b). Higher fishing intensity (e) increases p_C and reduces p_S as more hatchery fish are caught before they return to spawn, but the proportion hatchery-origin among spawners (p_{HOS}) and ocean catch (p_{HOC}) are unaltered because fishing intensity affects hatchery and natural-origin fish equally (see Fig. 2c). Higher stray rates (y) directly increase the proportion of hatchery-origin fish that end up spawning in natural areas (p_S) and the proportion of natural area spawners that are of hatchery origin (p_{HOS} , see Fig. 2d). 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 p_{HOS} saturation at 50% of natural-area spawners (see Fig. 2d). Neither p_C nor p_{HOC} respond to stray rates of fish that have already left the ocean to spawn (see Fig. 2d).

Hatchery contributions to natural-area spawning

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

$pHOS$ responds more to increasing stray rates when stray rates are initially low (Fig. 3a, d, e) but responds more to higher cohort ratios when cohort ratios are large (Fig. 3c, d, 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 fecundity ratios (ϕ_g) act in conjunction with higher stray rates (γ) to increase $pHOG$ (Fig. 4a) in exactly the same manner they interact with hatchery cohort ratios (ϕ_N , Fig. 4b). The two scalar multipliers ϕ_g and ϕ_N compound their effects on $pHOG$ (Fig. 4c). Like spawner proportions ($pHOS$, Fig. 3), egg proportions ($pHOG$) respond more to increasing maturation ratios (ϕ_b) when maturity is late

(low ϕ_b , Fig. 4d-g) and respond more to increasing cohort ratios (ϕ_N) when hatchery cohorts are large (high ϕ_N , Fig. 4b, c, and e), and $pHOG$ responds identically to changes in cohort ratios (ϕ_N) or fecundity ratios (ϕ_g , compare Fig. 4e and f). Also like spawner proportions, egg proportions show little response to increasing maturity ratios (ϕ_b) beyond ϕ_b^* (Fig. 4d-g). Higher fishing intensity (e) increases $pHOG$ when hatchery fish mature late ($\phi_b < 1$) and higher fishing intensity decreases $pHOG$ when hatchery fish mature early ($\phi_b > 1$, Fig. 4g).

Hatchery contributions to ocean harvest

The proportion of ocean catch comprising hatchery-origin fish ($pHOC$) goes up with larger cohort ratios (ϕ_N), with the largest effect from a given change in cohort ratios occurring when hatchery and natural-origin cohorts have similar initial abundance ($\phi_N \approx 1$, Fig. 5a, 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 (Fig. 5b, c). When hatchery fish mature late ($\phi_b < 1$), increasing fishing intensity (e) reduces the proportion hatchery-origin in ocean catch ($pHOC$) but when hatchery fish mature early ($\phi_b > 1$) increasing fishing intensity increases $pHOC$ (Fig. 5b).

Catch per stray spawner (CPS) increases with fishing intensity (e , Fig. 5d, e) and decreases with both stray rate (y , Fig. 5d, f) and maturation ratios (ϕ_b , Fig. 5e, 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 tradeoff.

By exploring the effects of multiple parameters individually or in concert, we have 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). Effects of straying and maturation rates on catch per stray spawner weaken but are not reversed if fishing vulnerability decreases with age (online supplement, Fig S2), 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, 2014b), 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 vs. 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) increase both the number of hatchery fish harvested and the number of hatchery fish escaping to natural spawning areas, exacerbating the tradeoff

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 tradeoff. 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 (*pS* and *pC*, the proportion straying or caught) 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 tradeoff 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 et al. 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 Healy 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., Vollestad 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 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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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 <i>natural areas</i>	(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 ($\phi_N, \phi_b, \phi_g, e, y$) along with (min, max) of perturbation

Figure Legends

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.

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.

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. Top row (*a-c*) predicts the proportion of ocean harvest that would be of hatchery-origin (*pHOC*) under different 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 ($\phi_N = 1$, $\phi_b = 1$, $e = 0.5$, $y = 0.3$). Bottom row (*d-f*) predicts 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 stray rates (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).

Natural production

Hatchery production

Supplementary materials

In the main text, we present sensitivity analyses to parameter values and multipliers individually and in pairwise combinations, but assume the same effects age on fecundity and fishery vulnerability throughout. In this supplement, we explore the consequences of relaxing this assumption for the effects of stray rate and maturation ratios on catch per stray spawner (*CPS*) or catch per stray egg (*CPG*). We focus on these metrics because they are independent of the overall scale of hatchery versus natural production, and focus on maturation and stray rates because we are most interested in the capacity for altered stray rates or maturation schedules to alter the tradeoff between hatchery contributions to harvest versus natural area spawning and egg production.

Fig. S1 shows the consequences of relaxing the assumption that fecundity increases with age. Since fecundity only affects egg number, we present the effects of stray rate and maturation ratios on *CPG* under different fecundity scenarios. In the baseline scenario, age specific fecundities $\{g_2, g_3, g_4, g_5\} = \{2100, 2900, 3000, 3700\}$, in the "flat" scenario $g_{2-5} = 3000$, and in the "reversed" scenario $\{g_2, g_3, g_4, g_5\} = \{3700, 3000, 2900, 2100\}$. Results are highly similar both qualitatively and quantitatively across this range of scenarios (Fig. S1a-S1c, note that close inspection reveals that the plots are not identical). To confirm that our model was capable of responding to extreme changes in the typical fecundity schedule, we verified that making the youngest fish much more fecund than older fish (biologically implausible, $g_2 = 3000$ and $g_{3-5} = 100$) yielded a detectable change in the contour plot, although the qualitative effects of increased stray rate or maturation rate are preserved (Fig. S1d).

Fig. S2 shows the consequences of replacing the default "selectivity" on different age classes by the fishery ($\{q_2, q_3, q_4, q_5\} = \{0.05, 0.5, 1, 1\}$, Fig. S2a) with weaker selectivity (making younger fish more vulnerable, and thus increasing overall exploitation for a given fishery intensity, $\{q_2, q_3, q_4, q_5\} = \{0.25, 0.75, 1, 1\}$, Fig. S2b) or a non-selective fishery (thus increasing total exploitation even further, $q_{2-5} = 1$, Fig. S2c). Finally, we explore an implausible decrease in vulnerability with

age ($\{q_2, q_3, q_4, q_5\} = \{1, 0.75, 0.5, 0.25\}$) in Fig. S2d. The qualitative pattern is the same in all cases, with *CPS* reduced by earlier maturation or higher stray rates. Overall catch per stray goes up as selectivity is reduced (young fish are more vulnerable) because total catch is higher and fewer fish survive to spawn.

Fig. S1. Natural log of catch per stray egg (*CPG*) as a function of maturation ratio and stray rate under the baseline scenario for fecundity increasing with age (a), no effect of age on fecundity (b), a decline of fecundity with age (c), or an extreme decline of fecundity with age (d).

Fig. S2. Natural log of catch per stray spawner (*CPS*) as a function of maturation ratio and stray rate under the baseline scenario for fishing vulnerability increasing with age (a), a less selective fishery in which old fish are still most vulnerable (b), a nonselective fishery (c), or a decline of fishery vulnerability with age (d).