

Unaccounted mortality in salmon fisheries: non-retention in gillnets and effects on estimates of spawners

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Summary

1. Effective and sustainable natural resource management is enhanced when the consequences of exploitative practices are fully understood and acknowledged. Commercial fisheries devote considerable resources to maximize the harvest of target species and minimize interference with non-target stocks. Appropriately, bycatch and discard of non-target stocks are recognized as critical economic and conservation concerns. Few studies, however, have examined non-retention mortality in target stocks. Non-retention, where fish are engaged by fishing gear but not landed, is rarely quantified and the effects on stocks are unknown. Mortality due to non-retention may have important effects on the dynamics of exploited populations.

2. We surveyed spawning populations of sockeye salmon *Oncorhynchus nerka* that had traversed commercial fisheries in Bristol Bay, Alaska, to estimate the incidence of non-retention in gillnets and the severity of injuries associated with entanglement. To better understand how gillnet injury affects spawning success, we tagged and monitored stream-spawning fish and applied a maximum likelihood model to mark–recapture data.

3. A substantial portion (11–29%) of spawning sockeye salmon exhibited clear signs of past entanglement with commercial gillnets. Survival among such fish was significantly reduced. More than half of the fish that reach natal spawning grounds with fishery-related injuries fail to reproduce. This suggests that estimates of spawning stocks are inflated by 5–15% at minimum.

4. *Synthesis and applications.* Our analyses indicate that non-retention in gillnet fisheries is an important and under-appreciated consequence of the exploitation of salmon. Stock estimates for exploited populations that do not account for non-retention mortality overestimate the number of reproductively viable fish. Unaccounted mortality and interannual variation in the magnitude of this mortality may prevent accurate estimates of viable spawners, confound our understanding of the relationship between stock size and recruitment, impede optimal management and obscure the ecosystem impacts of migratory stocks in coastal watersheds. Given the magnitude of non-retention in this fishery, explicit consideration of non-retention mortality may be warranted across a wide range of exploited populations.

Key-words: delayed mortality, ecosystem engineers, fishery-induced injury, mark–recapture analysis, natural resource management, Pacific salmon, population dynamics, stock-recruitment estimation

Introduction

Fishery-related injury in target stocks is rarely quantified but may be an important source of mortality in heavily exploited populations (Alverson 1997; Hall, Alverson & Metuzals 2000). Both immediate and delayed mortality caused by encounters

with commercial gear is often high (Chopin & Arimoto 1995). While bycatch, discard and release of non-target species is often considered (Harrington, Myers & Rosenberg 2005), damage sustained by target stocks is often ignored. Certain gear types have low retention rates, enabling a portion of fish that encounter gear to disentangle or escape, often leading to delayed mortality. Such delayed mortality may have important consequences for fisheries management and the sustainability

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of exploited populations, especially where these stocks are managed for explicit targets and fishing effort relative to stock size is variable.

Many Pacific salmon gillnet fisheries are managed according to escapement targets. These are terminal fisheries, which harvest salmon on their return migration to freshwater and are regulated to ensure that sufficient numbers of adults evade the fishery and spawn. While most fish intercepted by the fishery are harvested, many disentangle from nets and continue their migration to natal spawning areas. Many of these fish sustain serious injuries. Although counted as part of the aggregate escapement of viable spawners, fish damaged in the fishery experience physical trauma, physiological stress, exhaustion and increased susceptibility to disease (Ricker 1976; Davis 2002). These fish may die prior to spawning or have reduced spawning success. Such losses have a direct bearing on estimates of spawning adults. If a significant portion of the enumerated escapement fails to spawn, escapement estimates will not accurately reflect the effective population of viable spawners. This will also confound analyses of the relationship between spawning stock size and future recruitment to the population. Where delayed mortality affects a constant percentage of escaped stocks, this loss may be implicit in the stock-recruit function. In most fisheries, however, fishing effort is variable between years, dependent on the size and timing of the salmon run. The failure to account for inter-annual variability in fishery-related injury to spawning stocks may generate significant errors in stock assessment.

Survival for fish entangled by gillnets is the lowest for all gear types (ASFEC 1995). With regard to commercial salmon fisheries, there are no current estimates of gillnet-related injury in exploited populations nor has there been extensive research to determine the consequence of these injuries on spawning success among escaped fish. Studies of mortality associated with non-retention in salmonids have largely focused on catch-and-release sport fisheries (Vincent-Lang, Alexandersdottir & McBride 1993; Booth *et al.* 1995) or commercial fisheries using troll and seine gear (Parker, Black & Larkin 1959; Thomas & Associates Ltd 1997). The few existing studies that address non-retention mortality in gillnet fisheries either examine the issue in an experimental context (Thompson, Hunter & Patten 1971; Thompson & Hunter 1973), document outdated harvest regimes such as high seas fisheries (French *et al.* 1970; Ricker 1976), evaluate selective fisheries practices where entangled fish are deliberately released and revived (Buchanan *et al.* 2002; Vander Haegen *et al.* 2004) or exclude severely damaged fish from analysis (Thompson & Burgner 1952; Hartt 1963).

The Bristol Bay sockeye salmon *Oncorhynchus nerka* fishery is managed to achieve constant annual escapement. Our study was designed to quantify the impact of gillnet injury on escaped stocks, given the current operation of the fishery. We estimated the incidence and severity of injuries in fish returning to natal streams and the effect of such injuries on pre-spawning mortality. The findings suggest that gillnet injuries are common and, in many cases, inhibit spawning. The effects of such unaccounted mortality may have important implications for the designation of optimal escapement targets in exploited

populations, the estimation of spawner-recruit relationships, the understanding of evolutionary processes driven by fishery selection and the characterization of the ecosystem effects of spawning activity in coastal watersheds.

Materials and Methods

ESTIMATION OF THE INCIDENCE OF GILLNET INJURY

Analyses were conducted in the Wood River system in south-west Alaska (see Map Appendix S1, Supporting Information). The Wood River system is the primary watershed in the Nushagak district of the Bristol Bay fishery, supporting one of the world's largest stocks of commercially exploited sockeye salmon (Hilborn *et al.* 2003). Throughout the Wood River system, sockeye salmon gather within a 100 m range of their natal stream for a period of 1 month following migration through the fishery, entering spawning streams at maturation (Hendry, Berg & Quinn 1999). This behaviour allowed us to sample discrete populations immediately prior to their entry to spawning grounds. At Pick Creek, the site of our mark-recapture study, we used beach seines to sample 200–500 fish each year for three consecutive years (2005–2007) to determine the incidence and severity of gillnet injuries in the pre-spawning population of sockeye salmon that had successfully transited the fishery. In 2006 and 2007, we expanded sampling to include 10 populations throughout the Wood River system. All sampling occurred within a 2-week period (12–24 July). We sampled streams in accordance with historical peak spawning date (University of Washington, unpublished data), immediately prior to expected stream entry.

CLASSIFICATION OF GILLNET INJURY

All sockeye salmon were examined for fishery-related injury. Clear net marks, abrasions, contusions or scale loss spanning the circumference of the fish were considered evidence of gillnet entanglement. Gillnet marked fish were grouped according to the severity of the injury: (i) minor injuries included any evidence of gillnet entanglement, including net marks and/or scale loss; (ii) moderate injuries included open wounds and/or skin loss on 5–20% of the surface area of the fish; and (iii) severe injuries included large open wounds, fractured jaws or gill plates, and/or skin loss on >20% of the surface area of the fish (Fig. 1).

STREAM RESIDENCE AS AN INDICATOR OF PRE-SPAWNING MORTALITY

Our analysis sought to determine whether gillnet injury resulting from non-retention in commercial fisheries prevents injured fish from spawning. We examined a stream-spawning population of salmon, using stream residence as a proxy for successful reproduction. Direct observation of spawning activity was not possible given the spatial extent of the survey. Egg retention estimates were compromised by scavenging gulls *Larus glaucescens*. Therefore, a mark-recapture study was conducted at Pick Creek (59°33'00"N, 159°04'18"W) to determine relative differences in survival and stream residence between fish with and without fishery-related injuries. A second-order stream, Pick Creek originates in a series of spring-fed ponds and flows 2 km before entering Lake Nerka. The stream averages 33 cm deep and 7.8 m wide (Hendry 1998) with high water clarity and relatively constant discharge (Hendry *et al.* 1999). Spawning occurs at high densities throughout the lower 2 km of the stream, with an average of



Fig. 1. Photographs of relative severity of gillnet injury. Note that coloration is dark (red) and scales are absorbed in fish without injury. Fish have less coloration (red → bluish → silver) and retain scales as severity of injury increases. Morphological traits associated with sexual maturity in males (dorsal-ventral expansion and extended kype) are less pronounced among fish with injury. These trends suggest gillnet injury may retard or inhibit sexual maturation.

8000–10 000 adult spawners (Rogers & Schindler 2008) and a spawning season of c. 40 days. Due to the presumption that mortality of severely injured fish would increase as a function of distance travelled from the fishery, we sought to sample a population that represented the average distance from commercial fishery to natal stream for Bristol Bay stocks. Throughout Alaska, sockeye salmon stocks migrate a mean distance of 103 ± 70 km ($n = 32$) to an elevation 72 ± 104 m ($n = 32$). The average Bristol Bay sockeye migrates 94 km to 28 m (Burgner 1991). With a freshwater migration of 98 km to an elevation of 22 m (Hendry & Berg 1999), the Pick Creek population is representative of the post-fishery migration in Bristol Bay.

Pre-spawning mortality was assumed to occur where fish failed to demonstrate sufficient stream residence to allow spawning opportunities. Although sockeye salmon enter spawning areas at reproductive maturity, several days in-stream precede successful spawning at high density sites. The reproductive lifespan (stream entry to senescence) of Pick Creek fish is 17–20 days (Hendry *et al.* 1999). All sockeye salmon perish soon after spawning. Typically fish hold in tight schools during their first days of stream residence and disperse to colonize spawning habitat within a week of stream entry. Subsequent studies in Pick Creek indicate females secure territory and spawn towards the end of the first week of in-stream residence (mean days post-entry = 8.05 ± 5.56) and defend their redd site until senescence, typically maintaining a consistent presence for a week or more (mean days post-spawning = 6.93 ± 2.37 ; M. Baker, unpublished data). While movement does not preclude reproductive success in males, males establish dominance hierarchies on small spatial scales (Quinn, Adkison, & Ward 1996) and typically demonstrate strong site fidelity following a period of initial exploration (Foote 1990; Rich *et al.* 2006). Competitive advantage among males is driven by prior residence (Foote 1990) and, as males remain reproductively active until death, extended stream residence confers greater reproductive opportunities. Given these conditions, we determined any fish that failed to demonstrate a minimum stream residence of 3 days failed to spawn (sensitivity to this threshold value shown in Table 1).

MARK-RECAPTURE SAMPLING AND IN-STREAM OBSERVATION

From 15 to 17 July 2005, we sampled and tagged pre-spawning adult sockeye salmon at the mouth of Pick Creek. Fish were captured using a beach seine. A sample of 100 gillnet-marked fish was tagged, including 50 with minor injuries, 30 with moderate injuries and 20 with severe injuries (42 males and 58 females). This distribution of severity

of injury reflects a representative sampling of the injured population of fish at Pick Creek ($n = 1863$). A sample of 100 uninjured fish (50 males and 50 females) was also tagged as a control group. Each fish was anaesthetized with tricaine methanesulphonate (MS-222; Western Chemical, Inc., Ferndale, WA), tagged with an external uniquely coded 3-cm Petersen disc tag (Floy Tag Co., Seattle, WA), rejuvenated in cold water and released (Fig. 2). This method of tagging corresponds to a well-established procedure that neither accelerates mortality nor has lasting effects on fish behaviour (Quinn & Foote 1994). Presence and severity of fishery-related injury and presence of fungal infection (*Saprolegnia* spp.) was assessed at this stage. Photographs of all injured fish were reviewed at the conclusion of sampling to re-evaluate classification and ensure standard ranking over time.

Visual stream surveys of Pick Creek were conducted every other day throughout the lifespan of all tagged fish (17 July to 25 August). Surveys recorded the presence, absence and mortality of tagged fish. For analysis, each 2 day period was considered a sampling event.

NONPARAMETRIC ESTIMATOR FOR STREAM RESIDENCE TIME

Survival between sampling occasions and stream residence for each category of gillnet injury were estimated through a nonparametric estimator using a maximum likelihood approach. This allowed us to separately estimate survival and account for failures to detect fish during stream surveys. A model developed by Lady & Skalski (1998) was adapted and used to estimate stream residence, following approaches developed by Cormack (1964) and elaborated by Burnham *et al.* (1987), whereby conditional survival probabilities are estimated from one sampling event to the next based on release-recapture data for marked individuals.

Maximum likelihood estimation (MLE) was used to derive survival and detection probabilities, using the following function:

$$L(S, P, \lambda | a, c) \propto \left(\prod_{i=1}^{K-2} S_i^{a_i} \right) \left(\prod_{i=2}^{K-1} P_i^{c_i} (1 - P_i)^{1 - c_i} \right) \left(\prod_{i=1}^{K-1} \lambda_i^{c_i} \right) \lambda^{c_{K-1}}$$

where K is the number of sampling occasions; S_i is the probability that an individual alive at sampling occasion i will be alive at sampling occasion $i + 1$; P_i is the probability that an individual alive at sampling occasion i will be detected; λ is the product of final survival and detection probabilities ($S_{K-1}P_K$); a_i is the number of marked individuals detected at sampling occasion i ; c_i is

Table 1. Estimated stream residence time and pre-spawning mortality according to severity of gillnet injury and presence of *Saprolegnia* spp. infection

		Pre-spawning mortality		Stream residence time (days)			
				Maximum likelihood estimates		Individual mark-recapture histories	
		Threshold for successful spawning (minimum: 3 days; range: 1–9 days)					
Tagged fish (<i>n</i>)				All fish	Fish observed in stream	All fish	Fish observed in stream
Gillnet injury							
Uninjured	100	6%	(2–25%)	10.78	11.01	14.4 ± 8.3	14.7 ± 8.1
Gillnet injured	100	51%	(42–71%)	4.54	7.82	6.1 ± 7.8	10.5 ± 7.6
Minor	50	16%	(8–44%)	8.14	8.85	10.9 ± 8.0	11.9 ± 7.6
Moderate	30	80%	(67–93%)	1.37	4.11	1.7 ± 3.7	5.2 ± 4.8
Severe	20	95%	(90–100%)	–	–	0.4 ± 1.4	0.4 ± 1.4
Fungal infection (<i>Saprolegnia</i> spp.)							
No infection	157	11%	(4–35%)	9.84	10.30	12.8 ± 8.4	13.4 ± 8.1
Fungal infection	43	93%	(86–95%)	0.53	3.83	0.7 ± 2.5	5.2 ± 5.1

Stream residence was calculated for each category of gillnet injury through maximum likelihood estimation methods as a function of survival probabilities between 2-day sampling periods. Stream residence was also estimated on the basis of individual mark-recapture histories (± SD). Pre-spawning mortality was assumed in fish that failed to demonstrate in-stream survival over a minimum of two sampling periods (3 days). Sensitivity to this threshold stream residence is shown as a range of estimated pre-spawning mortality given threshold values of 1–9 days.

**Fig. 2.** Fish with Petersen disc tag (photograph: Michael Webster).

the number of marked individuals detected for the last time at sampling occasion i ; v_i is the number of marked individuals known to be alive at sampling occasion $i + 1$; χ_i is the probability that an individual alive at sampling occasion i will not be detected again ($\chi_i = c/a_i$). R is the number of individuals tagged at the initial sampling occasion.

where

$$v_i = R - \sum_{j=1}^i c_j$$

The maximum likelihood estimators for survival parameters (and their variances and covariances) are derived by Burnham *et al.* (1987) and reformulated by Lady & Skalski (1998):

$$\hat{S}_1 = \frac{a_2 v_2}{R(a_2 - c_2)}$$

$$\hat{S}_i = \frac{a_{i+1}(a_i - c_i)v_{i+1}}{a_i v_i(a_{i+1} - c_{i+1})} \quad \text{for } i = 2, \dots, K-2$$

Using these survival probabilities, Lady & Skalski (1998) developed the following estimator of stream residence time (T), operating on assumptions that: (i) the distribution of deaths between sampling periods is uniform and (ii) all individuals die prior to the final sampling occasion.

$$\hat{T} = \frac{1}{2} \sum_{i=1}^{K-2} \left\{ (t_i + t_{i+1})(1 - \hat{S}_i) \prod_{j=1}^{i-1} \hat{S}_j \right\} + \frac{1}{2} (t_{K-1} + t_K) \prod_{j=1}^{K-2} \hat{S}_j$$

where t_i is the time of the i th sampling occasion relative to the initial sampling occasion, $t_1 = 0$.

Although technically developed to derive estimates of stream residence time, this model was applied to data on a beach spawning population (Quinn & Foote 1994), where fish were marked and recaptured at the same location. In our study, fish were tagged at the stream mouth and surveys were conducted within the main stem of the stream. We therefore modified the model to estimate separate probabilities for: (i) whether or not a fish entered the stream and (ii) its survival and detection within the stream.

In our analysis, the first period describes the probability of stream entry or the interval between when a fish was marked (tagged at the stream mouth) and its first recapture (first in-stream observation). This is defined as the joint probability of survival and stream entry.

The second period describes survival after stream entry, which we characterize as stream residence. Stream residence was estimated only for fish that were observed in the stream and initiated at the first in-stream observation. For integration with the model above, we arranged the data such that the first in-stream observation (stream entry) for a given individual is considered the first sampling occasion (release) for that individual, regardless of calendar date. All subsequent sampling occasions for that individual are relative to that first in-stream observation, in effect, modelling stream residence as a first-order approximation by entry date rather than calendar date. Calendar date of spawning had no influence on the senescence schedule of fish (Appendix S2).

Results

INCIDENCE AND SEVERITY OF GILLNET INJURY

Fishery-related injuries due to gillnet entanglement were evident in 11% of fish sampled at Pick Creek in 2005. Subsequent sampling in 2006 and 2007 recorded gillnet injury rates of 29% and 18% respectively. Fungal infection was strongly associated with the severity of gillnet injury. No infection was observed in uninjured fish in 2005. Nearly half (43%) of gillnet-injured fish were infected, with rates of 6%, 76% and 100% for fish with minor, moderate and severe injuries respectively. Similar patterns were noted in 2006 and 2007.

In multi-year sampling at 10 streams, the incidence of gillnet injury ranged between 4–37% (mean = $18 \pm 13.1\%$) in 2006 and 7–29% (mean = $14 \pm 6.5\%$) in 2007 (Fig. 3). Among injured fish, both sexes exhibited 68% minor injury, 23% moderate injury and 9% severe injury in 2006 and 80% minor injury, 18% moderate injury and 2% severe injury in 2007. Fungal infection was associated with severity of gillnet injury (2×3 contingency tables: 2006: $\chi^2_2 = 748.20$, $P < 0.001$; 2007: $\chi^2_2 = 91.90$, $P < 0.001$). Infection rates for fish with minor, moderate and severe injuries were 9%, 41% and 77% (2006) and 5%, 33% and 62% (2007) respectively. Although excluded from our mark-recapture analyses, 2% of sockeye salmon sampled across 10 streams in both 2006 and 2007 also exhibited damage from boat propellers.

STREAM ENTRY AND IN-STREAM OBSERVATIONS

Fish must enter and maintain residence in the stream to successfully spawn. We tested the independence of severity of injury and whether or not fish entered the stream and found significant differences between groups ($\chi^2_3 = 117.79$,

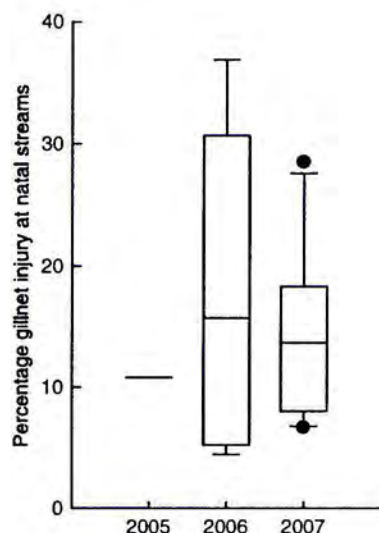


Fig. 3. Incidence of gillnet injury averaged across 10 streams in the Wood River system (2005–2007). Only one site was sampled in 2005 (Pick Creek).

$P < 0.001$). Virtually all (98%) uninjured fish and most (92%) fish with minor injuries entered the stream in contrast to 33% of fish with moderate injuries and 10% of fish with severe injuries. The presence of fungal infection was also a strong indicator of whether fish entered the stream ($\chi^2_1 = 130.94$, $P < 0.001$). Nearly all (96%) fish without fungal infection were observed in-stream in contrast to a minority (14%) with infection. Whether or not a fish was observed in-stream was independent of sex in the control group ($\chi^2_1 = 2.04$, $P = 0.153$).

Differences were also noted in the date of stream entry. Most control fish entered the stream 4 days after tagging. Fish with minor injuries held off the mouth more than twice as long. Both the mean ($t_{2,59} = 4.21$, $P < 0.001$) and variance ($F_{2,97,45} = 0.327$, $P < 0.001$) in stream entry date were distinguishable from control fish. There was no detectable difference ($t_{2,90} = 0.60$, $P = 0.549$) in mean stream entry date between control males (mean days to stream entry = 4.4 ± 4.8) and control females (3.8 ± 3.9). Similarly, no detectable difference was found ($t_{2,43} = 0.22$, $P = 0.829$) between males with minor injury (mean days to stream entry = 9.4 ± 7.8) and females with minor injury (9.0 ± 7.6). Few fish with moderate-to-severe injury entered the stream, which prevented accurate estimates.

SURVIVAL AND STREAM RESIDENCE TIME

Survival and detection probabilities

Using the maximum likelihood estimates of survival between sampling occasions, we calculated cumulative in-stream survival across sampling intervals as a function of entry date (Fig. 4). In-stream survival declined precipitously for fish with moderate to severe gillnet injury. Trends were even more pronounced for comparisons of fish with and without fungal infection. On any given sampling occasion, the probability of detecting a control fish known to have entered the stream was estimated at 0.718, taken as an average of MLE estimates over 20 sampling events. No differences were noted between males (0.700) and females (0.698). To enable estimation of detection probabilities independent of survival we also employed the Manly & Parr (1968) approach and recorded a detection probability of 0.702.

Stream residence by entry date

Maximum likelihood estimates of stream residence time ($\hat{T}$) were calculated as a function of survival probabilities between 2-day sampling periods. Gillnet injury had a direct bearing on stream residence time. We assumed fish that were never observed in the stream, never entered the stream. Among fish that entered the stream, uninjured fish had a mean stream residence of 11.01 (95% CI = 9.44–12.58) days in contrast to 8.85 (95% CI = 5.85–11.84) days for fish with minor injury and 4.11 (95% CI = 2.28–5.95) days for fish with moderate injury. Too few fish with severe injury entered the stream to estimate stream residence. Stream residence was also estimated as a

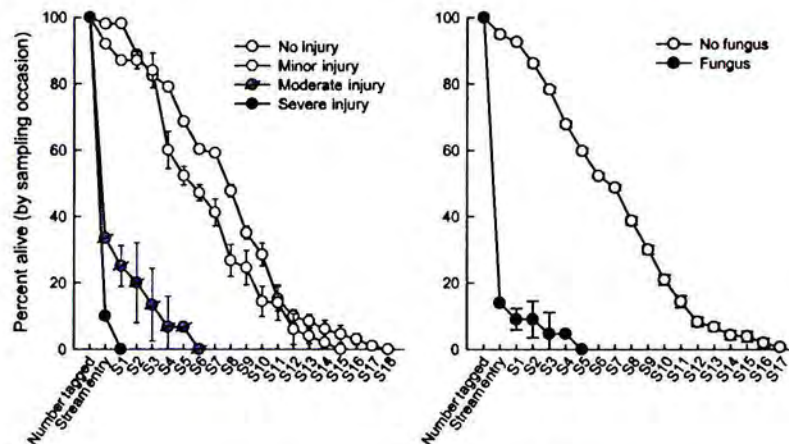


Fig. 4. Plots of in-stream survival according to severity of injury and presence of fungal infection. These estimates standardize by stream entry date, such that the plots illustrate total in-stream survival regardless of the timing of stream entry. The first interval reflects the number of fish tagged and released. The second interval is the percentage estimated to have entered the stream according to in-stream observations. Subsequent intervals (S1–S18) are calculated as the product of the number alive at the previous period and our MLE estimate for survival between the previous and the current period (95% confidence intervals are contained within error bars). Fish not observed in the stream were presumed dead.

function of all fish in each category (regardless of whether fish entered the stream) by integrating maximum likelihood estimates of stream residence for fish observed in the stream with estimates of zero for those never observed.

Longevity and stream residence by calendar date

Due to standardization by stream entry date, our maximum likelihood estimates do not provide estimates of survival for individual fish in real time nor allow us to characterize the number of fish in-stream at any given time. To analyse differences by calendar date, we estimated longevity for individual fish on the basis of the last observation for that individual. We estimated stream residence as the difference between the first and last in-stream observations. These methods confirmed the results achieved through maximum likelihood methods (Table 1).

Longevity (survival in days post-tagging) was greatly reduced ($t_{2,146} = 15.03$, $P < 0.001$) among moderately and severely injured fish relative to control fish. Interestingly, fish with minor injuries lived somewhat longer than the uninjured fish ($t_{2,78} = 1.36$, $P = 0.179$; Fig. 5a), but exhibited reduced stream residence ($t_{2,94} = 2.02$, $P = 0.046$), due to later stream entry (Fig. 5c). Pair-wise comparisons of stream residence between categories of gillnet injury confirmed significant differences between all groups ($P < 0.050$) except between those with moderate and severe injuries (ANOVA, *post hoc* Tukey HSD: $P = 0.912$). Distinct patterns in longevity were also noted as a function of fungal infection. Fish without fungal infections lived more than 15 times longer ($t_{2,173} = 16.95$, $P < 0.001$; Fig. 5b) and, among fish observed in-stream, spent more than twice as long in-stream ($t_{2,6} = 3.80$, $P = 0.005$; Fig. 5d). The longevity of control females (mean = 19.6 ± 7.7 , $n = 50$) was significantly longer ($t_{2,94} = 2.50$, $P = 0.014$) than control males (mean = 15.3 ± 9.2 , $n = 49$) and among those that entered the stream,

females demonstrated longer stream residence ($t_{2,95} = 2.65$, $P = 0.009$). Overall, however, males and females displayed similar patterns of decline in stream residence as a function of severity of gillnet injury (Fig. 6).

PRE-SPAWNING MORTALITY

The average stream residence for Pick Creek fish not killed through predation is 10–25 days (Hendry *et al.* 1999). We adopted a conservative estimate of pre-spawning mortality, assuming fish that failed to demonstrate in-stream survival for a minimum of 3 days failed to spawn. Using maximum likelihood estimates, pre-spawning mortality was calculated as a function of fish known alive at the second sampling occasion (v_1). According to our model, stream entry is considered the release date for each individual. Subsequent in-stream observations are in reference to this standardized release. Thus the percentage known alive at the second sampling occasion (v_1), includes all fish that survive a minimum of two sampling intervals (3 days) from stream entry. Given this criteria, the majority (51%) of fish with gillnet injuries were predicted to fail to spawn in contrast to 6% of control fish. Nearly all fish (93%) with fungal infection at the time of tagging failed to spawn (Table 1).

To account for predation effects, we surveyed all carcasses to determine the cause of death. Brown bears *Ursus arctos* are a major source of in-stream predation and pre-spawning mortality on sockeye salmon in south-west Alaska (Shuman 1950; Gard 1971) and are known to preferentially select fish in better condition in environments that facilitate foraging (Gende, Quinn & Willson 2001). We noted higher predation on control fish. Among fish with known fates ($n = 76$), bear predation was observed for 31% of uninjured males ($n = 17$) in contrast to 17% of gillnet-injured males ($n = 7$) and in 11% of uninjured females ($n = 39$) in contrast to 8% of gillnet-injured females ($n = 13$). While a significant portion of pre-spawning

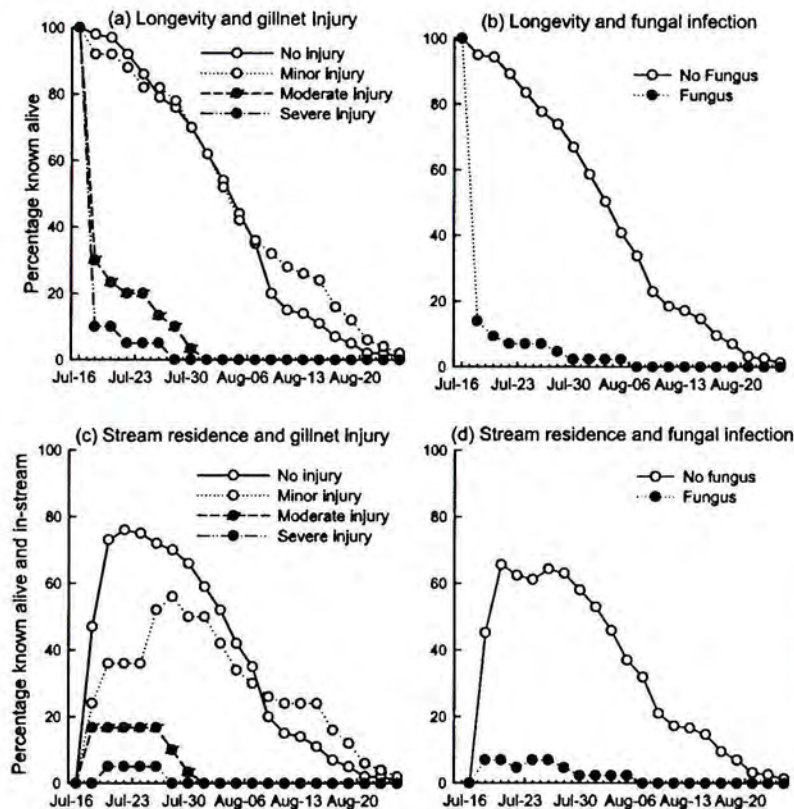


Fig. 5. (a–d) Longevity (post-tagging survival) and stream residence time according to severity of injury and presence of fungal infection. These estimates illustrate survival and stream residence by calendar date. Longevity estimates include fish known alive at any given sampling occasion. Stream residence estimates include fish known alive and known to have entered the stream.

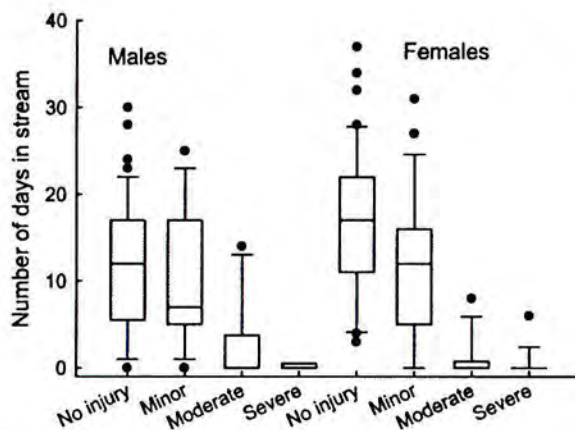


Fig. 6. Box plots of stream residence time according to sex and severity of gillnet injury.

mortality in our control group may be attributable to bear predation, it is unlikely that predation alone accounts for the high rates of pre-spawning mortality in fish injured through non-retention in gillnets.

MODEL PERFORMANCE AND ASSUMPTIONS

To analyse model performance, we utilized the release-recapture software SURPH 2.1 (Survival Under Proportional Hazards, 2002). To determine whether survival and detection are

the same across treatment groups, we applied TEST 1 developed by Burnham *et al.* (1987) and confirmed that survival parameters differ between fish with and without evident gillnet injury ($\chi^2_{39} = 117.73$, $P = 0.000$). To determine whether sex impacts survival or detection, we compared males and females within the control group and found no significant differences ($\chi^2_{39} = 34.23$, $P = 0.687$). Because our analysis standardized survival estimates according to stream entry date, we tested whether detection probabilities hold constant across sampling occasions to ensure different conditions at different sampling occasions would not bias this approach. Specifically we analysed mark-recapture data by calendar date and compared the relative performance of: (i) a model assuming unique detection parameters for each sampling period and (ii) a model assuming a common detection parameter across sampling periods. On the basis of the Akaike Information Criterion (Akaike 1973), we found the model with common detection parameters provided the best fit to the data (Table 2).

Discussion

IMPLICATIONS FOR NON-RETENTION AND DELAYED MORTALITY IN EXPLOITED STOCKS

Our results suggest that disentanglement from gillnets is a regular occurrence in commercial fisheries in Bristol Bay, Alaska. As a consequence, fishery-related injuries are common in spawning stocks of sockeye salmon. Mark-recapture results

Table 2. SURPH model comparison for unique vs. common detection parameters applied across sampling occasions

Model	No. parameters	Ln likelihood	AIC
Unique detection parameters for each sampling occasion	39	-852.618	1783.24
Common detection parameters for every sampling occasion	21	-786.366	1614.73

This analysis confirms our assumption that in-stream detection remained constant throughout the sampling period. It suggests that standardizing individual capture histories by stream entry date (rather than calendar date) did not bias survival estimates. AIC, Akaike Information Criterion.

demonstrate that survival on the spawning grounds is markedly reduced among gillnet-injured fish and inversely correlated with the severity of injury. Conservative estimates suggest that more than half of the fish that reach natal spawning grounds after contracting injuries in the fishery fail to reproduce. The incidence and severity of gillnet injury also appear to vary between years, probably as a function of fishing intensity and run size. Due to constant escapement targets, larger runs will experience higher rates of exploitation. During smaller runs managers implement more closures, which inadvertently improves the relative condition of the escaped stocks. Differences in the size of returning fish may also influence retention, given a relatively constant range of mesh sizes used in the fishery. For these reasons, distinguishing between total escapement (all fish that migrate past escapement towers) and effective escapement (fish that survive the migration and spawn) should be considered.

There are also broader ecological implications to decreased spawning activity in coastal watersheds. Recent attention has focused on the consequences to habitat and community structure related to the overexploitation of ecosystem engineers by commercial fisheries (Coleman & Williams 2002). Habitat modification by spawning salmon alters community organization in stream ecosystems and strongly influences the downstream flux of nutrients and resource subsidies (Moore, Schindler & Scheuerell 2004). Non-retention mortality in spawning stocks will reduce these effects relative to expectations based on escapement counts.

POTENTIAL FOR UNDERESTIMATING INCIDENCE OF GILLNET INJURY

Our estimates of the incidence of gillnet injury are almost certainly lower than actual rates of non-retention in escaped stocks of spawning salmon. To assess fish from discrete populations and minimize the inclusion of strays or migrants, our sampling was conducted at natal streams immediately prior to stream entry, roughly 2 weeks after stocks had migrated through the fishery and were enumerated at escapement counting towers. During this period, many injured fish probably do not survive the challenges associated with migration, osmoregulation, sexual maturation and maintenance metabolism.

Experimental studies of maturing sockeye salmon disentangled from gillnets found that 80% died within 1 week (Thompson *et al.* 1971; Thompson & Hunter 1973). Our estimates of the incidence of non-retention fail to account for fish that survive long enough to migrate past escapement towers but perish before our sampling occurs at natal streams. It is therefore reasonable to assume our estimate of 11–29% gillnet injury is conservative. Actual rates of injury in escaped stocks may be considerably higher (for further research, see Appendix S3).

PRE-SPAWNING MORTALITY AND PROXIMATE MECHANISMS

It is clear that virtually all fish with moderate to severe gillnet injury fail to spawn. In the case of fish with minor injuries, the delay in stream entry, abbreviated stream residence and the inhibition of morphological traits associated with sexual maturation (Fig. 1) suggest that even minor injuries retard maturation and reduce reproductive fitness. This delay in maturity may explain why fish with minor injuries live longer than uninjured fish despite reduced stream residence. Pre-spawning mortality was highly correlated with and was likely facilitated by fungal infection, caused by *Saprolegnia* spp., a facultative parasite common in freshwater ecosystems. *Saprolegnia* spp. causes tissue damage, loss of epithelial integrity and osmoregulatory failure (Bruno & Wood 1999). It is associated with damaged epidermal tissue (Hatai & Hoshiai 1994; Pickering 1994), suggesting fish with gillnet injuries are particularly susceptible to such infections. Fish with severe infections generally fail to recover (Pickering & Willoughby 1982). Of 43 fish with fungal infection at the time of our tagging, only one successfully spawned. Many injured fish without *Saprolegnia* spp. at tagging presumably developed infections subsequently. Due to the close correlation between fungal infection and pre-spawning mortality, *Saprolegnia* spp. is likely to be the proximate cause of pre-spawning mortality in gillnet injured fish.

BROADER APPLICATION OF NON-RETENTION MORTALITY AND SUSTAINABLE FISHERIES MANAGEMENT

Commercial gillnet fisheries harvest Pacific salmon on their return migration and are managed to ensure sufficient numbers of adults spawn and perpetuate discrete stocks. Complicating management, many salmon enumerated in escapement counts suffer injuries in the fishery and fail to spawn. Estimates of spawning potential based on such escapement counts fail to consider this loss. Our study indicates that gillnet injury affects a minimum of 11–29% of escaped fish. Roughly half of the injured fish fail to spawn. Even minor injuries may lead to adverse consequences, such as delayed maturation. The number of viable spawners in escapement counts may be overestimated by 5–15%, with repercussions for stock-recruitment analyses (Fig. 7). Currently, non-retention and delayed mortality are neither measured nor explicitly incorporated into stock assessment. The magnitude and inter-annual variation of non-retention in spawning stocks suggest that this source of

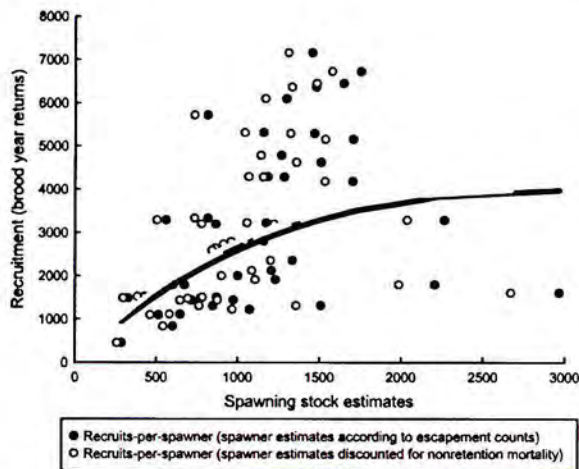


Fig. 7. Plots and Ricker (1954) model fit to spawner-recruit data in Wood River stocks (1956–2001). Failure to account for non-retention mortality in escaped stocks of salmonids will inflate estimates of viable spawners and underestimate recruits-per-spawner. We plot the stock recruitment relationship with spawning stock as enumerated at escapement towers (●) and discounted (–10%) for non-retention mortality (○). Mean recruits per spawner are 2.81 (escapement estimates) in contrast to 3.21 (discounted estimates). While a constant discount rate illustrates a significant difference in estimated productivity, accounting for interannual variance in non-retention (as a function of fishing intensity and size of returning fish) would be more informative to management and may improve our understanding of the relationship between spawning stock size and recruitment.

mortality is not adequately considered under current management assumptions. This additional unaccounted source of fishing mortality has not prevented sustainability in the Bristol Bay fishery due to a precautionary approach to management. It does, however, suggest that the productivity of these stocks has been systematically underestimated and indicates a means to improve efficiency if retention can be increased or mortality due to non-retention reduced. Management agencies across a wide range of commercial fisheries should carefully consider the potential for non-retention mortality in target stocks and instances where such mortality can be estimated and/or minimized.

Acknowledgements

We gratefully acknowledge J. Skalski, J. Lady and R. Hilborn for technical advice and guidance, G. Holtgrieve, T. Reed and T. Branch for review of the manuscript, managers and biologists at the Alaska Department of Fish and Game for data, permitting and consultation, and friends and colleagues in the University of Washington, Alaska Salmon Program for assistance in the field. Support and funding for this research was provided by the Gordon and Betty Moore Foundation, the National Science Foundation, the Environmental Protection Agency STAR fellowship programme, the H. Mason Keeler Endowment for Excellence, the John G. Peterson Scholarship, the Galen and Helen Maxfield Fisheries Scholarship, and Alaska salmon processors.

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Received 26 November 2008; accepted 11 May 2009

Handling Editor: Nick Dulvy

Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. Map of the Nushagak fishing district and Wood River system, Bristol Bay, Alaska

Appendix S2. Influence of spawning date on the senescence schedule of salmon

Appendix S3. Our results in the context of past research

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