

Relationship of size at return with environmental variation, hatchery production, and productivity of wild pink salmon in Prince William Sound, Alaska: does size matter?

Alex C. Wertheimer¹, William R. Heard¹, J. M. Maselko¹ & William W. Smoker²

¹National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Laboratory, 11305 Glacier Highway, Juneau, AK 99801, USA (Phone: +1-907-789-6040; Fax: +1-907-789-6094; E-mail: Alex.Wertheimer@noaa.gov); ²University of Alaska, Fairbanks, Juneau Center for Fisheries and Ocean Sciences, 11120 Glacier Highway, Juneau, AK 99801, USA

Accepted 5 August 2004

Contents

Abstract	page 321
Introduction	322
Methods	323
Data sources	
Analytic approach	
Simulation of hatchery effects	
Results	326
Factors affecting body size	
Body size and productivity	
Impact of the hatchery program on body size and productivity	
Discussion	330
Acknowledgements	332
References	332

Key words: hatchery interactions, salmon ranching, stock enhancement

Abstract

Pink salmon (*Oncorhynchus gorbuscha*) returning to Prince William Sound (PWS), Alaska, have increased to historically high levels of abundance in recent years, but average body size at return has declined. We examined how body size at return of PWS pink salmon was related to 10 biophysical factors, including the scale of hatchery production. We also examined the effect of body size at return on productivity of wild pink salmon in PWS. For the 1975–1999 brood years, we found that an index of total abundance of pink salmon in the Gulf of Alaska and sea surface temperature during the year of return best explained the variation in pink salmon body size over time. Body size at return was significantly correlated with productivity of wild pink salmon. We used stepwise-regression to fit a generalized linear version of the Ricker spawner-recruit model to determine if body size would explain significant variation in wild-stock productivity in context with other environmental variation, including hatchery production. The results indicate that variability in wild-stock productivity is primarily driven by density-independent factors in the marine environment, but that body size of wild spawners also significantly affects productivity of wild PWS pink salmon. We conclude that the success of large-scale enhancement increasing the total run in PWS may have contributed to the decline in body size because of density-dependent growth in the Gulf of Alaska. We used a simulation model to estimate the impact of hatchery-induced changes in adult body size on wild-stock production in PWS. We estimated an annual wild-stock yield loss of 1.03 million pink

salmon, less than 5% of the annual hatchery return of 24.2 million adult pink salmon for brood years 1990–1999.

Introduction

Hatcheries have been used to create or maintain fisheries by mitigating for habitat degradation and circumventing factors identified as limiting production from a specific locale or region (Radonski and Loftus, 1995). Billions of Pacific salmon are now cultured and released into coastal ecosystems throughout the North Pacific (Mahnken et al., 1998). Some hatchery programs have been very successful in producing fish for harvest; for example, Japanese chum salmon (*Oncorhynchus keta*) hatcheries have produced annual returns of 40–87 million adults since 1990, exceeding historical production levels by more than an order of magnitude (Kaeriyama, 1989; Mayama and Ishida, 2003). As the scale of hatchery production has increased, however, concern for potential ecological effects on wild stocks has also increased (Hilborn, 1992; Meffe, 1992; Levin et al., 2001).

In Prince William Sound (PWS), Alaska, pink salmon (*O. gorbuscha*) have increased to historically high levels of abundance in recent decades (Wertheimer et al., 2001). Total pink salmon returns to PWS have averaged 31 million fish annually from 1990 to 2000 (Johnson et al., 2002).

Many of these fish have been produced from a system of four large hatcheries. The numbers of juveniles released by the hatcheries increased rapidly until the mid-1980s (Figure 1); 500–600 million juvenile pink salmon have been released annually since then (Johnson et al., 2002). Hatchery returns from these releases have averaged 25.3 million fish annually from 1990 to 2000 (Johnson et al., 2002), ostensibly providing large benefits to the region (Pinkerton, 1994; Smoker and Linley, 1997).

Concurrent with increasing hatchery production, however, the number of wild pink salmon returning to PWS has declined from record high levels for brood years 1977–1983 (Figure 1), and productivity (returns per spawner) of wild pink salmon has generally declined. The role of hatcheries in regard to the wild-stock decline is controversial. Hilborn and Eggers (2000) have attributed the decline in wild-stock abundance to interactions with hatchery production; they concluded that hatchery fish had largely replaced wild fish, and estimated a net annual benefit from hatcheries of only 2 million fish. Wertheimer et al. (2004), however, found that conditions in the marine environment, rather than number of hatchery

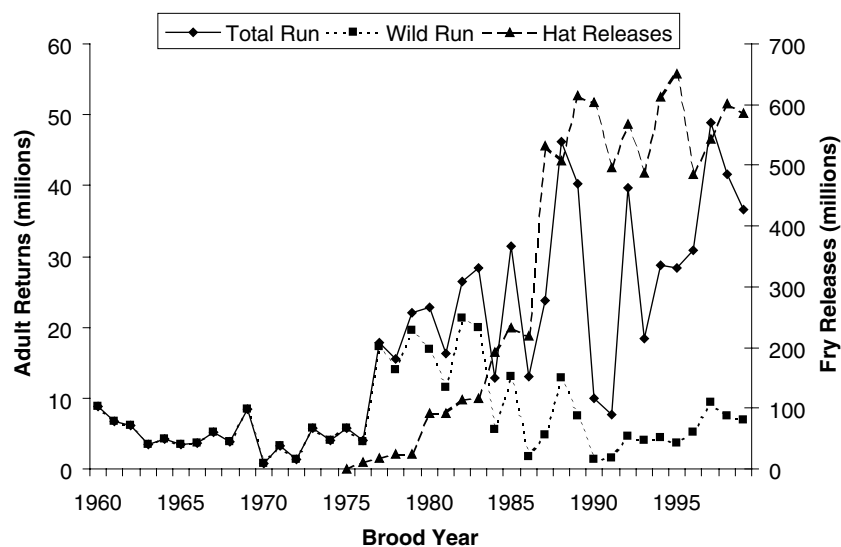


Figure 1. Total run, wild run, and hatchery releases of pink salmon in Prince William Sound, Alaska, 1960–2001.

juveniles released, best explained the variability in wild-stock productivity. They concluded that pink salmon productivity in PWS was driven primarily by density-independent marine conditions, and that the hatchery releases provided an annual net benefit of 20.6 million to 25.3 million pink salmon annually for the 1990–2000 returns.

None of the prior analyses investigating the interaction of large-scale enhancement and wild-stock productivity have considered the effect of body size at return. Abundance of Pacific salmon in the North Pacific Ocean has increased in recent decades, while body size of adult fish has generally decreased (Ishida et al., 1993; Bigler et al., 1996; Pyper and Peterman, 1999). Ricker (1995) noted that low adult growth rates and small body size of pink salmon have been associated with unusually high abundance in local regions. Bigler et al. (1996) found that the average body size of pink salmon in commercial fisheries throughout Alaska declined from 1970 to 1993, including PWS. Average body size of pink salmon in PWS has declined significantly since the inception of the hatchery program (Figure 2); average body size of adults at return from 1965 to 1975 was 1.86 kg, 26% larger than the 1.48 kg average for 1990–2000.

Our objectives in this paper are: (1) to use historical records of biophysical factors (including the scale of hatchery releases) to determine which of these factors significantly affect the body size at return of PWS pink salmon; (2) to examine the effect of body size of return on the productivity of PWS wild pink salmon in conjunction with the

scale of hatchery releases and other sources of environmental variation; and (3) to develop simulation models incorporating statistically significant factors to estimate the degree of impact of large-scale hatchery production on body size at return and wild-stock productivity.

Methods

Data sources

Productivity (returns per spawner) of wild pink salmon and body size at return of pink salmon in PWS, since the inception of the hatchery program (1975 brood) through the 1999 brood year, were evaluated in relation to parent body size and 10 measures or indexes of environmental conditions over time. The indexes reflect: (1) temperature experienced by pink salmon at different stages of their lives – a direct physiological determinant of growth and body size over the range of temperatures experienced by the salmon; (2) the abundance (density) of pink salmon – a putative depressor of growth, body size and survival; and (3) the aggregated effect of the biophysical environment on survival of pink salmon in the ocean, as indicated by the observed marine survival of hatchery releases. Variables used are listed in Table 1, and a short description of the parameters and the sources of the data are given below. Because pink salmon have an obligatory 2-year life cycle (Heard, 1991), returns (catch plus escapement) in a given year can be assigned entirely as the production from the brood

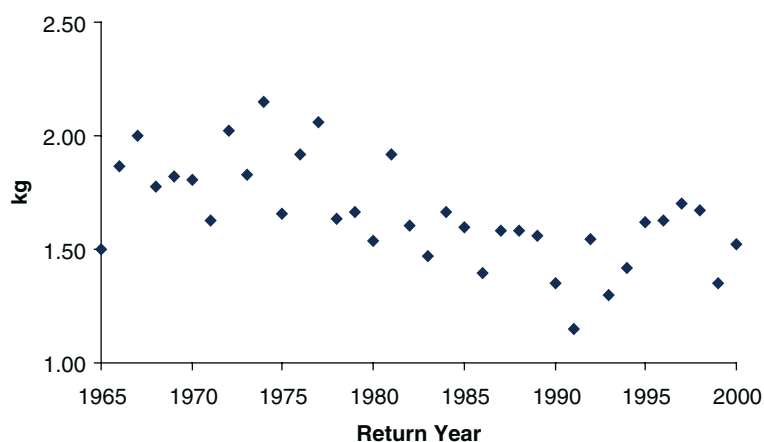


Figure 2. Average body size at return for pink salmon in Prince William Sound, Alaska, 1965–2000.

year 2 years prior to the return year. We identify the spawning or brood year as y , the year of entry into seawater of juvenile pink salmon as $y+1$, and the year of return as $y+2$.

Wild-stock spawners and returns by brood year

The numbers of wild-stock pink salmon harvested in PWS and spawning in PWS streams are estimated annually by the Alaska Department of Fish and Game (ADF&G). All commercial catches are reported to ADF&G; escapement estimates are based on weekly aerial surveys of 209 index streams. Data were available for the 1960–1999 brood years of pink salmon (Gray et al., 2002; Johnson et al., 2002).

Body size at return

Statistics on the average weight of pink salmon in the commercial fisheries in PWS are maintained by ADF&G (ADF&G, 2003). Average weight in the catch was used as the measure of adult body size (ParentSize, Table 1) of spawners for a given brood year y , and as the measure of body size at return of recruits in year $y+2$ (Table 1, Table 3).

Table 1. Correlations of body size at return of pink salmon to Prince William Sound and productivity (returns per spawner) of wild pink salmon with 10 biophysical variables

Variable	Body size at return r	Productivity r
ParentSize	0.198	0.543**
SpringAir	0.032	0.318
GOASST-0	0.150	0.505**
GOASST-1	0.442**	0.144
PDO-0	-0.077	0.073
PDO-1	0.426**	-0.106
HatFry	-0.479*	-0.394
HatRun	-0.491**	0.034
GOARun	-0.589**	-0.100
MSI	0.013	0.602***

Time period encompassed 1977 through 2001 return years. Variables are described in Methods. The correlation coefficients, r , that were significantly different from zero are indicated by asterisks, where * indicates $0.05 < p < 0.1$, ** $0.01 < p < 0.05$, and *** $p < 0.01$. Critical values for the statistical significance of r for each correlation were adjusted to account for autocorrelation in the data series (Pyper and Peterman, 1998).

Spring air temperatures

Spring air temperatures (SpringAir, Table 1) in Cordova, Alaska, were used as an index of sea surface temperature (SST) conditions affecting initial marine rearing of juvenile pink salmon in PWS ($y+1$). Air temperatures were used because a time series of SST observations for nearshore habitats in PWS extending prior to the 1990s was not available. Air temperatures in coastal areas have been shown to be related to the surface layer temperatures of nearby estuaries (Bruce et al., 1977), and have been used as a proxy for temperature regimes encountered by salmon (Adkison et al., 1996). Monthly average air temperatures for Cordova were retrieved from climate statistics summarized by the US National Weather Service, Alaska Region (www.wrcc.dri.edu/Summary/climsmak.html). Annual spring temperatures were computed as the average of the monthly averages for April, May, and June for a given year.

Gulf of Alaska summer SST

Summer sea surface temperatures in an area of the Gulf of Alaska (GOA) adjacent to PWS were used as an index of temperature conditions affecting PWS pink salmon: (1) in year $y+1$ as juveniles after they migrated from PWS into the GOA (GOASST-0, Table 1); and (2) in year $y+2$ as adults as they migrated from the GOA into PWS (GOASST-1, Table 1). Temperature records for the area lying between lat 58° N and lat 60° N, and long 146° E and long 149° E were extracted from the Comprehensive Ocean-Atmosphere Data Set (COADS; Mendelssohn and Roy, 1996) for 1976–1997 (affecting brood years 1975–1996) and from the Global Telecommunication System Data Base (www.pfeg.noaa.gov) for 1998–2000 (affecting brood years 1997–1999). Annual summer temperature was computed as the average of the temperatures recorded for July, August, and September in a given year.

Pacific Decadal Oscillation (PDO)

The PDO is an index of temperature changes in the north Pacific Ocean that has been related to basin-scale changes in the abundance and productivity of fishes in the north Pacific and GOA, including Pacific salmon (Mantua et al., 1997). Because the average PDO during winter is thought to be related to growth and survival conditions influencing sal-

mon populations in the subsequent spring and summer (Mantua et al., 1997), the annual PDO index was calculated as the average winter PDO. The average of the monthly averages for November of year y through March of the following year $y+1$ was used as a measure of basin-scale temperatures affecting juvenile pink salmon of brood year y in year $y+1$ (PDO-0, Table 1). The average of the monthly averages for November of year $y+1$ through March of the following year $y+2$ was used as a measure of basin-scale temperatures affecting juvenile pink salmon of brood year y in year $y+2$ (PDO-1, Table 1). Monthly PDO index values were extracted from data maintained by N. J. Mantua, University of Washington (<http://jisao.washington.edu/pdo/PDO.latest>).

Hatchery releases

The number of hatchery juveniles released into PWS in year $y+1$, where y is the brood year, was used as the measure of the impact of sea ranching (HatFry, Table 1). Hatchery fry could cause density-dependent interactions throughout the entire marine life history ($y+1$, $y+2$). Release numbers are from Johnson et al. (2002).

Hatchery returns

The number of hatchery fish returning in year $y+2$ (HatRun, Table 1) is an index of the density of hatchery fish in the marine environment during years $y+1$, $y+2$. Return numbers were from Johnson et al. (2002) and Gray et al. (2002).

GOA pink salmon abundance

The annual catch of pink salmon in fishing districts of Alaska adjacent to the GOA was used as an index of pink salmon abundance in the GOA (GOARun, Table 1) to examine potential density-dependent interactions (primarily in year $y+1$). Catch data were compiled from Byerly et al. (1999) and from ADF&G (2003).

Marine survival index

Average annual survival rates of hatchery juveniles released in PWS (Gray et al., 2002; Johnson et al., 2002) were used as an index of the marine survival conditions (MSI, Table 1) affecting wild-stock survival and productivity. The survival rate for a brood year y was computed by dividing the total hatchery return of pink salmon in year $y+2$ by the total number of hatchery pink salmon released as juveniles in year $y+1$.

Analytic approach

The association of wild-stock productivity and average body size at return to the biophysical factors in Table 1 was first examined by bivariate correlation. Wild-stock productivity was defined as $\text{Ln}(R_{y+2}/S_y)$, where R is the return, S is the spawning escapement, and y is the brood year. Time-series of data can be autocorrelated, which can affect the statistical evaluation of the correlation of two parameters. To account for autocorrelation, we adjusted the degrees of freedom for the hypothesis tests for significance of the correlation for each bivariate comparison using the methods recommended by Pyper and Peterman (1998).

We used a multiple linear regression model to determine which factors best explained the variability in body size at return:

$$\text{Size} = a + b_1X_1 + \dots + b_nX_n + \varepsilon_1 \quad (1)$$

where a is the intercept, b is the coefficient for variable X , and ε_1 is the residual error for the fit of Equation (1). The residuals of the final model were examined for significant autocorrelation or partial autocorrelation for time lags 1–6 years (Minitab, 2000).

We used the generalized linear version of the Ricker model (Quinn and Deriso, 1999) to determine which factors best explained the variability in wild-stock productivity:

$$\text{Ln}(R/S) = a + \beta S + \gamma_1X_1 + \dots + \gamma_nX_n + \varepsilon_2 \quad (2)$$

where a is the natural log of the Ricker productivity parameter α , β is the Ricker density-dependence parameter, γ is the coefficient for variable X , and ε_2 is the residual error for the fit of Equation (2).

We used forward–backward stepwise regression (Minitab, 2000) to identify significant variables in these models. A variable could enter a regression model at each step only if its coefficient was significantly different from zero at $p < 0.1$ (forward step); a variable already in the regression model would be dropped if its coefficient was not significantly different from zero at $p < 0.1$ after the addition of a new variable (backward step). The exception to this decision rule was that annual numbers of spawners, S , was kept in the regression model regardless of the p value for β , because it is

biologically appropriate for a spawner-and-recruit model. The Akaike Information Criterion (AIC) for multiple regression analysis (Gagne and Dayton, 2002), corrected for small sample size (Shono, 2000), and the coefficient of determination (R^2) were calculated at each step. The residuals of the final models were examined for significant autocorrelation or partial autocorrelation for time lags of one to six years (Minitab, 2000). The presence of significant autocorrelation in a regression model can affect the estimation of parameter coefficients and their statistical significance. No significant autocorrelation was detected for the residuals for either model, so no autocorrelative parameter was added to the models.

Simulation of hatchery effects

The models fit to Equations (1) and (2) were used to simulate the impact of hatchery production on body size at return and productivity of PWS wild-stock pink salmon. Hatchery releases or returns per se were not identified as significant parameters in either model. For Equation (1), however, GOARun and GOASST-1 were identified as significant. Because HatRun is a component of GOARun, we can simulate the annual effect on size at return in each year i in the absence of hatchery production by

$$\widehat{\text{Size}}_i = a + b_1(\text{GOARun}_i - \text{HatRun}_i) + b_2\text{GOASST-1} + \varepsilon_{1i} \quad (3)$$

where b_1 and b_2 are the coefficients estimated for GOARun and GOASST-1 by Equation (1), and ε_1 are the residuals from Equation (1). In turn, parent body size was identified as a significant parameter affecting wild-stock productivity. We can use the results from Equation (3) to simulate the annual effect of parent body size on the productivity of brood year y by

$$\widehat{\text{Ln}}(R_{y+2}/S_y) = a + \beta S_y + \gamma_1 \text{MSI}_y + \gamma_2 \text{ParentSize}_y + \varepsilon_{2y} \quad (4)$$

using the estimated average annual body size from Equation (3) for parent body size rather than the observed parent body size, and the parameter coefficients and residuals as estimated by Equation (2).

Confidence intervals for the point estimates from Equations (3) and (4) were generated by non-parametric bootstrapping of residuals from the regression models (Efron and Tibshirani, 1993). For body size at return, body size for each year for return years 1977–2001 were estimated by Equation (3), with ε_1 for each year of return selected randomly from the vector of residuals for all years from the model fit to Equation (1). This process was repeated 1000 times. Average values of body size for each of the 1000 permutations were computed, and the lowest and highest 50 values were truncated to identify the bootstrap 95% confidence interval. Similarly, bootstrap $\text{Ln}(R/S)$ values were estimated from Equation (4), using body size estimates from the bootstrap permutations of Equation (3), and adding ε_2 for each brood year selected randomly with replacement from the vector of residuals for all years from Equation (2). This process was also repeated 1000 times.

Results

Factors affecting body size

Five of the ten variables tested were significantly correlated with body size at return (Table 1). The two measures of temperature conditions affecting the adult ocean period, GOASST-1 and PDO-1, were positively associated with body size, while measures of temperature conditions affecting the juvenile marine period were not significantly correlated with body size. The three measures of pink salmon abundance, HatFry, HatRun, and GOARun, were negatively associated with body size at return. The correlation coefficient was greater for GOARun ($r = -0.589$), a basin-scale measure index of pink salmon density, than for HatFry or HatRun ($r = -0.479$ and -0.491 , respectively), which are more indicative of regional, PWS-scale pink salmon density (Table 1).

There was substantial cross-correlation among the variables identified as significantly associated with body size at return (Table 2). The three measures of pink salmon abundance that were significantly correlated and negatively correlated with adult body size were themselves significantly and positively correlated: larger hatchery releases (HatFry) were positively correlated with larger hatchery runs (HatRun), which were positively

Table 2. Cross-correlation matrix for variables with significant correlation ($p < 0.1$) with either body size at return or wild-stock productivity of Prince William Sound pink salmon (Table 1)

	GOASST-0	GOASST-1	PDO-1	HatFry	HatRun	GOARun	MSI
GOASST-0	–						
GOASST-1	.096	–					
PDO-1	.083	.277	–				
HatFry	–.210	–.190	–.477 **	–			
HatRun	–.001	–.230	–.436 **	.821 **	–		
GOARun	.093	–.260	–.459 **	.692 **	.689 **	–	
MSI	.120	–.128	.120	–.150	.282	.074	–
ParentSize	.279	.144	–.043	–.500 *	–.196	–.427 *	.126

The correlation coefficients, r , that were significantly different from zero are indicated by asterisks, where * indicates $0.05 < p < 0.1$, ** $0.01 < p < 0.05$, and *** $p < 0.01$. Critical values for the statistical significance of r for each correlation were adjusted to account for autocorrelation in the data series (Pyper and Peterman, 1998).

correlated with greater abundance of pink salmon in the Gulf of Alaska (GOARun). The PDO-1 was negatively and significantly correlated with these three measures of pink salmon abundance (Table 2). This inverse relationship of the PDO-1 to pink salmon abundance reflects the declining trend for the PDO over this time series ($r = -0.340$), a period during which hatchery releases and adult pink salmon abundance were generally increasing (Figure 1).

The stepwise regression fit for the linear model for body size at return (Equation (1)) identified two variables as explaining statistically significant variability in body size at return: GOARun and GOASST-1 (Table 3). The GOARun index was the first variable to enter the model and explained 31.9% of the variation in body size at return. The addition of GOASST-1 increased the R^2 to 38.5%. With these parameters in the model, no other variable of the 10 considered could be added at the $p = 0.1$ significance criterion. The AIC declined from Step 1 to Step 2, also indicating that the addition of the second parameter improved the model without decreasing information content.

Body size and productivity

Three of the 10 variables tested were significantly correlated with wild-stock productivity ($\ln(R/S)$), including ParentSize (Table 1). All of these variables were positively associated with wild-stock productivity: MSI ($r = 0.602$), the index of hatchery marine survivals; ParentSize ($r = 0.543$); and GOASST-0 ($r = 0.505$), an index of regional-

scale summer temperatures during juvenile ocean residency. The number of hatchery fry released, HatFry, was negatively associated with wild-stock productivity ($r = -0.394$), but the correlation coefficient was not significantly different from zero.

There was limited cross-correlation among the variables identified as significantly associated with wild-stock productivity. ParentSize was inversely and significantly correlated with HatFry and GOARun (Table 2), demonstrative of the same trends identified for body size at return. The correlation of MSI with HatFry was negative, but not significant ($r = -0.150$, $p > 0.5$), indicating that MSI was generally independent of the density of hatchery fry in PWS.

Table 3. Results of forward-backward stepwise regression fit of a multiple linear regression model for body size at return and associated biophysical variables for Prince William Sound pink salmon, brood years 1975–1999 (Equation (1), Methods)

Variable	Step 1	Step 2
Constant	4.07 (< 0.001)	1.82 (< 0.001)
GOARun	$-7.7 \times E^{-9}$ (0.002)	$-6.7 \times E^{-9}$ (0.006)
GOASST-1		0.18 (0.075)
R^2 (adjusted)	31.9	38.5
AIC _c	23.13	22.05

The regression coefficients, the associated probability, p , that a coefficient is significantly different from zero, adjusted R^2 (the coefficient of determination adjusted for degrees of freedom), and the Akaike Information Criterion corrected for small sample size (AIC_c) are shown for each step of the regression.

The stepwise regression fit of the generalized linear Ricker model (Equation (2)) identified four variables as explaining statistically significant variability in wild-stock $\ln(R/S)$: MSI, ParentSize, GOASST-0, and the index number of spawners (Table 4). Because the spawner index was arbitrarily kept in the model, this variable entered the model at the first step, although it was not statistically significant ($p = 0.261$) as the only predictive variable. When MSI entered the model at step 2, the adjusted R^2 increased from 1.4% to 43.5% (Table 4). ParentSize increased the R^2 to 64.0% and GOASST-0 to 69.2%. With these parameters in the model, no other variable of the ten considered could be added at the $P = 0.1$ significance criterion. The AIC declined for each step of the model, indicating that the addition of each parameter increased the amount of variability explained by the model without decreasing information content.

Impact of the hatchery program on body size and productivity

Estimates from Equation (3) of predicted body size at return in the absence of hatchery production are shown in Figure 3a. As hatchery runs increased, the predicted body size diverged positively from the observed body size. The predicted average body size at return from brood years 1990–1999 (return years 1992–2001) was 1.61 kg, 5% larger than the observed body size of 1.53 kg (Table 5). The bootstrap-predicted average for these years, 1.56 kg, was biased low relative to the determin-

istic point estimate. The bootstrap 95% confidence interval was 1.50–1.64 kg, which overlaps the observed body size; thus, the predicted hatchery effect on average body size was not significantly different from zero.

The effect of predicted body size changes in the absence of PWS hatchery fish on the productivity of wild fish over time is shown in Figure 3b. As the predicted body size effects become more pronounced, the predicted productivity from wild PWS pink salmon diverged positively from the observed. The predicted average $\ln(R/S)$ in the absence of hatchery fish from Equation (4) for brood years 1990–1999 was 1.26, 11% higher than the observed of 1.14 (Table 5). The bootstrap-predicted average of $\ln(R/S)$ was 1.39, biased high relative to the deterministic point estimate of 1.26. The bootstrap 95% confidence interval was 1.19–1.62 kg, and did not overlap the average observed productivity of 1.14; thus, the predicted body size effect on productivity was significantly different from zero. The exponents of the productivity values were calculated to estimate R/S , and applied to the average escapements for the 1990–1999 brood years to estimate average number of wild-stock returns at the different productivity levels (Table 5). The predicted average for Equation (4) were corrected for back-transformation bias by adding the variance divided by 2 before taking the exponent (Hilborn and Walters, 1992). The difference between the estimated wild-stock returns at observed and predicted productivities are estimates of yield loss from wild-stocks due to the hatchery production. We estimated a

Table 4. Results of forward–backward stepwise regression fit of the generalized linear version of the Ricker model for productivity ($\ln(R/S)$) to spawner/recruit data and associated biophysical variables for Prince William Sound wild-stock pink salmon, brood years 1975–1999

Variable	Step 1	Step 2	Step 3	Step 4
Constant	1.93 (<0.001)	0.97 (<0.014)	-1.74 (0.039)	-4.86 (<0.001)
Spawners	$-2.5 \times E^{-7}$ (0.261)	$-3.7 \times E^{-7}$ (0.034)	$-3.4 \times E^{-7}$ (0.017)	$-2.7 \times E^{-7}$ (0.057)
MSI		23.8 (<0.001)	21.6 (<0.001)	20.3 (<0.001)
Parent size			0.80 (0.001)	0.68 (0.004)
GOASST-0				0.29 (0.046)
R^2 (adjusted)	1.4	43.5	64.0	69.2
AIC _c	63.77	51.31	41.72	39.78

The regression coefficients, the associated probability, p , that a coefficient is significantly different from zero, adjusted R^2 (the coefficient of determination adjusted for degrees of freedom), and the Akaike Information Criterion corrected for small sample size (AIC_c) are shown for each step of the regression. Spawners were always included in the model; other variables could enter or remain in the model if $p < 0.1$.

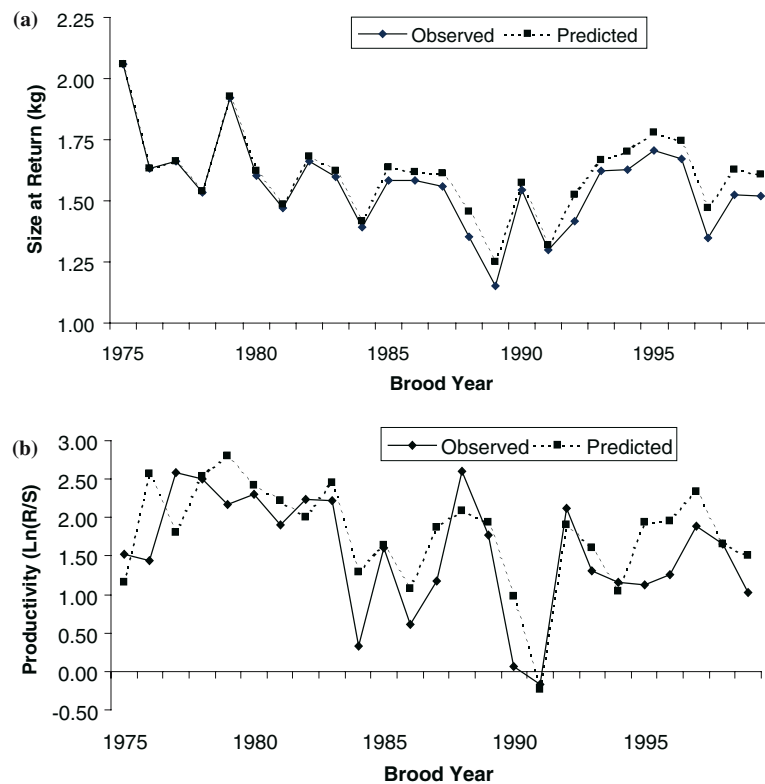


Figure 3. Observed and predicted body size at return (a) and wild-stock productivity (b) for 1975–1999 brood year pink salmon in Prince William Sound, Alaska. Predicted values are estimates from simulations of the effect of hatchery production of pink salmon.

wild-stock yield loss of 1.03 million fish, with a 95% confidence interval based on the bootstrap estimates of 0.21–2.70 million fish. The asymmet-

rical confidence interval is a result of the transformation from $\text{Ln}(R/S)$ to R/S for the bootstrap values.

Table 5. Observed and simulated averages for brood years 1990–1999 for body size at return and wild-stock productivity $\text{Ln}(R/S)$, where R is the recruits from spawners, S , of Prince William Sound pink salmon

	Observed	Simulations			
		Point estimates	Bootstrap average	Bootstrap 95% CI	
				Lower	Upper
Size at return (kg)	1.53	1.61	1.56	1.50	1.64
$\text{Ln}(R/S)$	1.14	1.26	1.39	1.19	1.62
R/S	3.14	3.86 ^a	4.03	3.28	5.04
Predicted average Wild-stock return (millions of fish)	4.45	5.48	5.72	4.66	7.15
Yield loss (millions of fish)	–	1.03	1.27	0.21	2.70

^aCorrected for back-transformation bias from log-transformed equation (Hilborn and Walters, 1992).

Point estimates and bootstrap predictions of body size and $\text{Ln}(R/S)$ in the absence of hatchery fish were derived from Equations (3) and (4) in the Methods. Yield loss is the difference between observed and simulated (absence of hatcheries) wild-stock productivity at average annual escapements of 1.42 million fish for the 1990–1999 brood years.

Discussion

The relationships between body size at return of PWS pink salmon with the index of abundance of pink salmon in the Gulf of Alaska and sea-surface temperature conditions during their last year at sea indicate that body size is significantly affected by the density of pink salmon in the Gulf of Alaska, and by environmental conditions during their adult growing season. These results are consistent with the paradigm that growth of salmon during their ocean life history is density-dependent and is affected by both regional and basin-scale abundance of conspecifics (Ishida et al., 1993; Ricker, 1995; Bigler et al., 1996; Pyper and Peterman, 1999).

Hatchery releases did not explain significant variation in body size at return when considered in the context of other biophysical factors such as the abundance of pink salmon in the Gulf of Alaska, although body size at return was significantly and inversely correlated with hatchery releases of pink salmon in a bivariate comparison. Hatchery releases were also significantly and positively correlated with the Gulf of Alaska abundance index. Because catches from PWS hatcheries comprised 24% of this index, we infer that hatchery production, by directly and substantially contributing to broad-scale pink salmon abundance, does affect body size at return.

We also found that parent body size explained a significant portion of the variation in wild-stock productivity of PWS pink salmon in the model relating productivity to biophysical factors. Both egg size and fecundity are positively correlated with body size in pink salmon (e.g., Foerster and Pritchard, 1941; Godfrey, 1959; Malecha, 2002). At a given escapement level, changes in fecundity directly affect the number of eggs transported into the spawning habitat (Forbes and Peterman, 1994). Smaller eggs result in smaller fry, which may have lower survival to adult (Bams, 1970; Parker, 1971). Because of these relationships, reductions in body size have been intuitively linked with reduced reproductive potential in salmon (Heard, 1991; Bigler et al., 1996; Cooney and Brodeur, 1998; Pyper and Peterman, 1999). Helle (1989) found that, for chum salmon in Olsen Creek in PWS, the larger the mean body size of spawners, the higher the survival to adulthood of their progeny. To our knowledge, our analysis is the

first time a direct association has been detected between body size and productivity of a pink salmon population.

While both egg size and fecundity are linked to body size, Malecha (2002) found that the relationship between an individual female's body size and egg size or fecundity was non-linear in a stock of pink salmon at the tails of the adult female size distribution. In the middle of the size distribution, egg size and fecundity changed linearly with body size, but within the lower end of the body size range, egg size was conserved and fecundity declined more rapidly with decreasing size. Because general decline in average body size will result in more fish returning in the size ranges at which egg size is conserved, the effects of decreasing egg size on productivity will diminish as fish become smaller, and the effect from reduced fecundity will increase. From a management perspective, the impact of reduced fecundity on potential egg deposition in a spawning stream could be mitigated by modifying annual escapement goals in response to inseason measures of body size at return.

We found that, while body size was a significant parameter affecting wild-stock productivity, density-independent conditions in the marine environment represented by the index of marine survival of hatchery fish and SST during the juvenile marine phase determined most of the variability in wild-stock productivity. The small and non-significant correlation of hatchery fry releases with hatchery survivals indicated that marine survival conditions were generally independent of the density of hatchery fry in PWS. The significant relationships of hatchery survivals with wild stock productivity indicated that hatchery and wild fish respond similarly to marine conditions. Coronado and Hilborn (1998a) also found that the marine survival trends were generally similar for hatchery and wild coho salmon (*O. kisutch*) within a geographic area, and Kovtun (2000) found a similar relationship for hatchery and wild chum salmon from the Tym River in Sakhalin, Russia. Boldt and Haldorson (2004) found that, while energy content of juvenile pink salmon in PWS varied by location, hatchery and wild juveniles were similar in energy content when captured at the same location.

Density-dependent marine growth and size at return and density-independent survival have also been observed for Japanese hatchery chum salmon (Kaeriyama, 1989; Mayama and Ishida, 2003). In

contrast to the evidence for density-dependent effects on adult size of salmon, evidence for density-dependent effects on survival is scarce (Broddeur et al., 2003; Ruggerone et al., 2003). However, Levin et al. (2001) concluded that density-dependent marine effects caused by large hatchery releases of 'spring/summer' Chinook salmon into the Columbia River basin reduced the marine survival of wild 'spring/summer' Chinook salmon stock in the Snake River, a tributary of the Columbia River; and Ruggerone et al. (2003) concluded that growth and survival of Bristol Bay sockeye salmon were reduced by density-dependent interactions with Asian pink salmon during their marine residency.

The association of productivity of PWS pink salmon with regional-scale rather than basin-scale temperatures (e.g., PDO) during the first year at sea is consistent with findings for pink, chum, and sockeye (*O. nerka*) salmon (Pyper et al., 2001; Mueter et al., 2002). Regional coherence in survival rates has also been observed for coho and Chinook (*O. tshawytscha*) salmon (Coronado and Hilborn, 1998a, b). Regional scale differences due to environmental variability, rather than the scale of hatchery production, is likely the primary reason for the differing trends in abundance and productivity of pink salmon that have been noted among different regions of Alaska (Hilborn and Eggers, 2000, 2001; Wertheimer et al., 2001, 2004).

Marine competition and freshwater genetic impacts have been proposed as possible mechanisms for hatchery impacts on the survival of wild pink salmon in PWS (Thomas and Mathisen, 1993; Hilborn and Eggers, 2000). The potential for ecological and genetic interactions of PWS pink salmon is well documented. Willette et al. (1999) found that growth of juvenile salmon in PWS was limited when juvenile densities were high. Reduced growth rates of juvenile pink salmon can directly affect survival (Parker, 1971; Mortensen et al., 2000; Willette et al., 2001). Also, Joyce and Evans (2002) have observed high rates of straying of hatchery adults into streams near the hatcheries in PWS, which could lead to negative genetic effects (Hindar et al., 1991; Busack and Currens, 1995).

Despite the potential for direct impacts on wild pink salmon, we did not find that the hatchery fry releases were significantly related to wild-stock productivity. In contrast, Hilborn and Eggers

(2000) found that hatchery fry releases were a significant parameter in their Ricker stock-recruit model. However, these authors did not consider other sources of environmental variation affecting PWS pink salmon, and thus fry releases were a proxy for other, more significant parameters such as the marine survival index and parent body size. In a previous analysis (Wertheimer et al., 2004), we also reported significant relationships between hatchery fry releases and wild-stock productivity for data for the 1975–1998 brood years, one of three time series of data we examined in that paper. However, we did not correct the significance test of the bivariate correlation for autocorrelation, and we did not consider the effect of parent body size in the spawner-recruit model for this time period. When parent body size was included in the stock-recruit model for this time period, hatchery fry releases no longer explained significant additional variation in productivity. We note that the bivariate correlations between fry releases and both wild-stock productivity and hatchery marine survival are negative (albeit not statistically significant), and thus we do not completely dismiss the possibility of density-dependent competition affecting survival. But we conclude that such impacts are small relative to the other parameters we have identified as significantly affecting wild-stock productivity.

Even though we found no direct effect of hatchery releases on wild-stock productivity, the impact of hatchery releases on body size at return represents an indirect effect because of the influence of parent body size on wild-stock productivity. This impact is contingent on the degree to which hatchery fish enhance, rather than replace, wild fish. Because our analyses indicate that productivity is largely driven by density-independent conditions in the marine environment, we attribute an incremental contribution to density-related body size changes in PWS pink salmon to the scale of hatchery production in PWS.

Based on these linkages between hatchery production, body size, and wild-stock productivity, we estimated that decreased adult body size due to hatchery production reduced yield of wild fish in PWS at 1.03 million fish annually, with a 95% confidence interval of 0.21 to 2.7 million, for brood years 1990–1999. This represents less than 5% of the average annual hatchery returns from these brood years of 24.2 million adult pink sal-

mon (Johnson et al., 2002). The resultant estimated net gain from hatchery production is 23.2 million fish, with a 95% confidence interval of 21.5 to 24.0 million.

The confidence intervals for our estimates accounted for process error in the underlying regression models. We did not, however, consider the effect of measurement errors in the data. The presence of substantial measurement error can obscure relationships among variables (Quinn and Deriso, 1999), but have not typically been considered when relating variation in size or productivity of salmon to environmental variation (e.g., Bigler et al., 1996; Pyper and Peterman, 1999; Pyper et al., 2001; Levin et al., 2001; Mueter et al., 2002; Ruggerone et al., 2003). Accounting for measurement error was outside the scope of this paper. Our objectives were to examine the relationship of indexes of size and wild stock productivity to a wide suite of environmental parameters or indexes, including the number of hatchery fry released, using modeling approaches similar to Hilborn & Eggers (2000) and Wertheimer et al. (2004); these authors also did not incorporate measurement error into their stock-recruit models.

Quantitative assessments of the impacts of sea ranching programs are essential to determine if programs are worth the economic and ecological costs (Blankenship and Leber, 1995; Laurec, 1999). The Alaska salmon hatchery program is designed to enhance the harvest of salmon while minimizing impacts to wild-stocks; policies, statutes, and regulations have been established to protect and maintain the productive potential of wild stocks (McGee, in press). Our results confirm the conclusions of several previous analyses: the hatchery program in PWS has provided large benefits and net increases in catch to the region (Pinkerton, 1994; Smoker and Linley, 1997; Wertheimer et al., 2001, 2004). Wild stocks of pink salmon in PWS remain highly productive, in relation to their historical performance and relative to the productivity of stocks in other regions of Alaska (Wertheimer et al., 2001). However, our results also indicate that there has been some loss of productivity of the wild stock due to the hatchery program. Evaluation of the magnitudes and the mechanisms of such interactions, as well as the level of enhancement to the fisheries, are essential to provide constituent groups, managers, and policy makers the information they need to assess

the success of hatchery programs and to refine hatchery strategies and regulations to minimize impacts to wild stocks.

Acknowledgements

A number of individuals generously provided us with information on Prince William Sound pink salmon and associated environmental data sets. We thank Steve Moffitt and Marianne McNair of the Alaska Department of Fish and Game; David Reggiani, Prince William Sound Aquaculture Corporation; Tim Joyce, USDA Forest Service; and Roy Mendelsohn and Richard Parish, National Oceanic and Atmospheric Administration. We also appreciate the insightful and helpful reviews by Jerry Pella, National Marine Fisheries Service, and two anonymous reviewers.

References

- ADF&G (2003) Recent years harvest statistics. Available from the Internet URL http://www.cf.adfg.state.ak.us/cf_home.htm
- Adkison, M.D., Peterman, R.M., Lapointe, M.F., Gillis, D.M. and Korman, J. (1996) Alternate models of climatic effects on sockeye salmon, *Oncorhynchus nerka*. *Fish. Oceanogr.* **5**, 137–152.
- Bams, R.A. (1970) Evaluation of a revised hatchery method tested on pink and chum salmon fry. *J. Fish. Res. Bd. Can.* **27**, 1429–1452.
- Bigler, B.S., Welch, D.W. and Helle, J.H. (1996) A review of the size trends among North Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* **53**, 455–465.
- Blankenship, H.L. and Leber, K.M. (1995) A responsible approach to marine stock enhancement. *Am. Fish. Soc. Symp.* **15**, 167–175.
- Boldt, J.L. and Haldorson, L.J. (2004) Size and condition of wild and hatchery pink salmon juveniles in Prince William Sound, Alaska. *Trans. Am. Fish. Soc.* **133**, 173–184.
- Brodeur, R.D., Myers, K.W. and Helle, J.H. (2003) Research conducted by the United States on the early ocean life history of Pacific salmon. *N. Pac. Anadr. Fish. Comm. Bull.* **3**, 89–131.
- Bruce, H.E., McLain, D.R. and Wing, B.L. (1977) Annual physical and chemical oceanographic cycles of Auke Bay, Southeastern Alaska. US Dep. Commerce NOAA Technical Report NMFS SSRF-712, 11 pp.
- Busack, C.A. and Currens, K.P. (1995) Genetic risks and hazards in hatchery operations: fundamental concepts and issues. *Am. Fish. Soc. Symp.* **15**, 71–80.
- Byerly, M., Brooks, B., Simonson, B., Savikko, H. and Gieger, H. (1999) Alaska commercial salmon catches, 1878–1997. Regional Information Report No. 5J99-05. Alaska Depart-

- ment of Fish and Game, Division of Commercial Fisheries, Juneau, 67 pp.
- Cooney, R.T. and Brodeur, R.D. (1998) Carrying capacity and North Pacific salmon production: stock-enhancement implications. *Bull. Mar. Sci.* **62**, 443–464.
- Coronado, C. and Hilborn, R. (1998a) Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kitsutch*) in the Pacific northwest. *Can. J. Fish. Aquat. Sci.* **55**, 2067–2077.
- Coronado, C. and Hilborn, R. (1998b) Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kitsutch*) in the Pacific northwest. *Bull. Mar. Sci.* **62**, 409–425.
- Efron, B. and Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman and Hall, New York, 436 pp.
- Foerster, R.E. and Pritchard, A.L. (1941) Observations on the relation of total egg content to total length and weight in the sockeye (*Oncorhynchus nerka*) and the pink salmon (*O. gorbuscha*). *Proc. Trans. Royal Soc. Can. Ser. 3* **35**(3), 51–60.
- Forbes, L.S. and Peterman, R.M. (1994) Simple size-structured models of recruitment and harvest in Pacific salmon (*Oncorhynchus* spp.) *Can. J. Fish. Aquat. Sci.* **51**, 603–616.
- Gagne, P. and Dayton, C.M. (2002) Best regression model using information criteria. *J. Mod. Appl. Statist. Meth.* **1**(2), 479–488.
- Godfrey, H. (1959) Variations in annual average weights of pink salmon, 1944–1958. *J. Fish. Res. Board Can.* **16**, 329–337.
- Gray, D., Ashe, D., Johnson, J., Merizon, R. and Moffitt, S. (2002) Prince William Sound management area 2001 annual finfish management report. Regional Information Report 2A02-20. Alaska Department of Fish and Game, Division of Commercial Fisheries, Anchorage, AK, 169 pp.
- Heard, W.R. (1991) Life history of pink salmon. In: Groot, C. and Margolis, L. (eds.), *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver, BC, pp. 119–230.
- Helle, J.H. (1989) Relation between size-at-maturity and survival of progeny in chum salmon, *Oncorhynchus keta* (Walbaum). *J. Fish. Biol.* **35**(A), 99–107.
- Hilborn, R. (1992) Hatcheries and the future of salmon in the Northwest. *Fisheries* **15**(1), 5–8.
- Hilborn, R. and Eggers, D. (2000) A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. *Trans. Am. Fish. Soc.* **129**, 333–350.
- Hilborn, R. and Eggers, D. (2001) A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska: response to comment. *Trans. Am. Fish. Soc.* **130**, 729–724.
- Hilborn, R. and Walters, C.J. (1992) *Quantitative Fisheries Stock Assessment: Choice, Dynamics, and Uncertainty*. Chapman and Hall, New York, 570 pp.
- Hindar, K., Ryman, N. and Utter, F. (1991) Genetic effects of cultured fish on natural fish populations. *Can. J. Fish. Aquat. Sci.* **48**, 945–957.
- Ishida, Y., Ito, S., Kaeriyama, M., McKinnell, S. and Nagasawa, K. (1993) Recent changes in age and size of chum salmon (*Oncorhynchus keta*) and possible causes. *Can. J. Fish. Aquat. Sci.* **50**, 290–295.
- Johnson, J., Sharp, D., Joyce, T. and Moffitt, S. (2002) Prince William Sound management area 2000 annual finfish management report. Regional Information Report 2A02-02. Alaska Department of Fish and Game, Division of Commercial Fisheries, Anchorage, 164 pp.
- Joyce, T. and Evans, D. (2002) Using thermally-marked otoliths to aid the management of Prince William Sound pink salmon. *N. Pac. Anad. Fish Comm. Tech. Rept.* **3**, 35–36.
- Kaeriyama, M. (1989) Aspects of salmon ranching in Japan. *Physiol. Ecol. Japan Spec. Vol.* **1**, 625–638.
- Kovton, A.A. (2000) Wild and hatchery production and recruitment of autumn chum salmon (*Oncorhynchus keta* Walbaum) in the Tym River, Sakhalin, 1960–1998. *N. Pac. Anad. Fish Comm. Bull.* **2**, 255–262.
- Laurec, A. (1999) Can the conditions for successful enhancement or sea ranching be defined? In: Howell, B.R., Moksness, E. and Svasand, T. (eds.), *Stock Enhancement and Sea Ranching*. Blackwell Science, Oxford, pp. 1–5.
- Levin, P. S., Zabel, R. W. and Williams, J. G. (2001) The road to extinction is paved with good intentions: negative association of fish hatcheries with threatened salmon. *Proc. R. Soc. Lond.* **268**(B), 1–6.
- Malecha, P.W. (2002) Survival and development of pink salmon (*Oncorhynchus gorbuscha*) embryos and fry as related to egg size and quantitative genetic variation. M.Sc. Thesis, University of Alaska Fairbanks, Juneau Center Fisheries Ocean Sciences, 68 pp.
- Mahnken, C., Ruggerone, G., Waknitz, W. and Flagg, T. (1998) A historical perspective on salmonid production from Pacific Rim hatcheries. *Nor. Pac. Anad. Fish Comm. Bull.* **1**, 38–53.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. and Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *J. Climatology* **8**, 241–253.
- Mayama, H. and Ishida, Y. (2003) Japanese studies on the early ocean life of juvenile salmon. *Nor. Pac. Anad. Fish Comm. Bull.* **3**, 41–67.
- McGee, S. (in press) Salmon hatcheries in Alaska-plans, permits, and policies that provide protection for wild stocks. In: Nickum, M.J., Mazik, P.M., Nickum, J.G. and MacKinlay, D.D. (eds.), *Propagated Fish in Resource Management*. American Fisheries Society, Bethesda, MD.
- Meffe, G.K. (1992) Techno-arrogance and halfway technologies: salmon hatcheries on the Pacific coast of North America. *Conserv. Biol.* **6**, 350–354.
- Mendelsohn, R. and Roy, C. (1996) *Comprehensive ocean dataset extraction's user guide*. US Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-228, 67 pp.
- Minitab (2000) *Minitab User's Guide 2: Data Analysis and Quality Tools*. Minitab Statistical Software, Release 13.
- Mortensen, D.M., Wertheimer, A.C., Taylor, S.G. and Landingham, J. (2000) Relationship between the early marine growth of pink salmon and marine water temperature, secondary production, and survival to adulthood. *Fish. Bull.* **98**, 319–335.
- Mueter, F.J., Peterman, R.M. and Pyper, B.J. (2002) Opposite effects of ocean temperature on survival rates of 120 stocks of Pacific salmon (*Oncorhynchus* spp.) in northern and southern areas. *Can. J. Fish. Aquat. Sci.* **59**, 456–463.
- Parker, R.R. (1971) Size selective predation among juvenile salmonid fishes in a British Columbia inlet. *J. Fish. Res. Bd. Can.* **28**, 1503–1510.

- Pinkerton, E. (1994) Economic and management benefits from the coordination of capture and culture fisheries: the case of Prince William Sound pink salmon. *N. Am. J. Fish. Manage.* **14**, 262–277.
- Pyper, B.J., Mueter, F.J., Peterman, R.M., Blackburn, D.J. and Wood, C.C. (2001) Spatial covariation in survival rates of Northeast Pacific pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. Aquat. Sci.* **58**, 1501–1515.
- Pyper, B.J. and Peterman, R.M. (1998) Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Can. J. Fish. Aquat. Sci.* **55**, 2127–2140.
- Pyper, B.J. and Peterman, R.M. (1999) Relationship among adult body length, abundance, and ocean temperature for British Columbia and Alaska sockeye salmon (*Oncorhynchus nerka*) 1967–1997. *Can. J. Fish. Aquat. Sci.* **56**, 1716–1720.
- Quinn, T.J. and Deriso, R.B. (1999) *Quantitative Fish Dynamics*. Oxford University Press, Oxford, 542 pp.
- Radonski, G.C. and Loftus, A.J. (1995) Fish genetics, fish hatcheries, wild fish, and other fables. *Amer. Fish. Soc. Symp.* **15**, 1–4.
- Ricker, W.E. (1995) Trends in the average size of Pacific salmon in Canadian catches. In: Beamish, R.J. (ed.), *Can. Spec. Publ. Fish. Aquat. Sci.* **121**, 593–602.
- Ruggerone, G.T., Zimmermann, M., Myers, K.M., Nielsen, J.L. and Rogers, D.E. (2003) Competition between Asian pink salmon (*Oncorhynchus gorbuscha*) and Alaskan sockeye salmon (*O. nerka*) in the North Pacific Ocean. *Fish. Oceanogr.* **12**(3), 209–219.
- Shono, H. (2000) Efficiency of the finite correction of Akaike's information criteria. *Fish. Sci.* **66**, 608–610.
- Smoker, W.W. and Linley, T.J. (1997) Are Prince William Sound salmon hatcheries a fool's bargain? *Alaska Fish. Res. Bull.* **43**(1), 75–78.
- Thomas, G.L. and Mathisen, O.A. (1993) Biological interactions of natural and enhanced stocks of salmon. *Fish. Res.* **18**, 1–18.
- Wertheimer, A.C., Smoker, W.W., Joyce, T.L. and Heard, W.R. (2001) Hatchery pink salmon in Prince William Sound: enhancement or replacement? *Trans. Am. Fish. Soc.* **130**, 712–720.
- Wertheimer, A.C., Heard, W.R. and Smoker W.W. (2004) Effects of hatchery releases and environmental variation on wild-stock productivity: consequences for sea ranching of pink salmon in Prince William Sound, Alaska. In: Leber, K.M., Kitada, S., Svasand, T. and Blankenship, H. L. (eds.), *Stock Enhancement and Sea Ranching 2*. Blackwell Science Ltd, Oxford, pp. 307–326.
- Willette, T.M., Cooney, T., and Hyer, K. (1999). Some processes affecting mortality of juvenile fishes during the spring bloom in Prince William Sound, Alaska. *Lowell Wakefield Symp. Ser.* **16**, 137–142.
- Willette, T.M., Cooney, R.T., Patrick, V., Mason, D.M., Thomas, G.L. and Scheel, D. (2001) Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska. *Fish. Oceanogr.* **10**(1), 14–41.