

ORIGINAL ARTICLE

Selection due to nonretention mortality in gillnet fisheries for salmon

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Abstract

Fisheries often exert selective pressures through elevated mortality on a non-random component of exploited stocks. Selective removal of individuals will alter the composition of a given population, with potential consequences for its size structure, stability and evolution. Gillnets are known to harvest fish according to size. It is not known, however, whether delayed mortality due to disentanglement from gillnets exerts selective pressures that reinforce or counteract harvest selection. We examined gillnet disentanglement in exploited populations of sockeye salmon (*Oncorhynchus nerka*) in Bristol Bay, Alaska, to characterize the length distribution of fish that disentangle from gillnets and determine whether nonretention mortality reinforces harvest selection and exerts common pressures according to sex and age. We also evaluated discrete spawning populations to determine whether nonretention affects populations with different morphologies in distinct ways. In aggregate, nonretention mortality in fish that disentangle from gillnets counters harvest selection but with different effects by sex and age. At the level of individual spawning populations, nonretention mortality may exert stabilizing, disruptive, or directional selection depending on the size distribution of a given population. Our analyses suggest nonretention mortality exerts significant selective pressures and should be explicitly included in analyses of fishery-induced selection.

Introduction

Selection occurs when individuals with distinct traits within a common population differ in their ability to withstand or respond to a particular pressure. In fisheries, selective removal of certain types of individuals before they reproduce will change the composition of an exploited population, particularly for traits related to maturation and growth (Ricker 1981; Trippel 1995; Law 2000). This may alter life history characteristics, including size-at-age, age-at-maturity, and morphology (Policansky 1993; Heino and Godo 2002). Heavy fishing pressure may induce plastic changes or, when traits have a genetic basis and selection is intense or persistent, may cause evolutionary change (Sharpe and Hendry 2009). To date, most studies have been limited in their ability to distinguish evolutionary responses from phenotypic plasticity (Hard et al. 2008). But research has demonstrated the potential

for genetic shifts in response to the selective effects of fishing (Stokes and Law 2000; Olsen et al. 2004; Swain et al. 2007). Moreover, phenotypic change itself may be cause for concern (Kinnison et al. 2009). Such shifts in wild stocks may occur rapidly (Law 2000; Conover and Munch 2002), may be difficult to reverse (Rowell 1993; Enberg et al. 2009; but see Conover et al. 2009), adversely affect long-term yield (Law and Grey 1989; Sheridan 1995; Heino 1998), and may pose a risk to sustainability of the exploited stock, fishing industry, or both (Heino and Godo 2002; Kuparinen and Merilä 2007; Allendorf and Hard 2009; Jorgensen et al. 2009).

Fishing gear is often size-selective. Harvest in commercial gillnet fisheries has been shown to cause directional selection towards smaller size (Todd and Larkin 1971; Law 2000). Fishing, however, not only removes fish directly through harvest. Interaction with gear may result in delayed mortality for fish not retained by the fishery.



Figure 1 Photographs of gillnet marking in male (left) and female (right) sockeye salmon due to disentanglement in commercial gillnet fisheries [Supporting Information, Appendix S1, Fig. A1 displays gillnet marking as apparent at sexual immaturity (sampling at entry to freshwater system) in contrast to gillnet marking at sexual maturity (sampling at natal streams)].

Fish may temporarily entangle in gillnets and subsequently disentangle and escape. Such encounters produce distinct marks (Fig. 1) and may cause serious injury in disentangled fish. Bristol Bay, Alaska sockeye salmon fisheries are terminal fisheries that harvest fish on their return migration to spawn, immediately prior to freshwater entry (Fig. 2). These fisheries are managed for explicit target escapements to individual watersheds, designed to ensure sufficient numbers of fish evade the fishery and

perpetuate discrete stocks. Harvest of sockeye salmon populations in the Wood River system in Bristol Bay has been shown to produce evident size differences between harvested and escaped fish (Kendall and Quinn 2009) and directional selection towards smaller fish (Kendall et al. 2009). Prespawning mortality in sockeye salmon that disentangle from commercial gillnets and are enumerated in the Wood River escapement has been documented by Baker and Schindler (2009). An important component of fishery selection that remains unstudied is whether unaccounted mortality in fish that disentangle from fishing gear and succumb to fishery-related injuries prior to reproduction compounds the selective effects of harvest.

The prevalence of disentanglement in gillnet fisheries is underappreciated but may be high. Experimental work (Thompson et al. 1971; Thompson and Hunter 1973), anecdotal evidence (Hartt 1963), and mark–recapture studies (Ashbrook et al. 2004; Baker and Schindler 2009) suggest high prespawning mortality rates and reduced reproductive fitness among fish subject to entanglement. Thus, evident gillnet marking indicates fish less likely to spawn and contribute to the reproductive capacity of escaped stocks. If gillnet disentanglement is size-selective, prespawning mortality due to nonretention in gillnets will

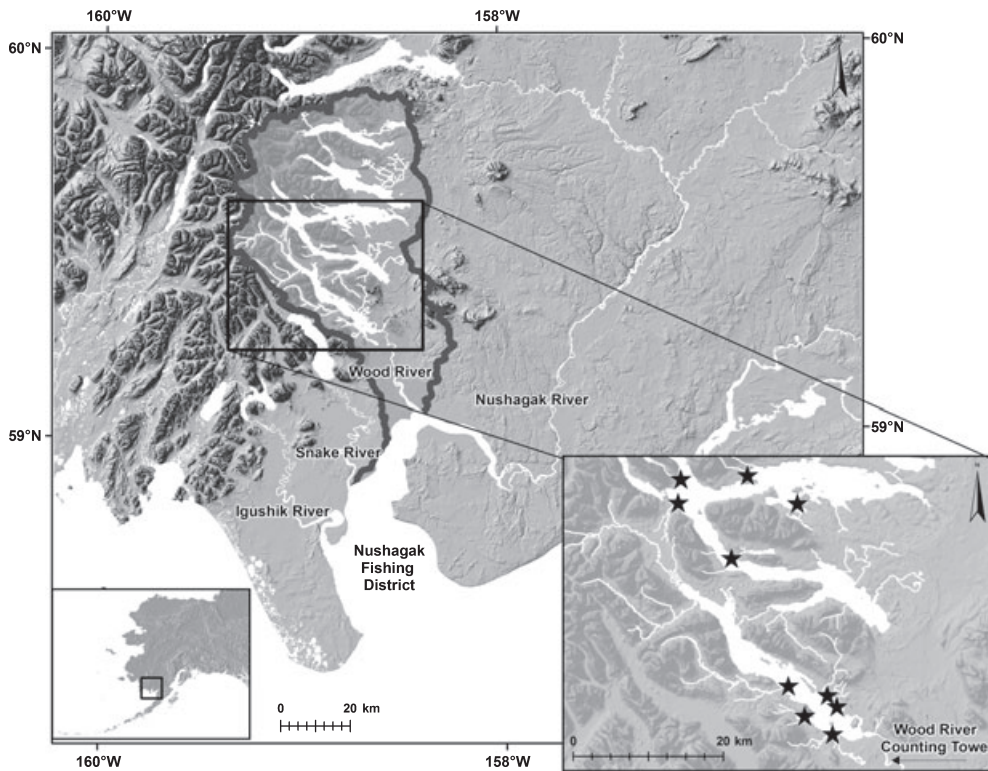


Figure 2 Map of Wood River system, Bristol Bay, Alaska. The main map displays the Nushagak fishing district and constituent watersheds (Wood River watershed outlined). The enlargement displays the sampling location for the aggregate Wood River system stock (Wood River counting tower), and the sampling locations for the 10 stream spawning populations surveyed in this study (★).

contribute to the selective pressures affecting exploited populations. To date, little attention has been directed to understanding the impacts of gillnet disentanglement injuries on escaped fish, whether the morphologies of gillnet marked fish are distinct from harvested fish or fish that escape without entanglement, and whether size-selective pressures due to nonretention mortality reinforce or counteract the selective effects of harvest.

Complicating these questions, gillnet fisheries for Pacific salmon exploit aggregate stocks that are in fact a composite of distinct locally adapted populations that may be impacted by harvest and nonretention mortality in distinct ways. Fine-scale homing of Pacific salmon to natal spawning sites (Dittman and Quinn 1996) and restricted flow between populations (Varnavskaya et al. 1994; Stewart et al. 2003) reinforces the reproductive isolation of populations. As a consequence, spawning aggregations separated by spatial, ecological, or temporal barriers demonstrate diverse life history strategies and local adaptation to variation in spawning and rearing habitats (Wood 1995; Hilborn et al. 2003). Genetic divergence between populations has been detected within a single rearing lake (Varnavskaya et al. 1994; Burger et al. 1997) and heritable phenotypic traits such as age-at-maturation, length, and body depth at length differ among sockeye salmon populations according to spawning habitat (Blair et al. 1993; Wood 1995; Quinn et al. 2001). In general, sexual selection and fecundity favor larger fish, while size-biased predation and habitat constraints related to mobility select against larger fish, such that fish morphology correlates with stream morphology in stream-spawning populations (Quinn et al. 2001). Exploitation occurs before aggregate stocks segregate into discrete spawning groups. Thus, selective pressures due to fishery harvest and nonretention mortality may affect discrete locally adapted populations with distinct morphologies in different ways (Burgner 1964; Hamon et al. 2000; Kendall and Quinn 2009).

We examined length-specific patterns of gillnet disentanglement marking in sockeye salmon escaping to spawn in the Wood River system, one of the Bristol Bay watersheds (Fig. 2). We hypothesized that fish of different lengths disentangle from gillnets at different rates, resulting in distinct differences in the length distributions of harvested fish and gillnet marked and unmarked fish in the escapement. We contrasted these length distributions to evaluate the relative patterns and pressures of fishery-induced selection and quantified selection differentials related to harvest, nonretention mortality and total selection on exploited stocks. We examined not only the Wood River system stock in aggregate, but also discrete spawning populations within the watershed to evaluate whether gillnet disentanglement has different effects on populations with distinct morphologies.

Materials and methods

Study site description

Bristol Bay, Alaska, located in the southeast Bering Sea, produces one of the most abundant sockeye salmon runs in the world. Bristol Bay salmon stocks have been exploited by a commercial gillnet fishery since 1884 (Bue 1986). Our research focused on the Wood River system. The Wood River drains a series of five interconnected lakes into the Nushagak Bay and is the primary watershed within the Nushagak district, one of five principle fishing districts of Bristol Bay (Fig. 2). Salmon migrate through Nushagak Bay and are either harvested in the Nushagak District fishery or escape to spawn as discrete populations in streams, rivers, and beaches in the Wood, Igushik, or Nushagak watersheds. Fishing pressure is intense, with a mean exploitation rate of 64% by the Nushagak District fishery over the past 25 years (1985–2009). The mean total run to the Nushagak District over this period was 6.9 million sockeye salmon and the mean annual escapement to the Wood River system was 1.29 million sockeye salmon (1985–2009). During the years of this study (2006–2008), the Wood River system received escapements of 4.0, 1.5, and 1.7 million sockeye salmon from annual runs of 15.9, 10.9, and 10.2 million in 2006, 2007, and 2008, respectively.

Mesh size in Bristol Bay commercial gillnet fisheries

Mesh size was regulated in Bristol Bay commercial fisheries for sockeye salmon from 1924 to 1984. Initial minimum mesh size was set at 146 mm and subsequently reduced to 137 mm in 1962. Although temporary regulations on minimum (137 mm) or maximum (140 mm) mesh size are occasionally declared through emergency orders to reduce incidental catch of Chinook salmon (*Oncorhynchus tshawytscha*) or pink salmon (*Oncorhynchus gorbuscha*) respectively, mesh size is no longer standardized.

Data collection

Sockeye salmon were sampled as an aggregate Wood River system stock via beach seine (nonselective gear) during their in-river migration immediately following passage through the fishery (Fig. 2). Sampling in 2006 occurred as part of an extensive tagging study investigating migration timing (Doctor et al. 2010). Sampling in 2007 and 2008 occurred as part of annual surveys of escapement conducted by the Alaska Department of Fish and Game (ADFG). Fish were sampled on 12 days in 2006 between June 23 and July 17 ($n = 2487$), daily in 2007 between July 1 and July 16 ($n = 1147$), and daily

in 2008 between June 25 and July 15 ($n = 1666$). Sampling periods were designed to best characterize all fish migrating through the Wood River throughout the season. The portion of the escapement that transited the river on days when sampling occurred was 69%, 59%, and 87%, for 2006 to 2008 respectively. Re-sampling was avoided by tagging in 2006 and by the removal of the adipose fin in 2007 and 2008. Estimates of total escapement to the Wood River system were based on ADFG visual tower counts (Thompson 1962; Woody 2007). The number of disentangled fish in the escapement on a given day was estimated as the percentage sampled with gillnet marking multiplied by the total number of fish that in the escapement that day. Incidence of gillnet disentanglement for a given year was estimated as the number of fish in the escapement with gillnet marking relative to the total escapement for days sampling occurred.

Sockeye salmon were also sampled at 10 natal spawning streams (Fig. 2) to investigate potential differences among discrete spawning populations. Sampling at stream mouths occurred between July 12 and July 27 (2006–2008) on fish that had begun to shoal along the lake shore at the outflow of natal spawning streams. Each stream population was sampled at the approximate historical date for stream entry to ensure sampling of the entire population while minimizing incidental sampling of fish in transit to other sites. Between 200 and 500 fish were sampled at each site. Where multiple sets were made, fish were pooled into holding pens to prevent re-sampling.

In all sampling events, fish were measured for length. The sex and presence of gillnet marking were also recorded. While the immediate trait under selection in a gillnet fishery is girth, length is positively correlated with girth and used as a proxy for girth (Regier 1969; Knudsen et al. 2001; Supporting Information, Appendix S2). Standard length metrics (mid-eye to fork of tail, MEFT) were used for in-river sampling. Length measurements at stream locations (mid-eye to hypural plate, MEHP) were designed to prevent measurement error associated with altered morphology (extended kype and dorsal–ventral elongation), related to sexual maturation (Blair et al. 1993). To facilitate comparisons, we converted the lengths of fish sampled at streams, in mm, from MEHP to MEFT, according to conversion equations estimated by Kendall and Quinn (2009) (Supporting information, Appendix S1).

$$\text{Females: } L_{\text{MEFT}} = 1.06(L_{\text{MEHP}}) + 22.85 \text{ mm } (r^2 = 0.91) \quad (1)$$

$$\text{Males: } L_{\text{MEFT}} = 1.10(L_{\text{MEHP}}) + 4.44 \text{ mm } (r^2 = 0.97) \quad (2)$$

Marks associated with gillnet disentanglement were defined as clear net marks, abrasions, or scale loss span-

ning the circumference of the fish (Fig. 1; Supporting Information, Appendix S1, Fig. A1). Fish with markings and injuries due to boat propellers, predators and parasites (marine mammals and lampreys), and other nonspecific causes were excluded.

Run reconstruction

The fishery operating in the Nushagak District exploits fish from the Wood, Nushagak, and Igushik river systems (Fig. 2). Due to this mixed stock fishery, the length distributions for Wood River fish harvested in the Nushagak district and for the total run (preharvest) to the Wood River system are not directly measurable. These were estimated as a function of a forward run reconstruction model (Branch and Hilborn 2010) that proportionately assigned fish in the Nushagak District harvest to their respective river system. This model utilized data on system-specific escapements, system-specific age compositions, district catch, and genetic estimates of catch composition (Dann et al. 2009) to estimate parameters for run size at length, gear selectivity, and stock availability. Parameters were estimated using maximum likelihood methods implemented through AD Model Builder (ADMB Project 2009). Model outputs on harvest selectivity (proportion harvested at length, by sex/year) are reported in the supporting information (Supporting Information, Appendix S3, Fig. C4) and were used to estimate numbers at length for Wood River fish in the Nushagak District harvest (by sex/year), such that:

$$H_l = \frac{p_l \cdot E_l}{1 - p_l} \quad (3)$$

where H_l is the number of fish harvested at length (l), p_l is proportion of fish harvested at length, and E_l is number of fish in the escapement at length.

Length frequency distributions for total run, harvest, escapement, and disentangled fish

To estimate the length distribution of fish that escaped to the Wood River, daily estimates of proportion of fish at length (based on daily in-river sampling of 80–100 fish) were weighted by the numbers of fish in the escapement that day (estimated by 24 h visual sampling at the Wood River counting tower; Woody 2007). Numbers at length for the total run to the Wood River system (preharvest fish) were estimated as the sum of the numbers at length for harvest and escapement. Numbers at length for fish that entangled in gillnets but subsequently disentangled and escaped (gillnet marked fish) were approximated from estimates of the proportion of disentangled fish at length, weighted by the number of

fish in the escapement and the incidence of disentanglement.

Relative distribution methods – comparative analysis of distributional change

To compare the length distributions of harvested and disentangled fish to the distribution of the total run (preharvest fish), we employed relative distribution methods, a nonparametric scale-invariant statistical tool for distributional comparison (Handcock and Morris 1999). The relative distribution displays the differences between two distributions as a ratio of their probability density functions. The reference group (in this case, preharvest fish) was re-scaled into proportional deciles, such that each length interval contained 10% of the group. The distributions for harvested fish and disentangled fish (separately) were then each scaled to this reference group such that differences in distributional form were distinctly displayed by the ratio of the proportion of harvested or disentangled fish at a given length interval to the proportion preharvest fish at that same length interval. The use of probability density functions and the scaling of the reference distribution to discrete quantiles enabled statistical analysis of differences in location (median) and shape (entropy and polarization) between the distributions (Supporting Information, Appendix S4).

Standardized selection differentials

To quantify total selection resulting from the fishery and to compare the relative effects of selection due to harvest mortality and nonretention mortality, we calculated length-based selection differentials (SD) for each year and sex. These values represent the difference in mean length of fish before and after a given selective event (either harvest or nonretention mortality). SDs were calculated as the mean length postselection minus the mean length preselection. Standardized selection differentials (SSDs) were also calculated to facilitate comparison across years. Standardized selection differentials were calculated as the mean length postselection minus the mean length preselection, divided by the standard deviation of the length of the preselection group (Law and Rowell 1993). Equations for SSDs used to determine harvest mortality, nonretention mortality, and total fishery-induced selection were, respectively:

$$SSD_{\text{Harvest}_{y,s}} = \frac{\bar{L}_{\text{TE}_{y,s}} - \bar{L}_{\text{R}_{y,s}}}{S_{\text{R}_{y,s}}} \quad (4)$$

where $\bar{L}_{\text{TE}_{y,s}}$ is the mean length of the total escapement and $\bar{L}_{\text{R}_{y,s}}$ is the mean length of the total run, and $S_{\text{R}_{y,s}}$ is the standard deviation of the total run.

$$SSD_{\text{Nonretention}_{y,s}} = \frac{\bar{L}_{\text{EE}_{y,s}} - \bar{L}_{\text{TE}_{y,s}}}{S_{\text{TE}_{y,s}}} \quad (5)$$

where $\bar{L}_{\text{EE}_{y,s}}$ is the mean length of the effective escapement (actual spawners), or the proportion of the total escapement that is expected to reproduce after accounting for nonretention mortality in the escapement, and is defined as:

$$\bar{L}_{\text{EE}_{y,s}} = \frac{\bar{L}_{\text{UE}_{y,s}}(1 - p_{\text{D}_{y,s}}) + \bar{L}_{\text{ME}_{y,s}}p_{\text{D}_{y,s}}(1 - p_{\text{M}})}{1 - p_{\text{D}_{y,s}}p_{\text{M}}} \quad (6)$$

where $\bar{L}_{\text{UE}_{y,s}}$ is the mean length of unmarked fish in the escapement, $\bar{L}_{\text{ME}_{y,s}}$ is the mean length of gillnet marked fish in the escapement, $p_{\text{D}_{y,s}}$ is the proportion of disentangled fish in the total escapement (incidence of gillnet disentanglement by year/sex), and p_{M} is the proportion of gillnet marked fish that fail to spawn. Pre-spawning mortality is estimated at 50% (Baker and Schindler 2009).

Total fishery-induced selection is calculated as:

$$SSD_{\text{Total}_{y,s}} = \frac{\bar{L}_{\text{EE}_{y,s}} - \bar{L}_{\text{R}_{y,s}}}{S_{\text{R}_{y,s}}} \quad (7)$$

Mean lengths ($\bar{L}_{\text{R}_{y,s}}, \bar{L}_{\text{TE}_{y,s}}, \bar{L}_{\text{UE}_{y,s}}, \bar{L}_{\text{ME}_{y,s}}, \bar{L}_{\text{EE}_{y,s}}$) and standard deviations of length ($S_{\text{R}_{y,s}}, S_{\text{TE}_{y,s}}$) for fish at each stage were estimated by bootstrapping length data 10 000 times with replacement. SSDs, SDs, and confidence intervals were calculated by randomly sampling (with replacement) the 10 000 bootstrapped mean lengths and standard deviations for each term in the SSD or SD function, calculating the differential and repeating the procedure through 10 000 replicates. The 95% confidence intervals for each SD and SSD are the 0.025 and 0.975 quantiles of the replicates (Effron 1982).

Evaluation of stream-specific populations and designation of stream-type morphologies

Length frequency distributions were estimated for each of 10 streams. Population-specific length-at-age distributions were also estimated based on otoliths collected from fish measured for length at the end of the spawning season, which had senesced in that stream (see Supporting Information, Appendix S1 for discussion on shifts in length related to maturation and senescence). Annuli were read from otoliths to determine freshwater and ocean residence time for individual fish ($n = 3597$, years 2006–2008) and composite length frequency distributions were constructed as a function of ocean age or years resident in the marine environment (2-ocean, 3-ocean). Distributions of length at age were corrected for an expected 5 mm reduction in length at senescence, given the results

of Quinn and Blair (1992) and were smoothed via local linear weighted regression (Loess: polynomial order = 1; proportion = 2).

Results

Incidence of gillnet disentanglement

Incidence of gillnet marking in the aggregate Wood River escapement was 20% in 2007, 35% in 2008, and 30% in 2009. Incidence of gillnet marking in the Wood River in 2006 was not directly estimable due to sampling

methods that may have overestimated incidence by sampling in stagnant areas of the river. Data from 2007 and 2008 suggested incidence of marking in-river was 1.77 times greater than incidence in streams. We estimated incidence of gillnet marking in 2006 at 36% based on the incidence of gillnet marking at natal streams in that year. Higher estimates at freshwater entry relative to estimates at natal streams likely reflects mortality among gillnet marked fish during the 2-week interval between river migration and our sampling of populations at natal streams.

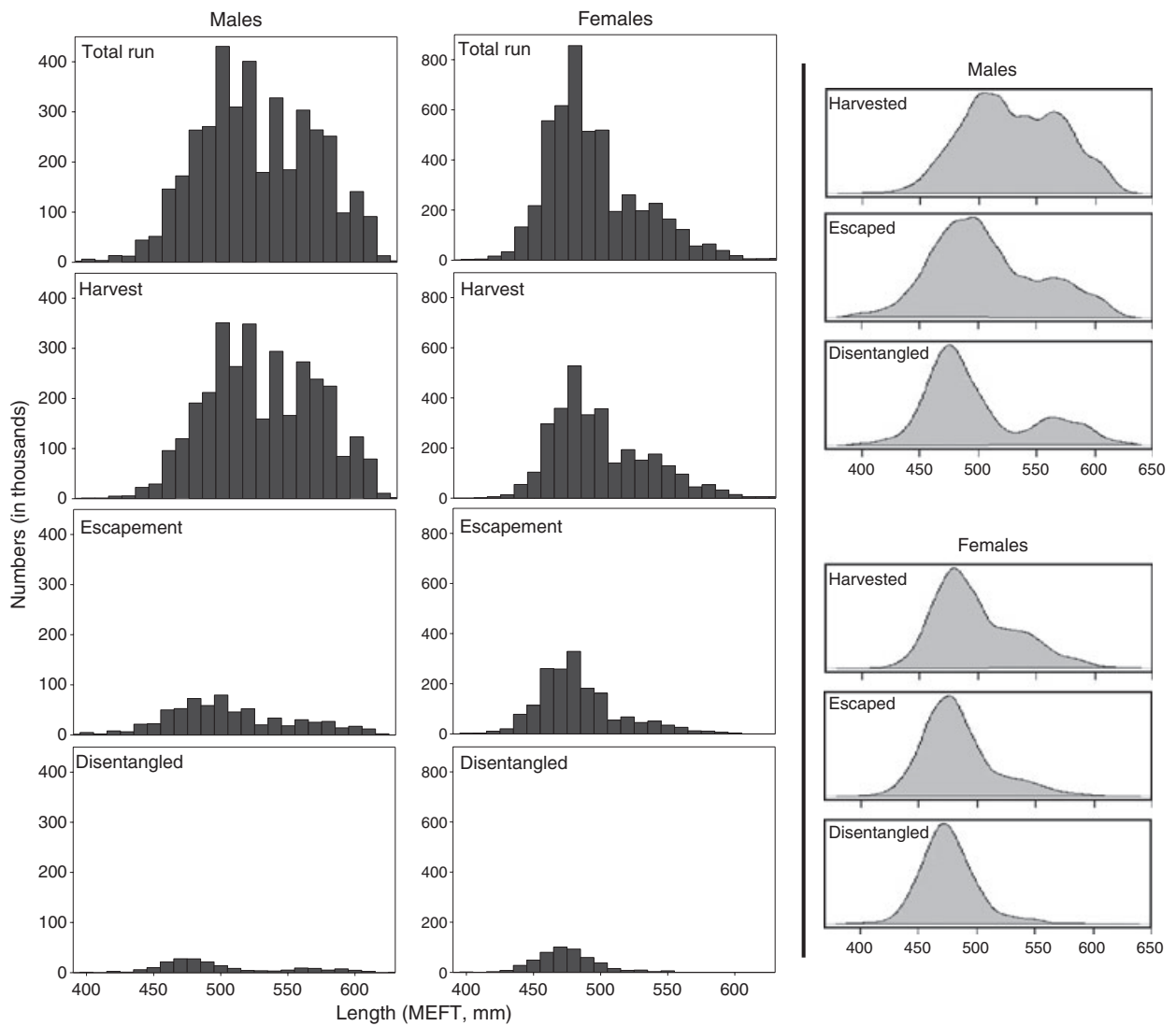


Figure 3 Histograms of estimated numbers at length (10 mm length bins) for the total run, harvest, escapement, and disentangled fish in the escapement for the aggregate Wood River system stock (mean, 2006–2008). Density plots on the right contrast the shape and location of the length distributions of harvested, escaped, and disentangled fish. (Supporting Information, Appendix S5, Figs E1–E3 display year-specific length distributions).

Patterns in fishery harvest and gillnet disentanglement by length

Several patterns emerged in the analyses of length distributions of Wood River system sockeye salmon, averaged across 2006–2008 (Fig. 3). Differences were noted between harvested fish, gillnet marked fish, and fish that escaped without entanglement. Gillnet marked fish of both sexes were smaller than fish that escaped the fishery unmarked and both gillnet marked and unmarked fish in the escape-ment were smaller than fish retained in the fishery (weighted mean length: gillnet marked males = 499 ± 48 mm SD, unmarked males = 511 ± 52 mm, harvested males = 530 ± 41 mm; female gillnet marked females = 477 ± 25 mm, unmarked females = 488 ± 34 mm, harvested females = 500 ± 38 mm). Differences in distributional variance were noted in the pair-wise comparison of harvested, gillnet marked, and unmarked fish (KS, two-sided: $P < 0.0001$). Within each group (harvested, gillnet marked, unmarked), length frequency distributions also differed by sex (KS, $P < 0.0001$). Bimodal trends were apparent for both male and females, which broadly reflected differences in the lengths of fish that spend 2 vs 3 years in ocean residence. Relative to harvest selection,

gillnet disentanglement had a distinct selective pressure. Although gillnet disentanglement affected some large (mostly 3-ocean) males, it had a greater proportional impact on smaller (mostly 2-ocean) males. In females, gillnet disentanglement occurred almost exclusively among smaller (mostly 2-ocean) fish. The length range for gillnet marked females was constrained in comparison to gillnet marked males, such that large females were either retained in nets or never entangled.

Inter-annual differences in gillnet disentanglement patterns were minor (Table 1; Supporting Information, Appendix S5, Figs E1–E3). Differences in the distributions of gillnet marked and unmarked fish in the aggregate Wood River stock (both sexes) were significant in all years (KS: $P < 0.0125$). In males, differences in mean length were complicated by the bimodal nature of the distributions. Notably, 2006 was distinguished by an unusually large return of sockeye salmon (Wood River system 25-year mean annual run = 4.1 million; 2006 run = 9.8 million) and characterized by small fish (mean Wood River system length: 2000–2008 = 536 mm; 2006 = 525 mm). This motivated some fishermen to use smaller mesh (designed to harvest pink salmon *O. gorbuscha*) late in the season (M. Baker, personal experience in fishery).

Table 1. Comparison of lengths (mean \pm SD) and length distributions of gillnet marked and unmarked populations of sockeye salmon on the basis of Mann–Whitney *U*-test (nonparametric test of variance) and Kolmogorov–Smirnov tests (distributional form). Rates of disentanglement are based on mean incidence of gillnet marking in the aggregate Wood River stock and mean incidence in 10 stream-spawning populations (Note that not all unmarked fish sampled were measured for length).

	Disentanglement (%)	Gillnet marked		Unmarked		M–W	K–S
		<i>N</i>	Length (mm)	<i>N</i>	Length (mm)		
Wood River System Stock							
Males							
2006	28†	203	496 \pm 49	294	500 \pm 54	NS	**
2007	12	36	518 \pm 51	326	519 \pm 53	NS	**
2008	30	156	498 \pm 46	355	517 \pm 51	***	***
Females							
2006	39†	602	474 \pm 25	687	483 \pm 32	***	***
2007	27	210	482 \pm 23	570	499 \pm 32	***	**
2008	38	508	475 \pm 24	660	487 \pm 37	***	***
Stream populations							
Males							
2006	16	132	505 \pm 48	460	499 \pm 53	NS	NS
2007	11	124	532 \pm 54	640	502 \pm 48	***	***
2008	13	160	491 \pm 50	560	506 \pm 42	***	***
Females							
2006	22	358	477 \pm 26	477	474 \pm 48	NS	NS
2007	16	188	478 \pm 24	523	488 \pm 34	***	***
2008	19	238	467 \pm 26	519	494 \pm 36	***	***

M–W, Mann–Whitney *U*-test; K–S, Kolmogorov–Smirnov test; NS, nonsignificant.

Significance: $P > 0.05 = NS$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

†Incidence of disentanglement in the Wood River system in 2006 is estimated as multiplier (1.77) of the incidence of gillnet disentanglement at streams in that year.

Selective effects of nonretention mortality in the context of harvest

Relative distributions: disentangled fish and harvested fish in contrast to preharvest fish

To distinguish the selective effects of harvest mortality and nonretention mortality, we contrasted the length distributions of harvested fish and gillnet marked fish against the length distribution of the total preharvest run to the Wood River (Fig. 4). Selective pressure due to gillnet disentanglement essentially counters the pressures of harvest selection, particularly in females. Harvested fish had a greater proportion of fish in the higher length categories relative to the preharvest stock (harvested fish were disproportionately larger), whereas gillnet marked fish had a greater proportion in lower length categories relative to the preharvest stock (gillnet marked fish were disproportionately smaller). Differences in the length distribution for harvested fish

relative to the preharvest stock were driven more by a shift in the median length than by differences in the shape of the distributions (harvested males: median effect = 91%; shape effect = 9%, harvested females: median effect = 91%; shape effect = 9%). Differences in the length distribution for gillnet marked fish relative to the preharvest stock, in contrast, were driven by both shifts in the shape and median (gillnet marked males: median effect = 68%; shape effect = 32%; gillnet marked females: median effect = 33%; shape effect = 67%). Differences in the spread of the distributions at the tails (polarization) were generally not significant (see Supporting Information, Appendix S4 for full results).

The effects of selection due to nonretention mortality across years

To compare how selective pressures due to nonretention mortality might augment or counteract harvest selection in a given year and the relative magnitude of their effects,

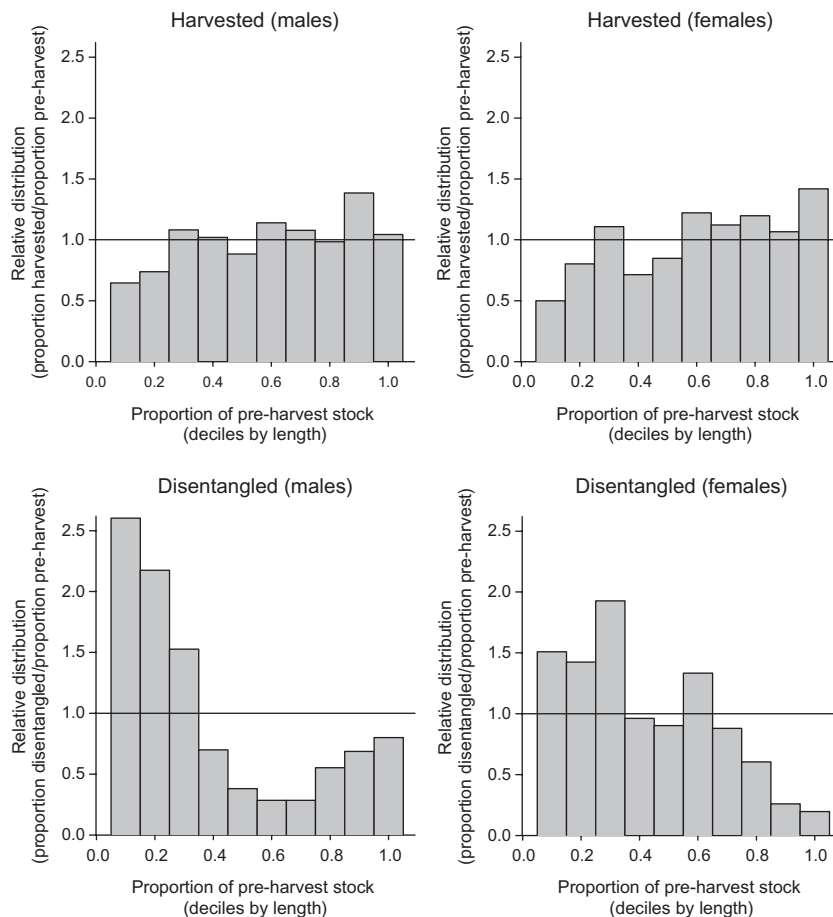


Figure 4 Selection pressure due to mortality via harvest (top graphs) and gillnet disentanglement (bottom graphs), contrasting harvested and disentangled fish to preharvest fish as a ratio of proportion at length. The preharvest stock is scaled to a uniform distribution (proportional deciles by length) and represented by the horizontal line at 1.0. Histograms display the relative densities for harvested and disentangled fish (the ratio of the relative proportion harvested/disentangled at length to the preharvest proportion at length), scaled to the uniform preharvest stock. In the case of identical distributions, the histogram would be uniform at 1.0.

we deconstructed the annual preharvest run to the Wood River system into the estimated numbers at length subject to harvest mortality and nonretention mortality and the remaining stock of effective spawners. Assuming 50% prespawning mortality for fish with evident signs of gillnet marking (Baker and Schindler 2009), the effective escapement (actual spawners) was calculated as total escapement minus half of the fish with gillnet marking for a given length category in a given year (Fig. 5). While we found that harvest mortality selected against the largest fish, selection due to nonretention mortality was directional with the opposite effect, predominantly selecting against smaller fish. In males, selection through nonretention mortality also had a stabilizing effect, selecting against fish in the shortest and longest length categories and further eroding the bimodal nature of the preharvest run. These broad scale patterns, evident at a system-wide level, however, differed at the finer scale of site-specific spawning populations.

Total selection: cumulative effects of harvest and nonretention mortality

Selection differentials for harvest, nonretention and total selection are listed (Table 2) and SSDs are displayed (Fig. 6). Our estimates of selection differentials for harvest (males: -30 to -3 mm, females: -15 to -1 mm) were negative indicating directional selection against larger fish. These estimates were similar to those reported in other analyses of harvest selection in this system (males: -14 to -2 mm, females: -14 to -6 mm, Kendall and Quinn 2009; males: -3.6 to $+0.3$ mm, females: -0.6 to -3.6 mm, Hamon et al. 2000). Standardized selection differentials were within 0 to ± 0.5 phenotypic standard deviations as reported in Hard et al. (2008) with the exception of 2006, a year characterized by extremely heavy exploitation rates due to an uncharacteristically large run. Selection differentials for nonretention were positive (males: $+0.5$ to $+4$ mm, females: $+1$ to $+3$ mm), indicating that the selective effects of nonretention mortality counteract those from harvest selection, though to a lesser extent.

Selective effects differ according to population-specific morphologies

Distinctions between the aggregate Wood River system stock and stream-spawning populations

Similar to the aggregate Wood River system stock, gillnet disentanglement disproportionately affected smaller females in stream-spawning populations, such that gillnet marked fish (weighted mean length across 10 streams 2006–2008 = 475 ± 32 mm) were smaller than fish that escaped the fishery unmarked (483 ± 35 mm). Among

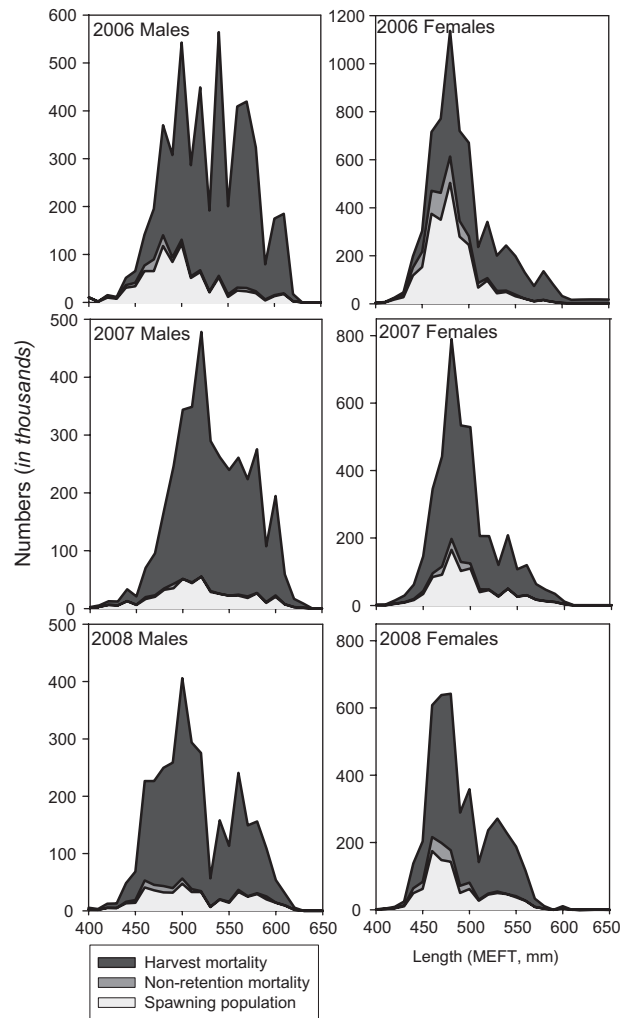


Figure 5 Length frequency area plots of the reconstructed aggregate Wood River system stock (total run, by sex and year) with mortality attributed to harvest extraction and nonretention. Nonretention mortality at length was estimated from the length distribution of disentangled fish, annual incidence of gillnet disentanglement in the escapement, and an estimated prespawning mortality rate of 50% for disentangled fish in the escapement. Total run is represented by the combined area. Total escapement is the area minus harvest mortality. The spawning population (effective escapement) is the total run minus harvest and nonretention mortality.

males, however, this trend was reversed (gillnet marked = 508 ± 32 mm, unmarked = 502 ± 45 mm) due to a relatively large proportion of gillnet marked males at longer length ranges. We noted differences in the length frequency distributions of gillnet marked and unmarked fish, calculated separately for males and females (KS: $P < 0.0001$) and differences between the sexes (KS: $P < 0.0001$). Each of these differed from the comparable length frequency distribution in the Wood River system as an aggregate stock.

Table 2. Selection differentials (in mm) and 95% confidence intervals for harvest selection, nonretention selection and total selection due to fisheries-induced pressures.

Selection mechanism	2006		2007		2008	
Males						
Harvest mortality	-29.9	(-32.8 to -27.0)	-12.7	(-16.9 to -8.4)	-3.4	(-7.8 to 1.0)
Nonretention mortality	0.5	(-3.9 to 5.0)	0.9	(-4.9 to 6.8)	3.5	(-1.9 to 8.9)
Total selection	-29.4	(-33.1 to -25.6)	-11.8	(-16.2 to -7.2)	0.2	(-3.5 to 4.0)
Females						
Harvest mortality	-15.2	(-16.6 to -13.8)	-1.1	(-3.4 to 1.3)	-7.3	(-9.4 to -5.2)
Nonretention mortality	0.8	(-0.8 to 2.4)	1.0	(-2.5 to 4.2)	2.7	(0.2 to 5.7)
Total selection	-14.5	(-17.0 to -11.7)	-0.1	(-2.8 to 2.7)	-4.7	(-7.3 to -2.1)

Distinctions among streams by population type

We also examined differences between these 10 stream-spawning populations to determine whether selective pressures from gillnet disentanglement were uniform across discrete spawning populations with distinct mean lengths (Fig. 7). The 10 stream populations differed in length among unmarked males (Kruskal–Wallis $\chi^2 = 241.61$, $df = 9$, $P < 0.0001$) and unmarked females (Kruskal–Wallis $\chi^2 = 390.59$, $df = 9$, $P < 0.0001$). We aggregated stream populations into two groups (small stream-type, large stream-type) on the basis of *post hoc* tests, which demonstrated that the three stream populations with the greatest length did not significantly differ from each other (Mann–Whitney *U*-tests: males: $P > 0.0749$, females: $P > 0.1089$), but differed from all other stream populations (males: $P < 0.0001$, females: $P < 0.0001$). Habitat metrics for flow and spawning area also differed by group (small stream-type: flow = $1.33 \text{ m}^3 \text{ s}^{-1}$, spawning area = $13\,272 \text{ m}^2$; large stream-type: flow = $1.67 \text{ m}^3 \text{ s}^{-1}$, spawning area = $79\,156 \text{ m}^2$; Marriott et al. 1964; Quinn et al. 2001). Our assignment of fish by stream-types into small (mean length: males = $496 \pm 47 \text{ mm}$, $n = 1441$, females = $477 \pm 30 \text{ mm}$, $n = 1243$) and large (mean length: males = $528 \pm 42 \text{ mm}$, $n = 410$, females = $515 \pm 32 \text{ mm}$, $n = 394$) types reflected significant differences between these aggregate groups for both males (Mann–Whitney *U*-test = 416430, $P < 0.0001$) and females (Mann–Whitney *U*-test = 393979, $P < 0.0001$). Differences in length were driven by longer ocean residence by large stream-types (proportion 3-ocean: males = 55%, females = 56%) as compared to small stream-types (proportion 3-ocean: males = 32%, females = 31%) (Quinn et al. 2001). Binary logistic regression suggested that gillnet disentanglement was a function of length ($P < 0.0127$), sex ($P < 0.0001$), and stream type ($P < 0.0001$).

Comparisons of length frequency distributions for gillnet marked and unmarked in small stream-type versus large stream-type fish suggested that nonretention mortality exerted different selective effects on populations with

distinct length ranges (Fig. 7; Supporting Information, Appendix S6). Among small stream-types, gillnet disentanglement had a stabilizing effect on the length frequency distribution of males, such that the smallest and the largest were most affected. Selection against smaller 2-ocean males and larger 3-ocean males may also reduce length differences between these two life histories. In small stream-type females the effect was somewhat disruptive, such that disentanglement occurred in larger 2-ocean and smaller 3-ocean fish. Among large stream-types, the effect was directional but with opposite effects on males and females. In males, disentanglement was almost exclusively limited to large 3-ocean fish. In females disentanglement was more common in smaller 2-ocean fish. Thus, selective pressures from nonretention mortality in large stream-types would reduce mean length in males and select against 3-ocean males but increase mean size in females and select against 2-ocean females.

Discussion

Human exploitation often drives change in natural populations (Allendorf and Hard 2009; Darimont et al. 2009). Previous research has identified selective pressures related to harvest mortality (Heino et al. 2002; Kendall et al. 2009). We found selection to also occur through delayed mortality related to injuries sustained by fish that disentangle from fishing gear. Prespawning mortality due to gillnet disentanglement (Baker and Schindler 2009), a secondary effect of fishery harvest, provides an additional selective pressure on exploited stocks. While a higher proportion of sockeye salmon in the Wood River system are subject to harvest mortality than to nonretention mortality, the latter has a significant impact. In years where harvest selection is weak and nonretention prevalent, nonretention selection may negate the selective effects of harvest.

Moreover, our estimates of nonretention mortality are conservative. The relative impact of nonretention mortality was predicated on an estimate of 50% prespawning

mortality (e.g. nonretention mortality was presumed to occur in half of disentangled fish), based on mark–recapture studies of spawning success among gillnet marked fish at natal streams (Baker and Schindler 2009). Higher rates of gillnet marking in fish sampled at freshwater entry (within 24 h of passage through the fishery) versus at natal streams (~2 weeks later) suggests high mortality (~44%) between freshwater entry and shoaling at natal spawning sites. This mortality would be in addition to the 50% mortality evident at natal streams. Thus, prespawning mortality among disentangled fish likely exceeds our estimates (~72% rather than ~50%) and the effects of nonretention are likely greater than estimated.

Harvest pressures represent a strong directional selection against larger fish. In aggregate, nonretention mortality appeared to counter harvest selection but with different effects by sex and age, such that it was stabilizing in males and directional in females. At the level of individual spawning populations, nonretention mortality may exert stabilizing, disruptive, or directional selection, depending on the length distribution and morphology (girth at length) of a given population. Additionally, while gillnet disentanglement appeared to occur at a consistent length range, the selective effects may vary temporally due to inter-annual differences in the length composition of the run and the gear employed to target that run. Thus, nonretention mortality may exert different selective pressures under different harvest circumstances.

We found convincing evidence that discrete populations of sockeye salmon with distinct length distributions are differentially affected by nonretention selection in a fishery exploiting these populations in aggregate. It is likely that harvest selection also differs in its effects on discrete populations, though we were not able to reconstruct the prefishery run for discrete populations and evaluate this directly. In the aggregate stock, prespawning mortality due to gillnet disentanglement may counter harvest selection and result in a spawning population that more closely reflects preharvest length distributions. However, both the selective pressure as well as the relative impact of harvest and nonretention mortality may differ for individual locally adapted populations that differ in morphology. At this scale, the additional selective effects of nonretention mortality may either counter or reinforce the effects of harvest, depending on the morphology, age-structure and size of the individual population. The issue of differential selection on discrete populations has particular relevance to salmon fisheries, given the importance of biocomplexity to the resilience of aggregate stock to exploitation and environmental change (Hilborn et al. 2003; Greene et al. 2010; Schindler et al. 2010).

Wood River sockeye salmon are characterized by trait divergence among discrete spawning populations. If

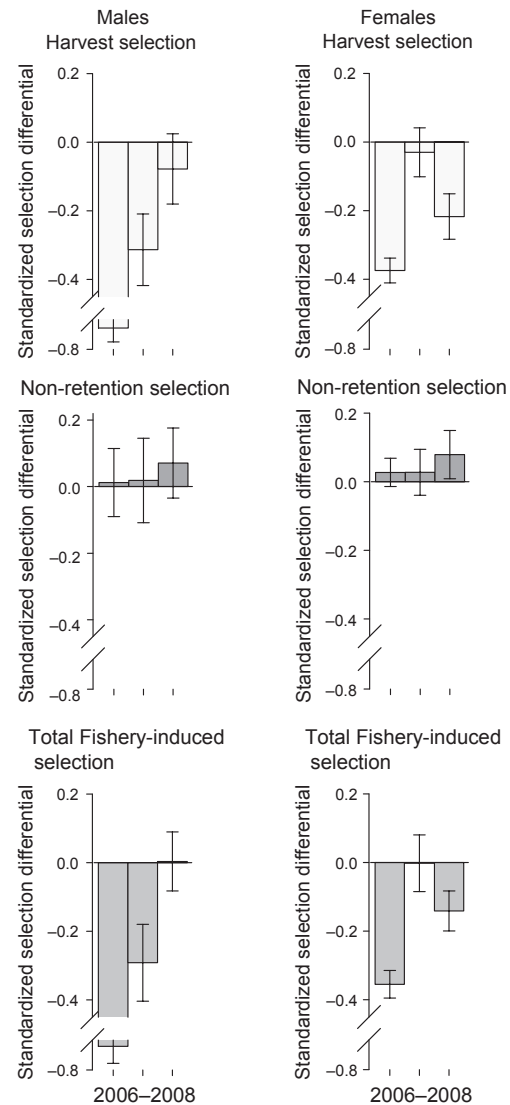


Figure 6 Standardized selection differentials (2006–2008) related to harvest mortality (top panels), nonretention mortality (middle panels) and totaled fisheries-induced selection (lower panels). Error bars represent 95% confidence intervals. Harvest selection produces a decrease in mean length in both sexes and is significant in most years. Nonretention selection produces an increase in length for both sexes but with higher variance in males, largely because nonretention affects males at both extremes of their length range. Total fisheries-induced selection is negative in most years but in years where harvest selection is relatively weak, the selective effects of nonretention mortality are enough to neutralize the selective effects of harvest.

adaptive divergence is complete, directional selection should be absent and stabilizing selection should prevail (Schluter 2000). Yet Carlson et al. (2009) found that sockeye salmon populations in the Wood River system have not attained equilibrium. This may be the result of opposing selection related to commercial fishing (Healey

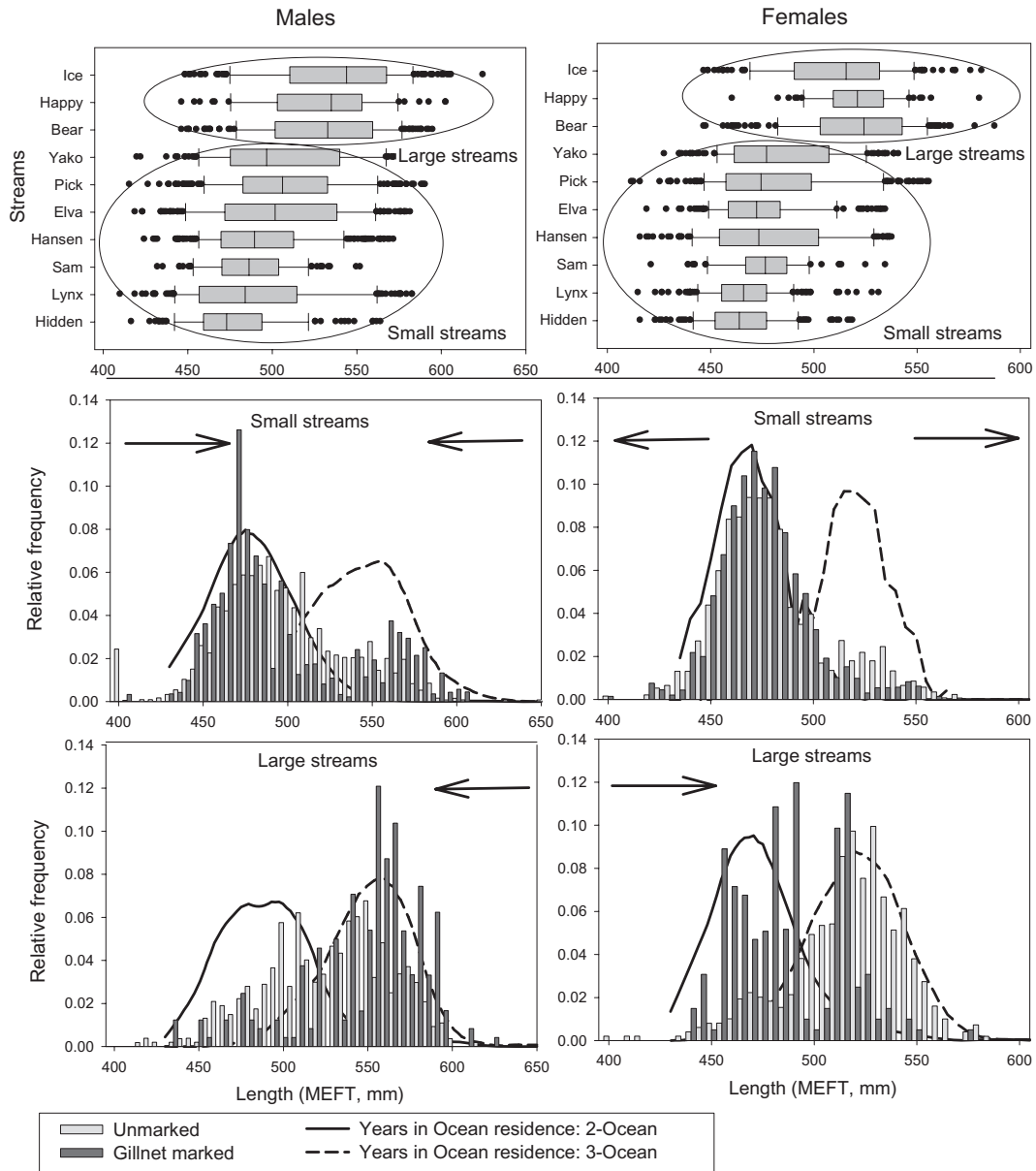


Figure 7 Top panels (boxplots) show individual stream populations as categorized into small- and large-stream types. Lower panels display the length frequency distributions for unmarked and gillnet marked fish that escape to natal streams (histograms) contrasted to length frequency distributions by age (years in ocean residence) of fish in these populations (solid and dashed lines). Arrows suggest how mortality due to gillnet disentanglement may exert directional, stabilizing, or disruptive selection in these population types (Supporting Information, Appendix S6 displays length distributions and selection pressures for individual streams).

1986), such that harvest and nonretention mortality restrict or retard ongoing population differentiation driven by natural selection. As in the case of harvest, nonretention likely confounds differentiation in many individual populations and may exert directional selection in some populations and disruptive selection in others. In investigating selective effects of nonretention mortality on

discrete populations we examined only stream-spawning fish. Further research is needed to determine the effects of nonretention in larger-bodied river-spawning and beach-spawning populations.

The presence of two ages (2-ocean and 3-ocean) complicates interpretation of fishery-induced selection. Fisheries-induced selection acts directly on size but has

implications for age as well and may affect the developmental processes of age-structured populations in ways that are difficult to discern (Hard et al. 2008). If the relationship between size and age is heritable, the evolutionary consequences of harvest and nonretention mortality will depend on the form of that relationship, i.e., the reaction norm. If a population tends to mature at a particular size regardless of age, harvest selection against larger individuals is likely to increase growth rates and reduce age at maturation, whereas if maturity is driven by age regardless of size, harvest selection would retard growth rates and reduce size at maturation. Nonretention mortality may counter these effects in aggregate, but the effects at the level of individual populations are difficult to predict without greater insight as to the relationship between size and maturity.

Determining the extent to which phenotypic shifts in exploited populations are genetic rather than an expression of phenotypic plasticity has proven elusive (Allendorf and Hard 2009). We demonstrate the opportunity for directional change through selection. Inferring evolutionary responses requires further information on genetic variability, heritability, and how fisheries-induced and other selective pressures may drive evolutionary change. Overall, reducing fishery-induced selectivity to preserve genetic and life history diversity in exploited populations is critical to reducing the long-term effects of fishing, maintaining biocomplexity in the stocks, and retaining the stabilizing effects of diverse population structure (Hard et al. 2008; Schindler et al. 2010). In this context, further research on the compounding effects of nonretention mortality is warranted.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Shifts in morphology and length related to maturation and senescence

Appendix S2. Use of length versus girth as metric for selection in gillnet fisheries and girth as further distinction between discrete population types

Appendix S3. Run reconstruction model

Appendix S4. Relative distribution methods

Appendix S5. Year-specific length distributions for the aggregate Wood River System stock (2006–2008)

Appendix S6. Stream-specific length distributions and selective pressures due to non-retention mortality

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