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ARTICLE

The effects of salmon abundance and run timing on the performance of management by emergency order

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Abstract: We examine the effect of uncertainty in salmon run abundance and run timing on the ability of managers to achieve escapement goals using in-season regulation of fishery openings using a detailed model of the arrival of salmon and operation of the fishery, the information available to managers, and managers' behavior. We supplement this management strategy evaluation by examining historical management performance of sockeye salmon (*Oncorhynchus nerka*) fisheries from Bristol Bay, Alaska. We find that uncertainty about run timing exacerbates the effects of uncertainty about salmon abundance. Early-arriving small runs and late-arriving large runs are especially problematic, as they produce in-season data that mimic that of a typically sized run with average run timing. Managers faced with an early-arriving small run will tend to overharvest the fish, particularly the earliest-arriving component. Managers faced with a late-arriving large run will tend to underharvest the fish, and harvest the latest-arriving components at a higher rate. This differential harvest of early or late components of the run is important because it might reduce the genetic diversity of the stock, thus reducing its future productivity.

Résumé : Nous examinons l'effet de l'incertitude relative à l'abondance et au moment de la montaison des saumons sur la capacité des gestionnaires d'atteindre les objectifs d'échappement à l'aide de la réglementation saisonnière des ouvertures de la pêche. Pour ce faire, nous utilisons un modèle détaillé de l'arrivée des saumons et du déroulement de la pêche, l'information dont disposent les gestionnaires et le comportement de ces derniers. Nous complétons cette évaluation des stratégies de gestion en examinant les résultats historiques de la gestion dans les pêches au saumon rouge (*Oncorhynchus nerka*) de la baie de Bristol (Alaska). Nous observons que l'incertitude relative au moment de la montaison exacerbe les effets de l'incertitude relative à l'abondance des saumons. Les petites montaisons précoces et les grandes montaisons tardives sont particulièrement problématiques puisqu'elles produisent des données saisonnières semblables à celles d'une montaison de taille typique dont le moment est dans la moyenne. Les gestionnaires en présence d'une petite montaison précoce tendent à surexploiter les poissons, particulièrement la composante qui arrive le plus tôt. Les gestionnaires en présence d'une grande montaison tardive tendent à sous-exploiter les poissons et à exploiter plus intensément les composantes arrivées le plus tardivement. Cette exploitation différentielle des composantes précoces et tardives de la montaison est importante parce qu'elle pourrait réduire la diversité génétique du stock, réduisant du coup sa productivité future. [Traduit par la Rédaction]

Introduction

Fixed escapement goal policies have a long history in Alaska, commencing soon after statehood (Clark et al. 2006). Maintaining escapements in years of poor returns is credited with preserving Alaska salmon runs in the aftermath of overharvest and through periods of poor environmental conditions (King 2009). A fixed escapement goal can be shown to maximize sustained yield from the stock (Clark 1976). However, a fixed harvest rate also has beneficial properties, with a similar yield and a lower variability (Bue et al. 2008; Steiner et al. 2011). Intermediate strategies can also be devised and are common in non-salmon fisheries; for example, Tier 1, 2, and 3 stocks in US federally managed fisheries (North Pacific Fisheries Management Council 2014). Currently, escapement goals for most salmon stocks in Alaska are given as a range (Alaska Statute 5AAC 39.223), affording managers some flexibility.

In Alaska, the management strategy most commonly used to achieve desired escapement goals is in-season management by emergency order (Clark et al. 2006). Managers open and close fisheries with as little as a few hours' notice based on the latest information on the state of the fishery. With perfect information (i.e., if managers knew the current year's total eventual return of fish, the timing of arrival of these fish on the fishing ground, and the efficiency of the fishing fleet, etc.), managers should in theory attain the desired escapement whenever the return exceeds the goal. However, managers' information is quite imperfect; in particular, preseason (Adkison 2002; Adkison and Peterman 2000; Burke et al. 2013; Costello et al. 1998; Fried and Hilborn 1988, Hyun et al. 2012; Noakes et al. 1990; Pulwarty and Redmond 1997; Scheuerell and Williams 2005) and in-season forecasts (Claytor and MacCrimmon 1988; Flynn and Hilborn 2004; Holt et al. 2009; Hyun et al. 2005; Link and Peterman 1998; Noakes 1989; Zheng and Mathisen 1998) of total returns and run timing (Hodgson et al. 2006; Hyun et al. 2005; Mundy and Evenson 2011; Springborn et al. 1998; Zheng and Mathisen 1998) are highly uncertain. Several authors (Bocking and Peterman 1988; Holt and Peterman 2006) have noted that weak runs tend to result in underescapement and strong runs in overescapement, sometimes to such a degree that the result more closely resembles a constant harvest rate than a constant escapement policy.

Several papers (Anderson and Beer 2009; Carney and Adkison 2014*a*; Quinn et al. 2007) have demonstrated differential harvest

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rates on seasonal components of some salmon runs. This raises concerns about fisheries-induced selection removing genetic diversity in run timing from a population, potentially reducing current or future productivity. Another concern is the potential extirpation of subpopulations with different run timings, whose timing may be a genetically based adaptation to the particular spawning location used (Brannon 1987). In the face of climate change it is important to preserve the biocomplexity of salmon populations so that both the genetic and demographic diversity are available to withstand future environmental variability.

In this study, we focus on escapement. We look at both the magnitude and the timing of escapement resulting from emergency order management. We examine the effects of the two major difficulties salmon managers must confront in attempting to achieve escapement goals: uncertainty about the abundance of the return and uncertainty about the timing of the return.

Materials and methods

Salmon fishery simulation

The salmon fishery simulation employed is a simplification of equations and parameter values previously developed for the sockeye salmon (*Oncorhynchus nerka*) stock in Egegik River, Alaska (Flynn et al. 2006). The arrival of salmon at the coastal fishing district is assumed to follow a noisy bell-shaped timing curve, governed by the following equation:

$$A_{i,y} = S_y \frac{\exp\left[-\frac{(i-\mu_y)^2}{2\sigma_a^2} + \varepsilon_i\right]}{\sum_i \exp\left[-\frac{(i-\mu_y)^2}{2\sigma_a^2} + \varepsilon_i\right]}$$
$$\varepsilon_i \sim \mathrm{N}(0, \sigma_d)$$

where

i = date, ranging from 1 to 60
$A_{i,y}$ = the number of fish arriving on day i in year y
S_y = the total number of fish arriving during year y
μ_y = the peak date of arrival in year y (for the base case, μ = 30)
σ_a = the spread in expected dates of arrival = 5
ε_i = random error in the number of fish arriving on day i (normally distributed with a mean of 0 and a standard deviation σ_d = 0.5)

Individual fish stay on the fishing ground for j days. For the base case, j = 1 day, but a value of 3 days was also explored. The number of fish on the fishing grounds on any date is simply those fish that have arrived within the last j days that have not yet been caught, or

$$D_k = \sum_{i=k-j+1}^{k} \left[A_i \times (1-h)^{\sum_{m=i}^{k-1} I_j}\right]$$

where

D_k = the total number of fish in the fishing district on day k
h = the harvest rate
I_j = an indicator variable with value 1 if fishing occurred on day j, 0 if it did not

For the base case, h was 0.90. Values of 0.70 and 0.99 were also explored.

In the daily simulation, harvest occurs before fish leave the fishing grounds. Thus, the daily catch (C_k) is simply the harvest rate times the number of fish available, and escapement (E_k) is simply the number of fish that arrived j days ago that have survived each day's fishing, including the current day:

$$C_k = hD_k$$
$$E_k = A_{k-j+1}(1-h)^{\sum_{m=k-j+1}^{k} I_m}$$

The fish were assumed to spend 3 days travelling between leaving the fishing district and reaching the tower where escapement is counted. Thus, counts of day k escapements are only available to managers with a lag of 3 days (lag = 3). Lags of 1 and 9 days were also explored. In-river mortality was assumed to be negligible.

Management strategy

Managers were assumed to have two objectives with regard to escapement: a total escapement of 1 000 000 fish and a temporal distribution of this escapement that matched the average arrival pattern of the stock (lagged j + lag days). To achieve these two goals, simulated managers employed a simple strategy to determine when to open fisheries. Prior to obtaining escapement information, they fished every other day. When escapement data were available, they compared their cumulative in-season escapement total to an in-season goal. This in-season goal was simply the desired final escapement multiplied by the fraction of the run that should have arrived on the spawning grounds, given the average (nonstochastic) run timing.

Managers compared the current escapement with the in-season goal using the following statistic:

$$\text{Escapement goal measure ET}_k = \frac{\left(\sum_{t=1}^{k-\text{lag}} E_t - G_{k-\text{lag}}\right)}{G_{60}} \times 100\%$$

where

k = the current date
lag = the number of days between when fish escape the fishery and when they are counted
G_t = manager's in-season escapement goal for date t (G_{60} = 1 000 000)
ET_k = statistic comparing current total escapement to the in-season goal.

This measure is simply the current escapement minus the date-specific in-season escapement goal, expressed as a percentage of the final escapement goal. Managers decided whether to open the fishery for the following day based on whether the escapement goal measure exceeded a critical value (Ecrit). For the base case, Ecrit was zero, but values of −5% and +5% were explored.

The effects of abundance and run timing

We explored the performance of the simulated management strategy across a range of abundance and run timing combinations. Abundance values ranged from 1 000 000 to 19 000 000 in increments of 2 000 000. Run timing ranged from 6 days earlier to 6 days later than the average timing, in steps of 2 days. One thousand simulations were performed for each combination of abundance and run timing.

Although we calculated a variety of indicators of management performance, we focused on the amount and timing of the escapement. The amount of escapement was the total number of fish that were not harvested in the simulated fishery. The timing of escapement was assessed in two ways. First, we compared escapement by date with a distribution with the average arrival timing (after accounting for the lag), which should match a manager's targeted timing if he or she were trying to minimize genetic selection resulting from differences in realized harvest rate for different components of the salmon run. Second, we compared escapement by date with a distribution with the current year's arrival timing, which would more accurately represent genetic selection.

Sensitivity analyses

We repeated the 1000 simulations for each of our abundance and arrival timing combinations using different values for the following: the number of days each fish was vulnerable to the fishery (j), the harvest rate when managers permitted a fishery (h), the number of days between when a fish left the fishery and when it was counted as escapement (lag), and the value of the in-season escapement statistic (Ecrit) that managers used to decide whether to open the fishery (Table 1).

Bristol Bay sockeye salmon data

We obtained daily catch and escapement data from six Bristol Bay sockeye salmon stocks for the years 1961–2010. These included the Ugashik, Egegik, Naknek, Kvichak, Nushagak, and Wood rivers; the Igushik and Alagnak were not included because of their relatively small contributions to their respective mixed stock fisheries, and the Togiak was omitted because of its atypical management strategy (Carney and Adkison 2014*a*). Yearly total abundance for each stock was calculated by summing the catch and escapement across days for each year.

Daily run reconstructions for Bristol Bay (Cunningham et al. 2012) provided estimates for the stock-specific mean date of arrival in each year. The daily run reconstruction partitioned daily catches in mixed-stock fishing districts and accounted for interception in neighboring fishing districts using age and genetic composition of catch data. For each stock, the average date across years was then subtracted to obtain the annual deviation in run timing (number of days early or late). A normal distribution was fit to the daily escapement counts for each stock in each year. The estimated mean of this distribution was used to characterize the timing of escapement for that year; the mean across years of this number was then subtracted to obtain the annual deviation in arrival timing of fish escaping to spawn from the arrival timing of all sockeye of that specific stock.

Escapement goals for Bristol Bay drainages are periodically re-evaluated and have changed over time. We obtained annual escapement goals for each drainage (Tim Baker, Alaska Department of Fish & Game (ADF&G), personal communication); where the goal was reported as a range, we used the midpoint of the range. For each drainage in each year, we calculated the logarithm of the ratio of the observed escapement to the goal.

We plotted the annual escapement, the log ratio of annual escapement to the escapement goal, and the annual escapement timing deviation for each stock as bubbleplots, with the annual abundance and run timing deviation as the axes. We fit linear models to each of these three variables using total abundance, run timing deviation, and their interaction as potential predictors. Fishermen's strikes could potentially reduce the ability of managers to control escapement and escapement timing; we examined the influence of data from 1980 and 1991, years of prolonged strikes, and found that excluding these years had little effect on our results.

Results

Simulations of the effects of abundance and run timing

Although the target escapement of our simulated managers was 1 000 000 fish, the mean escapement in the abundance and timing scenarios ranged from less than 500 000 to more than 4 000 000 fish (Table 2). Realized escapement increased with both the abundance of the return and later return timing.

The most problematic scenarios for managers for achieving escapement goals were either a small early run or a large, late run. In the case of a small early run, managers' in-season information suggested an adequate return and they initially followed a normal fishing schedule, consistent with a run of average size. When arrivals began to decline, managers reduced fishing but not enough fish remained to achieve the escapement goal (Fig. 1, top panels). With a large, late run, managers' in-season information again suggested a run of typical strength, and as a result they harvested at a moderate rate. The escapement goal was achieved fairly early in the run, and when managers responded to continued strong daily fish arrivals by increasing fishing opportunity, the limitations on fleet efficiency resulted in substantial additional escapement in excess of the seasonal target (Fig. 1, bottom panels).

Table 1. Scenarios used in sensitivity analyses.

Days on fishing grounds (j)	**1**, 3 days
Harvest rate (h)	0.7, **0.9**, 0.99
Delay in escapement counts (lag)	1, **3**, 9 days
Manager's decision criterion (Ecrit)	–5%, **0%**, 5%

Note: Values used in the base case are given in bold. Ecrit, an escapement goal measure.

The timing of escapements was found to depend upon both run timing and size, with a general tendency towards escapement timing that reflected run timing. Managers were unaware of each year's run timing, so their target escapement timing reflected the average run timing. Nonetheless, when an early run timing was simulated, the mean date of arrival of the escaping fish was generally earlier than the average timing, and vice versa (Table 3). Interestingly, the influence of abundance on this effect depended on whether the simulated run was early or late. For simulated runs with early timing, the deviation from average escapement timing was greatest for large runs. For simulated late runs, the relationship between abundance and escapement timing was less pronounced.

Scenarios where a run of only 1 000 000 fish arrived 2 or more days late were notable in a couple of respects. Managers' in-season information was that the run was quite weak (in fact, in-season information exaggerated the weakness), so little harvest occurred. The result was that escapement goals were achieved, and the timing of escapement matched the timing of fish arrival as harvest rates remained at or near zero.

A better indicator of artificial selection due to fisheries harvest is comparing the timing of escapement relative to the arrival timing of an average fish in a particular year. Because weak early runs tended to be overharvested early in the season before managers became aware they were weak, the escapement was biased towards the later component of these runs (Table 3). In contrast, late runs were underharvested early in the season when managers perceived them as being weaker; consequently, their escapement timing was biased towards the earlier fish. For very strong runs, this effect diminished as managers began fishing earlier, as cumulative escapement more quickly surpassed daily targets. The escapement timing of strong early runs mirrored arrival timing, as managers fished heavily on all components. Generally, earlier returning runs resulted in higher harvest rates early in the season and later timing of escapements relative to the timing of all arrivals. Similarly, later run timing resulted in higher exploitation of later arriving fish leading to earlier timing of escapements relative to the timing of all arrivals.

One initially puzzling finding was a decrease in escapement with higher abundance in some circumstances. For instance, with normal run timing escapements were higher on average when the total run was 7 000 000 – 9 000 000 than when it was 19 000 000 (Table 2). This phenomenon is built into the model structure; it persisted even after eliminating the variability (i.e., setting $\sigma_d = 0$) in the daily arrival fraction. The cause is the binary management action (harvest or not) and the lag (3 days) between the action and the indication of its effect (the escapement count). With a moderate-sized run, an in-season escapement can drop below the target early in the season, leading to a cessation of fishing just as

Table 2. Average escapement under the base case as a function of the arrival timing in days (columns) before or after the long-term mean and the abundance (rows) of the return.

	Days						
Abundance	–6	–4	–2	0	2	4	6
1 000 000	428 894	474 636	619 550	793 552	959 288	999 915	1 000 000
3 000 000	563 289	915 686	1 043 904	1 215 342	1 266 914	1 406 438	1 463 011
5 000 000	620 361	891 098	1 533 699	1 484 930	1 495 121	1 816 449	1 647 231
7 000 000	739 141	831 862	1 281 082	1 919 751	2 203 531	2 089 569	1 950 952
9 000 000	903 949	915 166	984 616	1 934 022	2 868 888	2 315 833	2 373 324
11 000 000	1 100 021	1 100 003	1 100 000	1 329 709	2 408 687	2 494 090	2 799 039
13 000 000	1 300 024	1 300 004	1 300 001	1 338 706	1 822 348	2 755 099	3 170 784
15 000 000	1 500 028	1 500 005	1 500 001	1 506 596	1 856 388	2 979 201	3 453 590
17 000 000	1 700 031	1 700 005	1 700 001	1 700 001	2 065 909	3 165 996	3 848 006
19 000 000	1 900 036	1 900 006	1 900 001	1 900 000	2 282 990	3 325 190	4 160 519

Note: Data represent mean of 1000 simulations with an escapement goal of 1 000 000.

Fig. 1. Typical simulations (trial 2 of 1000) for three total abundance and run timing scenarios. From top to bottom, abundance and timing were as follows: 1 000 000 fish 4 days early, 3 000 000 fish 0 days early, 9 000 000 fish 4 days late. Bars in left panels show abundance of fish arriving (millions) each day of the season; solid bars indicate fish that escape the fishery, open bars show fish that were caught. Right panels show in-season information (millions of fish) available to managers by date: bars = daily catch, circles = cumulative escapement counts, solid line = cumulative escapement target for each date. Midseason gaps in catch result from fishery closures.

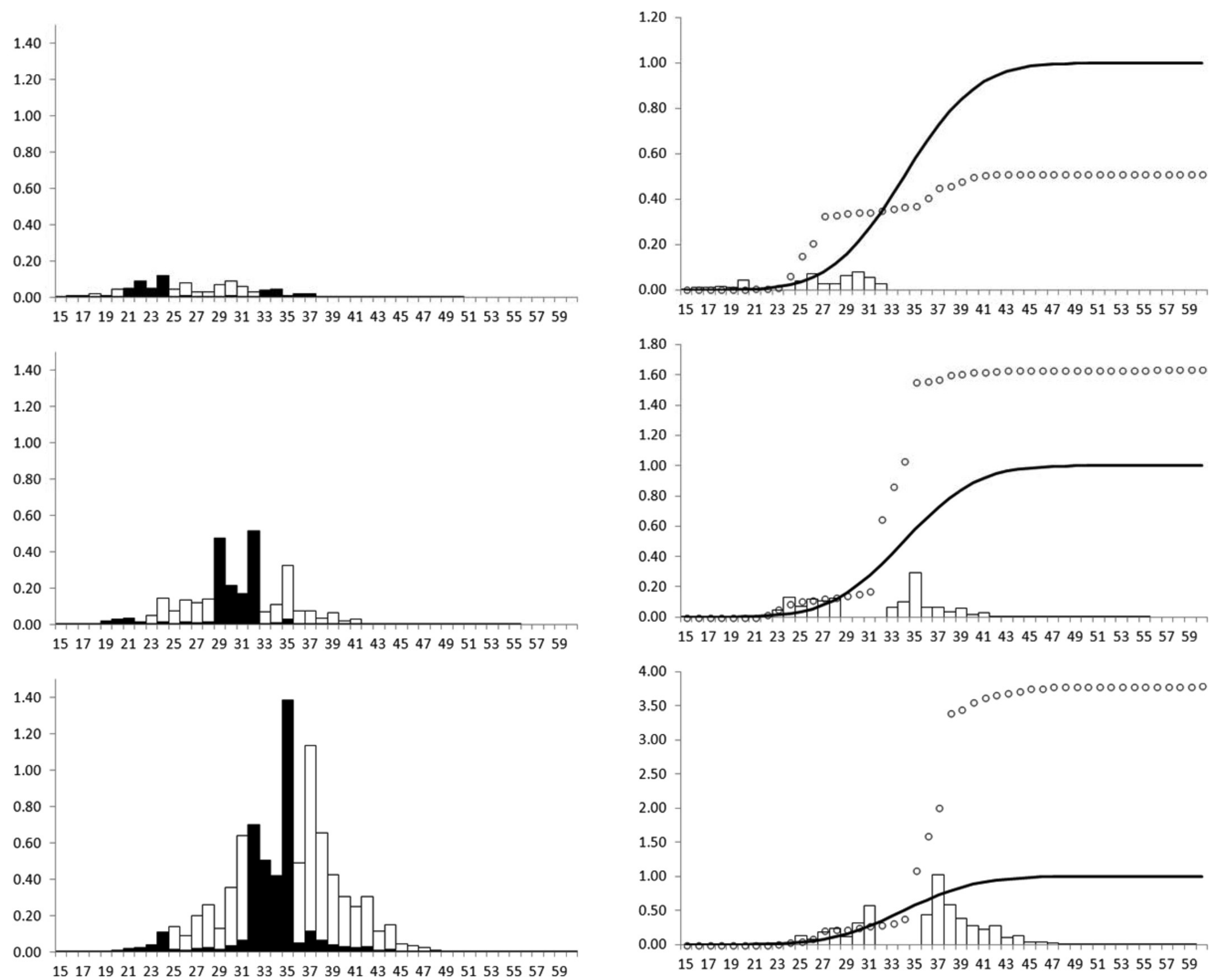


Table 3. Day of return (relative to the long-term mean) of fish that escape to spawn, as a function of the arrival timing in days (columns) before or after on the fishing ground and abundance (rows) of the return.

	Days						
Abundance	−6	−4	−2	0	2	4	6
1 000 000	−2.6	−2.9	−0.7	0.7	2.0	4.0	6.0
3 000 000	−1.9	−0.6	−2.3	0.5	0.8	2.3	2.6
5 000 000	−3.7	−0.2	0.3	−0.8	−0.5	2.0	2.5
7 000 000	−5.3	−2.1	1.4	−0.1	−0.2	1.6	3.0
9 000 000	−5.9	−3.7	−0.9	0.8	1.1	1.5	3.5
11 000 000	−6.0	−4.0	−2.0	−0.1	1.3	1.6	3.6
13 000 000	−6.0	−4.0	−2.0	−0.1	0.8	1.7	3.6
15 000 000	−6.0	−4.0	−2.0	0.0	0.5	1.7	3.5
17 000 000	−6.0	−4.0	−2.0	0.0	0.5	1.7	3.4
19 000 000	−6.0	−4.0	−2.0	0.0	0.7	1.7	3.3

Note: Data represent mean of 1000 simulations under the base case.

Table 4. Sensitivity analysis results for the mean (standard deviation in parentheses) of escapement under three scenarios: 1 million fish returning 4 days early, 3 million fish returning with typical timing, and 9 million fish returning 4 days late.

	(1, −4)	(3, 0)	(9, +4)
Base	474 636 (50 200)	1 215 342 (180 100)	2 315 833 (838 400)
lag = 1 day	546 891 (52 300)	1 050 951 (79 800)	1 773 588 (484 700)
lag = 9 days	396 289 (95 400)	736 291 (148 300)	2 051 093 (967 500)
$j = 3$	368 375 (50 300)	1 017 592 (160 600)	2 220 616 (799 600)
Ecrit = +5%	483 572 (49 300)	1 243 040 (157 700)	1 933 226 (889 900)
Ecrit = −5%	438 364 (58 000)	1 223 188 (179 900)	2 523 114 (430 900)
$h = 0.70$	498 914 (62 800)	1 188 981 (214 100)	3 074 954 (383 400)
$h = 0.99$	492 222 (65 500)	1 179 701 (179 600)	2 224 747 (823 500)

Note: Assumptions of the base case (Base) are modified as described in Table 1. Results are from 1000 simulations with an escapement goal of 1 000 000.

Table 5. Mean (standard deviation in parentheses) date of arrival of fish escaping the fishery relative to the overall mean date of arrival, under three scenarios: 1 million fish returning 4 days early, 3 million fish returning with typical timing, and 9 million fish returning 4 days late.

	(1, −4)	(3, 0)	(9, +4)
Base	1.0 (1.0)	0.4 (1.1)	−2.7 (1.3)
lag = 1 day	2.2 (0.5)	−0.1 (0.8)	−2.6 (0.8)
lag = 9 days	4.0 (0.5)	−2.1 (2.0)	−1.7 (2.9)
$j = 3$	1.8 (1.0)	3.9 (1.1)	−1.0 (3.0)
Ecrit = +5%	0.2 (1.0)	0.3 (0.8)	−2.7 (1.7)
Ecrit = −5%	3.9 (0.3)	0.0 (0.5)	−3.0 (0.4)
$h = 0.70$	2.3 (0.5)	0.4 (1.0)	−0.8 (0.7)
$h = 0.99$	1.4 (1.0)	−0.7 (1.0)	−3.1 (2.7)

Note: Assumptions of the base case (Base) are modified as described in Table 1. Results are from 1000 simulations.

large numbers of fish arrive at or near the peak in the arrival distribution. Because of the lag in counting escapement, multiple days of large escapement can occur before managers become aware that escapement is above target levels and resume fishing, leading to large overescapement. If the run is a little larger, the cumulative escapement never goes below daily targets, and the more continuous fishing prevents these large overescapements. Lowering the harvest rate (h) and spreading out the arrival timing (i.e., increasing σ_a) reduced but did not completely eliminate this phenomenon (not shown). Run timing was also important in determining at what abundance this low abundance peak in realized escapement occurred (Table 2). Earlier arrival meant that the peak in escapement occurred at a lower total abundance (i.e., 3 000 000 when 4 days early, 5 000 000 when 2 days early, and 9 000 000 with average arrival timing). This suggests that a smaller total abundance is required to result in high escapement or overescapement in years of earlier arrival, because a manager is more likely to restrict fishing opportunity early in the season based on the misperception of a larger run.

Table 6. Signs and significance of coefficients of the linear model predicting escapement as a function of abundance, arrival timing, and their interaction.

River	Arrival timing	Abundance	Interaction
Wood	+	+ (8.06e-11)	+
Nushagak	−	+ (3.31e-06)	+ (0.009)
Kvichak	−	+ (<2e-16)	+ (0.082)
Naknek	−	+ (1.84e-09)	+
Egegik	−	+ (7.51e-07)	+ (0.072)
Ugashik	+	+ (1.54e-08)	+

Note: P values less than 0.1 are shown in parentheses.

Table 7. Signs and significance of coefficients of the linear model predicting log(escapement/goal) as a function of abundance, arrival timing, and their interaction.

River	Arrival timing	Abundance	Interaction
Wood	+	+ (5.37e-08)	+
Nushagak	+	+ (6.69e-07)	+
Kvichak	−	+ (0.0001)	+
Naknek	−	+ (3.41e-07)	+
Egegik	+	+ (0.0257)	+
Ugashik	+	+ (1.14e-07)	−

Note: P values less than 0.1 are shown in parentheses.

Sensitivity analyses

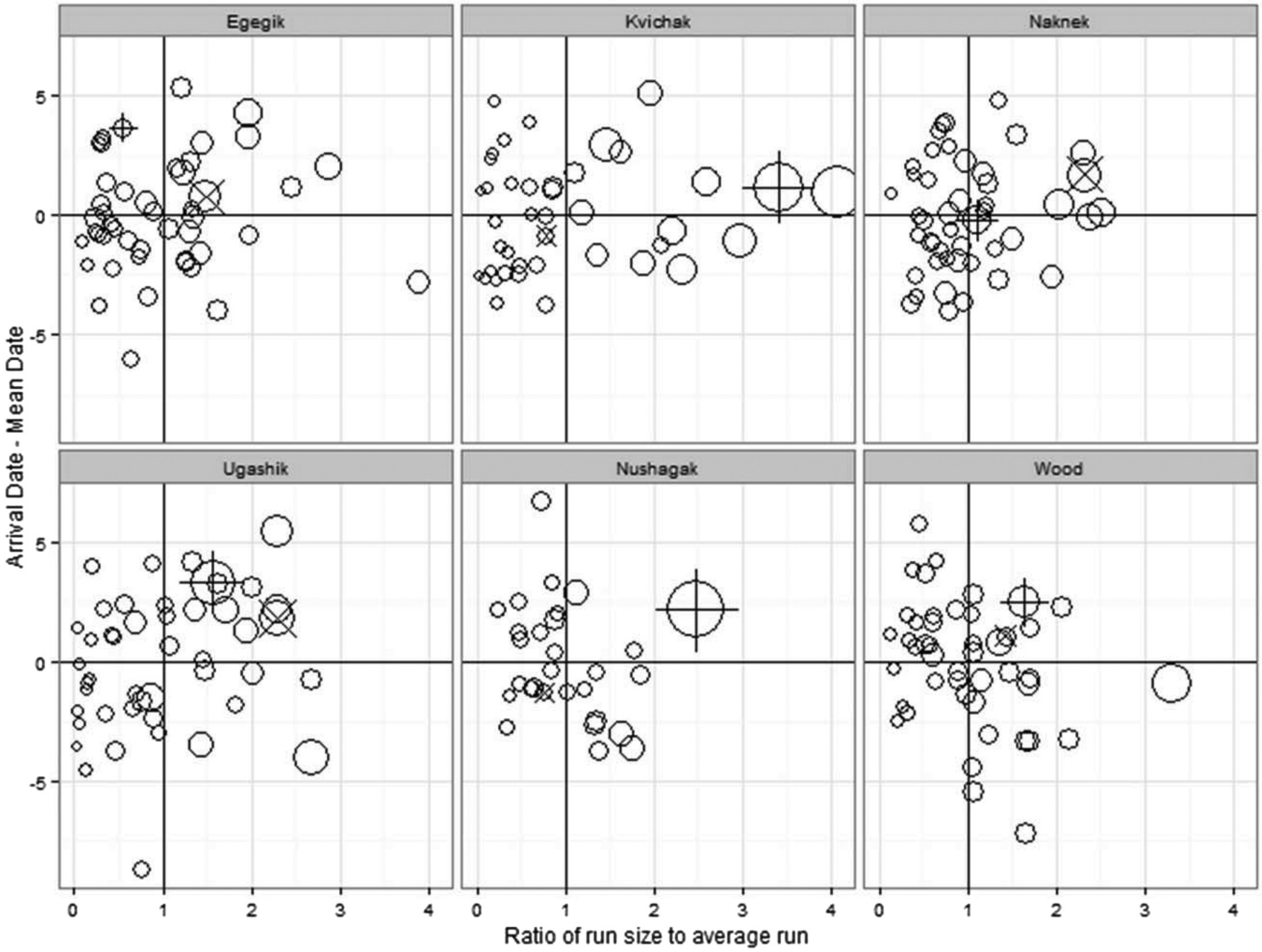
Although sensitivity analyses were run using all 70 combinations of run timing and abundance, for brevity we show results for three illustrative combinations. These include two combinations that were problematic in the base case (Tables 2–3): a run of only 1 000 000 arriving 4 days early and a run of 9 000 000 arriving 4 days late. The third combination, a run of 3 000 000 with average run timing, led to good management performance in the base case.

Although results were somewhat affected by changes in the assumptions, the general pattern of poor management performance in the face of a weak early run or a strong late run did not change. In all sensitivity analyses, a weak early run resulted in underescapement and a strong late run overescapement (Table 4). With a weak early run, escapement was biased towards the latest-arriving fish, while with a strong late run the opposite pattern was seen (Table 5).

The lag time between the fishery and the escapement enumeration site influenced management outcomes. More timely escapement data (lag = 1 day) improved the simulated managers' performance, with escapement closer to the target for both a small early run and a strong late run (Table 4). The timing of escapement was not, however, any closer to the average run timing with a reduction in lag time (Table 5). In addition, residence time on the fishing grounds (j) had an effect on escapement relative to targets. If the stock had a longer residence on the fishing grounds ($j = 3$), the managers' ability to achieve the escapement goal deteriorated slightly for the early, low scenario (1, −4), but led to outcomes closer to the escapement target for the two larger run scenarios (3, 0) and (9, +4) (Table 4). When managers were willing to fish while still 5% below the in-season escapement goal (Ecrit = −5%), the ability to achieve escapement was even poorer for early runs with low abundance (Table 4).

The harvest rate had little effect on performance with either a weak early run or a moderate run with typical timing. However, higher harvest rates did improve managers' ability to meet their escapement goals with a strong late run (Table 4). Late in the season, when managers became aware that the run was large, this ability to harvest at increased rates reduced the level of overescapement.

Fig. 2. The number of days the median date of arrival was early (–) or late (+) versus the abundance of fish in the run that year, relative to the long-term mean. The size of the circles gives the abundance of the escapement relative to the long-term mean. The data for 1980 and 1991, years with prolonged strikes, are labeled (+ and ×, respectively).



Bristol Bay sockeye salmon data

In real-world sockeye salmon fisheries in Bristol Bay, Alaska, both the magnitude of escapement and the log ratio of escapement to the goal were positively related to the strength of the run (Fig. 2; Tables 6 and 7); these relationships were significant at the 0.05 level in all six stocks. There was no consistent relationship between the timing of the run and the resultant escapement or ratio of the escapement to the goal. However, the interaction term was positive in all cases (5/6 for the ratio of escapement to goal), although statistically significant in only one case. This positive interaction term is consistent with the prediction from the simulations of the highest escapements resulting from strong, late runs, and the lowest escapements from early weak runs.

The timing of escapement was dependent on the strength of the run (Fig. 3). As predicted by our simulations, the average date of escapement was earlier when the run was stronger than average. This relationship was statistically significant at the 0.05 level in three of six stocks and of the correct sign in all six stocks (Table 8). The timing of the run did not show a consistent relationship with the timing of the escapement. However, the interaction between run timing and abundance was negative in five of six stocks, consistent with the prediction that a small early run should have a late-biased escapement and a large late run an early-biased escapement.

The deviation of the escapement timing from the arrival timing (Table 9; Fig. 4) was negatively related to both the arrival timing and the abundance for all six stocks; this coefficient was statistically significant at the 0.05 level in five and three of the six stocks, respectively. This supports the prediction that the latest arrivals in years when the run is early would be over-represented in the escapement, and the earliest arrivals would be over-represented when runs are late. It also supports the prediction that the earliest-arriving fish would be over-represented in the escapement in years with large runs, and vice versa when runs are small. The interaction term was negative for five of six stocks, again consistent with the prediction that escapement from a small early run should be biased toward late-arriving fish, while escapement from a large late run demonstrates early-biased escapement.

Discussion

The ability of salmon fishery managers to achieve their escapement objectives is hampered by large and largely unpredictable interannual fluctuations in abundance (Bocking and Peterman 1988). Managers must decide whether to allow harvests before run strength is known, and early-season decisions can greatly affect the final escapement totals. Consequently, a great deal of attention has been paid to preseason and in-season forecasts of salmon

Fig. 3. The number of days the median date of arrival was early (–) or late (+) versus the abundance of fish in the run that year, relative to the long-term mean. The size of the symbols is proportional to the number of days the escapement is early (circles) or late (triangles) relative to the mean. The data for 1980 and 1991, years with prolonged strikes, are labeled (+ and ×, respectively).

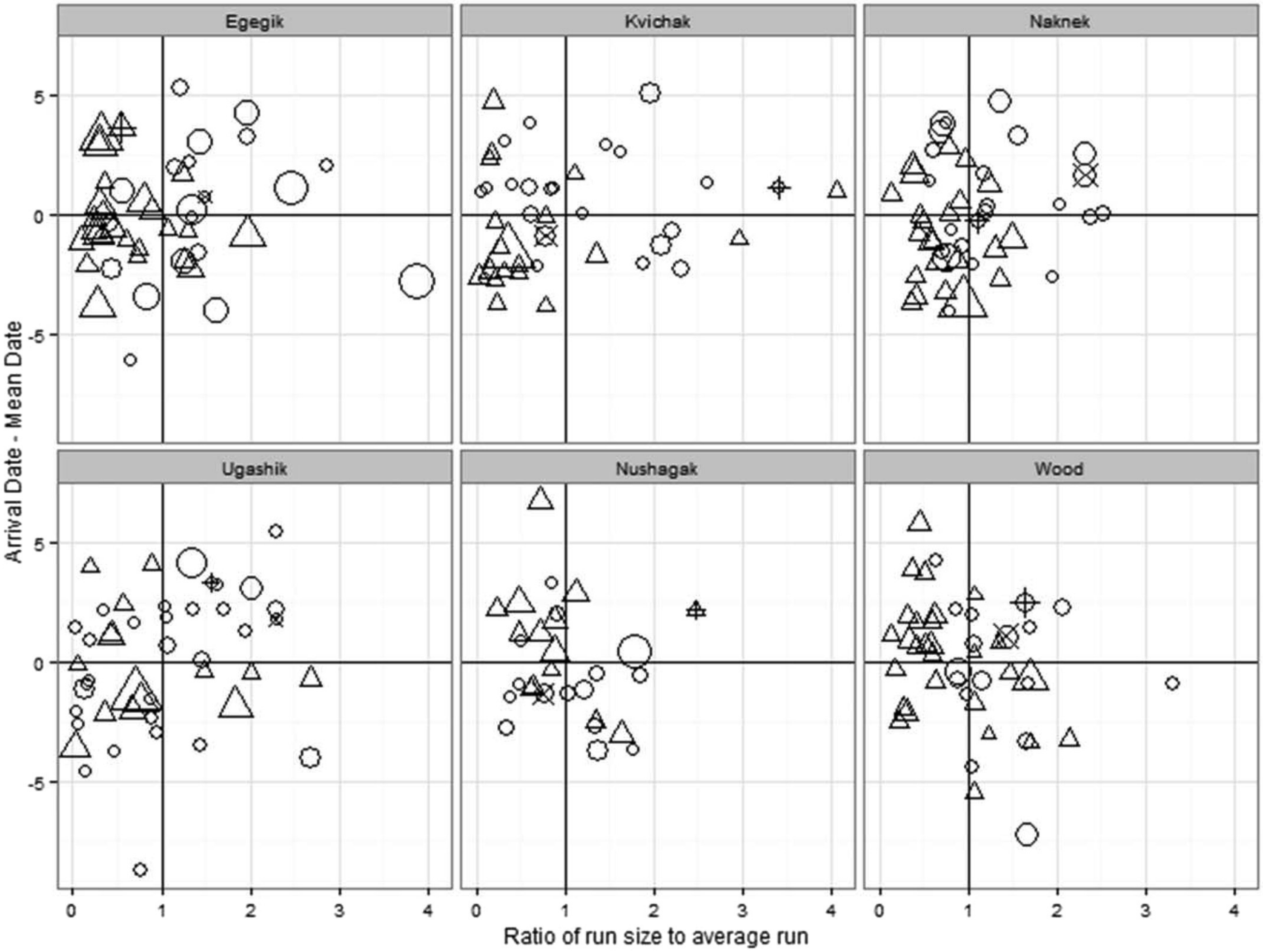


Table 8. Signs and significance of coefficients of the linear model predicting escapement timing as a function of abundance, arrival timing, and their interaction.

River	Arrival timing	Abundance	Interaction
Wood	+	– (0.015)	–
Nushagak	+	–	–
Kvichak	–	– (0.062)	+
Naknek	–	– (0.049)	–
Egegik	+	– (1.02e-05)	–
Ugashik	–	–	–

Note: *P* values less than 0.1 are shown in parentheses.

Table 9. Signs and significance of coefficients of the linear model predicting the deviation of escapement timing from run timing as a function of abundance, arrival timing, and their interaction.

River	Arrival timing	Abundance	Interaction
Wood	– (0.001)	– (0.014)	–
Nushagak	–	–	–
Kvichak	– (2.21e-07)	– (0.062)	+
Naknek	– (0.001)	– (0.049)	–
Egegik	– (0.037)	– (1.02e-05)	–
Ugashik	– (2.94e-05)	–	–

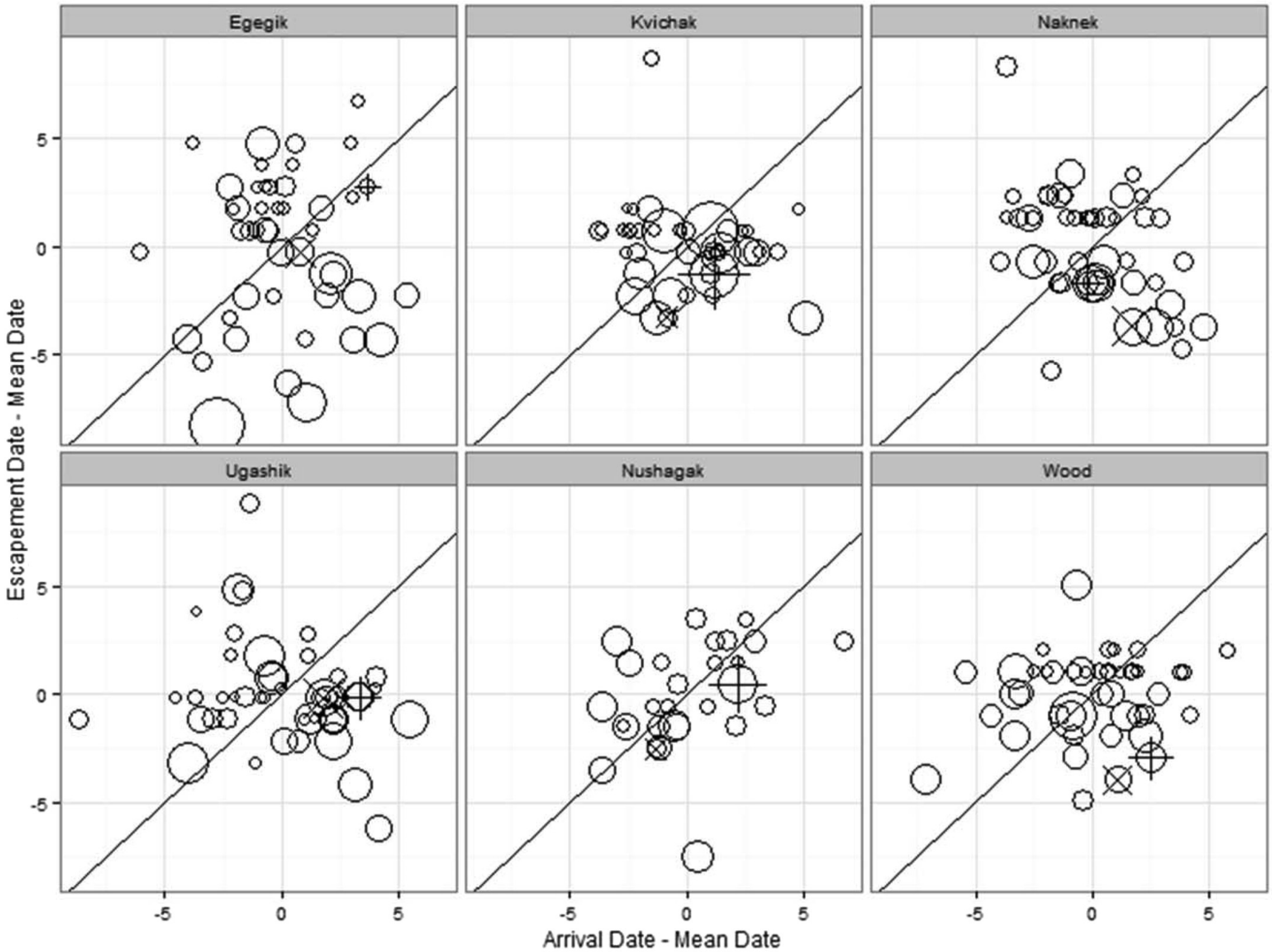
Note: *P* values less than 0.1 are shown in parentheses.

returns (Adkison and Peterman 2000; Chebanov 1989; Cross 1998; Farley 1996; Fried and Hilborn 1988; Fried and Yuen 1987; Hyun et al. 2005, 2012). However, preseason forecasts are usually highly uncertain, and in-season forecasts may not attain high certainty until later in the season when managers' ability to significantly affect escapement numbers has already passed (Adkison 2002).

The simulations presented here show that uncertainty about the timing of the run affects management performance as much as uncertainty about the abundance of the run. It is the interaction of unusual timing and abundance that presents managers with the greatest challenge. Both early weak runs and late strong runs can be perceived as normal, moderate strength runs early in the season, leading to escapements far from the target both in terms of abundance and in the equitable distribution of harvest rate across the season. With few exceptions (Mundy and Evenson 2011), forecasting run timing has received much less attention than forecasting run strength. These results show that improving run timing forecasts could produce substantial benefits.

Some of the phenomena predicted by our simulations were evident in data from Bristol Bay sockeye salmon stocks. As expected, stronger than average runs produced above-average and above-goal escapements despite a constant escapement goal policy (Fig. 2; Tables 6 and 7); this phenomenon has been demon-

Fig. 4. The number of days escapement was early (–) or late (+) versus the number of days fish arrival was early or late for six Bristol Bay rivers. Points below the line indicate escapements biased towards the earliest-arriving fish, and those above the line are biased towards the latest-arriving fish. The size of the circle is proportional to the abundance of fish relative to the long-term mean for the stock. The data for 1980 and 1991, years with prolonged strikes, are labeled (+ and ×, respectively).



strated previously in other salmon fisheries (Bocking and Peterman 1988; Holt and Peterman 2006). Larger runs also tended to produce escapements biased towards the earliest-arriving fish (Fig. 3; Tables 8 and 9), due to moderate early-season harvests in response to uncertainty about run strength during the fishing season. However, with respect to asymmetry in the imposed harvest rate across the season and biases in the contribution of early- or late-arriving fish to the escapement, simulation results indicate a much stronger influence of run timing relative to abundance.

Two of the six Bristol Bay sockeye salmon stocks, the Egegik and Ugashik, are harvested in (primarily) single-stock fisheries. In contrast, the others are harvested in fisheries that harvest a mixture of stocks. Management of these mixed-stock fisheries is more complicated than the simple strategy we simulated, particularly when the component stocks differ in both run strength and run timing in a particular year, and these complications might obviate some of the patterns we expected. For example, protecting a weak Kvichak stock by reducing harvest in the mixed-stock fishery can cause escapement of the Naknek stock to exceed its goal. Balancing multiple escapement objectives in a mixed-stock fishery is likely to result in greater differences between realized escapements and escapement targets for all stocks involved. Accurately predicting the timing of each component could aid managers in differentially harvesting the stronger stock.

Our simulations and previous empirical studies show that uncertainty about both run strength and run timing result in realized escapements that differ from escapement goals and that these differences are functions of the strength and timing of the run. More timely escapement counts resulted in an improved ability to achieve escapement goals. As long as the low escapements are neither too low nor prolonged, fluctuations in the magnitude of escapement are not too worrisome. Likewise, occasional large escapements mimic pre-fishery levels (Finney et al. 2000), and some components of the freshwater ecosystem will greatly benefit from these nutrient pulses (Moore et al. 2008).

Potentially more detrimental to future sustainability are the differential harvest rates that may be experienced by early- and late-arriving fish. Run timing may differ between substocks in the same drainage (Brannon 1987; Gharrett et al. 2001), and even within a population run timing differences may reflect heritable genetic differences (Kovach et al. 2012; Smoker et al. 1998). Harvest rate differences exerted on different portions of the run can cause artificial selection or differential harvest of substocks (Carney and Adkison 2014*b*; Quinn et al. 2007). With large late runs the later components of the run will be under-represented in the escapement, although the associated tendency towards overescapement may still ensure sufficient numbers of these later-running fish arrive on the spawning grounds. With early small runs very few individuals from the early component may escape the fishery. This could reduce the portfolio effect (Schindler et al. 2010) that stabilizes the productivity of these important fisheries and erode the genetic diversity that permits adaptation to future environmental change.

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