

Ghost runs: management and status assessment of Pacific salmon (*Oncorhynchus* spp.) returning to British Columbia's central and north coasts

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Abstract: The management of Pacific salmon (*Oncorhynchus* spp.) populations, which are spatially distributed across thousands of waterways in coastal British Columbia, Canada, presents considerable challenges to resource managers. We evaluated the efficacy of salmon management by Fisheries and Oceans Canada (DFO) over the past 55 years in two key areas: (i) the achievement of internally generated target escapement levels and (ii) escapement monitoring. We show that less than 4% of monitored streams ($n = 7$ of 215), which represent a small fraction of all salmon-bearing waterways ($n = 2592$), have consistently met escapement targets since 1950. During this same period, the number of streams monitored by DFO has simultaneously decreased. Further, current monitoring efforts fall short of encompassing the range of salmon diversity identified within recently designated conservation units. Importantly, we found that this erosion of monitoring effort has been biased towards dropping smaller runs that failed to meet target escapements in the previous decade. We suggest that such increasingly selective monitoring is presenting a progressively more biased evaluation of population health. In addition to fostering a "shifting baseline" syndrome, we conclude that these changes to monitoring can not provide data required for precautionary harvest management under the high exploitation levels that these runs experience.

Résumé : La gestion des populations de saumons du Pacifique (*Oncorhynchus* spp.), qui sont réparties spatialement dans des milliers de cours d'eau sur la côte de la Colombie-Britannique, présente des défis importants aux gestionnaires des ressources. Nous évaluons l'efficacité de la gestion des saumons faite par Pêches et Océans Canada (DFO) au cours des 55 dernières années dans deux domaines importants: (i) l'atteinte des cibles d'échappement par les processus intrinsèques et (ii) la surveillance de l'échappement. Nous montrons que moins de 4 % des cours d'eau suivis ($n = 7$ de 215), qui représentent une petite fraction des cours d'eau à saumons ($n = 2592$), ont régulièrement atteint leurs cibles d'échappement depuis 1950. Durant la même période, le nombre de cours d'eau suivis par DFO a simultanément décliné. De plus, les efforts de surveillance actuels n'arrivent pas à couvrir l'étendue de la diversité des saumons identifiée au sein des unités de conservation récemment définies. Ce qui est important de noter, c'est que cette érosion de l'effort de surveillance a frappé de façon disproportionnée les petits groupes de montaison qui n'ont pas réussi à atteindre leurs cibles d'échappement au cours de la dernière décennie. Nous croyons que cette surveillance de plus en plus sélective fournit une évaluation toujours plus faussée de la santé des populations. En plus de produire un syndrome de « données de base changeantes », ces modifications dans la surveillance ne permettent pas d'obtenir les données nécessaires pour une gestion prudente des récoltes dans les conditions de forte exploitation que connaissent ces groupes de montaison.

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Introduction

Salmon management presents complex biological, economic, and political challenges (Wright 1981; Hilborn and Luedke 1987). In British Columbia (BC), resource managers rely heavily on stock assessment programs to guide their decision-making processes. For example, annual enumeration monitoring of spawning salmon is thought to provide

critical information on stock status, trends, and productivity required to inform harvesting decisions and conservation plans (English et al. 2006). BC's Pacific Fisheries Resource Conservation Council (PFRCC 2004) considers consistent information on stock assessment a top management priority in successful salmon conservation. In contrast, ad hoc enumeration plans are thought to be inadequate to provide the quality of data needed to conserve salmon populations under heavy fisheries pressure (Routledge and Irvine 1999; PFRCC 2004; English et al. 2006).

Salmon (*Oncorhynchus* spp.) populations in BC and the entire Northeast Pacific have been, and continue to be, heavily exploited (Schmidt et al. 1998; Finney et al. 2000; English et al. 2006). They have disappeared from 40% of their historic spawning range in the continental US (Nehlsen et al. 1991) and are considered extinct in 142 watershed systems throughout BC (Slaney et al. 1996). Commercial catches in BC between 1995 and 2005 were the lowest on record (Walters and Korman 1999a; DFO 2008a). Additionally, the number of stocks contributing to this catch is also

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declining, shifting over the decades from many runs of diverse size to fewer large runs (Walters and Cahoon 1985; Wood 2001).

Under such exploitation pressures, stream-specific management escapement goals have been created by Fisheries and Oceans Canada (DFO) — the federal government agency responsible for salmon management in BC — with the aim to ensure adequate numbers of spawning salmon (Walters and Korman 1999b). These target escapements are based largely on professional judgement of habitat capacity, historic return records, and number of fish needed to adequately seed spawning grounds (Goruk and Winther 1992). Moreover, designed to maximize salmon production, these target escapements are considered widely relevant today (Walters et al. 2008). A primary strategy used by DFO to measure management performance relies on setting target escapement goals and detecting trends in abundance relative to these targets (Walters and Korman 1999a; DFO 2007). The ability to meet these escapement targets, therefore, provides a straightforward and objective way to evaluate whether basic management strategies by DFO have been achieved (Goruk and Winther 1992).

We have two objectives in assessing salmon management in BC by DFO. We first evaluate the frequency by which escapement targets have been achieved over the past half-century. In doing so, we thus also provide a contemporary assessment of the general status of salmon populations in BC relative to historical benchmarks. Second, we examine monitoring efforts by DFO over the same period. Specifically, we assess the changes to monitoring efforts over time and examine which factors have led to the considerable decrease in annual enumeration we document.

Materials and methods

We examined escapement data for BC's central and north coasts (DFO management areas 3 through 10; Fig. 1) between 1950 and 2005. This region consists of numerous isolated islands and mainland watersheds. Although this area includes several watersheds unmodified by roads or logging, fisheries exploitation and hatchery supplementation have occurred for more than a century. We assessed five commercially important salmon species: *Oncorhynchus tshawytscha* (Chinook), *Oncorhynchus kisutch* (coho), *Oncorhynchus nerka* (sockeye), *Oncorhynchus keta* (chum), and *Oncorhynchus gorbuscha* (pink). Given their consistent 2-year life cycle, we separated pink into even and odd years in analyses.

Trends in achieving target escapements

We assessed escapement trends in the study area for all years between 1950 and 2005 using DFO BC16 reports (DFO 1992) and DFO's Salmon Escapement Database System (NuSEDS; DFO 2008b). Although the accuracy of estimates contained within these databases has been questioned by some (e.g., Irvine and Nelson 1995), no alternative or complementary data are available.

We classified spawning records into three categories: indicator streams (sites defined by DFO and enumerated consistently over time); nonindicator streams (inconsistent enumeration of spawners); and streams without information (spawners confirmed, yet no enumeration data collected).

Although DFO infers general trends in abundance and productivity from indicator streams, many of these sites were not visited annually (particularly in recent years; see below). Accordingly, we described the monitoring of an indicator stream as unknown when enumeration information was gathered for less than 50% of the years within any one decade.

Using only indicator streams (and excluding unknown decades), we averaged annual escapement returns for each decade and compared them to management target escapement (MTE) values established by DFO. For each decade, we classified stream escapements as meets target (80% or more of the spawner target was met), depressed (40%–79%), and very depressed (<40%). Additionally, we examined the percentage of newly designated conservation units (CUs; DFO 2008c) for each species that was minimally monitored. We considered a CU meeting this minimal criterion if it contained a minimum of one enumerated stream during the period 2000–2005.

Evaluation of escapement monitoring

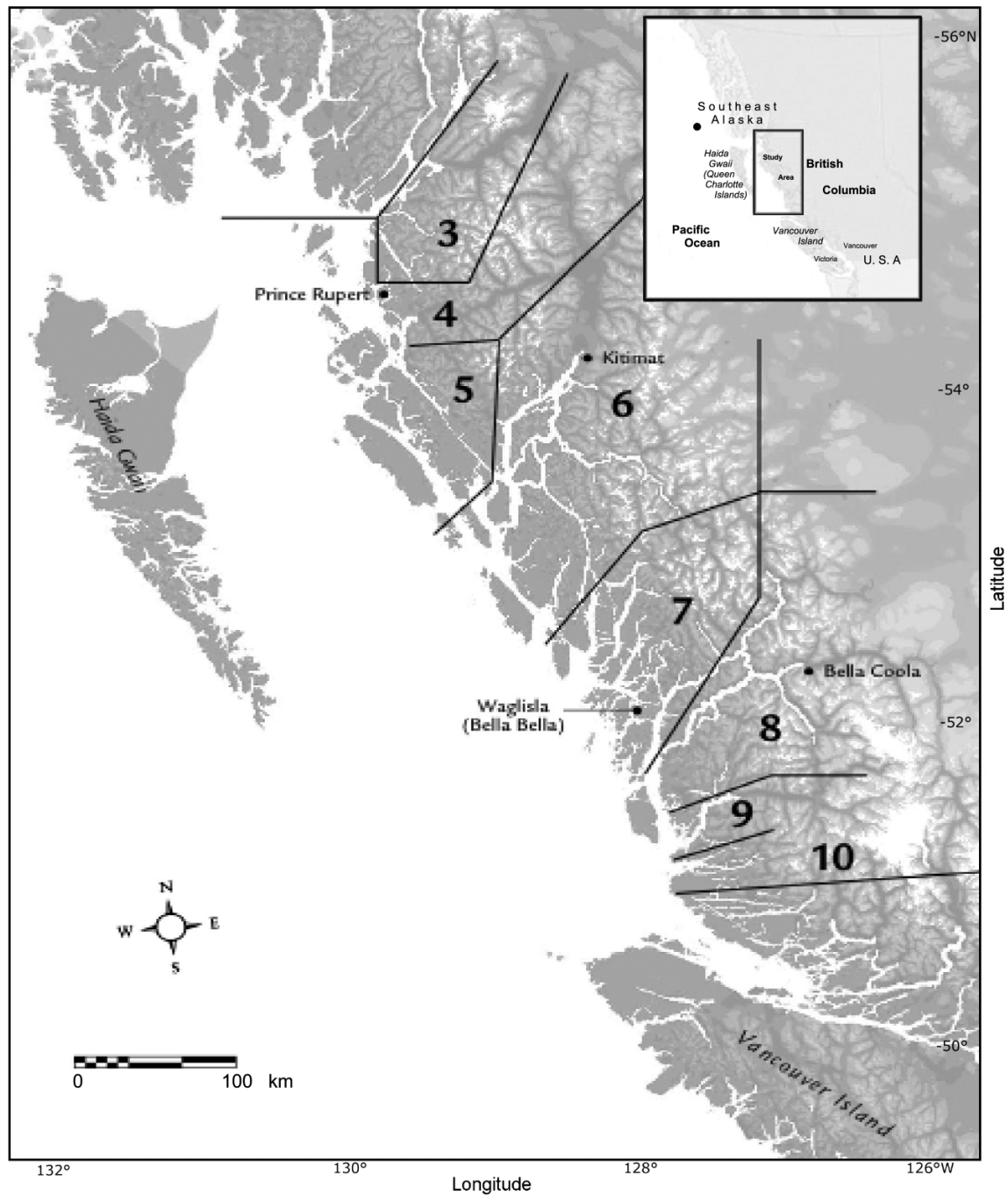
We were interested in which factors might influence changes in monitoring effort over the last half century. Specifically, we observed that fewer indicator streams were monitored each decade, but we did not know which factors were associated with monitoring cessation. Accordingly, we formed a priori hypotheses relating salmon run characteristics to the probability of runs ($n = 215$) being dropped from monitoring effort. Run characteristics included (*i*) run status during the previous decade (status; either meets target or not (i.e., depressed or very depressed)), (*ii*) potential run size (size; management target escapement values), and (*iii*) salmon species (species). From these hypotheses, we developed a set of candidate generalized linear regression models (binary logistic form). A Hosmer–Lemeshow goodness-of-fit statistic based on the global model showed the data did not depart from a logistic form ($P = 0.491$). For each model, we calculated Akaike's information criteria, following the formula: $AIC_c = -2(\log \text{likelihood}) + 2K + 2K(K + 1)/(n - K - 1)$, where K is the number of parameters and n is the number of indicator salmon runs. We then evaluated ΔAIC_c to select the best approximating model(s) and made appropriate inference, using $\Delta AIC_c < 4$ to describe the top model set. Finally, we summed Akaike weights (ω_i) across the top model set for each variable to rank them by importance (Burnham and Anderson 1998; Anderson et al. 2001). Tests were performed using SPSS 13.0 (SPSS Inc., Chicago, Illinois, USA).

Results

Trends in achieving target escapements

Evaluation of all species showed that the achievement of target escapements varied considerably by species over the last 55 years, but overall that less than 4% of monitored streams consistently met their decadal MTEs. Currently (i.e., between 2000 and 2005), and only when unknown systems that were dropped from monitoring efforts are omitted, coho and pink salmon are the only species to meet target escapements at more than 50% of their indicator streams (Table 1). Accordingly, under typical evaluation perspectives, the status of odd-year pink (72%; $n = 36$), even-year pink

Fig. 1. Study area, encompassing Fisheries Management Areas 3–10, for Pacific salmon (*Oncorhynchus* spp.) returning to British Columbia's central and north coasts during 1950–2005.



(66%; $n = 34$), and coho (63%; $n = 5$) appears to show relatively high levels of meeting escapement targets. Conversely, for Chinook, chum, and sockeye, runs currently classified as depressed or very depressed exceed 50% (Table 1).

Evaluation of escapement monitoring

DFO's BC16 reports identify 2592 runs of the five commercially harvested salmon species on BC's central and north coasts (Table 2). We found 30% of these runs ($n = 768$) were enumerated at least once between 1950 and 2005. Consistent data on abundance trends, however, exist

for only 8% ($n = 215$). Although coho streams are the most numerous among species, knowledge of spawner abundance is the poorest (<4%, $n = 33$ of total coho — $n = 891$). Chinook and sockeye have the greatest proportion of runs classified as indicator streams (13% each), followed by chum and pink (10% each). Though differing by species, streams with sufficient escapement data to evaluate trends have decreased from a high of 210 (98%) in 1980 to a low of 137 (64%) in 2005 (Fig. 2). Annual enumeration in the present decade is low for all species, but is particularly low for coho at only 2% ($n = 7$). Finally, our examination of

Table 1. Average escapement by species and decade and associated status categories for indicator streams ($n = 215$) of spawning Pacific salmon (*Oncorhynchus* spp.) returning to British Columbia's central and north coasts during 1950–2005.

| Species | No. of catalogued spawning runs | No. of classified indicator streams* | No. of indicator streams* annually enumerated 2000–2005 | No. of CUs [†] identified | Percent CUs [†] monitored by indicator streams* |
|-----------|---------------------------------|--------------------------------------|---|------------------------------------|--|
| Chinook | 215 | 27 | 6 | 22 | 41 |
| Coho | 891 | 33 | 6 | 15 | 40 |
| Sockeye | 320 | 40 | 8 | 119 | 13 |
| Chum | 492 | 49 | 8 | 16 | 75 |
| Pink | 674 | 66 | 27 | | |
| Odd-year | | | | 5 | 88 |
| Even-year | | | | 8 | 80 |
| Total | 2592 | 215 | | | |

*Indicator streams are salmon runs consistently enumerated, as classified by Fisheries and Oceans Canada.

[†]Enumeration of as few as one indicator stream in a conservation unit (CU) is classed as monitored.

Table 2. Synopsis of catalogued spawning runs, indicator streams, and current monitoring effort for Pacific salmon (*Oncorhynchus* spp.) returning to British Columbia's central and north coasts during 1950–2005.

| Decade | Assessment | Species | | | | | |
|------------------|--------------------|---------|---------|-----------|-----------|------------|-----------|
| | | Chinook | Coho | Sockeye | Chum | Pink, even | Pink, odd |
| 1950s | Escapement | 81 635 | 194 286 | 1 214 571 | 480 042 | 1 539 823 | 1 870 768 |
| | Meets target (%) | 19 | 15 | 25 | 22 | 23 | 14 |
| | Depressed (%) | 11 | 21 | 28 | 37 | 17 | 15 |
| | Very depressed (%) | 30 | 42 | 30 | 37 | 50 | 61 |
| | Unknown (%) | 41 | 21 | 15 | 4 | 11 | 11 |
| 1960s | Escapement | 71 320 | 192 022 | 1 529 056 | 472 922 | 4 339 656 | 2 034 378 |
| | Meets target (%) | 15 | 15 | 18 | 18 | 44 | 20 |
| | Depressed (%) | 11 | 21 | 40 | 41 | 21 | 24 |
| | Very depressed (%) | 48 | 36 | 40 | 39 | 26 | 50 |
| | Unknown (%) | 26 | 27 | 3 | 0 | 9 | 6 |
| 1970s | Escapement | 57 216 | 116 404 | 1 949 039 | 523 603 | 3 445 347 | 1 982 724 |
| | Meets target (%) | 0 | 9 | 23 | 22 | 52 | 15 |
| | Depressed (%) | 22 | 15 | 38 | 39 | 24 | 42 |
| | Very depressed (%) | 67 | 64 | 40 | 39 | 20 | 36 |
| | Unknown (%) | 11 | 12 | 0 | 0 | 5 | 6 |
| 1980s | Escapement | 77 077 | 104 189 | 2 841 318 | 512 508 | 3 648 158 | 4 257 666 |
| | Meets target (%) | 7 | 9 | 25 | 12 | 41 | 42 |
| | Depressed (%) | 19 | 33 | 40 | 45 | 33 | 33 |
| | Very depressed (%) | 67 | 48 | 35 | 43 | 26 | 24 |
| | Unknown (%) | 7 | 9 | 0 | 0 | 0 | 0 |
| 1990s | Escapement | 109 286 | 40 858 | 2 648 937 | 615 140 | 3 644 587 | 3 367 981 |
| | Meets target (%) | 11 | 15 | 20 | 16 | 29 | 29 |
| | Depressed (%) | 22 | 9 | 23 | 20 | 41 | 32 |
| | Very depressed (%) | 56 | 9 | 50 | 57 | 26 | 32 |
| | Unknown (%) | 11 | 67 | 8 | 6 | 5 | 8 |
| 2000s | Escapement | 62 116 | 62 246 | 1 407 130 | 716 146 | 3 697 642 | 4 769 329 |
| | Meets target (%) | 7 | 18 | 20 | 20 | 51 | 54 |
| | Depressed (%) | 15 | 3 | 5 | 27 | 11 | 17 |
| | Very depressed (%) | 26 | 6 | 48 | 24 | 21 | 6 |
| | Unknown (%) | 52 | 73 | 28 | 29 | 17 | 23 |
| Management goal* | | 210 175 | 444 000 | 2 218 250 | 1 092 000 | 4 384 000 | 4 384 000 |

*Management goal is Fisheries and Oceans Canada annual escapement target (MTE).

monitoring efforts within CU areas showed a range of minimal representation (at least one stream monitored) from 13% (sockeye) to 88% (odd-year pink), with an average of 28% across species (Table 2).

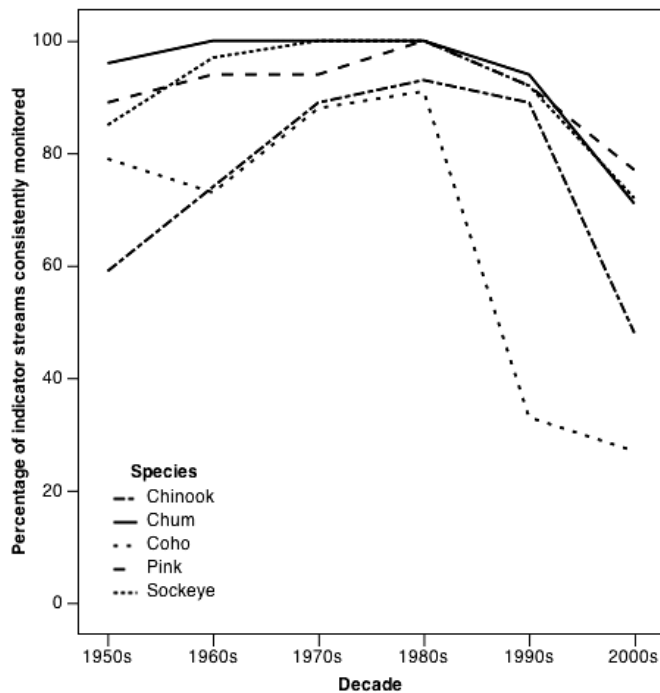
Model selection and multimodel inference suggested that status and size are the best predictors of monitoring cessation (Table 3). Specifically, the probability of runs being dropped from monitoring increased primarily with depressed

Table 3. Top generalized linear regression (logistic form) model set to predict the monitoring cessation of indicator salmon runs of British Columbia's central and north coasts.

| Model | K | Deviance | AIC_c | ΔAIC_c | ω_i | Nagelkerke R^2 |
|--|-----|----------|---------|----------------|------------|------------------|
| Status + size + (status \times size) | 4 | 260.872 | 269.327 | 0.000 | 0.434 | 0.121 |
| Status | 2 | 267.315 | 271.448 | 2.122 | 0.150 | 0.083 |
| Status + species | 3 | 265.239 | 271.509 | 2.182 | 0.146 | 0.096 |
| Status + size | 3 | 265.365 | 271.635 | 2.308 | 0.137 | 0.095 |
| Status + size + species | 4 | 264.209 | 272.664 | 3.337 | 0.082 | 0.102 |

Note: Nagelkerke R^2 values are always less for logistic models than for linear models. Model structure, deviance, corresponding ΔAIC_c , Akaike weight (ω_i), and Nagelkerke R^2 are included. Status is run status, size is run size, and species is salmon species.

Fig. 2. Decadal trends in monitoring effort for Pacific salmon (*Oncorhynchus* spp.) indicator streams on British Columbia's central and north coasts during 1950–2005.



or very depressed status, but less so with run size and species; all five models in the top model set (0–4 ΔAIC_c) contained status (Table 4). Summing the Akaike weights across top models ranked the variable status ($\Sigma\omega_i = 0.949$) higher than size, status \times size, and species by factors of 1.45, 2.19, and 4.16, respectively.

Discussion

Trends in achieving target escapements

Escapement enumeration is an important tool used by DFO in the assessment of abundance and subsequent establishment of harvest levels (Walters and Korman 1999b; English et al. 2006). Escapement data, ideally, should be continually compared with benchmark values to form the foundation of salmon management. Data we summarized, which span nearly six decades, show that management has repeatedly not met DFO's own target levels. This resulted in diminished runs for all species in nearly every decade,

Table 4. Summed Akaike's information criteria (AIC) weights ($\Sigma\omega_i$) across the top model set to rank parameters by relative importance in predicting the cessation of monitoring efforts of indicator salmon runs on British Columbia's central and north coasts.

| Parameter | $\Sigma\omega_i$ | Direction of association |
|----------------------|------------------|--|
| Status | 0.949 | Diminished status in previous decade |
| Size | 0.653 | Smaller runs |
| Status \times size | 0.434 | Diminished status when run size is small |
| Species | 0.228 | Order of species: coho, chum, pink, sockeye, Chinook |

Note: Status is run status, size is run size, species is salmon species, and direction of association describes in which manner the parameters are associated with monitoring cessation.

and as we describe below, was followed by increasingly selective monitoring programs that cannot accurately evaluate the health of salmon populations on BC's coast.

We acknowledge that meeting target escapements is an undoubtedly difficult task for managers given the complexity of Pacific salmon fisheries and the myriad of ecological factors that conspire to affect returning spawner numbers (Wright 1981; Hilborn and Luedke 1987). We point out, however, that MTEs were goals created by DFO, which by setting exploitation levels, would influence (at least in part) the health of salmon populations in BC (Goruk and Winther 1992; Walters and Korman 1999b; Walters et al. 2008).

Meeting internal management objectives is directly related to exploitation levels. Although climate and ocean survival likely play substantial roles, multiple lines of evidence suggest that overexploitation may be the greatest cause of salmon declines across the Northeast Pacific (Schmidt et al. 1998; Finney et al. 2000; Schindler et al. 2005). A recent report commissioned by DFO estimated that 48% of salmon runs in management areas 3 to 10 were either "highly exploited" or of "conservation concern" (English et al. 2006). For example, exploitation rates of Skeena River coho ranged from 40% to 90% between 1946 and 1997 (DFO 1999), resulting in an average 74% reduction in spawners over this period and subsequent fishery closure in 1998. Exploitation proportions of this magnitude have repeatedly resulted in decline and collapse of fisheries globally (Myers et al. 1996; Pitcher 2001; Belgrano and Fowler 2008). Coho numbers in the Skeena River system have steadily increased since this 1998 closure, and although increased marine survival likely contributed, the rebound of coho clearly demonstrates the efficacy of reducing fishing pressure as a

straightforward management prescription to rebuild diminished runs.

Evaluation of escapement monitoring

Not only are management targets consistently not being met, but also monitoring efforts are constantly eroding over the decades. As our data indicate, this handicaps current and future assessments of management and salmon population status. A constantly eroded effort and one biased to larger, healthier runs falls far short of the strategic effort required for informed fishery and salmon conservation decisions. A detailed report by the PFRCC (2004) concluded that the first priority in salmon conservation is consistent information (i.e., collected every year). Moreover, this current monitoring program is inadequate compared with specific recommendations made by an independent team commissioned by DFO (English et al. 2006), who called for a minimum of 407 streams enumerated yearly in this area, with an additional 152 runs enumerated every 2–4 years. Any effort less than this inhibits DFO's ability to accurately or precisely assess regional trends and can not provide the quality of data needed to conserve salmon populations under heavy fisheries pressure (PFRCC 2004; English et al. 2006). This is especially relevant for small runs (Routledge and Irvine 1999), which are disproportionately dropped from monitoring programs. If limited DFO resources earmarked for fieldwork are responsible for the monitoring patterns we document, we recommend that these responsibilities be increasingly shared with First Nations and nonprofit organizations, as has begun (e.g., Temple 2007). By sharing this responsibility, however, we suggest that these participants become increasingly involved in management decisions (i.e., setting exploitation limits).

How do our data on monitoring efforts relate to the most contemporary of management action plans? DFO recently published its CUs for wild salmon that identify the genetic and ecological scales at which salmon should be conserved and managed (DFO 2008c). It follows that these CUs should be adequately monitored. We show, however, a generally low monitoring effort, even applied at this scale. These data reinforce our conclusion that current monitoring efforts are inadequate to conserve salmon populations and indeed question the value of CUs, if largely unmonitored, as a new management tool for conservation.

Although budget shortfalls might contribute to monitoring declines in general (Slaney et al. 1996; PFRCC 2004), we present here some insight into how these decisions were made. Our data show that salmon runs that did not meet target escapements in the previous decade and were historically small were those most likely to be dropped from monitoring efforts. The consequence is an increasingly biased view of population health. Monitoring only healthy runs offers an uninformed and potentially perverse evaluation of regional population health. For example, the percentage of runs classified as depressed or very depressed during 2000–2005 for all species combined is 35%. Yet, if the number of runs classified likewise in the previous decade (and subsequently dropped from current monitoring) were to be included, the percentage increases to 72%. This can be likened to a “shifting baseline” (Pauly 1995) in the context of monitoring efforts.

Conservation implications

Why should managers be concerned with a monitoring effort increasingly biased towards large, healthy runs? Given that small spawning streams (i) far outnumber larger systems in this region (PFRCC 2004; English et al. 2006), (ii) are for the large part unmonitored, and (iii) those that are (or were) have (or had) a higher probability of monitoring cessation, several conservation implications arise.

Combined, small streams likely contribute disproportionately to ecosystem productivity and wider ecological and evolutionary processes. Coastal systems in this region are limited in nitrogen and phosphorous, which salmon carcasses provide, supplying important nutrients for aquatic and terrestrial primary productivity (Hyatt and Stockner 1985; Stockner and MacIsaac 1996). Small streams likely better enhance productivity of riparian communities compared with large streams by increasing carcass availability for terrestrial consumers and nutrient transporters (Quinn and Kinnison 1999; Quinn et al. 2003). Also, small streams facilitate carcasses flushing back into the ocean, providing estuarine nutrients that may serve as a positive feedback mechanism for salmon production (Fujiwara and Highsmith 1997; Gende et al. 2002). Moreover, wide distribution of such allochthonous resources can increase ecological and phenotypic diversity among individuals in receiving populations of terrestrial consumers (e.g., Hocking et al. 2007; Darimont et al. 2008a, 2008b).

Additionally, given current exploitation pressures and the prevailing mixed-stock harvest strategies, such biased monitoring might lead to harvest management that risks the extirpation of small runs. A notable example is Skeena River sockeye, for which harvest levels are based on the abundance returning to the Babine River spawning channels, a large and enhanced run. As a result, all other (and smaller) runs have declined substantially (Wood 2001; Walters et al. 2008). If current exploitation levels and monitoring efforts remain unchanged, waterways along BC's central and north coast might host only ghost runs — diminished or extirpated systems that once flourished with salmon.

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References

- Anderson, D.R., Link, W.A., Johnson, D.H., and Burnham, K.P. 2001. Suggestions for presenting the results of data analyses. *J. Wildl. Manage.* **65**: 373–378. doi:10.2307/3803088.
- Belgrano, A., and Fowler, C.W. 2008. Ecology for management: pattern-based policy. *In Ecology research progress. Edited by S.I. Munoz.* Nova Science Publishers, New York. pp. 5–31.
- Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Darimont, C.T., Paquet, P.C., and Reimchen, T.E. 2008a. Spawning salmon disrupt tight trophic coupling between wolves and ungulate prey in coastal British Columbia. *BMC Ecol.* **8**: 14. doi:10.1186/1472-6785-8-14.

- Darimont, C.T., Paquet, P.C., and Reimchen, T.E. 2008b. Landscape heterogeneity and marine subsidy generate extensive niche variation in a terrestrial carnivore. *J. Anim. Ecol.* In press.
- DFO. 1992. Stream survey catalogues. Fish Habitat Inventory and Information Program. North Coast Division Fisheries Branch, Sub-districts 3–10, Nass to Smith Inlet. Fisheries and Oceans Canada, Prince Rupert, B.C.
- DFO. 1999. Stock status of Skeena River coho salmon. Fisheries and Oceans Canada, Nanaimo, B.C. Science Stock Status Rep. No. D6-02
- DFO. 2007. Northern B.C. salmon integrated fisheries management plan 2007/2008. Fisheries and Oceans Canada, Prince Rupert, B.C.
- DFO. 2008a. Commercial salmon catch statistics by year [online]. Available from www.pac.dfo-mpo.gc.ca/sci/sa/Commercial/default_e.htm [accessed 09 July 2008].
- DFO. 2008b. NuSEDS V2.0 Regional adult salmon escapement database 1950–2005. Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, B.C.
- DFO. 2008c. Conservation units for Pacific salmon under the Wild Salmon Policy [online]. Available from www-comm.pac.dfo-mpo.gc.ca/publications/wsp/default_e.htm [accessed 24 November 2008].
- English, K.K., Peacock, D., and Spilsted, B. 2006. North and central coast core stock assessment program for salmon. Prepared for Pacific Salmon Foundation and Fisheries and Oceans Canada by LGL Limited Environmental Research Associates and Fisheries and Oceans Canada, Sidney, B.C.
- Finney, B.P., Gregory-Eaves, I., Sweetman, J., Douglas, M.S.V., and Smol, J.P. 2000. Impacts of climate change and fishing on Pacific salmon abundance over the past 300 years. *Science* (Washington, D.C.), **290**: 795–799. doi:10.1126/science.290.5492.795.
- Fujiwara, M., and Highsmith, R.C. 1997. Harpactoid copepods: potential link between inbound adult salmon and outbound juvenile salmon. *Mar. Ecol. Prog. Ser.* **158**: 205–213.
- Gende, S.M., Edwards, R.T., Willson, M.F., and Wipfli, M.S. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience*, **52**: 917–928. doi:10.1641/0006-3568(2002)052[0917:PSIAAT]2.0.CO;2.
- Goruk, R., and Winther, I. 1992. Salmon escapement and timing data for statistical areas 6 to 10 of the central coast of British Columbia 1980–1991. Supplement Edition II. DFO, Prince Rupert, B.C.
- Hilborn, R., and Luedke, W. 1987. Rationalizing the irrational: a case study in user group participation in Pacific salmon management. *Can. J. Fish. Aquat. Sci.* **44**: 1796–1805. doi:10.1139/f87-223.
- Hocking, M.D., Darimont, C.T., Christie, K.S., and Reimchen, T.E. 2007. Niche variation in burying beetles (*Nicrophorus* spp.) associated with marine and terrestrial consumers. *Can. J. Zool.* **85**: 437–442. doi:10.1139/Z07-016.
- Hyatt, K.D., and Stockner, J.G. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. *Can. J. Fish. Aquat. Sci.* **42**: 320–331. doi:10.1139/f85-041.
- Irvine, J.R., and Nelson, T.C. 1995. Proceedings of the 1994 Salmon Escapement Workshop and an Annotated Bibliography on Escapement Estimation Techniques. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 2305.
- Myers, R.A., Barrowman, N.J., Hoening, J.M., and Qu, Z. 1996. The collapse of cod in eastern Canada: the evidence from tagging data. *ICES J. Mar. Sci.* **53**: 629–640. doi:10.1006/jmsc.1996.0083.
- Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries*, **16**: 4–21.
- PFRCC. 2004. Advisory: salmon conservation challenges in British Columbia with particular reference to central and north coast. Pacific Fisheries Resource Conservation Council, Vancouver, B.C.
- Pauly, D. 1995. Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.* **10**: 430. doi:10.1016/S0169-5347(00)89171-5.
- Pitcher, T.J. 2001. Fisheries managed to rebuild ecosystems? Reconstructing the past to salvage the future. *Ecol. Appl.* **11**: 601–617. doi:10.1890/1051-0761(2001)011[0601:FMTRER]2.0.CO;2.
- Quinn, T.P., and Kinnison, M.T. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia* (Berlin), **121**: 273–282. doi:10.1007/s004420050929.
- Quinn, T.P., Gende, S.M., Ruggerone, G.T., and Rogers, D.E. 2003. Density-dependent predation by brown bears (*Ursus arctos*) on sockeye salmon (*Oncorhynchus nerka*). *Can. J. Fish. Aquat. Sci.* **60**: 553–562. doi:10.1139/f03-045.
- Routledge, R.D., and Irvine, J.R. 1999. Chance fluctuations and the survival of small salmon stocks. *Can. J. Fish. Aquat. Sci.* **56**: 1512–1519. doi:10.1139/cjfas-56-8-1512.
- Schindler, D.E., Leavitt, P.R., Brock, C.S., Johnson, S.P., and Quay, P.D. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. *Ecology*, **86**: 3225–3231. doi:10.1890/04-1730.
- Schmidt, D.C., Carlson, S.R., Kyle, G.B., and Finney, B.P. 1998. Influence of carcass-derived nutrients on sockeye salmon production of Karluk Lake, Alaska: importance in the assessment of an escapement goal. *N. Am. J. Fish. Manage.* **18**: 743–763. doi:10.1577/1548-8675(1998)018<0743:IOCDNO>2.0.CO;2.
- Slaney, T.L., Hyatt, K.D., Northcote, T.G., and Fielden, R.J. 1996. Status of anadromous salmon and trout in British Columbia and Yukon. *Fisheries*, **21**: 20–38. doi:10.1577/1548-8446(1996)021<0020:SOASAT>2.0.CO;2.
- Stockner, J.G., and MacIsaac, E.A. 1996. British Columbia lake enrichment programme: two decades of habitat enhancement for sockeye salmon. *Regul. Rivers*, **12**: 547–561. doi:10.1002/(SICI)1099-1646(199607)12:4/5<547::AID-RRR407>3.0.CO;2-M.
- Temple, N.N. 2007. Small stream surveys final report 2003–2006. Prepared for Raincoast Conservation Foundation, Victoria, B.C.
- Walters, C.J., and Cahoon, P. 1985. Evidence of decreasing spatial diversity in British Columbia salmon stocks. *Can. J. Fish. Aquat. Sci.* **42**: 1033–1037. doi:10.1139/f85-128.
- Walters, C.J., and Korman, J. 1999a. Salmon stocks: coast-wide stock status and trends, by species. *In* Pacific Fisheries Resource Conservation Council 1998–1999 annual report. PFRCC, Vancouver, B.C. p. 107.
- Walters, C.J., and Korman, J. 1999b. Salmon stocks: methods for analyzing productivity and for setting escapement and exploitation-rate goals. *In* Pacific Fisheries Resource Conservation Council 1998–1999 annual report. PFRCC, Vancouver, B.C. pp. 105–106.
- Walters, C.J., Lichatowich, J.A., Peterman, R.M., and Reynolds, J.D. 2008. Report of the Skeena Independent Science Review Panel. A report to the Canadian Department of Fisheries and Oceans and the British Columbia Ministry of the Environment, Vancouver, B.C.
- Wood, C.C. 2001. Managing biodiversity in Pacific salmon: the evolution of the Skeena River sockeye fishery in British Columbia [online]. Available from www.unep.org/bpsp/HTML%20files/TS-Fisheries2.html [accessed 10 July 2008].
- Wright, S. 1981. Contemporary Pacific salmon fisheries management. *N. Am. J. Fish. Manage.* **1**: 29–40. doi:10.1577/1548-8659(1981)1<29:CPSFM>2.0.CO;2.