Implications of Mark-Selective Fishing for Ocean Harvests and Escapements of Sacramento River Fall Chinook Salmon Populations

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Implications of Mark-Selective Fishing for Ocean Harvests and Escapements of Sacramento River Fall Chinook Salmon Populations

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Abstract
The need to protect imperiled salmon stocks along the Pacific coast of North America has led to an increasing use of mark-selective fisheries (MSFs) as a management strategy to reduce harvest mortality of wild salmon while allowing harvest of abundant hatchery salmon. However, MSFs remain untested in ocean fisheries for Chinook salmon Oncorhynchus tshawytscha off the coasts of California and Oregon, where hatchery fish have been estimated to compose the majority of Chinook salmon but where harvests have been restricted to protect several imperiled stocks. We developed a quantitative framework based on conventional cohort models to examine how aggregate ocean harvest and in-river escapement of Sacramento River fall-run Chinook salmon, the numerically dominant stock in the region, would have differed under MSF scenarios compared with the historic, traditional fishery. At historic contact rates (fishing effort) for 1988–2007, we estimated that annual in-river escapement of natural-origin fish would have increased by 119% on average under MSF scenarios, while reductions in harvest would have been inversely proportional to the fraction of hatchery-origin fish. During the more recent period of constrained fishing (2001–2007), we estimated MSF outcomes for a range of plausible contact rates (40–60% of age-4 fish) and hatchery fractions (40–80% of Chinook salmon). The combination of these factors determined the magnitude of estimated harvest reductions or gains under MSFs, with total MSF harvest (2001–2007) ranging from 46% lower to 48% higher than historic harvest. Increases in total escapement of natural-origin fish (2001–2007) under MSFs ranged from 24% to 48% depending on the contact rate. Comparisons between the traditional fishery and simulated MSF outcomes were robust to a wide range of cohort parameter values, suggesting that our aggregate results provide useful insights into potential MSF outcomes and the effects of key uncertainties.

The need to protect imperiled salmon stocks along the Pacific coast of North America (Good et al. 2007) has led to an increasing use of mark-selective fisheries (MSFs) as a management strategy for reducing harvest mortality on threatened or endangered wild salmon runs while allowing for harvest of abundant hatchery salmon (Hoffman and Patillo 2008; PSC 2009). Restrictions on harvesting to allow retention only of marked hatchery fish have enabled fisheries to continue at some times and in some areas where harvesting would otherwise be prohibited. The mass marking of hatchery juvenile salmon (i.e., removal of the adipose fin) is a necessary precursor to MSFs, enabling recreational and commercial harvesters to identify and legally retain hatchery fish in ocean and river fisheries. Currently, virtually all hatchery coho salmon Oncorhynchus kisutch from southern British Columbia, Washington, and Oregon are mass-marked, and numerous MSFs have been instituted in these regions to target hatchery fish (PSC 2009). Marking of hatchery Chinook salmon O. tshawytscha in Washington and Oregon increased from roughly 5% of juveniles released from the 1997 brood to 80% of the planned release of 135 million juveniles.
from the 2008 brood (PSC 2009). Washington State, which pioneered ocean MSFs for coho salmon and Chinook salmon in Puget Sound (Hoffman and Patillo 2008), is rapidly expanding the use of MSFs to many ocean and freshwater areas (PSC 2009).

The counterbalancing goals of society and fisheries management (i.e., to both conserve and exploit salmon populations) have fueled the debate as to whether hatchery-produced salmon are more of a risk or a benefit to the recovery of weak stocks (e.g., Brannon et al. 2004; HSRG 2005). Hatchery salmon can pose risks to the viability of wild populations through interbreeding and attraction of fishing effort (Ruckelshaus et al. 2002; Good et al. 2005). Under some circumstances, however, hatchery fish have been used as a tool to help sustain endangered populations while also providing alternative harvest opportunities (Brannon et al. 2004; Good et al. 2005; HSRG 2005). Broad regional efforts to design hatchery reforms that reduce impacts of hatchery fish on wild populations have concluded that hatcheries and harvest are integrally linked in current salmon management and that important hatchery reforms cannot succeed without harvest reform (Blankenship and Daniels 2004; HSRG 2005, 2009). To this end, mass marking has been recommended as a potentially valuable tool for both harvest management and hatchery reform, allowing fisheries to target hatchery fish and providing a means to identify, monitor, and potentially limit hatchery fish in natural spawning areas (Blankenship and Daniels 2004; Olson et al. 2004; HSRG 2005).

The use of mass marking in combination with MSFs has not been tested or formally proposed for Chinook salmon in the extensive ocean fisheries of California and southern Oregon (Figure 1), although several factors suggest that the use of MSFs would be beneficial. These mixed-stock fisheries are dominated by Sacramento River fall-run Chinook salmon (SRFC) of California’s Central Valley (CV; Winans et al. 2001; O’Farrell et al. 2008). Hatchery releases of SRFC (roughly 25 million juveniles/year) currently represent the largest predominately unmarked hatchery group south of British Columbia. The proportion of hatchery fish among the returning adult SRFC is unknown but may be as high as 90% (Barnett-Johnson et al. 2007). However, ocean fisheries that target abundant SRFC are constrained by regulations designed to limit harvests of Endangered Species Act (ESA)-listed Chinook salmon stocks (Sacramento River winter run, CV spring run, and California coastal [CC] fall run); in several recent years, fisheries were also heavily constrained to protect Klamath River Chinook salmon (PFMC and NMFS 2007; KRTAT 2009). Moreover, beginning in 2007, SRFC experienced dramatic declines in abundance (O’Farrell et al. 2008), raising concerns over the long-term viability of SRFC populations and the ocean fisheries they support.

For Chinook salmon, however, the expansion of MSF strategies is controversial (PSC 2005; PSC 2008). Broad-scale applications of MSFs will seriously undermine aspects of current management frameworks and monitoring programs that rely on the recovery of coded-wire tags (CWTs; PSC 2005, 2008). For several decades, the adipose fin clip has been the unique identifier of hatchery and wild Chinook salmon that have been tagged with CWTs. Consequently, under MSFs, it would not be possible to directly estimate fishery-specific exploitation rates and incidental mortality of unmarked (wild) fish by using CWTs (PSC 2005). The mass marking of hatchery juveniles is costly and also complicates sampling programs that are designed to recover CWTs in fishery and spawning areas (PSC 2005). Thus, implementation of MSF programs is expensive and logistically difficult and compromises key management information. Moreover, the ability of MSFs to protect depressed wild stocks will depend critically on the catch-and-release mortality rates of unmarked fish (Lawson and Sampson 1996), which may be substantial in some fisheries (e.g., Grover et al. 2002).

Clearly, a comprehensive evaluation of the potential utility of an MSF program directed at SRFC would require the consideration of numerous factors. Prominent among them is an examination of the potential effects of MSFs on harvest and spawning escapement of naturally producing populations. Indeed, while broad use of MSFs for ocean harvesting of salmon was recommended in the programmatic environmental impact statement prepared by the National Marine Fisheries Service (NMFS 2003), it was “with the caveat that the benefits to the fishery and to natural escapement would have to be evaluated against the cost on a case-by-case basis.”

In this paper, we use retrospective analyses to examine how ocean harvests and in-river escapements of SRFC would differ under MSF scenarios in comparison with the historic, traditional fishery. Current data limitations for SRFC present analytical challenges and preclude precise inferences of MSF outcomes, particularly for harvests, which depend on unknown abundances of hatchery fish. Thus, our goal was to develop a quantitative framework—based on conventional cohort models used in assessments of California Chinook salmon hatchery populations—to determine plausible and informative ranges of MSF outcomes for SRFC and the key uncertainties affecting those outcomes. We focus on aggregate measures of ocean harvest and in-river escapement, which provide useful insight for comparing the expected outcomes of transitioning from the traditional fishery to MSFs.

STUDY AREA AND FISHERIES

Ocean fisheries for Chinook salmon that extend from Cape Falcon, Oregon, to as far south as Monterey, California (Figure 1), are regulated by the Pacific Fishery Management Council (PFMC) in cooperation with state and tribal agencies. Commercial and recreational fishing is typically conducted by trolling, although a technique known as “mooching” has become popular in recreational fisheries of southern California (Boydstun 2001; Grover et al. 2002). Since the mid-1970s, commercial harvests have accounted for roughly 75% of the Chinook salmon landed at California ports (NMFS 2003; O’Farrell et al. 2008).

Ocean abundances in this region have been dominated by Chinook salmon from California’s CV, particularly the
FIGURE 1. Map of ocean fishery boundaries, major Chinook salmon hatcheries, and locations of Endangered Species Act-listed groups of Chinook salmon in California and southern Oregon. The hatcheries shown are those typically contributing to catches in the Central Valley Index Area and Klamath Management Zone (Mtn. = Mountain; R. = River).
hatchery-supplemented populations of SRFC (Winans et al. 2001; O’Farrell et al. 2008). For example, genetic sampling of Chinook salmon landed in test fisheries from 1997 to 1999 found that 89–95% of the fish caught from Point Conception to Bodega Bay (Figure 1) were CV fall-run Chinook salmon (Winans et al. 2001), while roughly 60% of the Chinook salmon sampled from central Oregon troll fisheries in 2006 were CV Chinook salmon (CROOS 2007a). These fisheries have frequently been constrained to protect ESA-listed Chinook salmon stocks (CV winter run, CV spring run, and CC), which constitute less than 10% of available Chinook salmon (Winans et al. 2001).

Abundances of hatchery-origin Chinook salmon in these fisheries have been substantial but rarely quantified. Currently, at least 30 hatchery programs produce and release about 32 million juvenile Chinook salmon in rivers south of Cape Falcon (Pacific States Marine Fisheries Commission, Regional Mark Processing Center, unpublished data). Roughly 77% (25 million) of released fish are from CV programs, and most are SRFC released from the Coleman National Fish Hatchery, Feather River Fish Hatchery, and Nimbus Fish Hatchery (Figure 1). Klamath Basin hatcheries produce about 18% of the total, while programs for other coastal rivers are relatively small. In the only study designed to distinguish between fish of hatchery and natural origin in California ocean harvests, an estimated 90% of Chinook salmon were found to be of hatchery origin based on otolith microstructure (Barnett-Johnson et al. 2007). In 2007, the California Department of Fish and Game (CDFG) initiated a “constant fractional marking” program to apply fin clips and CWTs to at least 25% of all Chinook salmon from CV hatcheries and up to 100% of Chinook salmon belonging to some special groups. However, most of the Chinook salmon that are currently released from CV hatcheries are unmarked.

The large-scale production of hatchery Chinook salmon that mingle with weak stocks off the California and Oregon coasts results in classic mixed-stock fisheries, and regulatory constraints on weak stocks have led to different management strategies and harvest rates in the region. In the area south of Point Arena, California (known as the CV Index Area), harvest is constrained by the weakest stock in the area during each year. Traditional regulations for protecting CV winter-run and spring-run Chinook salmon have included minimum size limits, seasonal and area closures, trip limits, and harvest quotas (Boydston 2001). South of Point Arena, harvest rates ranged from 50% to 80% during the 1980s but declined to a range of 25–60% after 1998 (PFMC 2008a). In addition, harvesting is highly constrained in the Klamath Management Zone (KMZ; northern California–southern Oregon; Figure 1), which was established to manage escapement objectives and in-river tribal harvest allocations of Klamath River fall-run Chinook salmon (KRFC). Harvest rates are greatest for age-4 KRFC; these rates averaged 45% during 1981–1990, but since 1991 the rates have been managed to achieve a target of 16% or less to protect ESA-listed CC Chinook salmon (NMFS 2000). In summary, weak stock concerns have increasingly constrained Chinook salmon harvest rates since the mid-1980s, resulting in large surpluses of CV hatchery Chinook salmon that go unharvested in some years (e.g., Williams 2006).

**METHODS**

We first describe a cohort model for tracking ocean abundances, fishery impacts, and spawning escapement for Chinook salmon populations under the traditional fishery as well as MSFs. We then apply the model to SRFC to examine how historic harvest and escapement might have differed under MSF scenarios.

**Generic Cohort Model**

The following cohort model accommodates the general life history and ocean fishery characteristics of California Chinook salmon populations. The model is largely based on methods used in cohort reconstruction of hatchery Chinook salmon populations (Goldwasser et al. 2001; Palmer-Zwahlen et al. 2006). There is no production function (e.g., stock–recruitment relationship) in the model; rather, annual ocean abundances (recruits) of an initial age are assumed or estimated and then propagated over time through fisheries and to spawner escapement. The key variables and notation of the cohort model are defined in Table 1. For brevity, the core equations (1)–(8)

| Symbol | Description |
|--------|-------------|
| a      | Subscript denoting age |
| t      | Subscript denoting year |
| N      | Ocean abundance at the beginning of a year |
| N*     | Ocean abundance at the end of a year |
| C      | Number of fish contacted (hooked and retrieved) by the fishery |
| H      | Number of fish harvested (retained) by the fishery |
| h      | Harvest rate (h = H/N) |
| R      | Number of catch-and-release deaths (shakers) |
| D      | Number of drop-off deaths |
| I      | Impact (number of fish killed by the fishery) |
| i      | Impact rate (i = I/N) |
| E      | Spawner escapement |
| c      | Contact rate |
| v      | Vulnerability to the fishery relative to age-4 fish |
| l      | Proportion of fish of legal size |
| r      | Catch-and-release mortality rate |
| d      | Drop-off mortality rate |
| s      | Annual survival rate in the absence of fishing |
| τ      | Fraction of the year in which fishery impacts occur |
| m      | Maturity rate |
| f      | Hatchery fraction; proportion of fish of hatchery origin |
of the model are summarized and referenced in Table 2, whereas equations (9)–(18) are displayed in the text.

We begin with the description of mortalities due to fishing, which closely follows the equations and notation of Prager and Mohr (2001). Calculations of fishing mortality start with ocean abundances by age \( (N_a) \) on September 1. While equations can be generalized to any set of age-classes, we limit ages \( (a) \) to the predominant “adult” age-classes (ages 3, 4, and 5) that are observed in harvests and escapements of California fall-run Chinook salmon populations (O’Farrell et al. 2008; KRTAT 2009). Thus, \( a \in \{3, 4, 5\} \), with ocean abundances of age-3 fish \( (N_3) \) representing the initial recruitment of a given cohort.

All sources of fishing mortality depend on the number of fish that are “contacted” by the ocean fishery (i.e., the number of fish that are hooked and successfully retrieved) as defined in equation (1) of Table 2. In equation (1), \( C_a \) denotes the number of contacts by age, \( c_i \) is the contact rate of fully recruited age-4 fish (i.e., \( c_4 = C_4/N_4 \)), and \( v_a \) is the contact vulnerability relative to age-4 fish (i.e., \( v_4 = c_4/c_4 \) and thus \( v_4 \equiv 1 \)). Given the specified contacts, three age-specific sources of fishing mortality are computed: harvests \( (H_a) \), which depend on the proportion \( (I_a) \) of fish that are of legal size; catch-and-release (or “shaker”) mortalities \( (R_a) \), consisting of sublegal-sized fish that are caught and released but later die of injury (with catch-and-release mortality rates \( r_a \)); and drop-off mortalities \( (D_a) \), which are fish that are assumed to have been hooked but lost before retrieval and to have died due to gear-inflicted injury or predation. These three sources of fishing mortality are defined in equations (2)–(4), where drop-offs \( (D_a) \) are assumed to be added fraction of \( d_a \) of the contacts (Table 2). Thus, the total fishing “impact” for age \( a \) \( (I_a) \) is the sum of \( H_a, R_a, \) and \( D_a \) (equation 5 in Table 2). Annual rates of harvest \( (h_a) \) and impact \( (i_a) \) are defined relative to the initial ocean abundance—that is, \( h_a = H_a/N_a \) and \( i_a = I_a/N_a \) (Table 1).

Applications of cohort reconstruction typically use monthly time steps to remove fishery impacts before applying natural mortality (or survival) rates (Goldwasser et al. 2001; Palmer-Zwahlen et al. 2006). The monthly sequence of calculations provides a final ocean abundance, denoted \( N^*_a \), on the last day of the last month (August 31) just prior to maturity. However, due to limited data, our application requires an annual time step. A simple and close approximation of the monthly based \( N^*_a \) can be obtained by assuming that all fishery impacts \( (I_a) \) occur at a specific fraction of the year, denoted \( \tau_a \). Partitioning the annual survival rate \( (s_a) \) in the absence of fishing between the initial period \( (\tau_a) \) and the remainder of the year \((1 - \tau_a) \) yields

\[
N^*_a = (N_a s_a \tau_a - I_a) s_a^{1-\tau_a},
\]

which simplifies to equation (6) in Table 2. When fishing occurs in various months, \( \tau_a \) represents the weighted mean fraction of the year, with weights equal to the monthly impacts (e.g., \( \tau = 0 \) corresponds to exclusive September fishing; \( \tau = 1/12 \) corresponds to weighted mean impacts occurring in October; etc.).

Given values of \( N^*_a \) and maturity rates \( (m_a) \) in year \( t \), the in-river spawner escapement \( (E) \) in year \( t \) and initial ocean abundance in year \( t + 1 \) are given by equations (7) and (8), respectively (Table 2). Thus, given initial recruitments \( (N_{3,t}) \), cohorts are propagated across years via equations (1)–(8) to provide \( H \) and \( E \) by age and year. Harvest and \( E \) will be conditional on the suite of cohort parameters \( (c_4, v, l, r, d, s, \tau, \text{ and } m) \); Table 1), the quantities of which may be age specific (except \( c_4 \)), fishery specific, year specific, or some combination of these.

**Traditional fishery.**—The above cohort model applies to traditional fisheries in which there are (1) set size limits above which fish may be retained and (2) no distinctions between hatchery-origin (hatchery) and natural-origin (natural) fish. However, to compare \( H \) and \( E \) between the traditional fishery and MSFs, we partition total ocean abundances into hatchery and natural components:

\[
N_a = N_{a, \text{hatchery}} + N_{a, \text{natural}} = f_a N_a + (1 - f_a) N_a, \tag{9}
\]
where $f$ is the “hatchery fraction” or proportion of fish of hatchery origin. Under a traditional fishery, $H$ and $E$ of hatchery and natural fish follow directly from equations (1)–(8), with initial abundances defined as in equation (9).

**Mark-selective fishery.**—The cohort model was adapted to an MSF scenario as follows. Under an MSF, we make several important assumptions: all fish of hatchery origin are marked and therefore identifiable in the ocean fishery; all hatchery fish of legal size are kept by the fishery, whereas all unmarked, natural-origin fish must be released; and the cohort parameters and ocean distributions of hatchery-origin and natural-origin fish are similar such that they have the same values of $s$, $m$, $v$, and so on. However, fishing regulations (e.g., effort and size limits) for hatchery fish under an MSF may differ from those of a traditional fishery depending on the management objectives for commercial and recreational fisheries. Under this scenario, MSF harvests ($H$) are limited to hatchery fish, with age-specific harvest and impact given by (from equations 1–5)

$$H_{a,\text{hatchery}} = f_a N_a \tilde{c}_a v_a \tilde{I}_a$$

and

$$I_{a,\text{hatchery}} = f_a N_a \tilde{c}_a v_a \left[ \tilde{I}_a + (1 - \tilde{I}_a) r_a + d_a \right].$$

where $\tilde{c}_a$ denotes the MSF age-4 contact rate and $\tilde{I}$ represents the MSF proportion of legal-sized hatchery fish.

In contrast, MSF impacts for natural-origin fish are limited to $R$ and $D$, as all natural fish that are contacted must be released (i.e., $I_a = 0$):

$$I_{a,\text{natural}} = (1 - f_a) N_a \tilde{c}_a v_a (r_a + d_a).$$

Here, the calculation of $R$ assumes that a given fish is contacted only once during the annual fishery. This “single-encounter” assumption is reasonable under the traditional fishery calculations (equation 3), in which proportions of sublegal-sized fish are generally low and such fish may grow during the fishing season to later exceed size limits. However, under an MSF, the single-encounter assumption will become increasingly unrealistic for natural fish as $c$ increases. This is because all contacted natural fish must be released and the majority of these fish will survive and may be vulnerable to recapture, especially when $c$ is high. Lawson and Sampson (1996) considered the case in which fish may be caught and released multiple times (a Poisson process), and they showed that the mortality rate ($R/N$) for unmarked fish under this “multiple-encounter” scenario is equal to

$$\frac{R}{N} = 1 - (1 - c)^y,$$

where $c$ is the contact rate (equivalent to the harvest rate assumed by Lawson and Sampson 1996; see their equation 14). In contrast, the mortality rate under the single-encounter assumption is simply defined as $R/N = cr$. The multiple-encounter mortality rate will always be greater than the single-encounter mortality rate, and the two rates will diverge as $c$ increases. Incorporating the multiple-encounter definition for $R$ (equation 13) gives the following expression for fishery impacts on natural fish:

$$I_{a,\text{natural}} = (1 - f_a) N_a \left[ 1 - (1 - \tilde{c}_a v_a)^y + \tilde{c}_a v_a d_a \right].$$

The key assumptions underlying the multiple-encounter scenario in equation (13) are that (1) all fish of a given age are randomly mixed and equally vulnerable to capture and (2) fish that survive capture and release are immediately available for recapture. When considering the total ocean fishery on an annual basis, as is done here, the impacts implied by the single- and multiple-encounter cases represent two extremes. Conditional on specific parameters, the single-encounter case represents a minimum assessment of impacts and is appropriate when all fishing occurs instantaneously such that no recaptures occur. In contrast, the multiple-encounter case provides a maximum assessment of impacts and is appropriate when all fishing applies to all fish equally, with each capture being processed before another capture takes place. The actual effect of fishing likely lies somewhere in between these two extremes, as would be the case when fish and fisheries are spatially segregated during discrete time periods, for example. To be conservative, however, we used the multiple-encounter assumption to compute natural impacts (equation 14) under MSFs in all analyses of SRFC.

**Fishery comparisons.**—Our interest lies in comparisons of $H$ and $E$ between the traditional fishery and MSFs. We are specifically interested in annual total harvest and natural-origin escapement, which are sums across adult ages:

$$H_a = \sum_{a=3}^{5} H_{a,t,\text{hatchery}} + \sum_{a=3}^{5} H_{a,t,\text{natural}},$$

and

$$E_{a,\text{natural}} = \sum_{a=3}^{5} E_{a,t,\text{natural}}.$$
(equation 3):

\[
\frac{\tilde{H}_a}{H_a} = \frac{f_a N_a \tilde{c}_4 v_a l_a}{N_a c_4 v_a l_a} = \frac{f_a \tilde{c}_4 l_a}{c_4 l_a}.
\]  

(17)

Thus, differences depend on a few key parameters, with relatively high MSF harvests observed when the hatchery fraction \( f \) is high or when either the MSF age-4 contact rate \( \tilde{c}_4 \) or the MSF proportion of legal-sized fish \( \tilde{l} \) is greater than that of the traditional fishery (i.e., \( c_4 \) or \( l \)).

Similarly, the ratio of age-specific natural \( E \) for an MSF to that for a traditional fishery can be expressed as (combining equations 5–7, 9, and 12, and simplifying):

\[
\frac{E_{a,natural} \tilde{E}_{a,natural}}{E_{a,natural} \tilde{E}_{a,natural}} = \frac{1 - \tilde{c}_4 v_a (r_a + d_a) s_a^{-r}}{1 - c_4 v_a [l_a + (1 - l_a) r_a + d_a] s_a^{-r}}.
\]  

(18)

Although this ratio depends on numerous variables, differences will largely be determined by the relative contact rates \( \tilde{c}_4 \) and \( c_4 \), the value of \( l \), and the value of \( r \). For example, when \( \tilde{c}_4 \) and \( c_4 \) are similar, natural \( E \) for an MSF will be relatively high when \( l \) is high and when \( r \) is low (i.e., when a high proportion of natural fish that would have been harvested under a traditional fishery are released under an MSF and have a high chance of surviving to escapement).

Sacramento River Fall-Run Chinook Salmon

There is very little information regarding age structure, maturity rates, and the proportion of hatchery fish for SRFC populations. Recently, an aggregate abundance index called the Sacramento index (SI) was developed for SRFC (O’Farrell et al. 2008). The components of the SI (Table 3) are the best available estimates of annual ocean harvest, river harvest, and spawning escapement for SRFC (O’Farrell et al. 2008). The SI provides total abundances across adult ages (3–5) of hatchery and natural fish combined. The definition of “year” used to compute the SI was consistent with cohort reconstructions—that is, ocean harvests were accrued annually from September 1 \( (t - 1) \) through August 31 of year \( t \) (O’Farrell et al. 2008). In our analysis, we define escapement as the total in-river run of SRFC, which includes river harvest (Table 3).

### Table 3. Total adult (ages 3–5) ocean harvest, river harvest, and spawners (in thousands of fish) for Sacramento River fall-run Chinook salmon populations \((H = \text{total harvest}; \ E = \text{total escapement})\). Data correspond to the Sacramento index (SI; O’Farrell et al. 2008).

| Year | Ocean harvest | In-river run (escapement) |
|------|---------------|--------------------------|
|      | Commercial    | Recreational | Total \((H)\) | Harvest | Spawners | Total \((E)\) | Total \((H + E = SI)\) |
| 1983 | 245.2         | 86.1          | 331.3         | 18.6    | 109.4    | 128.0       | 459.3 |
| 1984 | 266.2         | 87.0          | 353.1         | 26.9    | 158.2    | 185.1       | 538.2 |
| 1985 | 355.4         | 158.9         | 514.3         | 40.5    | 238.7    | 279.2       | 793.5 |
| 1986 | 618.7         | 137.5         | 756.3         | 40.5    | 238.2    | 278.6       | 1,034.9 |
| 1987 | 686.1         | 173.2         | 859.2         | 33.1    | 194.6    | 227.7       | 1,086.9 |
| 1988 | 1,162.6       | 188.3         | 1,350.9       | 38.2    | 224.7    | 262.9       | 1,613.8 |
| 1989 | 611.4         | 159.2         | 770.6         | 25.8    | 151.6    | 177.4       | 948.0 |
| 1990 | 514.2         | 150.5         | 664.7         | 17.8    | 104.9    | 122.8       | 787.5 |
| 1991 | 298.8         | 90.2          | 389.0         | 26.4    | 117.4    | 143.8       | 532.8 |
| 1992 | 232.5         | 70.1          | 302.6         | 13.9    | 81.1     | 95.0        | 397.6 |
| 1993 | 342.4         | 115.3         | 457.8         | 28.4    | 135.2    | 163.6       | 621.3 |
| 1994 | 302.3         | 164.7         | 467.1         | 29.5    | 163.6    | 193.2       | 660.2 |
| 1995 | 735.7         | 387.9         | 1,123.6       | 50.1    | 295.0    | 345.1       | 1,468.7 |
| 1996 | 426.7         | 157.0         | 583.7         | 50.9    | 299.6    | 350.5       | 934.2 |
| 1997 | 579.7         | 210.2         | 790.0         | 58.2    | 342.9    | 401.1       | 1,191.1 |
| 1998 | 292.8         | 113.9         | 406.7         | 72.3    | 238.1    | 310.4       | 717.1 |
| 1999 | 308.1         | 76.6          | 384.7         | 71.1    | 395.9    | 467.1       | 851.8 |
| 2000 | 431.4         | 153.2         | 584.5         | 62.0    | 416.8    | 478.8       | 1,063.3 |
| 2001 | 284.4         | 93.5          | 377.9         | 92.7    | 546.1    | 638.8       | 1,016.7 |
| 2002 | 447.6         | 184.1         | 631.7         | 90.3    | 775.5    | 865.8       | 1,497.4 |
| 2003 | 501.9         | 106.5         | 608.3         | 88.6    | 521.6    | 610.2       | 1,218.6 |
| 2004 | 621.9         | 212.6         | 834.5         | 48.2    | 283.6    | 331.7       | 1,166.3 |
| 2005 | 367.7         | 127.1         | 494.8         | 66.9    | 394.0    | 460.9       | 955.7 |
| 2006 | 149.9         | 107.7         | 257.6         | 45.5    | 267.9    | 313.4       | 571.0 |
| 2007 | 121.0         | 32.8          | 153.8         | 15.7    | 88.0     | 103.7       | 257.5 |
Despite a lack of the age-specific data required to rigorously reconstruct cohort abundances, useful approximations can be obtained by “deconvolving” the aggregate SI harvest and escapement time series (Table 3) into age-specific ocean abundances (Kope and Botsford 1988). As was described by Kope and Botsford (1988), the process of deconvolution is the opposite of convolution, in which annual (total) abundances are defined as a weighted sum (convolution) of past recruitments, such as those obtained via the cohort model described above. We adopt a slightly different approach to the multiyear matrix formulation used by Kope and Botsford (1988). Their formulation used annual effort data to model year-specific harvests and impacts by age, yielding a matrix solution for recruitment estimates across all years. In contrast, we used annual calculations in which we first solved for the recruitment value (age-3 ocean mates across all years. In contrast, we used annual calculations in which annual (total) abundances are defined as a weighted sum (convolution) of past recruitments, such as those obtained via the cohort model described above. We adopt a slightly different approach to the multiyear matrix formulation used by Kope and Botsford (1988). Their formulation used annual effort data to model year-specific harvests and impacts by age, yielding a matrix solution for recruitment estimates across all years. In contrast, we used annual calculations in which we first solved for the recruitment value (age-3 ocean abundance $N_3$) and then computed $c_4$. Thus, our approach did not require effort data to indirectly account for year-to-year variation in contact rates; rather, we estimated $c_4$ explicitly by using the SI time series of total ocean harvest and in-river escapement.

The equations we used to annually estimate $N_3$ and $c_4$ are provided in the Appendix. In brief, the deconvolution steps we used to estimate these values were as follows. First, equations for aggregate $H$ and $E$ (i.e., from the SI) were expressed in terms of the fixed cohort parameters, yielding a solution for $N_3$ that was independent of $c_4$. Given the estimate of $N_3$, the annual estimate of $c_4$ was obtained. To start the deconvolution, initial values were required for age-4 and age-5 ocean abundances ($N_4$ and $N_5$) in the first year (Kope and Botsford 1988). In all subsequent years, estimates of $N_4$ and $N_5$ were provided by the cohort model based on past estimates of recruitment, $N_3$ (e.g., equation 9). When the deconvolution is stable, the recruitment series converges within several years to a stable set of estimates regardless of the initial guesses for $N_4$ and $N_5$ (Kope and Botsford 1988). In sum, by using the aggregate $H$ and $E$ estimates provided by the SI (Table 3) and a set of assumed cohort parameters, we derived time series of age-specific SRFC ocean abundances and $c_4$ that would have produced the observed $H$ and $E$.

To generate abundance estimates and compare the traditional fishery and MSFs, baseline values for cohort parameters (Table 4) were set as follows. Some of the baseline values we used were rough approximations, and we do not provide all of the details of their derivation; rather, we evaluate the influence of each parameter on our results by using sensitivity analyses with broad ranges for parameter values. Values for $v$, $l$, $m$, and $\tau$ were obtained from data provided by Palmer-Zwahlen et al. (2006), who documented CWT-based cohort reconstructions of Feather River Fish Hatchery Chinook salmon releases for two brood years (1998 and 1999). (We are not aware of any other well-documented reconstructions for SRFC populations.) Monthly fishery impacts for total hatchery releases (Tables 15 and 16 of Palmer-Zwahlen et al. 2006) suggest a $v$ of roughly 0.75 for age-3 fish and 1.30 for age-5 fish and an average fishery timing ($\tau$) of roughly 0.75 (June) for age 3, 0.50 (March) for age 4, and 0.25 (December) for age 5. Proportions of legal-sized fish by month (Table 7 of Palmer-Zwahlen et al. 2006) provided annual $l$-values of 0.92 for age 3, 0.99 for age 4, and 1.00 for age 5. Maturity rates across hatchery release types (Table 13 of Palmer-Zwahlen et al. 2006), weighted by release numbers and averaged for the two brood years, provided $m$-values of 0.40 for age 3 and 0.95 for age 4. These values of $m$ are consistent with estimates reported by Kope (1987).

Baseline values for $d$, $r$, and $s$ were based on the conventional values used in PFMC analyses for California fall-run Chinook salmon populations. The value for $d$ was 0.05 for all ages (e.g., Goldwasser et al. 2001). On an annual basis, the conventional values of $s$ for ages 3–5 were 0.58, 0.80, and 0.80, respectively. The value of $r$ depends on the fishery (PFMC 2008b). For commercial troll fisheries, $r$ is equal to 0.26, while the $r$ for ocean recreational fisheries is 0.16 (based on values of 0.14 for trolling and 0.42 for mooching, weighted by their expected proportions; see PFMC 2008b). Finally, we derived a composite $r$ estimate of 0.24 for all ages by weighting the commercial and recreational $r$-values by the average proportion of commercial (75%) and recreational (25%) ocean harvests observed across years for the SI (Table 3).

The final—and critically important—parameter was the age-3 hatchery fraction ($f_3$), for which there is little data. The PFMC Salmon Technical Team assumed that 75% of CV Chinook salmon originated from hatcheries (NMFS 2003). More recent information indicated that roughly 90% of the Chinook salmon off the coast of California were of hatchery origin during the 2 years sampled (Barnett-Johnson et al. 2007). In contrast, estimates of adult returns counted at hatchery facilities account for a much lower proportion of total SRFC escapement (“GrandTabs” file; CDFG, unpublished data). The majority of spawners (GrandTabs) are designated as “natural-area” spawners, although the origin of such fish is highly uncertain (e.g., large natural-area spawning abundances often occur in reaches near hatchery facilities, but estimates of hatchery fish straying rates are lacking). We therefore selected a baseline $f_3$ value of 0.60 (i.e., 60% of age-3 recruits were assumed to be of hatchery origin and therefore marked), which is a relatively conservative estimate given the recent results of Barnett-Johnson et al. (2007).

TABLE 4. Baseline parameter values used for the Sacramento River fall-run Chinook salmon cohort analyses. Parameter symbols are defined in Table 1.

| Parameter | Age 3 | Age 4 | Age 5 |
|-----------|-------|-------|-------|
| $v$       | 0.75  | 1.00  | 1.30  |
| $l$       | 0.92  | 0.99  | 1.00  |
| $r$       | 0.24  | 0.24  | 0.24  |
| $d$       | 0.05  | 0.05  | 0.05  |
| $s$       | 0.58  | 0.80  | 0.80  |
| $\tau$    | 0.75  | 0.50  | 0.25  |
| $m$       | 0.40  | 0.95  | 1.00  |
| $f$       | 0.60  |       |       |
Comparisons and sensitivity analyses.—In our “baseline” analysis, we compared estimates for the traditional fishery and MSFs across the final 20 years of the SI (1988–2007; Table 3). Deconvolution of age composition for the full SI time series (1983–2007) required that abundances (N4 and N5) be supplied in the first year to initiate calculations. Deconvolved abundances converged to stable values by 1988 regardless of the initial values set for N4 and N5. Thus, we used 1988 as the initial year for comparison between historic fishery and MSF outcomes. Note that our baseline comparison refers to outcomes that were computed by using the baseline deconvolution—that is, the deconvolved estimates of age-specific ocean abundance and c4 that were calculated using the baseline cohort parameters (Table 4). Unless noted otherwise, MSF contact rates (c4) were set equal to the historic estimates (i.e., c4 for the traditional fishery), and no size limits for hatchery fish were assumed (i.e., t = 1).

We then conducted three distinct sensitivity analyses. First, to assess the implications of annual variability in key parameters affecting deconvolved abundances, we generated 500 separate deconvolutions (i.e., 500 sets of admissible age-specific abundances and c4) by using randomly generated values for age-3 maturity rate (m3,f) and age-3 vulnerability (v3,f) by year. These are the two key parameters for which we expected considerable year-to-year variation, and incidentally, they were the only cohort parameters that appreciably influenced deconvolved estimates. Both m3 and v3 were assumed to follow beta distributions with a mean equal to the baseline value (Table 4) and an SD of 0.1 (similar to the SDs of m3 and h3/h4 [a useful surrogate for v3,f] observed across years for postseason estimates of KRFC abundance and harvest; KRTAT 2009).

Second, we examined the sensitivity of the baseline results to fixed (across all years) changes in age-3 parameter values. In general, we examined parameter values that ranged from plus to minus one-third of the baseline value, except for l3 and τ3. For l3, we examined a range from 0.84 to 1.00; for τ3, we examined a range from 2 months earlier (April, τ3 = 0.58) to 2 months later (August, τ3 = 0.92) than the baseline value. In the case of r, the changes in r applied to all ages.

In our final set of analyses, we examined the implications of changing the MSF contact rate (c4,f) and the hatchery fraction (f3). For these analyses, we used the last 7 years of SI data (2001–2007), across which the average historic c4 was estimated to be 0.32 (32%). Ocean fisheries were frequently constrained during this period to protect weak stocks of concern. For 2001–2007, we estimated MSF outcomes by using three values for the f3 (40, 60, and 80%). For each f3, we examined three values of c4 (40, 50, and 60%) that could be used as management targets given that they are within the range of c4 observed over the past two decades.

RESULTS

Estimates of historic ocean abundances and contact rates (c4) for SRFC varied considerably across years from 1988 to 2007 (Figure 2). Conditional on the baseline cohort parameters (Table 4), estimates of age-3 ocean abundance (recruitment) ranged from a low of 358,000 in 2007 to a high of 2.97 million in 2002, averaging 1.58 million across years (Figure 2). Age-4 abundances ranged from 80,000 in 1993 to 762,000 in 2003 and averaged 293,000 across years (Figure 2). Age-5 abundance estimates averaged just 7,000, comprising less than 0.4% of ocean abundances across years. Estimates of c4 showed a declining
trend in recent years, ranging from a high of 63% in 1990 to a low of 19% in 2001 and averaging 43% across years. The addition of random variation in $m_3$ and $v_3$ resulted in considerable within-year variation in abundance estimates (especially for 1999–2005) but lower and more stable within-year variation for $c_4$ (Figure 2).

Under the assumptions of a constant $f_3$ of 60%, no MSF size limits on hatchery fish, and historic contact rates, the simulated harvest and escapement of SRFC for the MSF differed appreciably from those for historic fisheries (Figure 3). Mark-selective harvests were estimated to be 37% lower than historic $H$ across years, while in-river $E$ of natural fish increased by 119% on average. Despite high within-year variation in abundance estimates (Figure 2), there was relatively little within-year variation in MSF estimates of natural $E$ and almost no variation in $H$ estimates (Figure 3).

Comparisons between the historic and MSF scenarios were sensitive to a few key parameters. For $H$, average differences across years between historic and MSF estimates were influenced by assumed values for $f_3$ and the proportion of age-3 fish that were legal sized ($l_3$ for the traditional fishery; Figure 4). All other parameters had very little (<1%) or no effect on harvest comparisons across the ranges examined (within one-third of the baseline). Note that when MSF size limits for hatchery fish were assumed to equal those for the traditional fishery ($\tilde{l} = l$), the average decline in MSF harvest increased slightly from 37% to 40% ($\tilde{f} = 1 - f$), and in this scenario the changes in $l$ had no influence on harvest differences. Comparisons of natural $E$ were sensitive to more parameters; however, changes in the average difference were generally minimal (Figure 5). Over the ranges examined, values of $r$ (all ages) and $\tau_3$ had the largest influence on differences in natural $E$ (Figure 5).

Simulation of MSF to achieve a target $c$ in each year (2001–2007) showed that $H$ increased considerably as $\tilde{c}_4$ and $f_3$ increased (Table 5). The years chosen for this comparison

![Figure 3](https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science.on_10_Apr_2020)

![Figure 4](https://bioone.org/journals/Marine-and-Coastal-Fisheries:-Dynamics,-Management,-and-Ecosystem-Science.on_10_Apr_2020)
FIGURE 5. Sensitivity of changes in the in-river escapement of natural-origin Sacramento River fall-run Chinook salmon (1988–2007) simulated under mark-selective fishing due to varying the (A) age-3 vulnerability, (B) catch-and-release mortality rate, (C) age-3 maturity rate, (D) proportion of age-3 fish that are legal sized (traditional fishery only), (E) age-3 annual survival rate, and (F) timing of fishery impacts (fraction of the year, where 0.58 = April, 0.75 = June, and 0.92 = August). Solid dots indicate baseline parameter values; dashed lines indicate the baseline estimate of the average (20-year) change in escapement.
TABLE 5. Simulated ocean harvest (thousands) of Sacramento River fall-run Chinook salmon for 2001–2007 under mark-selective fishery scenarios based on different assumed age-3 hatchery fractions ($f_3$) and age-4 contact rates ($\tilde{c}_4$). Also shown is the percent change in total harvest relative to the historic (actual) ocean harvest reported for the Sacramento index (see Table 3).

| Ocean harvest year | $f_3$ (%) | $\tilde{c}_4$ (%) | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | Total | Change (%) |
|--------------------|-----------|-------------------|------|------|------|------|------|------|------|-------|-------------|
| Actual             | Actual    | 378               | 632  | 608  | 835  | 495  | 258  | 154  | 3,359 |       |             |
| 40                 |           | 330               | 425  | 283  | 283  | 293  | 126  | 61   | 1,801 | −46   |             |
| 50                 |           | 398               | 512  | 328  | 340  | 350  | 141  | 71   | 2,138 | −36   |             |
| 60                 |           | 460               | 591  | 363  | 390  | 400  | 149  | 79   | 2,432 | −28   |             |
| 60                 | 40        | 495               | 638  | 424  | 425  | 439  | 189  | 91   | 2,702 | −20   |             |
| 60                 | 50        | 597               | 768  | 492  | 509  | 524  | 212  | 106  | 3,208 | −4    |             |
| 60                 | 60        | 690               | 886  | 545  | 586  | 599  | 224  | 118  | 3,648 | 9     |             |
| 60                 | 80        | 659               | 851  | 565  | 567  | 586  | 253  | 122  | 3,603 | 7     |             |
| 60                 | 50        | 795               | 1,024| 656  | 679  | 699  | 282  | 142  | 4,277 | 27    |             |
| 60                 | 80        | 921               | 1,181| 726  | 781  | 799  | 298  | 157  | 4,864 | 45    |             |

provided a wide range of historic $c_4$ values (from 19% in 2001 to 48% in 2004; averaging 32%; Figure 2). The combination of $\tilde{c}_4$ and $f_3$ determined the magnitude of harvest reductions or gains for MSF in comparison with the historic harvests. For example, at a low $f_3$ of 40%, MSF harvests were lower than historic harvests in all years except 2001 (Table 5; Figure 6A). In contrast, at a high $f_3$ of 80%, MSF harvests were greater than historic harvests in several years (2001, 2002, and 2004), particularly for higher values of $\tilde{c}_4$ (Table 5; Figure 6B). Thus, total MSF harvest estimates across 2001–2007 varied widely across scenarios, ranging from a reduction of 46% (i.e., when $f_3 = 40\%$ and $c_4 = 40\%$) to an increase of 48% (i.e., when $f_3 = 80\%$ and $c_4 = 60\%$; Table 5) in comparison with historic harvests.

Escapement of SRFC natural spawners typically increased and the proportion of hatchery fish in escapements decreased with implementation of an MSF. Natural $E$ increased for all MSF scenarios in all 7 years (Figure 7). Total increases across years ranged from a low of 24% when $\tilde{c}_4$ was 60% to a high of 48% when $\tilde{c}_4$ was 40% (Table 6). In contrast, the $E$ of hatchery fish decreased for nearly all MSF scenarios (Figure 7). Regardless of the assumed $f_3$, higher MSF contact rates reduced the overall percentage of hatchery-origin adults in the total escapement for 2001–2007 (Figure 8).

DISCUSSION

Our retrospective analysis of SRFC indicated that a broadly implemented MSF would have resulted in large increases in escapement of natural fish and (depending on the proportion of hatchery fish) potentially large declines in ocean harvest relative to the values for the historic, traditional fishery. Increasing the MSF contact rates (relative to historic values) resulted in higher MSF harvests but lower gains in escapement of natural SRFC, illustrating the fundamental trade-off between providing harvest...
opportunity and protecting natural stocks—objectives that MSF managers strive to balance (Hoffman and Patillo 2008). Furthermore, we found that simulated MSF harvest and escapement were reasonably robust to all but a few key parameters, suggesting that the general outcomes of comparisons between the traditional fishery and MSFs follow straightforward and intuitive relationships that should be applicable to SRFC populations. Specifically, relative changes in harvest will be proportional to the number of marked hatchery adults that are available to the MSF and the relative fishing effort directed at those fish (Hoffman and Patillo 2008), while changes in escapement of natural fish will depend on the indirect MSF mortality on unmarked fish—specifically, their relative contact rates and subsequent release mortality (Lawson and Sampson 1996).

Of course, relative changes in harvest and escapement under an MSF depend on the choice of “traditional” fishery to which the MSF is compared. Our baseline comparison was between historic harvest and escapement (i.e., the traditional fishery) and

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**FIGURE 7.** Changes in the in-river escapement of natural (solid lines, open symbols) and hatchery (dashed lines, shaded symbols) Sacramento River fall-run Chinook salmon for 2001–2007 as simulated under mark-selective fishery (MSF) scenarios in comparison with estimated actual escapement. The displayed MSF scenarios are for an assumed age-3 hatchery fraction of 60% and three different age-4 contact rates: 40% (diamonds), 50% (squares), and 60% (triangles).

**FIGURE 8.** Simulated proportion of Sacramento River fall-run Chinook salmon in-river escapement composed of hatchery-origin spawners (across years 2001–2007) for the traditional (nonselective) fishery and for mark-selective fishery (MSF) scenarios with three age-4 contact rates ($\tilde{c}_4$) and three assumed age-3 hatchery fractions for ocean harvest ($f_3$).

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**TABLE 6.** Simulated in-river escapement (thousands) of natural-origin Sacramento River fall-run Chinook salmon for 2001–2007 under mark-selective fishery scenarios for different assumed age-3 hatchery fractions ($f_3$) and age-4 contact rates ($\tilde{c}_4$). Also shown is the percent change in total escapement relative to estimates of historic (actual) escapement of natural fish reported for the Sacramento index (see Table 3) given an assumed hatchery fraction.

| $f_3$ (%) | $\tilde{c}_4$ (%) | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | Total | Change (%) |
|----------|------------------|------|------|------|------|------|------|------|-------|------------|
| 40 Actual | 383              | 519  | 366  | 199  | 277  | 188  | 62   | 1,995 |       | 48         |
| 40       | 474              | 627  | 542  | 429  | 463  | 299  | 115  | 2,949 |       | 48         |
| 50       | 439              | 581  | 495  | 396  | 427  | 271  | 105  | 2,714 |       | 36         |
| 60       | 402              | 531  | 446  | 361  | 388  | 242  | 94   | 2,464 |       | 24         |
| 60 Actual | 256              | 346  | 244  | 133  | 184  | 125  | 41   | 1,330 |       | 36         |
| 40       | 316              | 418  | 361  | 286  | 308  | 200  | 77   | 1,966 |       | 48         |
| 50       | 293              | 387  | 330  | 264  | 284  | 181  | 70   | 1,809 |       | 36         |
| 60       | 268              | 354  | 297  | 240  | 259  | 161  | 62   | 1,643 |       | 24         |
| 80 Actual | 128              | 173  | 122  | 66   | 92   | 63   | 21   | 665   |       | 48         |
| 40       | 158              | 209  | 181  | 143  | 154  | 100  | 38   | 983   |       | 48         |
| 50       | 146              | 194  | 165  | 132  | 142  | 90   | 35   | 905   |       | 36         |
| 60       | 134              | 177  | 149  | 120  | 129  | 81   | 31   | 821   |       | 24         |
simulated MSF outcomes based on the historic contact rates. As a consequence of the relatively high historic contact rates, harvest decreased under the MSF, whereas natural escapement increased. However, if the default comparison had been between a restricted traditional fishery with minimal harvests and an MSF scenario with greater effort directed at marked (hatchery) fish, then under the MSF the harvest could have increased and natural escapement could have declined (i.e., if catch-and-release mortality under the MSF exceeds the traditional fishing mortality for natural fish). Actual MSF regulations would likely include catch quotas or season restrictions that are designed to constrain contact rates and incidental mortality on natural fish to within goals for weak stocks as mandated by PFMC. For example, MSFs for hatchery coho salmon off the coasts of Oregon and Washington are often constrained by the requirement that incidental mortality must remain under 15% for unmarked individuals (PMFC 2008b). Thus, we are cautious when interpreting our results for SRFC. Our projections of harvest reductions or gains in natural escapement under an MSF do not necessarily imply good or poor performance; rather, they demonstrate expected outcomes that are dependent on historic conditions as well as assumptions of the hypothetical scenario.

Our results demonstrated that MSF harvest predictions depended critically on the hatchery fraction assumed for SRFC. Unfortunately, there are few cohesive data for determining the historical hatchery fraction. At an assumed $f_3$ of 40%, MSF harvest (1988–2007) was 58% less than historic harvest, while at an $f_3$ of 80% the MSF harvest was only 16% lower than historic harvest (Figure 4A). Thus, a more informative evaluation of MSFs for SRFC will require improved estimates of the proportion of hatchery fish among ocean abundances. Although a 2-year study of otolith microstructure in ocean-caught Chinook salmon indicated that roughly 90% of the fish off the coast of California were of hatchery origin (Barnett-Johnson et al. 2007), the spatial and temporal resolution of the sampling was limited. If the hatchery fraction is indeed that high in a majority of years, it increases the potential for an MSF to maintain or increase harvest and to increase escapements of natural stocks. A recent CDFG program to mark at least 25% of all CV hatchery Chinook salmon will soon supply the first opportunity to directly measure the hatchery fraction. Of course, hatchery fractions are likely to vary from year to year depending on the relative production of hatchery and natural juveniles and the environmental conditions that might uniquely affect their rates of survival to adult recruitment. Although we did not examine such year-to-year variability, the general implications for SRFC would be straightforward: annual MSF harvest will vary in proportion to the annual hatchery fraction and fishery contact rates.

A key determinant of potential increases in SRFC natural escapement under an MSF versus the traditional fishery is $r$. This parameter will largely determine the degree of indirect fishing mortality on unmarked (natural) fish that are caught but must be released in selective fisheries (Lawson and Sampson 1996; Coggins et al. 2007). The implications of catch-and-release mortality are not unique to MSF programs. Such mortality is currently experienced by sublegal-sized fish in fisheries that impose size restrictions and by all fish of species that are subject to non-retention fisheries (PSC 2004). Thus, implicit in these existing regulatory measures is the assumption that $r$ is sufficiently low to provide the protection that is intended for these fish.

Differences in SRFC harvest and escapement between an MSF and a traditional fishery will also depend critically on the relative contact rates applied in each case. In some instances, managers may, for example, increase effort in an MSF to harvest surplus hatchery fish when the hatchery fraction is high (Hoffman and Patillo 2008), but this would be done at the expense of increasing incidental mortality on unmarked fish and reducing their escapement. Such trade-offs were evident for SRFC in our analysis of recent catch years under differing MSF contact rates (e.g., Tables 4, 5). On a fishery-by-fishery basis, the PFMC and the ESA consultation standards for harvest restrictions would set the upper limit for MSF contact rates to prevent depletion of weak stocks.

Our comparisons for harvest and escapement were robust to changes in many of the assumed cohort parameters. Although deconvolved estimates of abundance and contact rate were sensitive to annual variation in maturity and vulnerability rates, such variation did not translate into significant variability in simulated MSF harvest and translated into only modest variation in MSF escapement. The model structure ensured that historic (traditional) harvest and escapement were maintained; thus, uncertainty accrued only to MSF outcomes. Interannual variation in the simulated outcomes was essentially eliminated when results were examined as averages or totals across years. In essence, the model was internally consistent in that changes in parameter values that might affect MSF outcomes were simultaneously affecting the deconvolved estimates of abundance under the traditional fishery assumptions. Thus, changes in parameters that would affect traditional fisheries affected the MSF in a similar manner, often leading to little change in relative differences between the fisheries. Aside from the critical importance of the hatchery fraction in affecting simulated MSF harvest, the robustness of results to a wide range of parameter values suggests that our comparisons for SRFC are reasonably reliable and should be generally applicable to other Chinook salmon stocks, as discussed below.

**Model Limitations**

Our model contained simplifying assumptions and could be refined in several ways to provide additional insight. First, our calculations were aggregated across commercial and recreational ocean fisheries. For venues in which separate implications of MSF outcomes for recreational and commercial ocean fisheries (or their spatial or temporal strata) would be important, those evaluations would likely incorporate fishery-specific parameters (e.g., $c$, $r$, $v$, $l$, and $t$). For the purpose of our analyses, however, we would expect little difference in aggregate MSF outcomes from analyzing the fisheries...
Implications for Other California Chinook Salmon Stocks

Our analyses focused on SRFC, but under the simulated MSF scenarios, other natural populations of Chinook salmon would experience potential changes in fishing mortality and escapement. Chinook salmon stocks that share ocean distributions with SRFC include ESA-listed CV spring-run, CV winter-run, and CC stocks. The average age at maturity and the timing of river entry influence each population’s exposure to ocean fisheries. Because harvest impacts are lower for CV spring-run and winter-run Chinook salmon than for fall-run Chinook salmon (Grover et al. 2004), the relative increases in escapement experienced by spring- and winter-run stocks under MSFs would likely be lower than those simulated for SRFC. Spring-run Chinook salmon return to freshwater in the spring and thus avoid most ocean harvest during the year in which they mature. The limited data on age-specific harvest of spring Chinook salmon for the 1998 and 1999 broods indicate that the impact rate at age 3 averaged only 11% of the impact rate observed at age 4 (Grover et al. 2004). However, only about one-third of the fish matured at age 3, so those that remained in the ocean until age 4 experienced a full season of harvest at impact levels comparable to those of the SRFC. The CV winter-run Chinook salmon were harvested at even lower rates because they exit the ocean during winter of the year in which they mature, and therefore these fish entirely miss the last season of harvesting to which SRFC of the same age are exposed. Grover et al. (2004) estimated that on average, 96% of winter-run fish matured at age 3; individuals maturing at age 3 experienced an impact rate (in the prior summer) that averaged only 33% of the impact rate observed for fish remaining in the ocean to mature at age 4. Nevertheless, harvest impacts on spring-run and winter-run Chinook salmon are sufficiently high to be ranked as “very high” stressors to those populations according to the draft ESA recovery plan (NMFS 2009).

The MSF scenarios we simulated would also reduce impacts and allow increased escapement of natural CC Chinook salmon and KRFC; each of these has been the weak stock for which constraints on ocean harvesting have been implemented in California and southern Oregon during some years. Much of the harvest constraint on these stocks has been imposed by restricted seasons within the KMZ, but even if such restrictions remained in place under MSFs, both stocks are harvested in fisheries north and south of the KMZ (NMFS 2000; KRTAT 2009). The National Marine Fisheries Service (NMFS 2003) determined that CC Chinook salmon would be sufficiently protected from jeopardy by harvest restrictions that kept impact rates under 16% for natural age-4 KRFC. California coastal Chinook salmon originate from streams south of the Klamath River and tend to be captured more to the south than KRFC (NMFS 2000). Because their harvest vulnerability is believed to be intermediate to that of SRFC and KRFC (NMFS 2000), potential decreases in impact rate and increases in escapement for CC Chinook salmon under an MSF would likely be between those for SRFC and KRFC.
Related Management Issues

Although we assumed that mass marking and MSFs would be broadly implemented for SRFC, actual application to SRFC would involve a number of issues that are beyond the scope of this analysis. Application of MSFs would almost certainly include decisions on a mix of selective and nonselective fisheries—with simultaneous use of time, area, and gear restrictions—to achieve harvesting goals that are shaped each year by the regulatory review process of the PFMC. Implementation of MSFs would also compromise management information and require modification of existing harvest and escapement monitoring programs, which are based on the CWT recovery system that uses the adipose fin clip for recovery of tags (PSC 1995, 2005, 2009). Tools that may partially address monitoring problems include electronic detection of CWTs; use of double index tagging, wherein a second group of unmarked fish is given CWTs, to estimate overall impact rates on unmarked fish (PSC 1997); and genetic stock identification (Crane et al. 2000; CROOS 2007a, 2007b; Garza 2007; Parken et al. 2008). Additionally, effective use of MSFs for SRFC would require marking most or all of the fish released from hatcheries, although this may happen anyway as a necessary step toward CV hatchery reform (Blankenship and Daniels 2004; Olson et al. 2004; HSFR 2005) to allow reliable identification of hatchery fish and to potentially limit hatchery fish access to natural spawning areas, as recommended by the Hatchery Scientific Review Group (HSRG 2005). Finally, funding issues would have to be resolved, as the mass marking of hatchery Chinook salmon and the implementation of appropriate MSF monitoring and education programs will incur large costs.

Conclusions

Our retrospective analysis indicated that a broad implementation of an MSF (at historic contact rates) for SRFC would have resulted in (1) a doubling of in-river natural escapement relative to historic values but (2) potentially large reductions in ocean harvest depending on the proportion of hatchery fish. Comparisons between traditional fishery and simulated MSF outcomes were quite robust to a wide range of assumed cohort parameters, suggesting that our aggregate results provide useful insights into potential MSF outcomes and key uncertainties. As critical data on the proportion of hatchery fish among SRFC become available in future years, a much more rigorous evaluation of harvest implications will be possible. Although a careful assessment of the harvest and escapement consequences for SRFC is essential, it is only one aspect of a much broader evaluation of MSFs that would require consideration of numerous factors, such as other relevant Chinook salmon stocks, fisheries, hatchery reforms, impacts to CWT programs, and implementation costs.

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REFERENCES

Barnett-Johnson, R., C. B. Grimes, C. F. Royer, and C. J. Donohoe. 2007. Identifying the contribution of wild and hatchery Chinook salmon (Oncorhynchus tshawytscha) to the ocean fishery using otolith microstructure as natural tags. Canadian Journal of Fisheries and Aquatic Sciences 64:1683–1692.

Blankenship, H. L., and E. Daniels. 2004. A scientific and systematic redesign of Washington State salmonid hatcheries. Pages 561–572 in M. J. Nickum, P. M. Mazik, J. G. Nickum, and D. D. MacKinnal, editors. Propagated fish in source management. American Fisheries Society, Symposium 44, American Fisheries Society, Bethesda, Maryland.

Boydston, L. B. 2001. Ocean salmon fishery management. California Department of Fish and Game Fish Bulletin 179:183–195.

Brannon, E. L., D. F. Amend, M. A. Cronin, J. E. Lannan, S. LaPatra, W. J. McNeil, R. E. Noble, C. E. Smith, A. J. Talbot, G. A. Wedemeyer, and H. Westers. 2004. The controversy about salmon hatcheries. Fisheries 29(9): 12–31.

Coggins, L. G., Jr., M. J. Catalano, M. S. Allen, W. E. Pine III, and C. J. Walters. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish and Fisheries 8:196–210.

Crane, P. A., W. D. Templin, D. M. Eggers, and L. W. Seeb. 2000. Genetic stock identification of southeast Alaska Chinook salmon fishery catches. Alaska Department of Fish and Game, Regional Information Report 5J00–01, Anchorage.

CROOS (Collaborative Research on Oregon Ocean Salmon). 2007a. Project CROOS 2006, Final Report, Oregon Salmon Commission, Lincoln City. Available at: http://projectcroos.com/.(October 2008).

CROOS (Collaborative Research on Oregon Ocean Salmon). 2007b. 2007 sea- son report to the Pacific Fishery Management Council. Oregon Salmon Commission, Lincoln City. Available at: http://projectcroos.com/.(October 2008).

Garza, J. C. 2007. California genetic stock identification pilot project-2007. National Marine Fisheries Service, Southwest Fisheries Science Center, Final Report, La Jolla, California.

Goldwasser, L., M. S. Mohr, A. M. Grover, and M. L. Palmer-Zwahlen. 2001. The supporting databases and biological analyses for the revision of the Klamath Ocean Harvest Model. NOAA Technical Memorandum, Southwest Fisheries Science Center, Santa Cruz, California.

Good, T. P., T. J. Berechi, P. McElhany, M. M. McClure, and M. H. Ruckelshaus. 2007. Recovery planning for Endangered Species Act-listed Pacific salmon: using science to inform goals and strategies. Fisheries 32:426–440.

Good, T. P., R. S. Waples, and P. Adams. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Technical Memorandum NMFS-NWFS-C-66.

Grover, A., A. Low, P. Ward, J. Smith, M. Mohr, D. Viele, and C. Tracy. 2004. Recommendations for developing fishery management objectives for Sacramento River winter Chinook and Sacramento River spring Chinook. Pacific Fishery Management Council Interagency Work Group, Progress Report, Portland, Oregon.

Grover, A., M. S. Mohr, and M. L. Palmer-Zwahlen. 2002. Hook-and-release mortality of Chinook salmon from drift mooching with circle hooks: management implications for California’s ocean sport fishery. Pages 39–56 in J. A. Lucy and A. L. Studholme, editors. Catch and release in marine recreational fisheries. American Fisheries Society, Symposium 30, Bethesda, Maryland.

Hoffman, A., and P. L. Patillo. 2008. The practical application of mark-selective fisheries. Pages 451–459 in J. L. Nielsen, J. J. Dodson, K. Friedland, T. R. Hamon, J. Musick, and A. Verspoor, editors. Reconciling fisheries with conservation: proceedings of the fourth world fisheries congress. American Fisheries Society, Symposium 49, Bethesda, Maryland.

HSRG (Hatchery Scientific Review Group). 2005. Hatchery reform in Washington: principles and emerging issues. Fisheries 30(6):11–23.

HSRG (Hatchery Scientific Review Group). 2009. Report to Congress on Columbia River Basin hatchery reform. Available: www.hatcheryreform.us. (November 2010).
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Kope, R. G. 1987. Separable virtual population analysis of Pacific salmon with application to marked Chinook salmon, Oncorhynchus tshawytscha, from California’s Central Valley, Canadian Journal of Fisheries and Aquatic Sciences 11:1213–1220.

Kope, R. G., and L. W. Botsford. 1988. Detection of environmental influence on recruitment using abundance data. Canadian Journal of Fisheries and Aquatic Sciences 45:1448–1458.

KRTAT (Klamath River Technical Advisory Team). 2009. Ocean abundance projections and prospective harvest levels for Klamath River fall Chinook, 2009 season. Available: http://www.pcnouncl.org/wp-content/uploads/KRTAT-2009_SkPrj_Rept_26Feb2009.pdf. (November 2010).

Lawson, P. W., and D. B. Sampson. 1996. Gear-related mortality in selective fisheries for ocean salmon. North American Journal of Fisheries Management 16:512–520.

NMFS (National Marine Fisheries Service). 2000. Biological opinion and incidental take statement: effects of the Pacific Coast Salmon Plan on California Central Valley spring-run Chinook, and California coastal Chinook salmon. NMFS, Protected Resources Division, Silver Spring, Maryland.

NMFS (National Marine Fisheries Service). 2003. Pacific salmon fisheries management off the coasts of southeast Alaska, Washington, Oregon and California and in the Columbia River basin. NMFS Northwest Region, Final Programmatic Environmental Impact Statement, Seattle.

NMFS (National Marine Fisheries Service). 2009. Public draft recovery plan for the evolutionarily significant units of Sacramento River winter-run Chinook salmon and Central Valley spring-run Chinook salmon and the distinct population segment of Central Valley steelhead. NMFS, Southwest Regional Office, Sacramento, California. Available: http://swfsc.nmfs.noaa.gov/recovery/centralvalleypplan.htm. (November 2009).

O’Farrell, M. R., M. S. Mohr, M. L. Palmer-Zwahlen, and A. M. Grover. 2008. The Sacramento index. Pacific Fishery Management Council, Report, Portland, Oregon. Available: http://www.pcouncil.org/bb/2008/1108/D1a ATT2-1108.pdf. (November 2010).

Olson, D. E., B. Spateholts, M. Paiya, and D. E. Campton. 2004. Salmon hatcheries for the 21st century: a model at Warm Springs National Fish Hatchery. Pages 585–602 in M. J. Nickum, P. M. Mazik, J. G. Nickum, and D. D. MacKinlay, editors. Propagated fish in resource management. American Fisheries Society, Symposium 44, Bethesda, Maryland.

Palmer-Zwahlen, M. L., A. M. Grover, and J. A. Duran. 2006. Feather River Chinook cohort reconstruction brood years 1998 and 1999 fall and spring runs. California Department of Fish and Game, Final Report, Santa Rosa.

Parken, C. K., J. R. Candy, J. R. Irvine, and T. D. Beacham. 2008. Genetic and coded wire tag results combine to allow more-precise management of a complex Chinook salmon aggregate. North American Journal of Fisheries Management 28:328–340.

PFMC (Pacific Fishery Management Council). 2008a. Stock abundance analysis for 2008 ocean salmon fisheries. Pacific Fishery Management Council, Preseason Report I, Portland, Oregon.

PFMC (Pacific Fishery Management Council). 2008b. Analysis of council adopted management measures for 2008 ocean salmon fisheries. Pacific Fishery Management Council, Preseason Report III, Portland, Oregon.

PFMC and NMFS (Pacific Fishery Management Council and National Marine Fisheries Service). 2007. Final environmental assessment for Pacific coast salmon plan amendment 13: an initiative to provide de minimis fishing opportunity for Klamath River fall-run Chinook salmon. Pacific Fishery Management Council, Portland, Oregon.

Prager, M. H., and M. S. Mohr. 2001. The harvest rate model for Klamath River fall Chinook, 2009 season. Available: http://www.pcouncil.org/wp-content/uploads/KRTAT-2009_SkPrj_Rept_26Feb2009.pdf. (November 2010).

Prager, M. H., and M. S. Mohr. 2001. The harvest rate model for Klamath River fall Chinook salmon, with management applications and comments on model development and documentation. North American Journal of Fisheries Management 21:533–547.

PSC (Pacific Salmon Commission). 1995. Pacific Salmon Commission, Selective Fishery Evaluation TCASFEC (95)-1, Vancouver.

PSC (Pacific Salmon Commission). 1997. Reliability and feasibility of using electronic detection for recovery of coded wire tags in coho salmon. Pacific Salmon Commission, Selective Fishery Evaluation TCASFEC (97)-1, Vancouver.

PSC (Pacific Salmon Commission). 2004. Estimation and application of incidental fishing mortality in Chinook salmon management under the 1999 agreement to the Pacific Salmon Treaty. Pacific Salmon Commission, Joint Chinook Technical Committee Report TCCChinook (04)-1, Vancouver.

PSC (Pacific Salmon Commission). 2005. Report of the expert panel on the future of the coded wire tag program for Pacific salmon. Pacific Salmon Commission, Technical Report 18, Vancouver. Available: www.psc.org/pubs/pstr18.pdf. (October 2008).

PSC (Pacific Salmon Commission). 2008. Review of 2008 mass marking and mark selective fishery proposals. Pacific Salmon Commission, Selective Fisheries Evaluation Committee Report SFEC (08)-1, Vancouver.

PSC (Pacific Salmon Commission). 2009. Review of 2009 mass marking and mark selective fishery proposals. Pacific Salmon Commission, Selective Fisheries Evaluation Committee Report SFEC (09)-1, Vancouver.

Ruckelshaus, M. H., P. Levin, J. B. Johnson, and P. M. Kareiva. 2002. The Pacific salmon wars: what science brings to the challenge of recovering species. Annual Review of Ecology and Systematics 33:665–706.

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(Article 2). Available: http://repositories.cdlib.org/jmie/ffews/vol4/iss3/art2. (October 2008).

Winans, G. A., D. Viele, A. Grover, M. Palmer-Zwahlen, D. Teel, and D. Van Doornik. 2001. An update on genetic stock identification of Chinook salmon in the Pacific Northwest: test fisheries in California. Reviews in Fisheries Science 9:213–237.

APPENDIX: ESTIMATION OF RECRUITMENT AND CONTACT RATES FOR SACRAMENTO RIVER FALL-RUN CHINOOK SALMON

In a given year, the Sacramento index (SI) provides values of total harvest (H) and in-river escapement (E). As a cohort is propagated forward in time, values of age-4 and age-5 ocean abundance (N4 and N5) in year t are calculated conditional on previous values of age-3 abundance (N3) and age-4 contact rates (c4). Given values of H, E, N4, and N5 in year t, the values of N3 and c4 in year t can be computed as follows.

First, we express H and E as the sums across ages (a = 3–5) defined in terms of the assumed cohort parameters (c, v, l, r, d, s, and m; Table 1):

\[ H = c_4 \sum_a N_a v_a I_a \]  

\[ E = \sum_a \left[ N_a s_a + I_a \left(1 - v_a\right)\right]m_a \]

\[ = \sum_a N_a v_a [I_a + (1 - l_a) r + d] s_a \left(1 - v_a\right) m_a . \]

Next, we derive expressions for c4 via equations (A.1) and (A.2):

\[ c_4 = \frac{H}{\sum_a N_a v_a I_a} \]  

\[ c_4 = \frac{\sum_a N_a s_a m_a - E}{\sum_a N_a v_a [I_a + (1 - l_a) r + d] s_a \left(1 - v_a\right) m_a} . \]
When equations (A.3) and (A.4) are equated and rearranged, the result is

\[ H \sum_a N_a v_a [I_a + (1 - l_a) r + d] s_a^{(1 - r_a)} m_a = \left( \sum_a N_a s_a m_a - E \right) \left( \sum_a N_a v_a l_a \right). \] (A.5)

To simplify notation, we redefine equation (A.5) as

\[ H \sum_a N_a \gamma_1 a = \left( \sum_a N_a \gamma_2 a - E \right) \left( \sum_a N_a \gamma_3 a \right), \] (A.6)

where

\[ \gamma_1 a = v_a [I_a + (1 - l_a) r + d] s_a^{(1 - r_a)} m_a \]
\[ \gamma_2 a = s_a m_a \]
\[ \gamma_3 a = v_a l_a. \] (A.7)

To express equation (A.6) in terms of \( N_3 \), we expand all relevant terms:

\[ H N_3 \gamma_1 3 + H \sum_{a=4,5} N_a \gamma_1 a = N_3^2 \gamma_23 \gamma_33 + N_3 \gamma_23 \sum_{a=4,5} N_a \gamma_2 a + N_3 \gamma_33 \sum_{a=4,5} N_a \gamma_3 a - E N_3 \gamma_33 \sum_{a=4,5} N_a \gamma_2 a \sum_{a=4,5} N_a \gamma_3 a - E \sum_{a=4,5} N_a \gamma_3 a \sum_{a=4,5} N_a \gamma_3 a. \] (A.8)

Rearrangement of equation (A.8) gives

\[ N_3^2 \gamma_23 \gamma_33 + N_3 \left( \gamma_23 \sum_{a=4,5} N_a \gamma_2 a + \gamma_33 \sum_{a=4,5} N_a \gamma_3 a - E \gamma_33 \right) - H \gamma_33 = H \sum_{a=4,5} N_a \gamma_1 a - \sum_{a=4,5} N_a \gamma_2 a \sum_{a=4,5} N_a \gamma_3 a \times \sum_{a=4,5} N_a \gamma_3 a + E \sum_{a=4,5} N_a \gamma_3 a. \] (A.9)

This quadratic equation for \( N_3 \) is then solved by “completing the square.” We further simplify notation by defining equation (A.9) as

\[ N_3^2 \gamma_23 \gamma_33 + N_3 Q_1 = Q_2, \] (A.10)

where

\[ Q_1 = \gamma_23 \sum_{a=4,5} N_a \gamma_2 a + \gamma_33 \sum_{a=4,5} N_a \gamma_3 a - E \gamma_33 - H \gamma_33 \]
\[ Q_2 = H \sum_{a=4,5} N_a \gamma_1 a - \sum_{a=4,5} N_a \gamma_2 a \sum_{a=4,5} N_a \gamma_3 a + E \sum_{a=4,5} N_a \gamma_3 a. \] (A.11)

Completing the square in equation (A.10) and solving for \( N_3 \) will result in

\[ N_3 = -\frac{Q_1}{2 \gamma_23 \gamma_33} \pm \sqrt{\frac{Q_2}{\gamma_23 \gamma_33} + \left( \frac{Q_1}{2 \gamma_23 \gamma_33} \right)^2}. \]

The real solution, if admissible (i.e., \( N_3 > 0 \)), is given by

\[ N_3 = \sqrt{\frac{Q_2}{\gamma_23 \gamma_33} + \left( \frac{Q_1}{2 \gamma_23 \gamma_33} \right)^2} - \frac{Q_1}{2 \gamma_23 \gamma_33}. \] (A.12)

Finally, the computed value of \( N_3 \) is combined with the other known values \((N_4, N_5, H, v_a, \text{ and } l_a)\) in year \( t \) to compute \( c_4 \) via equation (A.3). The deconvolution proceeds to the next year. To start the deconvolution, initial values are required for \( N_4 \) and \( N_5 \). However, if the deconvolution is stable (Kope and Botsford 1988), the effect of these initial values will last only for a few years, after which the convolution will converge to identical time series of values \( \{N_3, N_4, N_5, c_4\} \) regardless of the values of \( N_4 \) and \( N_5 \) in the first year.