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Measuring the net biological impact of fisheries enhancement: pink salmon hatcheries can increase yield, but with apparent costs to wild populations

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Abstract: Hatchery production of juvenile fish for release into the wild has been practiced for well over a century in an effort to increase the number of salmon available to harvest. In this study, we evaluate the net impact of the largest such program in North America, the hatchery program for pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound (PWS), Alaska. At the same time the hatchery program was increasing in output, there was a major change in productivity in the North Pacific so that throughout Alaska pink salmon increased dramatically in abundance between the 1970s and the 2000s. Using other regions of Alaska as reference sites, we estimate that the PWS hatchery program has increased the total catch by an average of 17 million fish, of which 8 million have been allocated to pay hatchery operating expenses. We estimate that the maximum sustainable yield (MSY) of wild spawning fish in PWS has increased slightly (28%), while in regions of Alaska without pink salmon hatchery programs the MSY has tripled. Our results support the use of a precautionary approach to future large-scale stock enhancement efforts.

Résumé : La production en alevinières de poissons juvéniles destinés à être relâchés dans la nature est pratiquée depuis plus d'un siècle dans le but d'accroître le nombre de saumons disponibles pour la pêche. Nous évaluons l'incidence nette du plus grand programme du genre en Amérique du Nord, le programme de production en alevinières de saumons roses (*Oncorhynchus gorbuscha*) dans le golfe du Prince William (GPW), en Alaska. Au même moment où la production de ce programme augmentait, un changement majeur de la productivité dans le Pacifique Nord s'est produit, de sorte que l'abondance des saumons roses à la grandeur de l'Alaska a connu une augmentation très marquée entre les années 1970 et 2000. En utilisant d'autres régions de l'Alaska comme sites de référence, nous estimons que le programme de production en alevinières du GPW s'est traduit par une augmentation moyenne des prises totales de 17 millions de poissons, dont 8 millions ont été alloués pour payer les dépenses d'exploitation des alevinières. Nous estimons que le rendement équilibré maximum (REM) des poissons se reproduisant à l'état sauvage dans le GPW a augmenté légèrement (28 %), alors que dans des régions de l'Alaska sans programme de production de saumons roses en alevinières, le REM a triplé. Nos résultats appuient l'adoption d'une approche prudente dans les efforts futurs de mise en valeur des stocks à grande échelle. [Traduit par la Rédaction]

Introduction

Despite increasing global demand for seafood, the production of marine capture fisheries has remained essentially stable over the past three decades (FAO 2014). Although there remains the potential for some increase by improved management (Worm and Branch 2012; Watson et al. 2013), the plateau in capture fisheries is generally believed to reflect a fundamental limitation in the capacity of the world's oceans to generate food (Worm et al. 2009; Chassot et al. 2010; Worm and Branch 2012). Intensive aquaculture appears to offer an opportunity to circumvent this limitation, and indeed, the rapid expansion of the industry has allowed continued growth in fish production in recent decades (FAO 2014). However, in many cases intensive culture of marine species is infeasible for technical, economic, or political reasons (Bostock et al. 2010). The enhancement of wild populations through release of hatchery-reared juveniles is an intermediate approach that has been practiced in a variety of marine fish and invertebrate species for over a century (Hilborn 1998; Bell et al. 2006; Lorenzen et al. 2013). Also known as stock enhancement or ocean ranching, this type of aquaculture generally involves the rearing of juveniles in a hatch-

ery past some critical stage before release in to the wild, thereby circumventing high levels of mortality or habitat limitations associated with early life-history stages (Leber et al. 2004). Surviving individuals are then expected to be available for capture after several years of ocean growth. These methods may also be suitable for hastening the recovery from historical overfishing (Molony et al. 2003). As such, there is a great deal of interest in the use of fisheries enhancement to rebuild depleted fisheries and to bolster the productivity of healthy stocks. However, despite a long history of experimentation, successful enhancement of marine species is rare, and most efforts remain in a research and development phase (Lorenzen et al. 2013; Trushenski et al. 2014).

In contrast with the limited success of marine stock enhancement, large-scale hatchery programs for anadromous salmonids — especially Pacific salmon (*Oncorhynchus* spp.) — have been operating for decades, and today it is estimated that nearly one in four salmon in the Pacific Ocean are of hatchery origin (Larkin 1974; Ruggerone et al. 2010) and overall abundance of Pacific salmon in the ocean has increased greatly (Wertheimer et al. 2005; Ruggerone et al. 2010; Peterman et al. 2012). Despite the long history and massive scale of hatchery salmon production, the
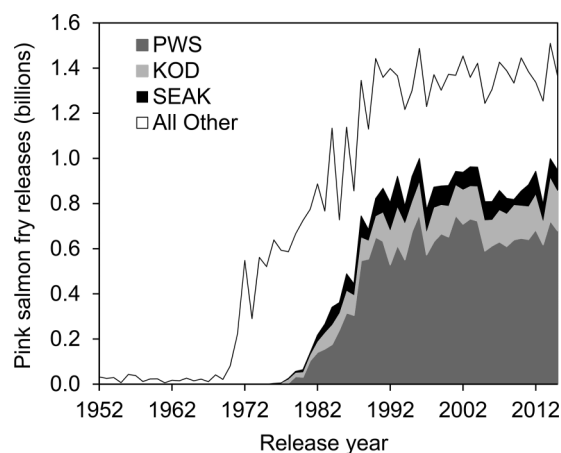
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Fig. 1. Annual releases of pink salmon fry to the North Pacific Ocean between 1952 and 2015. PWS, Prince William Sound; KOD, Kodiak; SEAK, Southeast Alaska. Data from North Pacific Anadromous Fish Commission (NPAFC 2016).

Table 1. The ten largest Pacific salmon hatchery-producing regions, ranked by average juvenile releases for the 10 years ending in 2015.

Country	Region	Species	Juvenile releases (millions)	
			2006–2015 (mean)	1952–2015 (total)
USA	**Alaska — PWS**	**Pink**	**649.1**	**19 546.8**
Japan	Hokkaido — Pacific	Chum	613.7	30 059.7
Japan	Honshu — Pacific	Chum	531.7	24 742.6
USA	Alaska — SEAK	Chum	443.4	11 104.9
Japan	Hokkaido — West	Chum	427.1	18 427.4
Russia	Sakhalin Coast	Chum	222.9	7 140.9
USA	Wash., Ore., Calif., Idaho	Chinook	202.7	10 335.2
Russia	Sakhalin Coast	Pink	200.1	9 491.0
Japan	Honshu — West	Chum	150.3	9 230.0
USA	**Alaska — KOD**	**Pink**	**147.8**	**4 456.6**

Note: Programs addressed in this study are bolded. PWS, Prince William Sound; SEAK, Southeast Alaska; KOD, Kodiak. Data summarized from North Pacific Anadromous Fish Commission (NPAFC 2016).

efficacy of salmon enhancement programs as a tool for increasing fisheries productivity has rarely been rigorously demonstrated (Larkin 1974; Lorenzen 2005; Naish et al. 2007; Paquet et al. 2011). It has been repeatedly suggested over the past 30 years that to improve enhancement efforts it is necessary to specify clear, measureable goals and monitor outcomes relative to these goals (Peterman 1991; Hilborn 1998; Naish et al. 2007; Paquet et al. 2011). Nevertheless, monitoring and evaluation of salmon hatchery programs remains largely insufficient (Naish et al. 2007). To ensure that expected enhancement effects are being achieved, evaluation of hatchery programs must consider all relevant risks and benefits (Hilborn 1998).

Much of the difficulty in evaluating salmon hatchery programs results from a lack of suitable controls that would allow for isolation of any enhancement effect. Manipulation of stocking rates provides one avenue for distinguishing environmental and hatchery influences on fisheries production (Buhle et al. 2009), but experimental reductions in hatchery production are typically precluded by legal, political, or economic considerations (Naish et al. 2007). Retrospective analyses that attempt to explain trends in abundance using time series of environmental variables and stocking rates have become more common as data on enhanced populations is increasingly available (Wertheimer et al. 2004; Morita et al. 2006; Scheuerell et al. 2015). Alaska's pink salmon (*Oncorhynchus gorbuscha*) enhancement programs provide a unique opportunity to examine the net biological impact of large-scale stock enhancement both because of its scale and the quality of available data. Compared with other salmon-producing regions in the Pacific, Alaska's hatchery programs are relatively young, and as a result reliable catch and abundance data exist for both pre- and posthatchery periods (Olsen 1993). Additionally, since 1995 most hatchery pink salmon have been thermally marked, which allows for reliable attribution in the catch (Hilborn and Eggers 2000). Hatchery releases began during the mid-1970s (Olsen 1993) and combined releases from the two largest programs have been stable around 750 million since about 1990 (Brenner et al. 2012). These programs constitute around 10% of the total number of salmon juveniles released to the North Pacific and more than half the total pink salmon (NPAFC 2016; Fig. 1; Table 1).

Four regions account for the majority of the pink salmon catch in Alaska. Prior to hatchery supplementation, pink salmon were most abundant in Southeast Alaska (SEAK; ~20 million annual run), followed by Kodiak (KOD; ~10 million), Prince William Sound (PWS; ~7 million), and the south Alaska Peninsula (SPEN; ~3 million). Enhancement occurs in three of the regions, though

the scale of operations varies by orders of magnitude. PWS pink salmon is currently the largest hatchery program in the world by annual number of releases (NPAFC 2016). Since 1990, on average, 77 (SD = 48) hatchery fry have been released for each returning wild adult fish in PWS, while in KOD this ratio is about 8:1 (SD = 3.6) and in SEAK close to 1:1 (SD = 0.5). Unlike many other regions where hatcheries are intended to mitigate declines in salmon populations resulting from habitat degradation, Alaska's hatcheries are designed to produce harvestable fish to supplement relatively healthy wild populations (Naish et al. 2007). Since the inception of the hatchery programs, pink salmon catches have increased dramatically, especially in PWS where hatchery returns now average over 35 million fish and peaked at 76 million in 2013. The majority of these fish are harvested in common-property commercial fisheries, though hatchery operators also harvest on average 30% of returning fish to cover production costs (Botz et al. 2013). Despite the ostensible success of enhancement, uncertainties regarding impacts of hatchery-origin fish on wild salmon and other species continue to cause concern among many stakeholders (Pearson et al. 2012; Brenner et al. 2012; Jasper et al. 2013). Since 2012 these concerns have contributed to delays in the recertification of Alaska salmon by the Marine Stewardship Council, resulted in a "Category C" grade for PWS salmon from the Fisheries Sustainability Partnership, and motivated an intensive research program by the Alaska Department of Fish and Game.

Recent analysis of hatchery programs from around the Pacific have found limited evidence of a large enhancement effect and in many cases identified concerns about negative impacts on wild populations. For example, Morita et al. (2006) modeled pink salmon catch in relation to hatchery output and climate factors and found that intensive stocking contributed little to a dramatic increase in abundance after 1990. Ohnuki et al. (2015) used tagging data to confirm the minor contribution hatchery-origin fish to commercial pink salmon catches in Japan and suggest that the costs of hatchery production likely outweigh the benefits. Kaev (2012) examined the population dynamics of chum (*Oncorhynchus keta*) and pink salmon in the Sakhalin–Kuril region of Russia and found evidence of an enhancement effect in hatchery-supplemented chum populations, but not in pink salmon populations. Sahashi et al. (2015) found that hatchery stocking of masu salmon (*Oncorhynchus masou*) in the Shari River tended to displace rather than supplement natural production. Similarly, Scheuerell et al. (2015) compared supplemented and natural populations of Snake River Chinook salmon (*Oncorhynchus tshawytscha*) and identified only minor increases (~3% on average) in adult density attributable to enhancement efforts. Buhle et al. (2009) identified negative im-

Fig. 2. Study area map showing the four Gulf of Alaska pink salmon-producing regions. Triangles indicate the location of major pink salmon hatcheries. PWS, Prince William Sound; KOD, Kodiak; SEAK, Southeast Alaska; SPEN, south Alaska Peninsula. Basemap created from TM World Borders 0.3 (https://koordinates.com/layer/7354-tm-world-borders-03/).
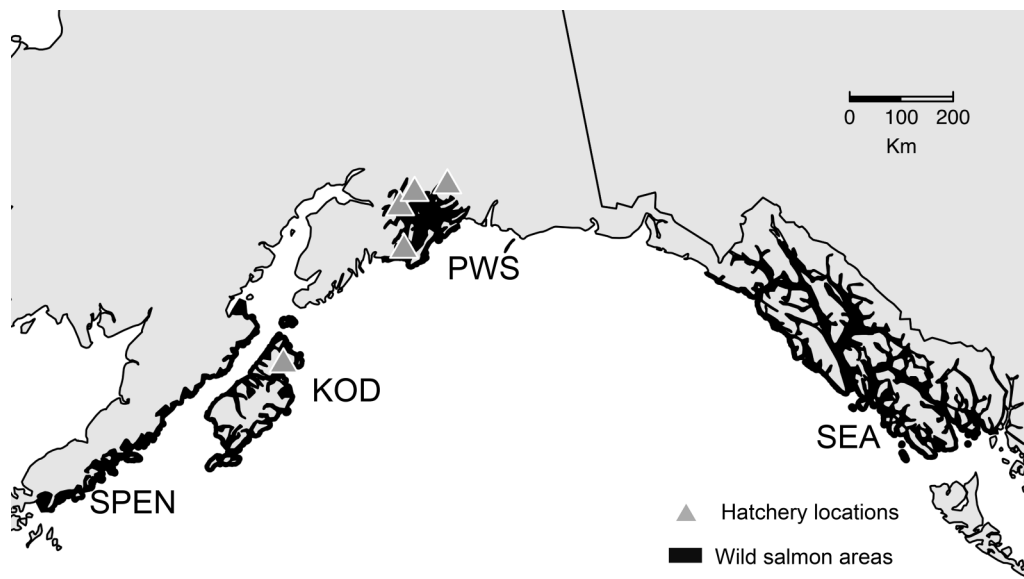
pacts of hatchery coho (*Oncorhynchus kisutch*) on wild Oregon coast populations and documented increased wild productivity following large reductions in hatchery supplementation. Finally, Zhivotovsky et al. (2012) used genetic and demographic analyses to show that rapid expansion of a chum hatchery program on Iturup Island led to the extirpation of a distinct beach-spawning ecotype by abundant hatchery strays.

Given the limited success demonstrated by these recent hatchery studies, it is not surprising that the net biological impact of Alaska's pink salmon hatchery programs have been a matter of considerable debate. Consistent with reports of limited benefits of hatchery programs, several previous studies have concluded that improved ocean survival associated with a large-scale shift in marine environmental conditions would have led to increased pink salmon catch even in the absence of hatchery production (Eggers et al. 1991; Tarbox and Bendock 1996; Hilborn and Eggers 2000, 2001). Others have argued that hatchery production is primarily responsible for increasing catches and conclude that the enhancement program is highly successful (Smoker and Linley 1997; Wertheimer et al. 2001; Heard 2003; Wertheimer et al. 2004). Hilborn and Eggers (2001) describe these two hypotheses as "augmentation" and "replacement". Under the augmentation hypothesis, hatchery production adds additional productivity to the fishery without impacting existing wild stocks. Alternatively, the replacement hypothesis asserts that hatchery production reduces wild stock productivity, and thus hatchery fish effectively replace wild fish in the catch. In practice these hypotheses define the ends of a gradient; under complete replacement the net value of one hatchery fish approaches zero, while under complete augmentation each hatchery fish could be considered equal to one additional wild fish.

To make predictions about the trajectory of the PWS pink salmon fishery in the absence of the hatchery program, we rely on two key patterns of productivity in salmon populations. First, oscillation between North Pacific climate regimes has been shown to predictably influence salmon abundance (Hare et al. 1999; Beamish et al. 1999, 2004). Second, covariation in the productivity of salmon stocks has been shown to be highest in geographically proximate populations (Pyper et al. 2001; Wertheimer et al. 2001), and indeed Alaskan salmon populations have shown strong spatial coherence in decadal-scale patterns of productivity (Hare et al.

1999). Thus, to establish an empirical estimate of net biological benefit, we examine over 50 years of catch and abundance data from four pink salmon-producing regions in Alaska (Fig. 2) to predict catch and wild stock productivity in the absence of enhancement efforts. The present study builds on previous reviews of Alaska's pink salmon hatcheries, including Eggers et al. (1991), Hilborn and Eggers (2000), and Wertheimer et al. (2001), and benefits from over 15 recent years of data, a period of consistently intense hatchery stocking (Fig. 1). With this extended data set, we are also able to compare spawner–recruit relationships for wild pink salmon populations before and after the implementation of hatchery programs. In addition, we consider the impact of hatchery production on interannual variability in pink salmon abundance.

Methods

The data set

Data on wild escapement, total catch, hatchery fry releases, wild catch, and cost recovery catch were obtained from annual Management and Fisheries Enhancement reports published by Alaska Department of Fish and Game (e.g., Botz et al. 2013). We followed the conventions described in Hilborn and Eggers (2000) for classifying hatchery and wild fish in the catch and escapement. In short, for stock identification purposes, hatchery salmon in PWS have been monitored with tagging programs since 1987 and with 100% thermal otolith marking since 1996. In the KOD region, hatchery pink salmon return to and are harvested in several bays with little natural production and are therefore distinguished from wild fish based on reported harvest location. In SEAK, the vast majority of hatchery pink salmon are harvested for cost recovery in terminal areas and are therefore distinguished by harvest location. No hatchery production occurs in the South Peninsula (SPEN) region. Thermal otolith marking and intensive catch sampling provide reliable estimates of hatchery contribution to harvest, but despite widespread marking of hatchery pink salmon there is no systematic effort to evaluate the proportion of wild stock escapement made up by hatchery strays (Brenner et al. 2012). As such, we assume all naturally spawning fish to be wild, though straying is likely common. In total we analyzed data on catch and escapement beginning with calendar year 1960 and

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Fig. 3. Stacked area plot showing catch and total abundance (catch + escapement/broodstock) of hatchery and wild pink salmon in four management areas of Alaska, 1960–2013.
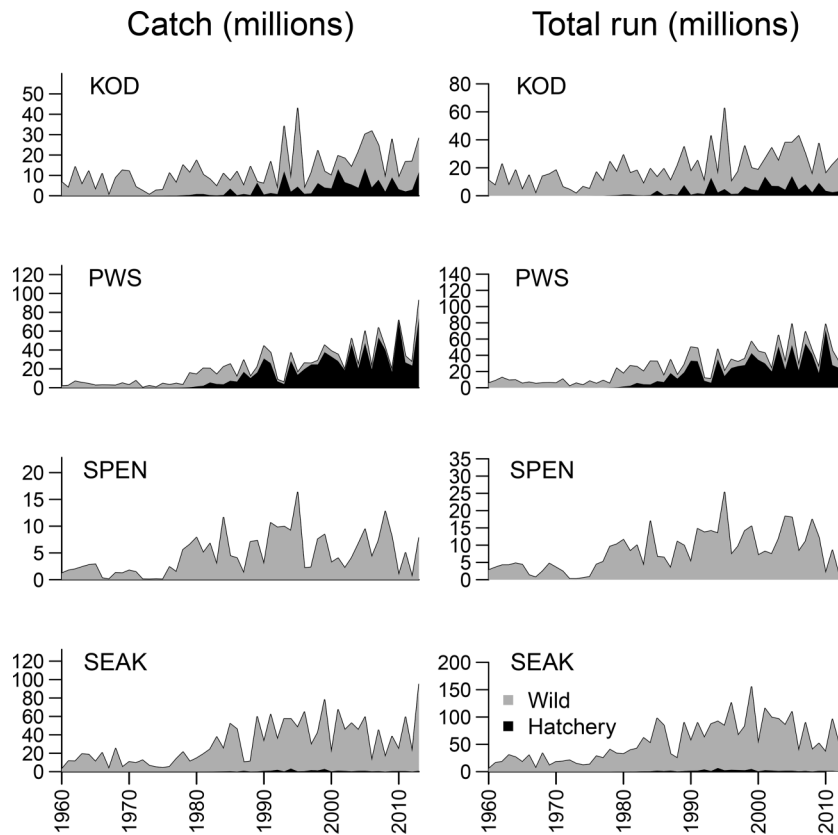
ending with the wild return in 2013 and, given the 2-year life cycle of pink salmon, were thus able to construct spawner–recruit data for brood years 1960 to 2011.

For the purposes of our analyses, we identified three distinct periods in the abundance and catch data and compared four adjacent areas of Alaska with major pink salmon production. Brood years 1960–1976 represent preregime shift natural productivity; 1977–1987 is a period of transition when the productivity of wild stocks throughout Alaska had increased, but hatchery production was not yet at its current capacity; and 1988–2011 represents when catch was generally higher in all areas and total hatchery releases were relatively stable at around 750 million (Fig. 3). Rapid change in the climate, ecology, and fisheries productivity of the North Pacific occurred in 1977 (Mantua et al. 1997; Hare et al. 1999), and we used this well-documented phenomenon to define the first period assuming that the 1977 brood year would be the first pink salmon to be fully impacted by changes in marine conditions. These fish returned 2 years later, and for the catch analysis the break between periods therefore occurs between 1978 and 1979.

Magnitude and drivers of increased catch

Because releases of hatchery pink salmon began in PWS at the same time as a large shift in natural salmon productivity in Alaska, it is difficult to separate the influence of these two factors on the observed increase in catch that has occurred since the late 1970s. Although there is no perfect control for the influence of hatcheries, the spatial coherence of Alaskan salmon productivity trends on a decadal scale allows nearby pink salmon-producing regions to serve as pseudo-controls (Hilborn and Eggers 2000). Thus, to assess the relative contribution of the environment and fry release on the temporal changes observed in catches, we fit two models to catch data for the four harvest areas: one that

included hatchery releases as a predictor variable and one that did not:

Model (1) $\log(\text{catch}_{S,t}) = p_1 + p_2 S + p_3 P + \varepsilon$

Model (2) $\log(\text{catch}_{S,t}) = p_1 + p_2 S + p_3 P + p_4 H_{S,t} + \varepsilon$

where S is a fixed area effect, P is a fixed period effect (before and after the regime shift), H is the number of fry released in area S in the year t, p_i are estimated coefficients, and ε is a normally distributed random error term. The Akaike information criterion (AIC) was computed for each model and used to compare their relative support. The difference between observed mean catch and mean catch predicted by Model 1 in the postregime shift period can be interpreted as the contribution of hatchery production to catch after accounting for the shift in natural productivity. Subtracting mean cost-recovery catch from this value gives the net contribution of hatchery production to the common-property fisheries.

Hatchery impacts on wild stock productivity

To evaluate the impact of hatchery production to wild stock productivity for the four management areas during two periods — the preregime shift period (1960–1976) and the most recent period (1988–2011) — we fit the Ricker spawner–recruit curve by period and area.

$$R = S e^{\alpha - \beta S + \varepsilon}$$

where R is the number of returns (catch plus escapement) produced by spawners, S, in a brood year, α and β are the estimated

Table 2. Pink salmon catch and variability for the preregime shift (period 1: 1960–1976) and postregime shift, full hatchery production (period 3: 1988–2013) periods in four management areas in Alaska.

District	Period	Mean catch (millions)	Standard deviation	Variance	Coefficient of variation	Normality (Shapiro test p value)	Homogeneity of variance (F test p value)
KOD	1	7.3	4.8	22.4	0.65	0.13	
	3	18.2	10.4	108.2	0.57	0.44	9.7E-04
PWS	1	3.9	3.3	10.9	0.84	2.1E-03	
	3	36.3	20.4	416.2	0.56	0.16	3.7E-11
SPEN	1	1.7	1.7	3.0	0.99	2.0E-02	
	3	6.4	4.0	15.9	0.61	0.37	5.7E-04
SEAK	1	11.3	6.6	43.8	0.58	0.14	
	3	46.0	20.4	416.6	0.44	0.85	6.2E-06

Note: KOD, Kodiak; PWS, Prince William Sound; SPEN, south Alaska Peninsula; SEAK, Southeast Alaska.

Fig. 4. Observed (grey lines and points) and model-predicted (black solid and dashed lines) pink salmon catch for four management areas in Alaska, 1960–2013. Model 1 includes period and area effects, while Model 2 adds hatchery releases as a predictor.
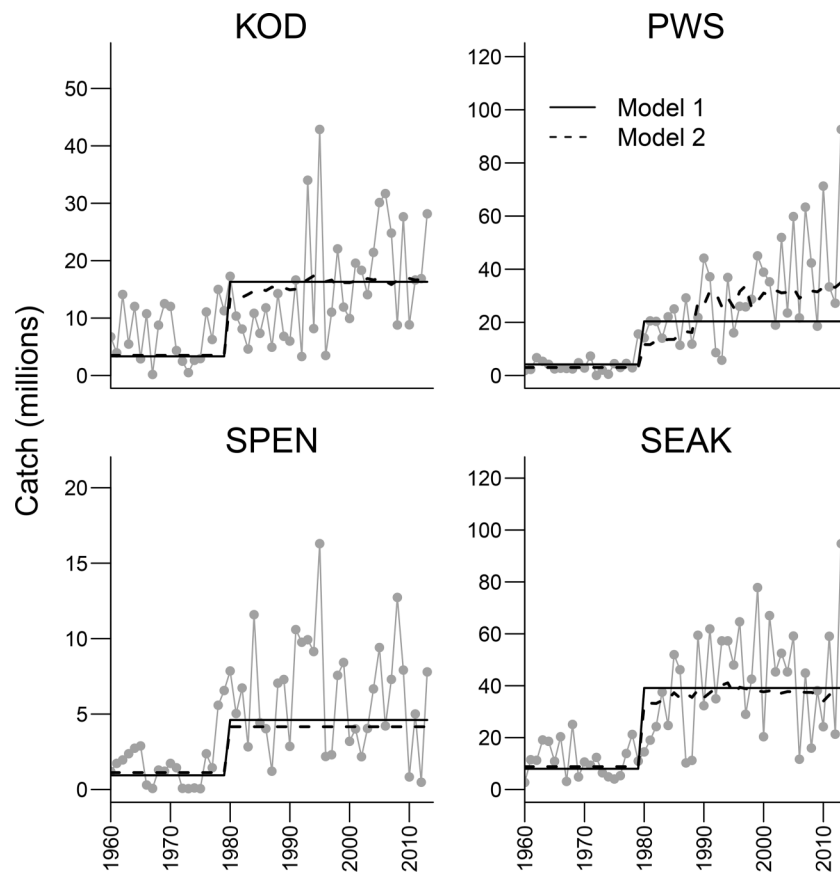
Ricker maximum recruits per spawner and density-dependence parameters, respectively, and ε is a normally distributed random error term. For each area we assessed eight hypotheses that could account for changes in wild productivity between periods: a null hypothesis of no change (α, β, and ε remain equal), and all possible combinations of changes in growth rate, density dependence, and error variance between periods. We calculated the AIC and AIC weights for each model. AIC model averaging (Burnham and Anderson 2002) was used to calculate the magnitude of change and standard deviation of the parameters across models.

The estimated parameters were used to compute the biological reference points maximum sustainable yield (MSY), biomass producing MSY (BMSY), and the optimal harvest rate for achieving MSY (Hilborn 1985):

$$BMSY = (0.5 - 0.07\alpha)\beta$$

$$MSY = BMSYe^{\alpha(1-BMSY/\beta)} - BMSY$$

Hatchery influence on variability of catch

Two indicators of catch variability were computed for each area and time period: the variance and the coefficient of variation (CV = σ^2/μ). Variance tends to increase with increasing mean, which can confound a comparison of variances. The CV is a normalized measure of variability that accounts for differences in mean and therefore removes the influence of differences in means between time periods. After testing for normality (Shapiro test), an F test was conducted to test the hypothesis that the variances observed in each area during the first (1960–1976) and last

Fig. 5. Lowest AIC Ricker model parameter estimates for preregime shift (period 1: 1960–1976) and postregime shift, full hatchery production (period 3: 1988–2011) periods in four pink salmon management areas in Alaska. α values have been multiplied by 10 to aid in visualization. Error bars show standard errors as calculated using the delta method.
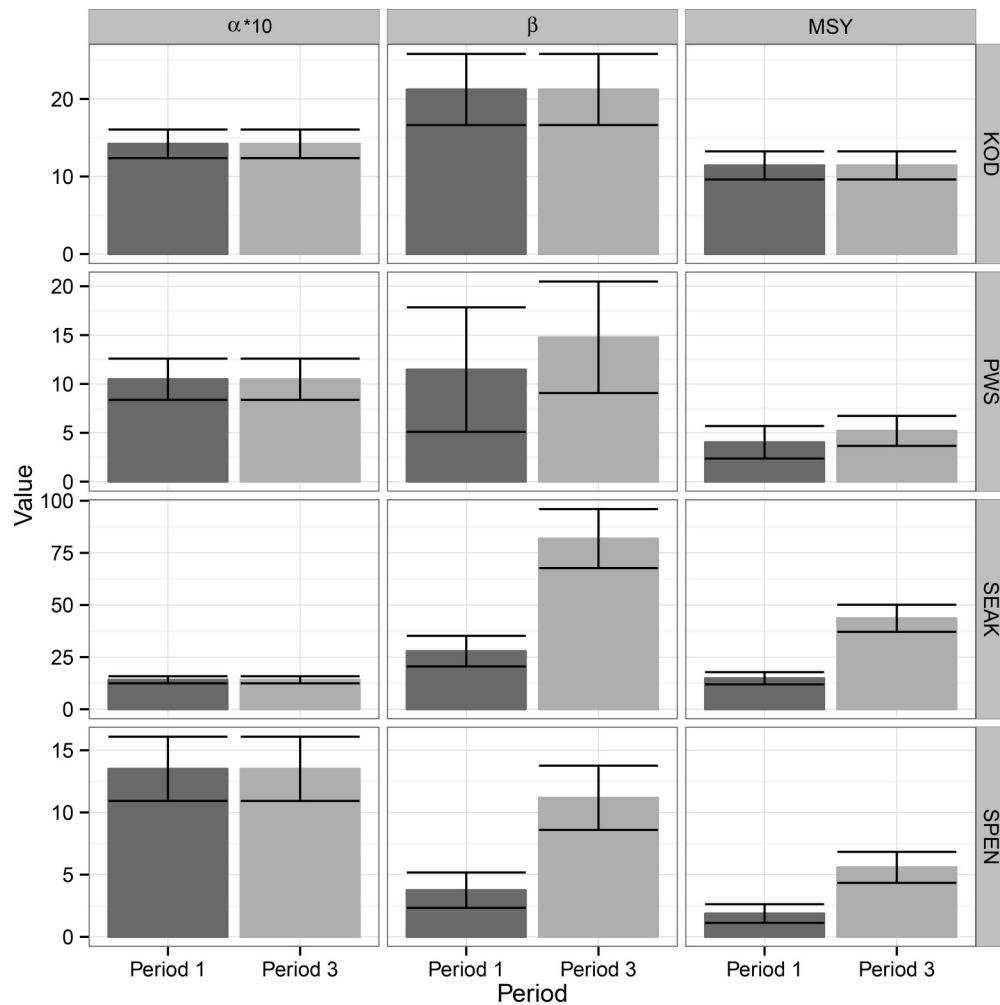
(1988–2011) periods were different. The modified Bennet's test was used to test the hypothesis that all the CVs (one for each combination of period and area) belong to the same population of CVs.

Results

Magnitude and drivers of increased catch

In all management areas examined, pink salmon catch increased following a regime shift in the late 1970s (Fig. 3; Table 2). However, in PWS, catch increased nearly tenfold between the low-productivity, prehatchery period (period 1) and the high-productivity, full hatchery production period (period 3). Meanwhile, in all other management areas (KOD, SEAK, and SPEN) catch increased approximately threefold. The disproportionate increase in catch observed in PWS compared with the other areas suggests a considerable contribution by the PWS hatchery program, even after accounting for potentially increased wild stock productivity following the shift to improved environmental conditions. We compared a model that explains changes in catch as only affected by the productivity change from periods 1 to 3 (Model 1) and a model that also uses hatchery releases as a covariate (Model 2). Including hatchery releases as a covariate improves model performance substantially compared with an environment–area only model (Model 1 AIC = 553; Model 2 AIC = 540; Fig. 4). In particular, for PWS the model that ignores hatchery releases failed to explain the large catches observed after 1990 (period 3);

the model using only regime changes predicts a mean catch of 19 million fish (Fig. 4), while the mean observed catch for that period was 36 million, a difference of 17 million. Since 1990, an average of 8 million fish per year have been harvested by the hatcheries to pay their operating expenses, suggesting that the hatcheries in PWS had an average net contribution to the commercial fleet of 9 million fish. Meanwhile, there is very little difference between predicted catch in the absence hatcheries and observed catch for KOD and SEAK, which suggests a negligible effect of enhancement in these areas.

Hatchery impacts on wild stock productivity

The estimated parameters α and β of the Ricker stock–recruitment function represent intrinsic population growth rate and carrying capacity, respectively. Thus, changes in either value reflect altered productivity for salmon stocks. Following from the notion of spatial coherence in trends of salmon productivity (Beamish et al. 1999; Finney et al. 2002), it is reasonable to assume that in the absence of region-specific factors, the productivity of wild pink salmon stocks would show similar trends in productivity. However, following the climate regime shift in the late 1970s, the period-specific stock–recruit relationships appear to show a commensurate shift in productivity in the SEAK and SPEN management areas, but not in KOD or PWS (Fig. 5; Table 3). The two regions without major hatchery programs experienced increases

Table 3. Candidate models assessed to explain changes in production between periods and the respective AIC and AIC weights.

District	Model specification	Best model	ΔAIC	AIC weight
KOD	$\alpha 1 = \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 = \sigma 2$	0	5.01	0.02
	$\alpha 1 \neq \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 \neq \sigma 2$	0	2.44	0.07
	$\alpha 1 \neq \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 = \sigma 2$	0	2.41	0.08
	$\alpha 1 = \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 \neq \sigma 2$	1	0.00	0.25
	$\alpha 1 \neq \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 = \sigma 2$	0	0.68	0.18
	$\alpha 1 = \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 \neq \sigma 2$	0	1.78	0.10
	$\alpha 1 = \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 = \sigma 2$	0	1.70	0.11
	$\alpha 1 \neq \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 \neq \sigma 2$	0	0.65	0.18
PWS	$\alpha 1 = \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 = \sigma 2$	0	0.37	0.15
	$\alpha 1 \neq \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 \neq \sigma 2$	0	2.54	0.05
	$\alpha 1 \neq \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 = \sigma 2$	0	0.54	0.14
	$\alpha 1 = \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 \neq \sigma 2$	0	0.16	0.17
	$\alpha 1 \neq \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 = \sigma 2$	0	0.09	0.17
	$\alpha 1 = \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 \neq \sigma 2$	0	1.99	0.07
	$\alpha 1 = \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 = \sigma 2$	1	0.00	0.18
	$\alpha 1 \neq \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 \neq \sigma 2$	0	2.06	0.07
SPEN	$\alpha 1 = \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 = \sigma 2$	0	2.67	0.01
	$\alpha 1 \neq \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 \neq \sigma 2$	0	3.06	0.14
	$\alpha 1 \neq \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 = \sigma 2$	0	1.63	0.01
	$\alpha 1 = \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 \neq \sigma 2$	0	3.26	0.25
	$\alpha 1 \neq \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 = \sigma 2$	0	3.92	0.01
	$\alpha 1 = \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 \neq \sigma 2$	1	1.44	0.32
	$\alpha 1 = \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 = \sigma 2$	0	0.00	0.01
	$\alpha 1 \neq \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 \neq \sigma 2$	0	4.58	0.27
SEAK	$\alpha 1 = \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 = \sigma 2$	0	8.08	0.09
	$\alpha 1 \neq \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 \neq \sigma 2$	0	1.69	0.08
	$\alpha 1 \neq \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 = \sigma 2$	0	7.86	0.16
	$\alpha 1 = \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 \neq \sigma 2$	0	0.50	0.07
	$\alpha 1 \neq \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 = \sigma 2$	0	6.91	0.05
	$\alpha 1 = \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 \neq \sigma 2$	0	0.00	0.17
	$\alpha 1 = \alpha 2,\ \beta 1 \neq \beta 2,\ \sigma 1 = \sigma 2$	1	6.14	0.35
	$\alpha 1 \neq \alpha 2,\ \beta 1 = \beta 2,\ \sigma 1 \neq \sigma 2$	0	0.34	0.04

in MSY of nearly 200%, while in KOD and PWS no significant change in productivity parameters or MSY was detected (Table 4).

In SEAK and SPEN, a large increase in the β parameter of the Ricker model best explains the differences between periods. Although several candidate models have similar weights (Table 3), when averaged across models the general pattern still holds; large increases in MSY are observed in SEA and SPEN, while little or no increase in productivity is observed in PWS and KOD. That these regions could have experienced similar productivity increases in the absence of hatcheries seems plausible given that during the early 1980s, a period in which environmental conditions had improved but hatchery production averaged less than 20% of its current level, the mean return of wild pink salmon to PWS was 22.3 million fish, and wild catch averaged over 15 million. Since 1988 when hatchery releases stabilized around 600 million fish, the mean wild return and catch have been 10.7 and 5.4 million fish, respectively, less than 50% of the prehatchery peak for returns and 35% for catch.

Hatchery influence on variability of catch

The four areas showed a similar general pattern in the temporal evolution of catch variability; as the mean catches increased, the variability tended to be larger. However, the increase in variability appeared to be sharper in PWS and KOD after 1990 (Fig. 3). Statistical tests comparing the variance between periods 1 and 3 showed a significant increase in all management areas (Table 2). Although the absolute variability increased between periods, the CV decreased from period 1 to period 3 (note that in SEAK the reduction was markedly larger). Despite this apparent trend, the Bennet's test failed to reject the hypothesis that all the CVs were equal (value = 5.42; $p = 0.12$; df = 7). These findings suggest that hatchery production has not had a stabilizing effect on pink salmon catch over time.

Discussion

Enhancement of pink salmon in Alaska — particularly in the PWS management area — has succeeded in producing a substantial and sustained enhancement effect and contributed to an order of magnitude increase in catch since the 1960s. At the same time, local wild populations have remained "sustainable" insofar as their abundances remain stable and they appear at no immediate risk of collapse. While increased variability in catch resulting from high abundances may be problematic from a fisheries and processing perspective, overall the hatchery program appears to provide a net contribution to harvest. However, our results also demonstrate that if reduced wild productivity and the costs of hatchery production are not accounted for, the benefits of enhancement may be considerably overestimated. The magnitude of increased catch in PWS has been at least twice as great as nearby areas, implying a large contribution from hatchery production, but comparisons with adjacent regions also suggest that favorable ocean conditions would have resulted in an increasing abundance trend even in the absence of an enhancement program. Therefore, in the case of PWS, although the mean catch of hatchery fish since 1990 has been 30 million, our best estimate of the net enhancement effect to the commercial fishery (9 million) is less than one-third of the apparent contribution when impacts on wild production and cost-recovery are ignored. In regions with smaller hatchery programs — KOD and SEAK — our models suggest a negligible contribution of hatcheries to increased catches. Thus, overall our results are consistent with previous studies that find enhancement effects of salmon hatcheries to be relatively minor (Morita et al. 2006; Scheuerell et al. 2015) and context-dependent (Kaev 2012).

The utilization of adjacent management areas as pseudo-replicates leaves the possibility that some local phenomenon has caused the atypical trajectory of wild pink salmon productivity in PWS and KOD. At a larger spatial scale, wild pink salmon populations from throughout the species range have increased in abundance by an average of 90% since the 1976–1977 ocean regime shift, further suggesting some unique factor at play in PWS and KOD (Morita et al. 2006; Ruggerone et al. 2010). A continued upward trend in hatchery returns despite relatively steady release levels since 1990 demonstrate that local marine conditions are not limiting productivity in hatchery pink salmon. Some persistent change in the productivity of the freshwater life-history phase would therefore be required to explain constant productivity despite improved marine conditions. Wertheimer et al. (2001) posited that the 1989 *Exxon Valdez* oil spill could account for the divergent pattern of abundance in PWS wild pink salmon. However, recent estimates of the impact of the spill on PWS pink salmon are modest, and the populations have been considered fully recovered from spill impacts since 2002 (Quinn et al. 2002; Brannon et al. 2012; EVOSTC 2014).

Based on our analysis of wild pink salmon productivity in Alaska, we conclude that the release of hatchery pink salmon has likely reduced productivity of the wild populations that interact substantially with hatchery salmon. While wild stocks in the SPEN and SEAK regions experienced dramatic increases in MSY (~200%) — apparently as a result of increased carrying capacity (Fig. 5) — no such increases were observed in PWS or KOD. This pattern suggests that natural carrying capacity may have also increased in PWS and KOD, but is utilized by hatchery fish and thus no change is apparent for the wild stocks, essentially the pattern predicted by the replacement hypothesis (Hilborn and Eggers 2001). Our analyses do not, however, implicate any particular mechanism for negative impacts of hatchery–wild interaction. Understanding the mechanism or mechanisms by which

Table 4. Parameters of the lowest AIC Ricker model, optimum escapement, maximum sustainable yield (MSY), and harvest rate (HR) producing MSY for each stock in for the preregime shift (1: 1960–1976) and postregime shift, full hatchery production (3: 1988–2013) periods.

	KOD 1	KOD 3	PWS 1	PWS 3	SEAK 1	SEAK 3	SPEN 1	SPEN 3
α	1.42	1.42	1.04	1.04	1.39	1.39	1.25	1.25
β	21.22	21.22	11.46	14.77	28.36	82.76	3.92	11.87
σ	0.67	0.49	0.57	0.57	0.47	0.39	0.88	0.88
BMSY	8.49	8.49	4.89	6.30	11.17	33.30	1.61	4.89
MSY	11.42	11.42	4.03	5.19	14.85	43.33	1.76	5.33
ΔMSY	0%		28%		202.7%		191.8%	
Optimal HR	57%	57%	45%	45%	56%	56%	52%	52%

Note: α, intrinsic population growth rate; β, density dependence; σ, standard deviation; BMSY, biomass producing MSY.

hatchery production reduces wild stock productivity is critical for quantifying the long-term risk to wild stocks and identifying appropriate management responses. If reduced productivity is primarily a result of ecological interactions that reduce wild pink salmon survival or spawning success, then wild stocks would presumably recover quickly in response to reduced hatchery releases. Although salmon are well known for their ability to reliably return to their natal streams, some proportion of a population will enter and spawn in other streams, a phenomenon known as straying (Westley et al. 2013). Hatchery salmon commonly stray and often interbreed with wild conspecifics, but generally produce fewer successful offspring than their wild counterparts (Naish et al. 2007; Christie et al. 2014). The long-term effects of regular hatchery introgression are uncertain, but in any case genetic impacts on productivity would be expected to persist for multiple generations (Grant 2011; Baskett and Waples 2013; Harbicht et al. 2014).

Previous studies have identified the potential for both ecological and genetic interaction between hatchery and wild pink salmon in Alaska. As noted previously, despite widespread marking of hatchery pink salmon in Alaska, there is no systematic effort to quantify rates of straying by hatchery fish. However, recent studies have provided evidence that straying rates by PWS hatchery pink salmon may be significant. Brenner et al. (2012) found that in some PWS streams up to 98% of fish on spawning grounds were of hatchery origin. The degree to which these fish successfully breed with wild individuals is unknown, but recent genetic analyses have found significant hatchery introgression in PWS and SEAK wild chum salmon (Jasper et al. 2013). Notwithstanding breeding success, high rates of straying reduce the validity of escapement estimates and can therefore diminish the effectiveness of wild stock management.

High straying rates indicate large potential for ecological or genetic interaction between hatchery and wild fish and also confound efforts to estimate wild escapement. With hundreds of millions of hatchery releases occurring in PWS, even low absolute straying rates can result in high proportions of hatchery fish on some wild spawning grounds. Further research on the prevalence of straying and the genetic contribution of hatchery strays to the wild gene pool should be a priority. Though high stray rates implicate reproductive interaction as a likely mechanism for hatchery impacts, interactions at other life-history stages should not be ignored. The period immediately following ocean entry is thought to be very important to lifetime survival of anadromous salmon, and localized resource depletion by large numbers of hatchery fry may potentially impact growth and survival of wild fish (Cross et al. 2008). Increased abundance is also thought to be driving a downward trend in adult body size in PWS hatchery and wild pink salmon, which suggests competition during ocean rearing and homeward migration (Wertheimer et al. 2005). Taken together, these various interactions between hatchery and wild pink salmon demonstrate that a variety of plausible mechanisms exist for hatchery program impacts on wild productivity. It seems fea-

sible that with improved understanding of these mechanisms, an effective accounting of the benefits and risks of hatchery operations for Alaska salmon enhancement could be accomplished. However, because pink salmon migrate long distances and potentially interact with many other salmon populations and species, the net benefits of enhancement will ultimately be sensitive to the geographic scope of analysis.

There is accumulating evidence that pink salmon have far-reaching impacts on ocean ecosystems. Patterns of alternating abundance in species that share ocean habitat with pink salmon strongly suggest impacts of competition (Ruggerone and Nielsen 2004). Such patterns have been observed in other salmon species, including comparatively valuable Bristol Bay sockeye salmon (*Oncorhynchus nerka*) (Ruggerone et al. 2003) and threatened Puget Sound Chinook salmon populations (Ruggerone and Goetz 2004). Recent analysis of long-term data on seabird populations in the North Pacific demonstrated similar patterns in reproductive success, implying that pink salmon also compete directly or indirectly with higher trophic levels (Springer and van Vliet 2014). There is also growing concern that large hatchery releases from around the North Pacific may be resulting in density-dependent declines in growth and survival for all salmon species as oceanic carrying capacity is approached (Cooney and Brodeur 1998; Kaeriyama et al. 2009). When considered in this broader ecosystem context, the analysis of stock enhancement becomes much more complex. With an increasing focus on ecosystem-based management of the oceans, the broader impacts of future enhancement efforts are likely to be heavily scrutinized (Pikitch et al. 2004; Samhouri et al. 2014). Ultimately, if these efforts are to be compatible with ecosystem-based principles, it will be critical to understand the biological capacity for enhancement and the potential unintended consequences of large-scale hatchery releases.

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