Evolutionary Applications www.evolutionaryapplications.org

Evolutionary Applications ISSN 1752-4571

ORIGINAL ARTICLE

Is fishing selective for physiological and energetic characteristics in migratory adult sockeye salmon?

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Keywords
biotelemetry, fishing, harvest, individual variation, phenotypic, selectivity.

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Received: 13 December 2008
Accepted: 1 April 2009

doi:10.1111/j.1752-4571.2009.00076.x

Abstract

There is extensive evidence that fishing is often selective for specific phenotypic characteristics, and that selective harvest can thus result in genotypic change. To date, however, there are no studies that evaluate whether fishing is selective for certain physiological or energetic characteristics that may influence fish behaviour and thus vulnerability to capture. Here, adult sockeye salmon (*Oncorhynchus nerka*) were used as a model to test the null hypothesis that fishing is not selective for specific physiological or energetic traits. Fish were intercepted during their spawning migrations, implanted with a gastric radio transmitter, and biopsied (i.e., non-lethally sampled for blood, gill tissue and quantification of energetic status). In both 2003 and 2006, we tagged and biopsied 301 and 770 sockeye salmon, respectively, in the marine environment en route to their natal river system to spawn. In 2006 an additional 378 individuals were tagged and biopsied in freshwater. We found that 23 (7.6%) of the marine fish tagged in 2003, 78 (10.1%) of the marine fish tagged in 2006 and 57 (15.1%) of the freshwater fish tagged in 2006 were harvested by one of three fisheries sectors that operate in the coastal marine environment and the Fraser River (i.e. commercial, recreational or First Nations fisheries between the site of release and Hell's Gate in the Fraser River, approximately 250 km upriver and 465 km from the ocean tagging site). However, fisheries were not open continually or consistently in different locations and for different fisheries sectors necessitating a paired analytical approach. As such, for statistical analyses we paired individual fish that were harvested with another fish of the same genetic stock that was released on the same date and exhibited similar migration behaviour, except that they successfully evaded capture and reached natal spawning grounds. Using two-tailed Wilcoxon matched pairs signed-rank tests, we revealed that the physiological and energetic characteristics of harvested fish did not differ from those of the successful migrants despite evaluating a number of biochemical (e.g. plasma metabolites, cortisol, plasma ions, gill Na^+/K^+-ATPase) and energetic (e.g. gross somatic energy density) variables (P's all >0.10). However, for some analyses we suffered low statistical power and the study design had several shortcomings that could have made detection of differences difficult. We suggest that additional research explore the concept of fishing-induced selection for physiological characteristics

because physiology is closely linked to three traits where fisheries-induced selection does occur (i.e. life-history, behaviour and morphology).

Introduction

Many economically valuable marine fish stocks are heavily exploited by commercial (Pauly et al. 2002; Christensen et al. 2003; Myers and Worm 2003) and even recreational fisheries (Coleman et al. 2004; Cooke and Cowx 2004, 2006), often representing the primary source of adult mortality. These exploitative fishing practices tend to be highly selective for traits such as size, sex, maturity, behaviour and spatial distribution of fish (See review in Heino and Godø 2002). Research has revealed that fisheries-induced selection may promote genetic change in individual stocks (Stokes and Law 2000) that may result in long-term changes in yield, age-at-maturity and other stock properties (Sheridan 1995; Conover 2000). Heino and Godø (2002) have categorized traits that are sensitive to fishing into three broad categories: life-history, behavioural, and morphological. Interestingly, existing studies (summarized in Heino and Godø 2002) rarely acknowledge that physiological traits could also be subject to fishing-induced selection. Indeed, physiology is intimately linked to both life-history (Ricklefs and Wikelski 2002; Young et al. 2007) and behaviour (Altmann and Altmann 2003), and as such, is covered to some degree by these three categories. However, many physiological traits directly affect organismal performance, environmental tolerances and, ultimately, fitness and survival, linking the gene to the phenotype (Spicer and Gaston 1999; Pörtner and Farrell 2008). In experimental artificial selection studies (Hill and Caballero 1992; Gibbs 1999) and in aquaculture settings (Gjedrem 1983, 1997), researchers recognized that selection for different physiological traits can influence animal performance and fitness. Furthermore, studies of inter-individual variability have documented high levels of physiological diversity among fishes (Prosser 1955; Bennett 1987; Spicer and Gaston 1999).

Lacking to date, however, has been the consideration of a selection for physiological traits in the context of fisheries. Selection of this nature is especially important for fish stocks such as semelparous Pacific salmon where failure to reach spawning grounds and successfully spawn ultimately results in zero lifetime fitness. As salmon are harvested during reproductive migrations and reproductive migrations represent perhaps the most complex interaction between behaviour and physiology (Hinch et al. 2005). Pacific salmon present themselves as an interesting model to evaluate whether fishing is indeed selective for different physiological phenotypes. Moreover, Pacific salmon fisheries such as gill nets have previously been determined to be selective for fish morphology, size, age, and behaviour (Todd and Larkin 1971; Ricker 1981; Hamon et al. 2000).

There are several reasons why physiological characteristics may be important. Pacific salmon are fished heavily by commercial fishers (purse seine, troll, gill net), recreational anglers (rod and reel) and First Nations members (purse seine, gill net, rod and reel, dip net) during spawning migrations in coastal, estuarine, and freshwater settings (Groot and Margolis 1991). Nevertheless, they navigate to natal spawning grounds while facing these fishing pressures. In of themselves, these migrations are physically challenging, with a segment of any population dying en route to spawning grounds. Severe river migration conditions can greatly exacerbate this mortality (Macdonald 2000; Macdonald et al. 2000; Farrell et al. 2008). Salmon are in a catabolic state during migration, having ceased feeding before moving into coastal waters. Therefore, energy stored prior to river entry must fuel the river migration, as well as reproductive maturation and mating activities (Brett 1995; Hinch et al. 2005). Salmon must also adjust their osmoregulatory and hydromineral balance as they move from a marine to a freshwater environment (Shrimpton et al. 2005). Given these challenges and the fact that the migratory process can elevate indicators of chronic and acute stress (Cooke et al. 2006a,b), physiological and energetic condition can be associated with different behaviours and fate (i.e. whether fish are successful in reaching natal spawning grounds or die en route; Cooke et al. 2006a,b; Young et al. 2006; Crossin et al. 2007). However, it is unknown whether fishing is selective for any physiological or energetic characteristics.

Certain physiological and energetic states can influence behaviour and certain fish behaviours may make them more or less vulnerable to capture. For example, osmoregulatory preparedness for freshwater entry (e.g. low gill Na^+/K^+-ATPase activity) could be associated with individuals being preferentially distributed in the upper water column near estuaries (i.e. lower salinity), making them more susceptible to certain types of fishing gear. In another example, fish with high energy levels may be more capable of escaping fishing gear and swimming mid-current (and avoiding nearshore fishing gear).

Furthermore, some physiological traits may be associated with catchability without any *a priori* logical explanation as to why this may be (e.g. aggression or different metabolic rates; Cooke et al. 2007; Redpath et al. 2009). Such relationships could help to identify behavioural components that have not previously been considered in selection studies.

The greatest challenge with addressing this information gap is obtaining meaningful data from migrating salmon. Techniques are needed that combine information on individual fate, behaviour and physiology of free-swimming migratory fish. We have developed an approach to address this deficiency by working with local fishers to intercept adult sockeye salmon *(Oncorhynchus nerka)* during their spawning migration, and implanting individual salmon with radio transmitters to follow their subsequent migration behaviour and to determine their fate throughout the Fraser River and its tributaries over a distance of up to 1200 km. These same individuals were also biopsied, (blood and gill tissue samples, and energetic status) to assess the physiological and energetic correlates of migration success in sockeye salmon (Cooke et al. 2005, 2008b). Because our samples were part of fishery harvests, it was possible to test for the first time the hypothesis that fishing is selective for specific physiological and/or energetic traits by comparing fish that successfully reached spawning grounds with those that were harvested by fisheries. Our null hypothesis was that fishing is not selective for specific physiological (i.e. plasma glucose, lactate, cortisol, osmolality, Na^+, Cl^-, and K^+, and gill Na^+/K^+-ATPase) or energetic (i.e. gross somatic energy) traits in adult migrating sockeye salmon and is based on the premise that our initial collection techniques for tagging were themselves not selective (see Discussion). The parameters that we measured are indicative of organismal stress, osmoregulatory status, and energetic condition and have been widely used in the study of Pacific salmon migration biology (Cooke et al. 2006a,b; Crossin et al. 2007).

Materials and methods

Sampling strategy

The present investigation was part of two larger telemetry studies in which sockeye salmon were intercepted during their spawning migration at the southern end of Johnstone Strait, BC, Canada in 2003 and at Johnstone Strait, Juan de Fuca Strait and the lower Fraser River in 2006 (in the ocean $N = 559$ in 2003 and $N = 770$ in 2006; and $N = 378$ in freshwater in 2006) (Fig. 1; See English et al. 2004; Robichaud and English 2007). In the marine environment in 2003 and 2006, fish were collected using a large purse seine net deployed from a commercial fishing vessel, which also served as the platform for biopsy, radio-tagging and fish release. A fine-mesh drift gill net

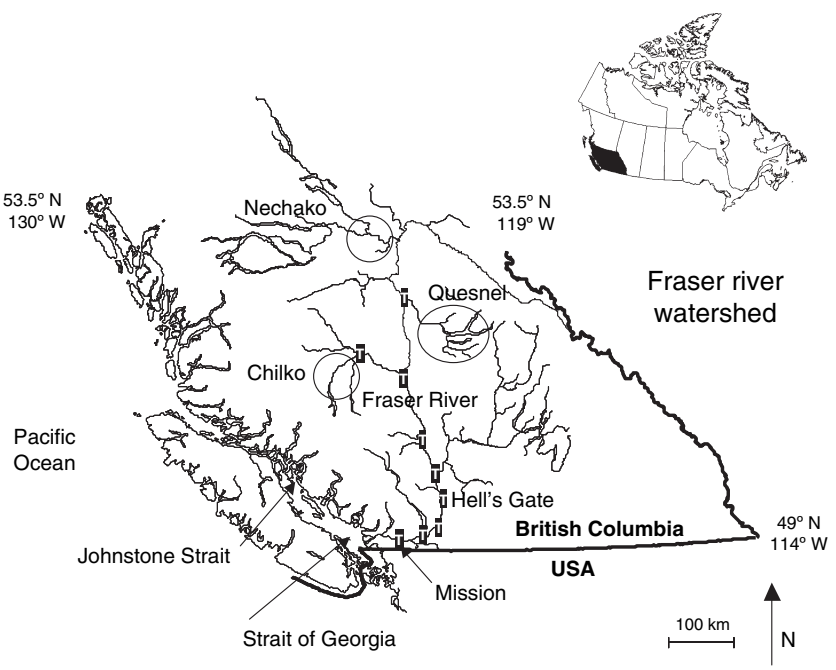

Figure 1 Map of Canada with an inset of the Fraser River Watershed of British Columbia. Key locations are identified on the map including the river entry telemetry station at Mission. Additional telemetry stations are indicated by the 'T' in black boxes. Natal spawning watersheds and general terminal spawning locations are circled. Fish were tagged in Johnstone Strait. The Fraser Estuary is considered to be the tidal region of the Fraser River which reaches to just below Mission.

(8.9 cm mesh size, net measuring 30 m long and 3.3 m deep) was used to collect fish in the freshwater environment. Our protocols, which were approved by the University of British Columbia and Carleton University Animal Care Committees, were validated in a parallel study involving three independent assessments to demonstrate biopsy and insertion of a biotelemetery device was without deleterious effects to immediate behaviour or survival of sockeye salmon (Cooke et al. 2005). We biopsied fish without anaesthesia because the possibility existed that the fish we released might be subsequently caught and consumed by fishers and animals and the regulation that anaesthetics currently approved for use on fish should not be ingested by humans.

Fish were sampled, tagged and released over a 3-week period between August 11 and August 28, 2003, between August 6 and 10 in Juan de Fuca Strait and August 11 and 27 in Johnstone Strait in 2006 for marine-tagged fish. Freshwater fish were tagged and released over 22 days from July 9 to September 1, 2006, 69 km from the Fraser River mouth, near Crescent Island. The released fish from each location were first detected by two radio telemetry stations 85 km upstream from the mouth of the river at Mission, BC (Fig. 1) and beyond the tidal boundary. To follow the progress of the fish up river, additional telemetry stations equipped with up to three antennas and a data logging radio receiver (SRX_400; Lotek Engineering Inc., Newmarket, ON), as detailed in English et al. (2004) and Robichaud and English (2007) were strategically deployed throughout the mainstem Fraser River and at the entrances to the natal sub-watershed (Fig. 1). Mobile tracking was also conducted by foot and boat and mobile tracking surveys were conducted to confirm arrival of individuals at spawning grounds. To encourage reporting of fish harvested by commercial fishers, recreational anglers, and First Nations members, we implemented a public awareness campaign and offered a small reward for information and transmitter return in both 2003 and 2006. Receivers were also used to scan for transmitters at three of the largest (by volume) fish processing plants in BC. Reporting compliance was believed to be high (English et al. 2004).

Biopsy and tagging techniques

In the marine environment, individual fish were removed from the purse seine (which remained in the water and was gathered at the side of the vessel) by a hand net and placed in large, flow-through totes on deck. For the freshwater component of the study, individual fish were rapidly recovered from the drift gill net by hand and placed in on-board, aerated holding totes containing ambient freshwater, then transferred to holding totes on-shore for sampling. In both the marine and freshwater environments, individuals were removed from the holding totes, placed ventral side up in a V-shaped trough that was lined with foam, and provided with a continuous supply of fresh ambient water via a tube placed near the mouth. Fish were manually restrained for <3 min during which time fork length (FL) was measured, tissues were biopsied and a radio transmitter was inserted. The biopsy procedure involved: (i) removing a small piece (0.5 g) of the adipose fin for DNA stock identification, (ii) removing one scale for ageing, (iii) removing 3 mL of blood from the caudal vessel using a vacutainer syringe (1.5″, 21 gauge; Houston 1990) for assessing plasma chemistry, and (iv) removing <4 mm from the tips of 6 to 8 filaments (0.03 g) from the first gill arch (McCormick 1993) for assessing gill enzyme activity. Gill tissue and centrifuged plasma samples were stored on dry ice for several days until transfer to a −80°C freezer where they were held until analysis. A hand-held micro-wave energy meter (Distell Fish Fatmeter model 692; Distell Inc, West Lothian, Scotland, UK) was placed on the left side of the fish in two locations to quantify somatic energy levels (see Crossin and Hinch 2005). Radio transmitters, which measured 16 mm in diameter and 51 mm in length and weighed 16.1 g in air and 6.2 g in water (MCFT-3A; Lotek Inc., Newmarket, ON), were orally inserted into the stomach using a plastic applicator.

Assays

Stock origin was ascribed to individual fish by a combination of DNA analyses (Beacham et al. 1995) and the recovery of radio transmitters at spawning grounds. Plasma ions (Na^+, K^+, Cl^-), cortisol, lactate, glucose and osmolality measurements followed the procedures described by Farrell et al. (2001) and Cooke et al. (2006a,b). Gill tissue Na^+/K^+-ATPase activity was determined with a kinetic assay (McCormick 1993) and expressed as μmol ADP mg^{-1} protein h^{-1}. Detailed description of all assays presented here including the inter-assay variability and quality control criteria are provided in Farrell et al. (2001) and Cooke et al. (2006a,b).

Statistical analysis

Individual fish known to have been captured based upon tag return from fisheries were individually paired with a fish of the same genetic stock that successfully reached natal spawning grounds. Previous multivariate analysis of variance (MANOVA) on log(10) transformed data (McGarigal et al. 2000) revealed that stocks and sexes differed in background physiological and energetic condition (Cooke et al. 2006a), necessitating stock- and sex-specific

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pairing. Although we tagged a large number of fish, because of all the factors involved the number of fish available for analysis was too low to enable multivariate analysis. All pairings were from fish released on the same date and an effort was made to reduce the time between capture and tagging on an individual day.

When possible, we paired fish that were most similar in size (fork length). We also considered the migration behaviour of fish with respect to river entry timing (for fish that reached the river) and attempted to pair fish with similar river entry dates and times. This was done because physiological condition can influence river entry time (Crossin et al. 2007; Cooke et al. 2008a) and migration rate (Crossin et al. 2007; Hanson et al. 2008) which would potentially expose fish to a different suite of fishing activities. Indeed, sockeye salmon fisheries are opened and closed in different areas and for different gear types throughout the season. A fish released on one day may simply never encounter an anglers hook because all fisheries are closed yet a fish released 2 days later may experience intense fishing pressure. We assumed that pairs of fish were exposed to fishing threats at the same rate and in the same river locations equally throughout the duration of the study. Two-sample *t*-tests were used to assess our ability to pair control and harvested fish with similar size (fork length) and migration speed (time between release and river entry). For core analyses, we contrasted individuals that were harvested with those that successfully reached their natal sub-watershed. In instances where data were missing (e.g. not all physiological assays were conducted for all individuals), we excluded the pair of fish from analyses. Because data did not always meet the normality assumption (i.e. that the source population from which differences have been drawn can be reasonably supposed to have a normal distribution) for a parametric paired *t*-test, we used two-tailed Wilcoxon matched pairs signed-rank tests (non-parametric analogue to the paired *t*-test; Wilcoxon 1945; Wilcoxon et al. 1970) to test the null hypothesis of no difference between individual harvested sockeye and paired control fish that successfully reached terminal spawning grounds. Prior to conducting Wilcoxon matched pairs signed-rank test, we confirmed that the data met the three primary assumptions of this test, namely: (i) that the paired values of X^A and X^B are randomly and independently drawn (i.e. each pair is drawn independently of all other pairs); (ii) that the dependent variable is intrinsically continuous, capable in principle, if not in practice, of producing measures carried out to the nth decimal place; and (iii) that the measures of X^A and X^B have the properties of at least an ordinal scale of measurement (Siegel and Castellan 1988). Wilcoxon matched pairs signed-rank tests are more robust than paired *t*-tests for dealing with outliers in the case of small sample sizes even following transformations (Wilcoxon 1945). All analyses were conducted using JMP 7.0 (SAS Institute, Raleigh, NC) and were assessed for significance at alpha = 0.05. However, for physiological assessments the *P*-value was Bonferroni corrected to reflect multiple comparisons and control for spurious relationships yielding a final alpha = 0.005 for assessment of the primary null hypothesis.

Results

All harvested and paired control fish were tagged and released on the same day. Overall, the mean (±SE) difference in release time between the fish that were harvested relative to those that reached spawning grounds was similar for fish in each tagging session (Table 1). For fish that successfully reached the Fraser River at Mission (65 km from river mouth and the first radio telemetry station) but were later harvested ($N = 19$ of 24 in 2003 and $N = 5$ of 35 for marine-tagged fish in 2003 and 2006 respectively, and $N = 19$ of 23 for 2006 freshwater-tagged fish), travel times between release and detection at Mission were similar to fish that successfully spawned ($t = 0.053$, df = 19, $P = 0.960$ in 2003; $t = -1.154$, df = 3, $P = 0.166$ for 2006 marine-tagged fish; $t = -0.37$, df = 22, $P = 0.644$ for 2006 freshwater-tagged fish; Table 1). Overall, fish that were harvested were of similar size to fish that we selected as control fish ($t = 1.063$, df = 23, $P = 0.294$ in 2003; df = 34, $P = 0.639$ for 2006 marine-tagged fish; $t = 0.051$, df = 22, $P = 0.520$ for 2006 freshwater-tagged fish; Table 1).

In the ocean in 2003 and 2006, and in the river in 2006, respectively, at least 23 of 301 (7.6%), 78 of 770 (10.1%), 57 of 378 (15.1%) fish were harvested before reaching spawning grounds. In the ocean in 2003 and 2006, respectively, 4 and 37 of the fish that were harvested were captured in marine or estuarine waters by commercial or First Nations fishers. For ocean-tagged fish in 2003 and 2006, and river-tagged fish in 2006, respectively, 19, 33 and 35 fish were captured by commercial or First Nations fisheries in the mainstem of the Fraser River. In 2003, all of the recreationally harvested fish were captured downstream of Hope, whereas the First Nations sector harvested fish from just upstream of Mission to the Fraser-Thompson confluence at Lytton. In 2006, three ocean-tagged fish were harvested by the marine sport fishery and six fish were captured by the freshwater sport fishery between Mission and Sawmill Creek. Twenty-one river-tagged fish from 2006 were harvested by the recreational fisheries sector between Mission and Sawmill Creek and one fish was harvested by the recreational sector upriver of Sawmill Creek. Fish were harvested between 1 and 18 days (median, 9) for marine-tagged fish in 2003, 2 and 61 days (median, 12) for marine-tagged fish in 2006

Table 1. Summary of fish characteristics for Fraser sockeye salmon tagged in 2003 (marine) and 2006 (marine and freshwater).

Tagging details	2003 Ocean tagging	2006 Ocean tagging	2006 In-River tagging
Mean ± SE time between release of tagged fish	14.4 ± 42 min	7.4 ± 36.4 min	31.7 ± 22.1 min
Mean ± SE travel times between release and detection at mission for survivors	7.06 ± 0.43 days	10.84 ± 1.12 days	1.96 ± 1.59 days
Mean ± SE travel times between release and detection at mission for fish the were harvested prior to arrival at spawning grounds	7.09 ± 0.43 days	7.68 ± 2.22 days	2.17 ± 1.98 days
Mean ± SE size (total length in cm) of tagged fish that reached spawning grounds	60.5 ± 0.5 cm	59.5 ± 0.5 cm	60.0 ± 0.5 cm
Mean ± SE size (total length in cm) of tagged fish that were harvested prior to arrival at spawning grounds	61.2 ± 0.5 cm	59.8 ± 0.5 cm	60.0 ± 0.7 cm
Mean Time ± SE in days between tagging and harvest for those fish that were harvested after release	9 ± 1 days	14.3 ± 2.1 days	8.9 ± 1.9 days

Table 2. Characteristics of summer run sockeye salmon that were harvested and paired control fish. Time between the release of the harvested fish and the control fish is provided. When zero, the fish were tagged at the same time. Positive numbers indicate instances where the control fish was released later than the harvested fish and negative numbers indicate instances where the harvested fish were released later than the control fish. Time before capture is provided only for fish that were harvested. Fate of harvested fish is provided with respect to the location of the capture as well as the fishing sector. Time until river entry is a behavioral metric and represents the time (in days) between release and arrival at Mission (See Fig. 1) and is provided for both harvested and control fish.

Stock	Tagging date in 2003	Time between releases (min)	Time before capture (days)	Fate of harvested fish (location and fishing sector)	Time until river entry (days)		Fork length (cm)	
					Harvested fish	Control fish	Harvested fish	Control fish
Chilcotin	11-Aug	0	13	In River – recreational	8.78	7.9	59	61
Chilcotin	12-Aug	0	2	Marine – commercial	NA	8.57	53	63
Chilcotin	12-Aug	429+	3	Marine – commercial	NA	10.31	59	60
Chilcotin	13-Aug	153+	11	In River – recreational	5.94	5.43	62	61
Chilcotin	14-Aug	0	18	In River – First Nations	7.25	6.91	65	58
Chilcotin	14-Aug	0	7	In River – recreational	6.36	6.34	65	60
Chilcotin	14-Aug	0	4	Estuary – First Nations	NA	5.61	60	60
Chilcotin	15-Aug	0	1	Marine – commercial	NA	6.77	59	59
Chilcotin	20-Aug	0	10	In River – First Nations	6	5.83	61	60
Chilcotin	20-Aug	0	16	In River – First Nations	10.47	10.64	59	59
Chilcotin	21-Aug	0	9	In River – First Nations	7.25	8.91	63	62
Chilcotin	22-Aug	0	9	In River – First Nations	5.19	10.72	61	60
Chilcotin	22-Aug	134–	12	In River – First Nations	6.74	10.72	59	60
Chilcotin	28-Aug	65–	13	In River – First Nations	11.86	4.74	62	64
Nechako	13-Aug	450+	9	In River – First Nations	7	6.98	63	58
Nechako	14-Aug	0	15	In River – First Nations	6.34	5.62	62	64
Nechako	14-Aug	460–	10	In River – First Nations	5.91	7.84	57	58
Quesnel	11-Aug	145–	14	In River – First Nations	7.56	7.73	61	65
Quesnel	14-Aug	270–	6	In River – First Nations	4.77	4.49	60	59
Quesnel	14-Aug	150+	7	In River – recreational	5.74	5.43	62	58
Quesnel	14-Aug	175–	1	Marine – commercial	NA	4.49	56	59
Quesnel	15-Aug	335+	7	In River – First Nations	5.92	5.94	62	58
Quesnel	28-Aug	65+	11	In River – First Nations	8.65	4.53	59	65

and 1 and 31 days (median, 5) for river-tagged fish in 2006 following biosampling and tagging procedures (Tables 1–4).

We tested the null hypothesis that there was no difference in the physiology or energetic status of individual sockeye salmon that were harvested by fisheries and those

Table 3. Characteristics of sockeye salmon that were harvested and paired control fish for individuals that were tagged in the marine environment in 2006. Time between the release of the harvested fish and the control fish is provided. Positive numbers indicate instances where the control fish was released later than the harvested fish and negative numbers indicate instances where the harvested fish were released later than the control fish. Time before capture provided only for fish that were harvested. Fate of harvested fish provided with respect to the location of the capture as well as the fishing sector. Time until river entry is a behavioral metric and represents the time (in days) between release and arrival at Mission (See Fig. 1) and is provided for both harvested and control fish.

Stock	Tagging date in 2006	Time between releases (min)	Time before capture (days)	Fate of harvested fish (location and fishing sector)	Time until river entry (days)		Fork length (cm)	
					Harvested fish	Control fish	Harvested fish	Control fish
Scotch	8-Aug	3+	6	Marine – commercial	NA	7.20	61	63
Scotch	8-Aug	262–	20	In River – First Nations	12.45	6.78	56	61.5
Scotch	8-Aug	19–	7	In River – commercial	NA	NA	62	57
Scotch	16-Aug	11–	12	In River – recreational	NA	6.08	59	54.5
Seymour	6-Aug	9+	6	Marine – commercial	NA	8.92	58	55
Seymour	7-Aug	3+	16	In River – First Nations	8.23	NA	55	62
Chilko	6-Aug	18+	28	In River – First Nations	18.04	8.47	56	61
Chilko	6-Aug	41–	5	Marine – commercial	NA	0.00	64	60.5
Chilko	7-Aug	98–	16	Marine – commercial	NA	8.07	56	56
Chilko	7-Aug	197–	13	In River – First Nations	NA	7.64	58	54
Chilko	16-Aug	294–	7	In River – commercial	NA	5.19	56	60.5
Chilko	17-Aug	173–	12	In River – commercial	NA	7.53	59	60
Chilko	25-Aug	196–	15	In River – First Nations	6.12	6.29	60	58
Quesnel	8-Aug	28+	2	Marine – commercial	NA	13.58	60.5	63.5
Stellako	7-Aug	251–	12	In River – commercial	NA	9.57	53.5	65
Stellako	8-Aug	12+	12	In River – First Nations	NA	NA	57	57
Adams	9-Aug	5+	13	In River – commercial	NA	19.69	55.5	62
Adams	9-Aug	244–	9	In River – First Nations	NA	15.20	59.5	58.5
Adams	10-Aug	117+	13	Marine – commercial	NA	NA	63	57.5
Adams	10-Aug	6+	13	Marine – commercial	NA	11.14	61	63
Adams	11-Aug	351+	12	In River – recreational	NA	9.07	62	57
Adams	16-Aug	24+	6	In River – commercial	NA	12.34	62	58
Adams	16-Aug	9–	3	In River – First Nations	NA	NA	62.5	64
Adams	16-Aug	11+	20	In River – recreational	NA	30.65	56	61
Adams	18-Aug	230+	3	Marine – commercial	NA	7.78	55	60
Adams	19-Aug	5–	61	Marine – commercial	NA	11.34	64	60.5
Adams	19-Aug	4+	20	In River – commercial	6.75	9.19	58	57
Adams	19-Aug	3+	17	In River – commercial	NA	19.87	63	61
Adams	19-Aug	30+	10	In River – commercial	NA	16.48	62.5	64
Adams	25-Aug	10+	27	In River – First Nations	NA	NA	58	60
Adams	25-Aug	158–	55	In River – commercial	NA	11.54	67	60
Adams	26-Aug	6+	13	Marine – commercial	NA	12.94	60	60
Little River	17-Aug	22+	5	In River – commercial	NA	8.20	63	60
Little River	18-Aug	3–	3	Marine – commercial	NA	11.97	61	62
Shuswap	6-Aug	40–	9	Marine – commercial	NA	22.05	60	59

that reached spawning grounds. Using two-tailed Wilcoxon matched pairs signed-rank tests, we failed to reject our null hypothesis. Following Bonferroni corrections, there were no significant differences ($P > 0.005$) in any of the physiological variables measured from plasma (i.e. lactate, glucose, cortisol, osmolality, Na^+, K^+, Cl^-) or gill tissue (gill Na^+/K^+-ATPase) or in energetic status (i.e. gross somatic energy) for fish tagged in the marine environment in 2003 (Tables 2 and 5) and 2006 (Tables 3 and 6) and freshwater environment in 2006 (Tables 4 and 7). Even prior to Bonferroni adjustments (i.e. original *P*-value of 0.05), none of the variables examined were approaching significance (Tables 5–7). There were few consistencies in how paired values compared between harvested and control fish in 2003 or 2006 (i.e. no obvious trends with respect to higher or lower values). Power analysis revealed that we had low probability (range of 1-ß from 0.051 to 0.150 in 2003; 0.05 to 0.491 in the ocean in 2006; 0.051 to 0.087 in freshwater in 2006) of detecting differences as a result of the effect size (variability of the data) and low sample sizes (Tables 5–7).

Table 4. Characteristics of harvested sockeye salmon and paired control fish for individuals that were tagged in-river in 2006. Time between the release of the harvested fish and the control fish is provided. Positive numbers indicate instances where the control fish was released later than the harvested fish and negative numbers indicate instances where the harvested fish were released later than the control fish. Time before capture is provided only for fish that were harvested. Fate of harvested fish is provided with respect to the location of the capture as well as the fishing sector. Time to Mission is a behavioral metric and represents the time (in days) between release and arrival at Mission (See Fig. 1) and is provided for both harvested and control fish.

Stock	Tagging date in 2006	Time between releases (min)	Time before capture (days)	Fate of harvested fish (location and fishing sector)	Time between release and mission (days)		Fork length (cm)	
					Harvested fish	Control fish	Harvested fish	Control fish
Fennell	1-Aug	46+	24	In River - First Nations	1.68	1.33	54	60
Scotch	2-Aug	66–	6	In River - First Nations	1.92	1.94	63	60
Scotch	2-Aug	37+	4	In River – recreational	3.18	2.46	58	61
Scotch	3-Aug	8+	2	In River – recreational	0.75	1.80	62	62
Scotch	10-Aug	93+	1	In River – recreational	1.42	1.83	63	61
Seymour	15-Aug	239+	3	In River – recreational	NA	NA	66	63
Chilko	1-Aug	94–	23	In River – First Nations	1.40	4.16	57	57
Chilko	1-Aug	161–	6	In River – First Nations	1.83	5.31	58	58
Chilko	3-Aug	3+	3	In River – First Nations	1.40	4.11	60	59
Chilko	10-Aug	3–	19	In River – First Nations	1.49	1.68	58	58
Chilko	14-Aug	111+	2	In River – recreational	1.68	1.08	62	63
Chilko	15-Aug	153–	13	In River – First Nations	3.00	1.29	60	58
Chilko	31-Aug	275–	5	In River – commercial	1.42	1.83	60	58
Chilko	1-Sep	365+	10	In River – First Nations	2.24	1.42	56	58
Quesnel	3-Aug	77–	9	In River – First Nations	3.48	NA	57	65
Quesnel	10-Aug	381–	2	In River – recreational	1.91	0.90	60	59
Quesnel	31-Aug	16+	2	In River – recreational	1.56	0.94	64	55
Stellako	1-Aug	260+	5	In River – First Nations	9.86	2.17	56	61
Stellako	2-Aug	48+	24	In River – First Nations	1.44	6.09	61	59
Stellako	8-Aug	3+	31	In River – commercial	4.86	NA	66	58
Adams	31-Aug	111+	3	In River – recreational	NA	1.43	61	61
Shuswap	10-Aug	294–	3	In River – recreational	1.28	2.52	59	61
Shuswap	31-Aug	5–	5	In River – First Nations	2.075	0.83	59	66

Table 5. Summary statistics from the two-tailed Wilcoxon matched pairs signed-rank tests used to test the null hypothesis of no difference between individual harvested sockeye and paired control fish that successfully reached terminal spawning grounds. Power was calculated a posteriori to reflect actual variation at a P of 0.05. P values were interpreted using Bonferroni corrected P-values ($P = 0.005$). Note that not all fish were used in all analyses as not all physiological samples were collected from all individuals.

Variables	*N*	W	*Z*-Score	Probability	Power (1 – ß)
Gross somatic energy (MJ kg^{-1})	21	–41	–0.7	0.484	0.147
Plasma Na^+ (mmol l^{-1})	17	–40	–0.93	0.352	0.063
Plasma K^+ (mmol L^{-1})	17	–16	–0.37	0.711	0.058
Plasma Cl^- (mmol L^{-1})	17	15	0.34	0.734	0.079
Plasma osmolality (mOsmo kg^{-1})	17	–29	–0.67	0.503	0.081
Plasma cortisol (ng mL^{-1})	16	56	1.43	0.153	0.150
Plasma lactate (mmol L^{-1})	17	–11	–0.25	0.803	0.051
Plasma glucose (mmol L^{-1})	17	–23	–0.53	0.596	0.067
Gill Na^+/K^+-ATPase (μmol ADP mg^{-1} protein h^{-1})	15	–18	–0.5	0.617	0.050

Discussion

To date, no previous research has tested the hypothesis that fisheries are selective for physiological and energetic characteristics (but see Cooke et al. 2007 for an artificial selection experiment). We relied on coupling individual behaviour and fate (i.e. spawning versus fisheries harvest) using biotelemetry (Cooke et al. 2008b) with nonlethal physiological biopsy techniques (Cooke et al. 2005) to contrast the condition of fish that were harvested with those that successfully reached terminal spawning grounds. We paired individual harvested fish with the

Table 6. Summary statistics from the two-tailed Wilcoxon matched pairs signed-rank tests used to test the null hypothesis of no difference between individual harvested sockeye and paired control fish that successfully reached terminal spawning grounds for individuals that were tagged in the marine environment in 2006. Power was calculated a posteriori to reflect actual variation at a *P* of 0.05. *P*-values were interpreted using Bonferroni corrected *P*-values ($P = 0.005$). Note that not all fish were used in all analyses as not all physiological samples were collected from all individuals.

Variables	*N*	W	*Z*-Score	Probability	Power (1 − ß)
Gross somatic energy (MJ kg^{-1})	31	37.5	0.28	0.449	0.491
Plasma Na^+ (mmol L^{-1})	35	77.5	0.13	0.189	0.051
Plasma Cl^- (mmol L^{-1})	35	−50	−0.29	0.421	0.065
Plasma osmolality (mOsmo kg^{-1})	35	2	0.35	0.973	0.225
Plasma cortisol (ng mL^{-1})	10	−4.5	−0.66	0.695	0.050
Plasma lactate (mmol L^{-1})	35	25	0.05	0.688	0.067
Plasma glucose (mmol L^{-1})	35	−29.5	−0.02	0.636	0.159
Gill Na^+/K^+-ATPase (μmol ADP mg^{-1} protein h^{-1})	33	36.5	0.45	0.523	0.126

Table 7. Summary statistics from the two-tailed Wilcoxon matched pairs signed-rank tests used to test the null hypothesis of no difference between individual harvested sockeye and paired control fish that successfully reached terminal spawning grounds for individuals that were tagged in-river in 2006. Power was calculated a posteriori to reflect actual variation at a *P* of 0.05. *P*-values were interpreted using Bonferroni corrected *P*-values ($P = 0.005$). Note that not all fish were used in all analyses as not all physiological samples were collected from all individuals.

Variables	*N*	W	*Z*-Score	Probability	Power (1 − ß)
Gross somatic energy (MJ kg^{-1})	23	29	0.65	0.334	0.077
Plasma Na^+ (mmol L^{-1})	23	7	0.15	0.828	0.051
Plasma Cl^- (mmol L^{-1})	23	28	0.04	0.384	0.055
Plasma osmolality (mOsmo kg^{-1})	23	39	0.28	0.219	0.051
Plasma lactate (mmol L^{-1})	23	22	0.09	0.468	0.056
Plasma glucose (mmol L^{-1})	23	4	0.54	0.913	0.083
Gill Na^+/K^+-ATPase (μmol ADP mg^{-1} protein h^{-1})	22	−53	0.13	0.088	0.087

most similar individual that successfully spawned based on date of release (all paired fish were released on the same day), time of release (all paired fish were released within 7 h of each other with a mean difference of less than 30 min), stock (all paired fish were of the same stock), total length (there were no differences in the sizes of fish in either group), and finally time between tagging and river entry (there were no differences in the travel times for fish in either group). Using adult migrating sockeye salmon as a model, we revealed that despite intense fishing pressure from three fishing sectors (commercial, recreational and First Nations) in marine, estuarine, and in river (freshwater) environments, we failed to detect differences in the physiological status of fish that were harvested relative to those that successfully reached spawning grounds. However, it is also important to acknowledge that the study design had several shortcomings including (i) low statistical power as a result of relatively few data points, (ii) the paired analysis approach potentially limiting ability to detect differences, (iii) all fish including those classified as un-fished in the 'control' treatment, had to be initially captured by fishing gear for tagging and sampling, and (iv) fish were recaptured using a variety of gear types each with different selective characteristics. We discuss all of these factors in an effort to aid in the interpretation of our data set and to also propose a way forward for future research aimed at evaluating whether fishing is selective for physiological traits.

Our result may be viewed as equivocal for various reasons discussed below. Foremost, it is still plausible that sockeye fisheries were selective for physiological characteristics that were not measured here. Although we evaluated multiple physiological response variables, there was little literature to assist in developing rational predictions. One prediction was that fish that were harvested would have had elevated plasma lactate (an anaerobic metabolite) which would have affected organismal behaviour and activity (e.g. Black 1958; Hinch and Bratty 2000) and potentially increased susceptibility to capture and harvest. However, high lactate could have also be a result of the capture itself with individuals that struggle the most and presumably have the highest lactate being the ones most likely to escape. In either instance, our data did not reveal any significant difference in plasma lactate concentrations in control or harvested fish. An additional variable that we predicted to be relevant was gross somatic energy. Energy density in upriver migrants is linked strongly to

migratory performance (Crossin et al. 2004; Cooke et al. 2006a,b) and swimming speeds (Hanson et al. 2008). Again, we had little support for this prediction so although we attempted to link physiology to capture, we were unable to detect any relationships.

A common problem in fisheries selectivity studies is low statistical power (Heino and Godø 2002). Our analysis was no exception. Using our 2003 marine-tagging results as an example, given the variability observed in our data and assuming that it would have been consistent with larger sample sizes, we would have required ~500 samples (250 harvested fish and 250 controls) to have an 80% probability of detecting a 5% difference. Given that harvest rates were about 7% across summer run stocks in 2003, we would have had to tag 3570 sockeye to achieve this level of power, i.e. 10-times the sample size we had in 2003. Given that the telemetry studies that we implemented in 2003 and 2006 were among the biggest in Canadian history (Cooke and Thorstad In Review), and given that, based on our 2003 data set alone, it is unlikely that a better dataset will emerge for some time. Only on the Columbia River in the United States are there telemetry studies that approach or exceed those sample sizes (largest to our knowledge is approaching 20 000 transmitters), however, all of the studies of that magnitude have been performed on downstream migrating smolts, which are not harvested by any fishing sector and not individually biopsied and released (e.g. Schreck et al. 2006). Consequently, we recommend continual collection of data through time such that it may be possible to combine discrete data sets to achieve necessary power.

A fundamental issue with these data is the fact that all of the fish in the study were captured by commercial fishing gear (an ocean purse seine) and had already been 'selected' as part of a fishery. In fact, all of the tagged fish (both those that were harvested and those that were paired controls) would have been harvested at this initial capture had this not been an experimental test fishing charter. In essence, a requirement to tag and biopsy a wild fish for a fisheries harvest study is the fact that the fish must first be captured and, when working in an ocean environment, fisheries are the only available method of capture. Almost all fisheries gear and sampling techniques are selective in some way (e.g. size, sex, behaviour, location), so it is difficult to not expose fish to fisheries selection as part of the fisheries technique. However, purse seines are generally deemed to be less selective than most other fisheries methods given that they rapidly encompass and trap all adult fish in a relatively large area, providing little opportunity for gear avoidance or escape based on swim performance or size. Likely, only fish in deeper water could potentially avoid capture better than those swimming in shallower water. For marine tagged fish, any potential selectivity from our initial purse seine capture techniques would be minimized by pairing fish based on similar characteristics (i.e. date and time of capture, total length, stock and time from capture to river entry). Accordingly, pairing similar fish allows us to identify potential characteristics that could be selected for by subsequent fisheries recaptures. Thus, of all potential capture techniques, the purse seine (as used here) is likely the best approach for collecting, tagging, and biopsying fish for selectivity experiments.

Fraser River salmon are exposed to multiple fishing sectors and fishing gear. At the sites of capture and release, there were active commercial, recreational, and First Nations fisheries. As marine-tagged fish approach the estuary, recreational fishing decreased and there was increased fishing pressure from commercial and First Nations fisheries using trolling and gill nets. In the lower Fraser River (Mission to Hope), recreational fishing is popular, as well as First Nations gill netting. Upriver from Hope, the fisheries are almost exclusively First Nations, relying on dipnet and gill net (both fixed and drifting) for capture. Because of the low sample sizes in this study, we can only partially assess the potential physiological aspects of selectivity in different sectors (i.e. marine purse seine and freshwater gill net), or environments (marine vs freshwater). Because fishing gear is differentially selective for sizes, sex, morphology, behaviour, etc., of Pacific salmon (e.g. Todd and Larkin 1971; Ricker 1981; Hamon et al. 2000), it is plausible that the grouping of all our data into a composite of 'harvested' actually obscured potential trends. Another challenge with the analysis was the fact that we were forced to use a paired analytical approach because of the variation in fishing effort (i.e. openings and closings) throughout the season. Future studies would benefit from exposing fish to consistent fishing effort over a more protracted period in order to enable more robust techniques such as MANOVA or logistic regression to test the null hypothesis of no difference in physiological and energetic condition between fates. Moreover, although we mounted an extensive public awareness campaign in both years, including the provision of rewards, and despite the fact that we believe that tag reporting compliance was high, our fisheries harvest rates are surely an underestimate of actual harvest. Because we paired individual harvested fish with a non-harvested control that reached spawning grounds, it is not possible to erroneously pair a known harvested fish with a control fish that was actually harvested.

In summary, we failed to reject our null hypothesis of no difference in the physiological or energetic condition of migratory adult sockeye salmon that successfully reached natal spawning grounds versus those fish that were harvested by one of the three fisheries sectors operating in

coastal BC or the Fraser River. The main caveats to this result are a low statistical power and physiological indices that we did not consider. Improved statistical power would require an order of magnitude more telemetry data and biopsies. However, as physiology is closely linked to two traits where fisheries-induced selection does occur (i.e. life-history and behaviour), we suggest that additional research explore the concept of fishing-induced selection for physiological characteristics using controlled laboratory and mesocosm experiments and larger scale field physiology (coupling telemetry and biopsy) techniques (Conover and Baumann 2009). In addition, genomics tools (gene arrays) would enable more comprehensive physiological analyses than were possible in this study using conventional blood-based physiological assays. The notion that physiological characteristics could preclude fish to be selectively harvested is particularly relevant to diadromous fish or other species that undertake large scale migrations where physiological and energetic tolerances and capacity interact with organismal behaviour to influence fitness (Hinch et al. 2005). As global aquatic environments continue to be exploited by commercial, recreational, and subsistence fisheries, it is important to understand fisheries selectivity and the evolutionary consequences of angling. Given the demonstrable links between physiology, behaviour, and life-history (e.g. Spicer and Gaston 1999; Ricklefs and Wikelski 2002; Young et al. 2007), it is conceivable that fisheries are selective for specific physiological and energetic characteristics (phenotypes). Knowledge of the fisheries selectivity for physiological characteristics will be needed to conserve and manage global fisheries (Wikelski and Cooke 2006; Young et al. 2007) using evolutionarily enlightened strategies (Ashley et al. 2003).

Acknowledgements

All procedures used in this study were developed with approvals and guidance from the Canadian Council on Animal Care administered by the University of British Columbia and Fisheries and Oceans Canada. We thank Al Cass, Laura Richards, Jim Cave, Jim Woodey, Mike Lapointe, Carmen McConnell, and others from the Pacific Salmon Commission for facilitating this project. Tagging, biopsy, and data management support was provided by Richard Alexander, Dave Robichaud, Ivan Olsson, Jay Sitar, Trisha Watson, Louise Kuchel, Jayme Davidson, Jim Ferguson, Bill Koski, Nathan Blakley, Cezary Sliwinski, Troy Ganzeveld, and Stephanie Green. We also thank the skippers and the crew of the *Royal Mariner 1* and the *Sunfisher*. Physiological assays were conducted by Jayme Davidson, Janette Garries, and Jeff Young. Several anonymous referees and the guest editors provided valuable comments on the manuscript. Funding for the telemetry component of the study was provided by a contract to LGL Limited from Fisheries and Oceans Canada. The bio-sampling component of the project was funded by a Natural Sciences and Engineering Research Council (NSERC) Strategic Grant, NSERC discovery grants, and the DFO Fraser River E-Watch Program. The lead author was supported by NSERC and Izaak Walton Killam postdoctoral fellowships and institutional funds from Carleton University.

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