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Merits and Limits of Ecosystem Protection for Conserving Wild Salmon in a Northern Coastal British Columbia River

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ABSTRACT. Loss and degradation of freshwater habitat reduces the ability of wild salmon populations to endure other anthropogenic stressors such as climate change, harvest, and interactions with artificially propagated fishes. Preservation of pristine salmon rivers has thus been advocated as a cost-effective way of sustaining wild Pacific salmon populations. We examine the value of freshwater habitat protection in conserving salmon and fostering resilience in the Kitlope watershed in northern coastal British Columbia—a large (3186 km²) and undeveloped temperate rainforest ecosystem with legislated protected status. In comparison with other pristine Pacific Rim salmon rivers we studied, the Kitlope is characterized by abundant and complex habitats for salmon that should contribute to high resilience. However, biological productivity in this system is constrained by naturally cold, light limited, ultra-oligotrophic growing conditions; and the mean (\pm SD) density of river-rearing salmonids is currently low (0.32 ± 0.27 fish per square meter; $n = 36$) compared to our other four study rivers (grand mean = 2.55 ± 2.98 fish per square meter; $n = 224$). Existing data and traditional ecological knowledge suggest that current returns of adult salmon to the Kitlope, particularly sockeye, are declining or depressed relative to historic levels. This poor stock status—presumably owing to unfavorable conditions in the marine environment and ongoing harvest in coastal mixed-stock fisheries—reduces the salmon-mediated transfer of marine-derived nutrients and energy to the system’s nutrient-poor aquatic and terrestrial food webs. In fact, Kitlope Lake sediments and riparian tree leaves had marine nitrogen signatures ($\delta^{15}\text{N}$) among the lowest recorded in a salmon ecosystem. The protection of the Kitlope watershed is undoubtedly a conservation success story. However, “salmon strongholds” of pristine watersheds may not adequately sustain salmon populations and foster social and ecological resilience without more holistic and risk-averse management that accounts for uncertainty and interactions between ecosystem fertility, harvest, climate dynamics, and food web dynamics in the marine and freshwater environments encompassed by the life cycle of the fish.

Key Words: *conservation; ecology; fisheries management; habitat; Kitlope River; Pacific salmon; resilience; salmon stronghold*

INTRODUCTION

Ecosystem protection in the form of reserves and special management areas reduces or prevents the direct human impacts of resource extraction, land development, and waste disposal. Such impacts can reduce ecosystem resilience (Folke et al. 2004), defined here as “the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks” after Walker et al. (2004). Protecting both marine and terrestrial habitats has been advocated as a necessary supplement to traditional population

management practices that have generally failed to prevent widespread extinctions and ecosystem collapse (Roberts 1997, World Conservation Union 2003). In North America, marine protected areas with “no-take” zones have sometimes proven successful at increasing mean biomass, size, density, and egg production in populations targeted by fisheries (Tetreault and Ambrose 2007). Large terrestrial protected areas can aid in the conservation of wide-ranging mammals, especially apex predators, that are vulnerable to human disturbance (Noss et al. 1996). Moreover, the net direct and indirect economic benefits that accrue from undeveloped wilderness through ecosystem goods

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and services can be greater than those that accrue from developed landscapes (Balmford et al. 2002). In this paper, we examine whether the protected status of a large catchment in northern British Columbia (B.C.) can insure resilience of Pacific salmon (*Oncorhynchus* spp.) populations.

In freshwater ecosystems, physical and biological diversity are maintained by biophysical processes operating at multiple spatial scales (Stanford et al. 2005), and protection at the catchment scale provides the ultimate safeguard against human interruption of these processes (Dudgeon et al. 2006). Such process interruptions include flow regulation through dams, channelization and bank armoring (Hauer et al. 2003), and increased soil erosion and instability due to deforestation and road building (Hartman et al. 1996). Indeed, alluvial floodplains are some of the most endangered landscapes on earth (Tockner and Stanford 2002), and whole catchments, especially large ones, seldom are fully protected (Naiman et al. 2002).

Pacific salmon are icons of social and ecological well-being to aboriginal and other fishing cultures of the Northern Pacific Rim. Degradation and loss of freshwater habitat has been a major contributing factor in declines and extinctions of wild Pacific salmon populations over the past century (Nehlsen et al. 1991). Salmon are highly adapted to their natal waters (Quinn 2005); therefore, habitat perturbations that alter natural selection can reduce genetic and phenotypic diversity and fitness (McClure et al. 2008). This diversity is considered essential in maintaining resilience in Pacific salmon populations, especially where other anthropogenic and natural sources of mortality (e.g., harvest, climate change) are significant (Hilborn et al. 2003).

Conversely, the health and resilience of salmon-based ecosystems is often dependent on the health and resilience of their component salmon populations due to the tremendous net nutrient and energy subsidies that salmon carcasses provide to freshwater and riparian ecosystems when they return to spawn (Naiman et al. 2002). Throughout southern British Columbia and the U.S. Pacific Northwest, large and long-term declines in salmon abundance have led to order-of-magnitude decreases in marine-derived-nutrient influx to riparian floodplain ecosystems (Schoonmaker et al. 2003), prompting concern for the productivity of these systems and their ability to support wildlife, including salmon (Schindler et al. 2003 and

references therein). While ecological relationships between productivity and resilience in general are variable and non-linear (Stone et al. 1996), aquatic productivity is positively correlated with the productivity of some salmon populations (Hyatt and Stockner 1985, Finney et al. 2000), thus contributing to the maintenance of biological diversity.

In Canada and the U.S., vast monetary and human resources have been dedicated to the restoration of the freshwater habitats of endangered or threatened salmon populations (Williams 2006). However, some have advocated for an alternative, more proactive approach – a Salmon Sanctuary Strategy to create a network of headwaters-to-ocean protected areas for salmon (Rahr et al. 1998, Lichatowich et al. 2000). Rahr and Augerot (2006) define these salmon sanctuaries as watersheds with intact and ecologically connected habitats (undeveloped floodplains, no dams, no channelization) with abundant and diverse wild salmon populations (no artificial propagation), and a management regime that is mandated to maintain that diversity and abundance.

Maintenance of abundant and high-quality freshwater habitat likely buttresses the resilience of anadromous salmon populations in the face of other threats, such as climate change, overharvest, and genetic introgression from cultured stocks (Lichatowich et al. 1999, Mantua and Francis 2004). However, it is unclear to what extent protection of freshwater habitat can be an effective salmon conservation tool if other pressures are not identified and reduced, or if subsequent management does not effectively provide for population maintenance (Augerot 2005). Indeed, for many species, the creation of protected areas in other ecosystems has too often proven insufficient for conserving biological diversity and abundance without additional conservation measures (Allison et al. 1998, Pressey et al. 2007).

In this paper, we evaluate the efficacy of ecosystem protection and current management practices in conserving sockeye (*Oncorhynchus nerka*) and other salmon populations in a so-called “salmon sanctuary” – the Kitlope watershed in the northern coastal region of British Columbia. We contrast biological and physical attributes that foster both resilience and precariousness (proximity to an undesirable threshold: Walker et al. 2004) in the Kitlope River ecosystem and its anadromous

salmon. We examine how these attributes – status of the sockeye salmon population, external factors such as salmon harvest and climate change, and various physical and chemical attributes of watershed condition relative to other watersheds under similar study by the authors – are affected by ecosystem protection and current management.

SITE DESCRIPTION AND MANAGEMENT HISTORY

The topography of the Kitlope River catchment is steep with several glaciers at the headwaters (Fig. 1), and the biogeoclimatic classification is Coastal Western Hemlock at lower elevations and Mountain Hemlock and Alpine Tundra at higher elevations (Meidinger and Pojar 1991). The regional climate is determined by wet, warm conditions due to ocean proximity interacting with colder continental air masses. Average annual precipitation for the Kitlope watershed is approximately 190 cm (Environment Canada data), often with intense rainfall or rain on snow, causing regular scouring floods, with bankfull or higher flows occurring multiple times per year (Stockner et al. 1993; *personal observations*).

The Kitlope is a classic gravel-bedded, floodplain river with a diverse array of habitat types including braided and anastomosed channel networks with many spring brooks persisting in flood channels, expansive gravel bars with pioneering vegetation, wood jams, backwaters, beaver ponds, and bogs and other wetlands, all embedded in expansive, forested floodplains. The system is also defined by its two lakes and a large, productive estuary. The Kitlope River empties into a 30 km long fjord (Gardner Canal) at 53°15' N, 127°55' W on the north coast of British Columbia (Fig. 1) and drains the largest catchment (3186 km²) within the largest contiguous area of undeveloped coastal temperate rainforest basins on Earth (Travers 1991).

The Kitlope watershed is the ancestral home to the Henaaksiala people, who in 1946 emigrated and amalgamated with the Haisla people to the north after their population was decimated by epidemics (Pritchard 1977, Barbetti 2005). The basin was scheduled to be logged in the 1990s, but under pressure from the Haisla Nation and conservationists, West Fraser Timber Ltd. relinquished all harvest rights without compensation and the Kitlope watershed was given legislated protected status in 1994. The resultant Kitlope Heritage Conservancy

is adjacent to other large protected areas to the east, west, and south, forming a larger contiguous protected area of more than 17,000 km². While the Conservancy lands and waters are jointly managed by the B.C. provincial government and the Haisla Nation through the Kitlope Management Committee, Kitlope salmon populations are managed by the federal department of Fisheries and Oceans Canada (DFO). Recreational and subsistence fishing and hunting are permitted in the Conservancy, but fishers and hunters, predominantly from the Haisla Nation, are rare compared to less remote areas.

Although aquatic productivity in the Kitlope River is low (ultra-oligotrophic), five species of Pacific salmon support diverse and abundant predators (we observed evidence of bears, seals, Bald Eagles, and wolves feeding on salmon) and ongoing subsistence, commercial, and recreational fisheries. Other salmonid fishes present in the Kitlope are Dolly Varden (*Salvelinus malma*), steelhead (*O. mykiss*), and coastal cutthroat trout (*O. clarkii clarkii*).

Sockeye and coho (*O. kisutch*) are the most abundant and commonly harvested salmon in the system. The Kitlope sockeye population is substantially larger (10–100x) than any other in the Area 6 fisheries management region (Fig. 1; DFO, *unpublished data*). Kitlope sockeye are used by DFO as an “indicator” stock for this region, and the dominant lake-spawning sockeye comprise a Conservation Unit under Canada’s Wild Salmon Policy (DFO 2005). Annual sockeye returns to Kitlope Lake have been trending downward since the mid-1980s (Fig. 2), with a mean decline rate of 61% over the past three sockeye generations analyzed (1990–2005: Rand 2008). Returning spawners have not met DFO’s Management Target Escapement with any consistency since the 1960s (Fig. 2), similar to most salmon stocks in the region (Price et al. 2008).

In an effort to boost sockeye production, Kitlope Lake was artificially fertilized with ammonium nitrate and ammonium phosphate from 1979 to 1985. Phytoplankton and zooplankton abundance and sockeye fry size all increased in the two-year sampling period after fertilization began, but due to a limited sampling effort prior to fertilization (1 year), it is unclear whether the fertilizer applications led to increased fry and smolt production and/or survival (Shortreed et al. 2001).

Fig. 1. Location map with top portion showing the 3200 km² Kitlope drainage basin and protected area boundary (solid black line) and (1) Kitlope Lake, (2) Kitlope River mouth/estuary, (3) Kemano River estuary and village site, (4) entrance to Gardner Canal, (5) Kitimat River estuary and hatchery, (6) Douglas Channel, and (7) former Butedale cannery site. The dashed line demarks the marine boundaries of federal fisheries Management Area 6.

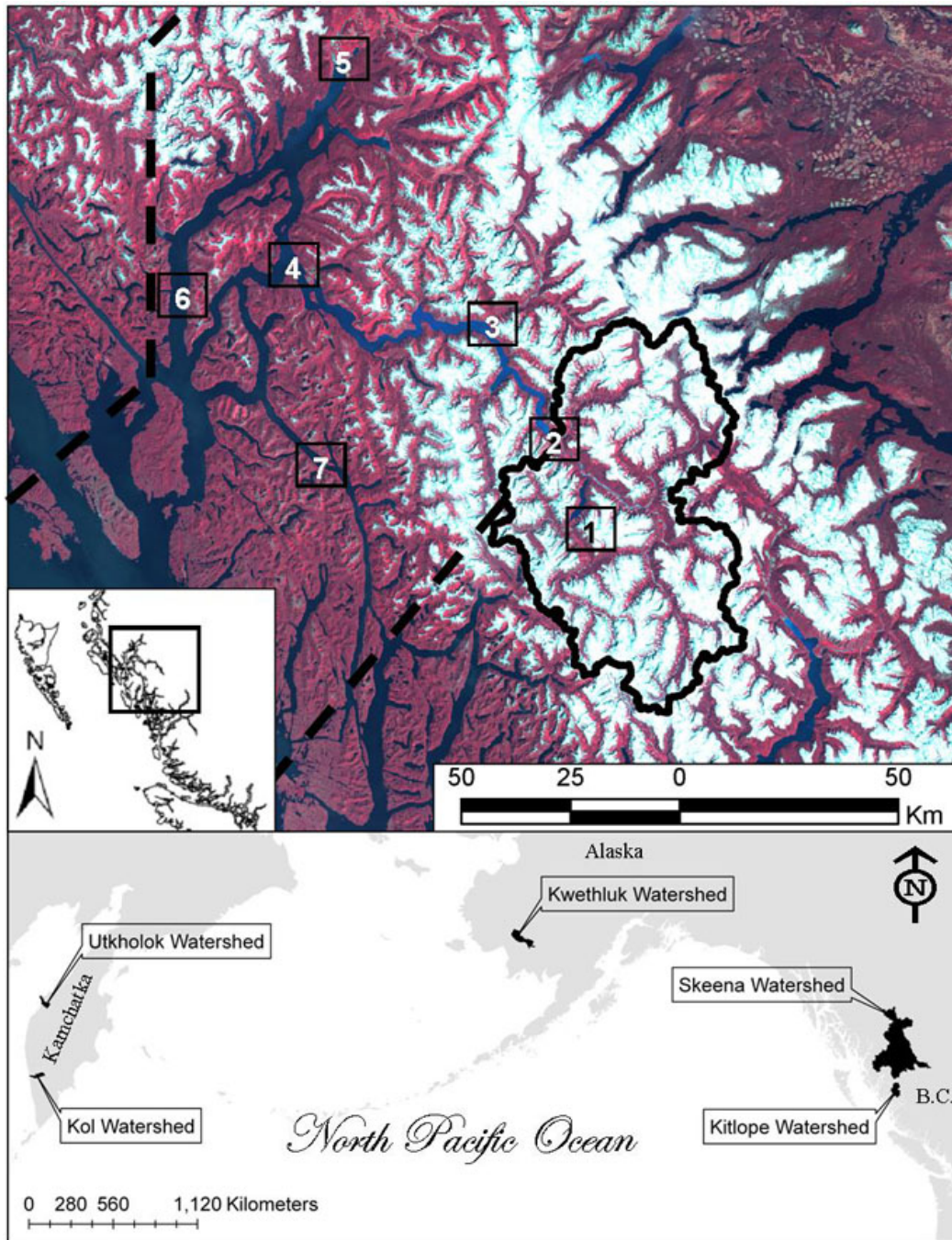
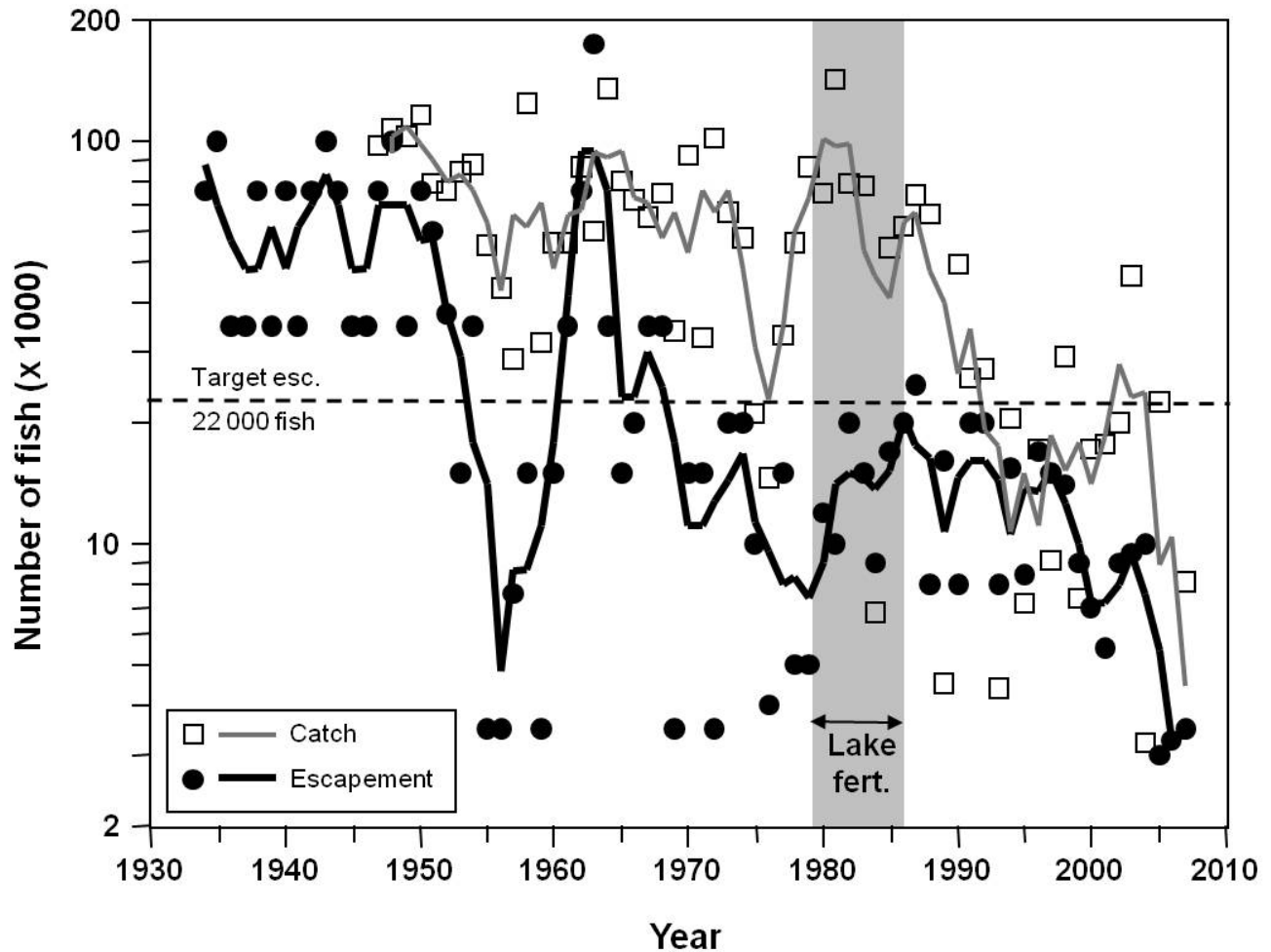


Fig. 2. Estimated escapement of Kitlope River sockeye salmon (1934–2007) and commercial sockeye catch (seine + gillnet + troll) from coastal approach waters (Management Area 6; 1947–2007; DFO, unpublished data). Lines represent 3-year running averages, the shaded area represents the period of artificial lake fertilization, and the dashed line represents the management target escapement. Note log10 scale.



Other salmon stocks (pink [*O. gorbuscha*], chum [*O. keta*], Chinook [*O. tshawytscha*]) also appear to be declining, depressed, or fluctuating at low abundance (with occasional exceptions), although numerical escapement data are inconsistent or non-existent (Riddell 2004; DFO, unpublished data). As of 2004, Kitlope River Chinook salmon were considered “very depressed” based on available data (Riddell 2004), but escapements have not been routinely estimated since 1999. Data are insufficient

to discern any long-term trends in pink, chum, and coho stocks, but the limited spawning surveys conducted by DFO, the Haisla Fisheries Commission, and researchers from the Salmonid Rivers Observatory Network suggest that DFO escapement targets routinely are not met.

The Kitlope watershed was a study site (observatory) for the Salmonid Rivers Observatory Network (SaRON), a research program of the

Flathead Lake Biological Station of the University of Montana, from 2004 to 2008 (University of Montana 2010). The five primary SaRON watersheds are the Kitlope and Skeena Rivers, B. C.; Kwethluk River, southwest Alaska; and the Kol and Utkholok Rivers, Kamchatka, Russia (Fig. 1). These rivers were selected primarily for their abundant, complex, and intact floodplain habitats with minimal near-term development threats, which allowed for long-term study of natural ecosystem processes, and for their regional representation of habitat characteristics and composition. Within each observatory watershed, a floodplain study reach was selected for extensive biological and physical sampling. Study reaches ranged from 20 to 80 km in length and were selected for having comparable physical characteristics to one another, such as habitat diversity and complexity and proximity to tidewater relative to watershed size.

METHODS

To describe the biophysical attributes of the Kitlope watershed that confer both resilience and precariousness upon the Kitlope's anadromous salmon, we collected and synthesized information on juvenile salmonid density, habitat complexity, aquatic production indicators, marine nutrient subsidies, and external factors such as salmon harvest and climate change. In order to present these salient biophysical attributes of the Kitlope River in a basin-wide comparative context, we synthesized data (2004–2006) collected at the five SaRON sites around the Pacific Rim. Additionally, we collected and interpreted past published studies conducted in the system (Rosberg et al. 1982, Stockner et al. 1993 and references therein, Hill et al. 2009), and unpublished agency data and reports, and we collected local and traditional ecological knowledge from Haisla elders and fishermen.

Physical habitat characteristics

Classified multispectral satellite (Quickbird) images (Lorang et al. 2005) of the floodplain study reaches were used to produce comparative data on river complexity, specifically channel separations and returns (nodes) per kilometer and floodplain area (%) covered by vegetation (a proxy for relative flood disturbance severity) and driftwood jams (important juvenile salmon habitat: Fausch and Northcote 1992).

Regional climate

To assess regional climate patterns, mean daily air temperature data (1951–2006) were obtained from an Environment Canada weather station 46 km north of Kitlope Lake, and missing monthly values were excluded or replaced with interpolated (5-point average) values. Pacific Decadal Oscillation (PDO) index values – indicators of Pacific Ocean climate variability affecting salmon production (Mantua et al. 1997) – were obtained from the website of the Joint Institute for the Study of Atmosphere and Oceans (JISAO 2007).

Water quality, marine-derived nutrients, and food web characteristics

Water quality samples and leaves from dominant non-nitrogen fixing riparian tree and understory species were collected at the five SaRON rivers from May to October 2004–2006 (2005–2006 for Skeena), using a single standardized sampling protocol. At each river, two individual locations accessible to spawning salmon were selected for repeated sampling in each of the following habitats: orthofluvial spring brooks, parafluvial spring brooks, and main channel shallow shorelines (defined in Stanford et al. 2005).

We synthesized data from the following water quality variables to compare aquatic habitat characteristics among study rivers: water temperature, dissolved nitrogen (ammonium, nitrate/nitrite), soluble reactive phosphorus, and specific conductance. For this paper, we restricted our data synthesis to shallow shoreline habitats to simplify comparisons among rivers. We also obtained water quality data from Kitlope Lake (Stockner et al. 1993; A.C. Hill, *unpublished data*) and from a 48-year radioisotope-dated sediment core that was extracted in June 2005 from Kitlope Lake in order to examine historic changes in lake algal production and marine-derived-nutrient import in relation to sockeye salmon returns and climate change (Hill et al. 2009).

All vegetation samples were collected from riparian areas adjacent to the sampling sites used for fish and water variables. Foliar $\delta^{15}\text{N}$ in the plant leaves, measured using standard methods (Morris 2008), allowed us to compare marine nitrogen import across study sites. Food web sampling at these sites also included measures of periphyton biomass and

benthic invertebrate size and density as proxies for productivity.

Kitlope River salmon populations

Juvenile salmonid densities (fish per square meter) were measured 2–3 times annually at all study rivers by multi-pass depletion electrofishing (May–Oct. 2005–2006 [Skeena] and 2004–2006 [all other rivers]) using a standardized sampling protocol at the same main channel shallow shoreline sites selected for water and vegetation sampling (*Methods: Water quality, marine-derived nutrients, and food web characteristics*). Juvenile salmonid densities were calculated using Bayesian statistical population estimates (Wyatt 2002).

We obtained local salmon escapement estimates based on visual counts of spawners (Spilsted and Spencer 2009), commercial fishery catch data from DFO databases for 1950–2005, and additional data from unpublished annual DFO fishery reports dated back to 1934 (B. Spilsted, DFO, *personal communication*). Error in the escapement data is unknown; nonetheless, these estimates were considered suitable by DFO for interpreting long-term patterns in spawner abundance (Riddell 2004).

Local and traditional ecological knowledge

We supplemented the catch, escapement, and climate data with local and traditional ecological knowledge gathered through semi-directed interviews (Huntington 2000) with six Haisla elders (Table 1). Participants were asked questions by the primary author regarding their memories of salmon population and fishery dynamics within Haisla and Henaaksiala ancestral territory. Questions emphasized sockeye fishing in Gardner Canal and various fishing localities in the Kitlope watershed because sockeye are usually the favoured subsistence food fish harvested in the system by Haisla people. Questions also focused on regional climate dynamics. The interviewees each had extensive firsthand and hereditary (traditional) knowledge of the Kitlope and Gardner Canal area, as well as firsthand, multi-year experience in the commercial fishing industry.

RESULTS

Physical habitat characteristics

Our proxy for habitat complexity (nodes per kilometer) ranked the Kitlope River in the upper third of values (10 of 33) for North Pacific Rim rivers that we analyzed (J.A. Stanford, *unpublished data*) and put the Kitlope in the upper range of the five SaRON rivers (Table 2). Driftwood jams were notably abundant and populated with very large boles throughout the system. Indeed, nearly 1% of our floodplain study reach, measured from valley wall to valley wall, was covered by large driftwood deposits (Table 2). Qualitative snorkelling surveys and fry trapping showed that the driftwood deposits within the channel network were preferred habitats for coho and Chinook fry and parr relative to adjacent pools without wood. Quantitative estimates of available spawning habitat do not exist for the Kitlope River and its tributaries; however, it appears to be abundant (Rosberg et al. 1982, Travers 1991) but underutilized, owing to depressed and/or declining stocks.

Headwater glaciers ensure moderate-high flows and cool water temperatures in the Kitlope River during the warm summer months after the melt of the seasonal snow pack (Table 2). Floods typically occur at least once during both the spring melt and fall spawning seasons in this system (G. Amos, C. Paul Sr., *personal communication* [Table 1]; *personal observations*), similar to the nearby Kemano River (Fig. 1; Environment Canada hydrology data), causing strong scouring, and resulting in a higher proportion of water and cobble to vegetated cover in the floodplain compared to the other four study rivers (Table 2). Redd scouring during floods is known to increase egg mortality (Montgomery et al. 1996) and suspension of fine sediments, which reduces light penetration.

Regional climate

Mean annual air temperatures were significantly correlated with PDO index values for the period 1952–2006 ($r = 0.48$, $P < 0.001$ for first-difference residuals; Fig. 3; Hill et al. 2009), confirming strong coherence between local and oceanic climate patterns. A clear warming trend occurred in the region beginning with the c.1976 climatic regime shift (Fig. 3), and according to all Haisla elders we

Table 1. Members of the Haisla First Nation who were interviewed for local and traditional knowledge of Kitlope River salmon, associated fisheries, and local climate trends.

Initials	Given Name	Haisla name	Haisla title
JW	John Wilson	Sunahead	Hereditary Chief; Elder
BW	Beatrice Wilson		Elder
KH	Ken Hall	C'ekwikas	Hereditary Chief; Elder
CP	Cecil Paul Sr.	Wahxed	Elder
GA	Gerald Amos	Ga Gaum Guist	Elder
GS	Glen Smith		Elder

interviewed, annual ice-free periods in Gardner Canal (as a proxy for Kitlope Lake) increased concordantly.

Water quality, marine-derived nutrients, and food web characteristics

The Kitlope River exhibited the lowest carbon and dissolved ion (specific conductance) concentrations and a colder annual water temperature maximum compared to the other SaRON sites; however, concentrations of ambient nutrients (nitrogen and phosphorus) were similarly low in the Skeena and Kwethluk Rivers (Table 2). Seasonal minimums for soluble reactive phosphorus, nitrate/nitrite, ammonia, and total and dissolved organic carbon in the Kitlope River were less than or equal to those in any other SaRON study river (Table 2). The Kitlope also exhibited comparatively high light limitation due to high inputs of glacial sediments (Stockner et al. 1993; *personal observations*). Likewise, Kitlope Lake was cold, weakly stratified, glacially turbid, mildly acidic, poorly buffered, and fast flushing, with ambient phosphorus concentrations often below detection limits (Stockner et al. 1993; Table 3).

Recent import of marine-derived nutrients to the Kitlope River via returning adult salmon appeared to be negligible. The mean (\pm SD) $\delta^{15}\text{N}$ from leaves of Kitlope River riparian vegetation (-4.11

$\pm 1.94\text{‰}$) was substantially lower than that measured not only at other SaRON rivers (Table 2) but also at other salmon rivers around the Pacific Rim, and was even lower than reference sites without salmon ($-1.4 \pm 1.6\text{‰}$; Morris 2008). Indeed, the mean value for temperate forests is -2.8‰ (Martinelli et al. 1999). Moreover, sedimentary $\delta^{15}\text{N}$ in Kitlope Lake was among the lowest yet recorded in a sockeye nursery lake ($\sim 0\text{‰}$; Hill et al. 2009 and references therein). However, order-of-magnitude changes in sockeye escapements in the early 1960s (Fig. 2) coincided with the largest changes in $\delta^{15}\text{N}$ and proxy measures of lake algal production (carbon/nitrogen ratio and fossil pigment concentrations) that we observed in our lake sediment core, suggesting that the marine nutrient subsidy provided by large salmon returns can boost fertility in Kitlope Lake (Hill et al. 2009).

Instream production is low in the Kitlope River due to nutrient, carbon, light, and temperature limitations and high flushing rates (Table 2). Standing crops of periphytic algae from main channel riffles were low (3.48 mg C m^{-2}) and benthic invertebrates in mainstem riffles were sparse (38.1 ± 36.6 SD individuals m^{-2}), small, and less diverse than in any of the other SaRON rivers (J.A. Stanford, *unpublished data*). In 1978–1980, DFO researchers found lake plankton biomass to be low and species poor, and chlorophyll concentration and primary production were among the lowest measured in any B.C. sockeye nursery lake (Stockner et al. 1993, Shortreed et al. 2001, A.C. Hill, *unpublished data*;

Table 2. Measures of habitat complexity, water quality, fish density, and marine-derived nutrients among five pan-Pacific Rim sites in the Salmonid Rivers Observatory Network (SaRON). Water chemistry values are means \pm standard deviation, with range below. Bracketed values are sample sizes. Fish and water quality data are from main channel shallow shoreline sites only. Vegetation species/types sampled: Co = cottonwood (*Populus* spp.); W = willow (*Salix* spp.); D = red osier dogwood (*Cornus sericea*); F = *Filipendula kamtschatica*; Bl = Arctic blackberry (*Rubus arcticus*); Bi = paper birch (*Betula papyrifera*); G = grass (Poaceae); Sa = salmonberry (*Rubus spectabilis*); E = elderberry (*Sambucus* spp.); Se = *Senecio cannabifolius*; Ch = *Chosenia arbutifolia*; N = stinging nettle (*Urtica dioica*). All data are from SaRON 2004–2006 except for Skeena River (data from 2005–2006) and * Riverscape Analysis Project (2010); ** Quickbird floodplain imagery (Lorang et al. 2005).

	Kitlope	Skeena	Kwethluk	Kol	Utkholok
Latitude *	53°15' N	54°12' N	60°49' N	53°49' N	57°43' N
Longitude *	127°54' W	129°35' W	116°24' W	155°57' E	156°52' E
Catchment area (km ²) *	3206	51,383	3787	1502	1371
Channel complexity (nodes per kilometer) **	18.03	21.65	21.49	16.32	4.96
Non-vegetative cover of floodplain study reach **	49%	44%	11%	8%	18%
Large wood cover of floodplain study reach **	0.88%	0.55%	0.01%	n/a	n/a
Annual max. water temp. (°C)	13.5	16.8	16.8	15.1	18.8
Nitrate and nitrite ($\mu\text{g L}^{-1}$)	23.63 \pm 23.60 (13) 88.40 – 96.32	19.80 \pm 11.60 (9) 7.53 – 47.53	14.52 \pm 6.50 (52) 4.94 – 40.52	167.23 \pm 129.27 (27) 8.84 – 591.02	51.65 \pm 42.79 (18) 0.49 – 118.658
Ammonium ($\mu\text{g L}^{-1}$)	19.21 \pm 43.18 (26) 0 – 206.59	13.23 \pm 13.81 (52) 0 – 67.42	13.45 \pm 13.81 (78) 0 – 65.30	241.26 \pm 307.12 (123) 0 – 2600	45.57 \pm 28.89 (29) 9.22 – 151.64
Soluble reactive phosphorus ($\mu\text{g L}^{-1}$)	4.53 \pm 5.16 (13) 0.71 – 15.55	2.29 \pm 1.56 (9) 0.40 – 5.18	3.28 \pm 1.44 (52) 0.51 – 66.54	13.95 \pm 14.59 (28) 5.20 – 77.35	26.05 \pm 27.18 (18) 7.06 – 107.14
Total organic carbon (mg L ⁻¹)	0.79 \pm 0.56 (11) 0.17 – 1.65	1.33 \pm 0.66 (9) 0.56 – 2.42	2.43 \pm 1.66 (51) 0.77 – 6.98	1.32 \pm 0.38 (4) 1.02 – 1.86	8.92 \pm 4.53 (14) 3.02 – 17.74
Dissolved organic carbon (mg L ⁻¹)	0.47 \pm 0.47 (24) 0 – 1.72	1.11 \pm 0.64 (24) 0.26 – 2.69	1.92 \pm 1.42 (77) 0.36 – 6.49	1.75 \pm 0.82 1.03 – 3.56	7.46 \pm 0.64 0.26 – 2.69
Specific conductance (μS)	15.8 \pm 2.1 (22)	68.9 \pm 5.9 (28)	105.8 \pm 7.7 (87)	54.7 \pm 6.9 (129)	71.8 \pm 14.1 (98)

(con'd)

Juvenile salmonid density (fish per square meter)	0.14 ± 0.08 (19)	0.20 ± 0.10 (11)	2.59 ± 5.70 (16)	3.71 ± 3.13 (16)	3.13 ± 4.04 (17)
Riparian plant foliar δ ¹⁵ N (‰)	-4.11 ± 1.94 (74) -5.83 - -3.73	-1.36 ± 1.05 (54) -2.47 - -0.06	0.56 ± 1.48 (57) -2.70 - 1.55	3.32 ± 1.52 (74) 3.29 - 4.43	3.85 ± 2.20 (21) 1.38 - 5.58
Plants sampled for δ ¹⁵ N	Co, E, G, D, Sa, W	Co, G, D, W	Bi, G, Bl, W(3), Co	Ch, G, F, Se, N, W	G, F, W

Table 3). However, the sediment core from Kitlope Lake indicated that the recent warming trend (Fig. 3) increased aquatic production potential (Hill et al. 2009), possibly increasing the forage base for juvenile salmon (as in Schindler et al. 2005).

Kitlope River salmon populations

The spatial and life history diversity of salmon stocks in the Kitlope watershed appeared to be moderate. All five species were known to spawn at accessible locations throughout the catchment, and Chinook and sockeye appeared to employ multiple life history strategies (Rosberg et al. 1982; *personal observations*). We observed lake-type sockeye spawning on numerous alluvial fans on the shoreline of Kitlope Lake and in spring-fed and mainstem channels upstream from the lake, as well as in the lake outlet. We also observed a small number of presumed river-type sockeye spawning in spring-fed channels in the upper Kitlope River. Age composition among Chinook was found by Rosberg et al. (1982) to include both river-type (overwintering) and ocean-type (early smolting).

Juvenile salmonids in Kitlope River electrofishing surveys consisted of *O. kisutch* (52%), *O. mykiss* (33%), *O. tshawytscha* (10%), *S. malma* (3%), and *O. clarkii clarkii* (2%); these and additional salmonid species were encountered in the other study rivers. Except for the Skeena River, estimated mean juvenile salmonid densities in main channel shallow shoreline habitats were more than an order of magnitude lower in the Kitlope River than in the other SaRON rivers (Table 2). For all riverine habitats sampled (main channel shallow shoreline, orthofluvial springs, parafluvial springs), the combined mean (± SD) salmonid density in the Kitlope River (n = 36) was 0.32 ± 0.27 fish per square meter versus 2.55 ± 2.98 fish per square

meter for the other four SaRON rivers combined (n = 224).

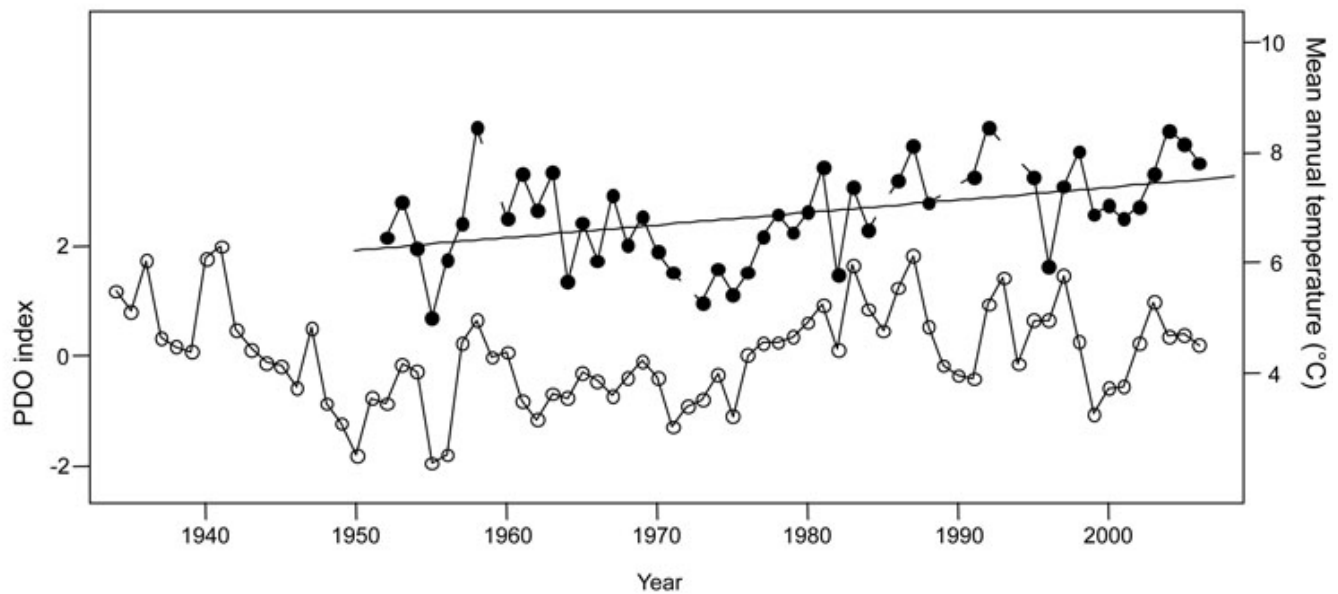
Earlier studies by DFO showed that mean (and 95% CI) sockeye smolt weight (2.14 ± 0.30 g; N = 25) and estimated density (310 fish per hectare) in Kitlope Lake were among the lowest measured for any large sockeye nursery lake in British Columbia, presumably as a result of the low aquatic productivity due to cold temperatures, poor light penetration, and high flushing rates (Hyatt and Stockner 1985, Shortreed et al. 2001). Historic estimates of juvenile salmon density cannot be compared with these recent data because they do not exist for Kitlope River and Lake.

All Haisla interviewees stated that salmon abundance in the Gardner Canal area has declined substantially over their lifetimes, corroborating trends in DFO escapement data for sockeye (Fig. 2). For example, when asked about trends in Kitlope Lake sockeye, C. Paul Sr. described recent returns as being “almost down to zero” compared to those in his youth, and G. Smith stated that these runs had become “a lot smaller...a lot (original emphasis)” over his lifetime with the most recent years being the worst. Today it is difficult and rare for Haisla fishers to obtain subsistence salmon catches in the Kitlope watershed on par with amounts commonly obtained in past decades (C. Paul Sr., G. Amos, G. Smith, J. Wilson, *personal communication*; Table 1).

Management characteristics of the Kitlope ecosystem

The freshwater habitat of Kitlope River salmon is entirely protected, but fisheries were and often still are a significant source of salmon mortality. Until 1955, targeted commercial fisheries were

Fig. 3. Mean annual air temperature (solid circles) at Kemano (53°33.8' N, 127°56.9' W, elevation 87 m above sea level, data from Environment Canada), and mean annual Pacific Decadal Oscillation (PDO) index values (Source: University of Washington Joint Institute for the Atmosphere and Oceans; open circles) (rtemp-PDO = 0.48, $P < 0.001$, for 1st-difference residuals). Originally published in Hill et al. 2009 by NRC Research Press.



conducted at the mouth of Gardner Canal (seine) and in the Canal itself (gillnet). Interviewee narratives from the 1920s and 1930s described large harvests of Kitlope-bound sockeye in the commercial fishery. The earliest account was relayed by G. Amos, whose uncle noted from reading log books at the Butedale cannery (Fig. 1) in the 1920s and 1930s that seine boats took up to 20,000 sockeye per cumulative net-set at the entrance to Gardner Canal, delivered the fish to the cannery, and returned for an equivalent catch in the same day. Conservation concerns for numerous local stocks, including Kitlope sockeye (Fig. 2), led to a moratorium on these fisheries in 1955, which has never been lifted (C. Paul Sr., G. Amos, J. Wilson, *personal communication*; DFO, *unpublished data*). Since then, the fishery has been conducted primarily in the coastal approach waters to Douglas Channel (i.e., west and northwest of Butedale in Fig. 1), where interceptions of Kitlope-bound fish occur. However, harvest rates of Kitlope salmon in these fisheries are uncertain due to a lack of stock-specific

catch data (i.e., identification using genetic markers). According to low-resolution genetic data collected through the Canada-U.S. salmon treaty, Kitlope-bound sockeye also appear to be intercepted in other B.C. coastal fisheries further to the north (DFO, *unpublished data*, methods in Beacham et al. 2005).

A cannery (Price and Co.) operating near the Kitlope River estuary from 1890 to 1893 had annual packs averaging 191,840 kg, most of which were likely sockeye (Lyons 1969, Pritchard 1977), which translates to ~53,000 fish per year based on conversion factors in Argue and Shepard (2005). Total production (catch + escapement) for Kitlope Lake sockeye has likely not exceeded 20,000 fish during the most recent decade (Fig. 2), although the lack of stock composition data for the mixed-stock commercial and aboriginal catches preclude a reliable estimate of annual production of Kitlope sockeye.

Table 3. General limnological information for Kitlope Lake. The 1978–1980 data are means from weekly sampling through the growing season taken from Stockner et al. (1993); our 2005 data are means from four sampling events (7/05, 8/02, 8/23, 9/26) for nitrogen (N) and phosphorus (P) and two additional sampling events (5/30, 6/18) for all other variables. Originally published in Hill et al. 2009 by NRC Research Press.

	1978 (Unfertilized)	1979–1980 (Fertilized)	2005
Total nitrogen ($\mu\text{g N L}^{-1}$)	--	--	121.4
Mean epilimnetic nitrate ($\mu\text{g N L}^{-1}$)	19	18	48
Total phosphorus ($\mu\text{g P L}^{-1}$)	1.5 – 8.0	--	7.1
Soluble reactive phosphorus ($\mu\text{g P L}^{-1}$)	< 1	< 1	2.0
Chlorophyll ($\mu\text{g L}^{-1}$)	0.56	0.60 – 1.10	0.96
Total alkalinity ($\text{mg CaCO}_3 \text{ L}^{-1}$)	1.6	1.5	--
Daily photosynthetic rate (mg C m^{-2})	54	65	--
Zooplankton biomass (mg dry wt m^{-2})	53	88	--
Euphotic zone (m)	7.6	8.6	9.7
Secchi disk depth (m)		1 – 6 m	1.3 – 4.2 m
Turbidity (NTU)	--	--	2.18
Seasonal average surface temp. ($^{\circ}\text{C}$)		10.5	15.3
pH	6.22	6.10	6.46
Specific conductance (μS)	--	--	8.21

DISCUSSION

In the context of salmon ecology, the Kitlope watershed features an interesting dichotomy of resilience and precariousness attributes (Table 4). Resilience is likely fostered by the large size of the catchment, its protected status, and its complex, connected habitats for salmon. These habitats are produced by the natural interaction of flooding, sediment and driftwood loading, and rain forest succession on the expansive floodplains. This shifting habitat mosaic is considered essential to the maintenance of natural riverine biodiversity and bioproductivity (Stanford et al. 2005), and is synonymous with resilience in salmon ecosystems (Bisson et al. 2009, Waples et al. 2009).

In contrast, the Kitlope's aquatic ecosystem is glacially turbid, cold, and ultra-oligotrophic – potentially precarious conditions for salmon, especially if salmon populations are weakened by decades of over-exploitation by humans. These same salmon must also contend with the rigors of density-dependent food web interactions in an unforgiving marine environment (Ruggerone and Nielsen 2004), as well as warming sea surface temperatures in the North Pacific, and other changing ocean conditions stemming from unprecedented global warming (reviewed by Chittenden et al. 2009).

Precariousness could be buffered by the persistence of salmon populations with diverse life histories

Table 4. Summary of attributes likely to foster resilience and precariousness in Kitlope River salmon populations.

Resilience attributes	Precariousness attributes
Size (abundant habitat)	Poor aquatic growing conditions
Undeveloped/ protected status	- Low background nutrient concentrations
Water quality: no eutrophication or pollution	- Low primary and secondary production
Habitat complexity	Hydrology
- Moderate to high floodplain channel complexity	- Flashy hydrograph
- Array of habitat types	- Fast flushing
Hydrology	Low juvenile salmon abundance compared to other systems
- Glaciers maintain flows during warm summer/fall months	Constraints on adult spawning success (harvest, ocean climate, and food web dynamics)
- Natural flow variability	Climate: warming trend is likely to change system hydrology and salmon production through multiple pathways at multiple scales
Biological complexity	
- Multiple salmon species with multiple life history strategies	
Climate: warming trend is increasing production potential	

alternating contributions to overall production in the watershed ecosystem (Hilborn et al. 2003). While life history diversity certainly exists within some Kitlope salmonid populations (Rosberg et al. 1982; C. Paul Sr., G. Amos, *personal communication*), this aspect of their ecology has not been thoroughly documented. In any case, existing quantitative and qualitative data indicate that annual returns of all five species of salmon to the Kitlope River are declining or depressed. Therefore, simply placing a protected area umbrella over the watershed may not by itself mitigate other important factors that constrain salmon production.

Merits and limits of ecosystem protection

The creation of the Kitlope Heritage Conservancy protected area has clearly fostered social resilience and human “response diversity” (concept discussed in Bottom et al. 2009). For example, the Conservancy provides an important venue for the dissemination and maintenance of Haisla local and traditional ecological knowledge through cultural

rediscovery field camps for children (Lertzman 2002) and local field-based college courses where Haisla and non-Haisla students are exposed to traditional and scientific ecological knowledge in an integrated framework. Numerous Haisla and non-Haisla people have enjoyed employment as watchmen (also known as park rangers), field scientists, research technicians, and ecotourism guides in the Conservancy.

Ecologically, the protection of such a large, intact watershed adjacent to other large protected areas has obvious potential benefits, such as the provision of diverse and connected habitats for wide-ranging vertebrates (Noss et al. 1996). Moreover, it is difficult to overstate the inherent benefits that accrue to salmon and salmon consumer species by simply making a large alluvial river system, including 94 km² of complex floodplain, more than 200 km of mainstem river (J.A. Stanford, *unpublished data*), and an estuarine landscape off limits to human settlement and industrial development (Lichatowich et al. 2000, Mantua and Francis 2004). Indeed, many river systems in the

region with similar geomorphology, geochemistry, hydrology, and historic salmon runs have suffered substantial reductions in floodplain habitat and increases in sedimentation as a result of logging and associated road building (Gottesfeld and Rabnett 2008).

While not a result of ecosystem protection, the absence of a salmon hatchery in the watershed minimizes potential genetic introgression and competition from cultured stocks (reviewed by Naish et al. 2008), and the absence of salmon farms in the region reduces potential for sea lice-induced mortality of out-migrating smolts (Krkosek et al. 2007), providing *de facto* protections relative to many other salmon populations in British Columbia.

Despite the many inherent benefits of protected status for the Kitlope watershed and its component salmon populations, other factors appear to be constraining salmon production. Salmon population dynamics in general are strongly influenced by long-term, transoceanic climatic regimes and associated variations in productivity (Mantua et al. 1997, Beamish et al. 1999). Early marine residency is an especially crucial phase for salmon (Mueter et al. 2005, Pyper et al. 2005), and poor marine survival associated with climate change has been implicated in precipitous declines in major sockeye populations (Owikeno Lake, Long Lake) only 200 km south of the Kitlope (McKinnell et al. 2001, Riddell 2004). On the other hand, climate warming may be increasing the productivity of cold, ultra-oligotrophic Kitlope Lake (Hill et al. 2009) as has occurred in other sockeye nursery lakes (Schindler et al. 2005). However, warming air temperatures may be offset by hydrologic and thermal effects of glacial recession and changing precipitation patterns (Bryant 2009), combined with changing marine conditions, and ongoing fishing mortality. The net outcomes for salmon are decidedly uncertain.

Resilience of Kitlope salmon

Populations of many species exhibit low stability (i. e., large fluctuations) while remaining highly resilient (Holling 1973), and this is often the case among individual salmon populations (Quinn 2005). Maintenance of complexity and connectivity in freshwater and estuarine habitats is important for fostering resilience in salmon populations in an era

of increasingly unpredictable climatic variability, but such resilience is also fostered by maintaining biocomplexity through sustained spawning escapements (Mantua and Francis 2004). For example, Hilborn et al. (2003) demonstrated that the sustained productivity of the Bristol Bay, Alaska sockeye stock complex through numerous climatic regime shifts was a result of a management strategy that preserved biocomplexity within the larger aggregate population by curtailing fisheries on less productive (precarious) stocks. In turn, diverse and abundant salmon populations drive ecosystem processes in ways that directly and indirectly benefit many other species (Gende et al. 2002), and foster resilience in human communities (Bottom et al. 2009).

There is concern about Kitlope River salmon because recent stock status appears to have been concurrently poor to moderate among all species (i. e., usually < 50% of Management Target Escapement where estimates exist), rather than substantially variable among years and species. Moreover, many other wild salmon stocks in northern coastal British Columbia are also trending downward or fluctuating at low abundance relative to historic levels (Rand 2008, Walters et al. 2008), and less than 4% of monitored streams have consistently met escapement targets since 1950 (Price et al. 2008). Annual harvests of Kitlope River salmon in commercial and subsistence mixed-stock marine fisheries have not been precisely estimated, but given the poor escapements of multiple stocks, even moderate catches may represent inordinately high exploitation rates. In addition to the direct impact on population size, recruitment overfishing can jeopardize resilience of small populations through deleterious evolutionary effects (Hard et al. 2008).

From a watershed ecosystem perspective, reduced escapements of spawning salmon relative to historic levels may be exacerbating the already extreme paucity of ambient nutrients in the system. Indeed, the lack of a substantive marine nutrient subsidy in the Kitlope watershed was readily apparent in $\delta^{15}\text{N}$ values observed in lake sediments (Hill et al. 2009) and riparian vegetation – some of the lowest yet measured in a salmon-producing system. Given the known strong role of salmon nutrients in freshwater and riparian ecosystems (Gende et al. 2002), this nutrient deficit likely undermines the health and resilience of this ostensibly pristine watershed.

Conceptual foundation for management

In order to achieve greater efficacy as a salmon stronghold, the current management of the Kitlope ecosystem could benefit by addressing the current mismatch between the scale of anadromous salmon life cycles and ecological interactions, and the different scales at which salmon populations and ecosystems are managed (Bottom et al. 2009). The stronghold concept need not be confined to freshwater and the conceptual foundation for the management of the Conservancy should be explicitly holistic in the context of salmon life history requirements. Also, sources of mortality at key life stages should be quantified (Schindler et al. 2008) and minimized until stocks recover.

Relocation of fishing effort closer to or into rivers – and using low-mortality capture methods such as beach seines, tangle nets (Vander Haegen et al. 2004), fish wheels (Link and Peterman 1998), or fish traps (Stewart 1977) – is recommended elsewhere as a viable risk-averse alternative to mixed-stock gauntlet fisheries (Walters et al. 2008, Healey 2009). Such terminal and in-river fisheries also make it easier to obtain stock assessment data, especially in places like the Kitlope River where visual spawner counts are often hampered by turbid waters and difficult access. In the nearby Nass River, for example, stock assessment procedures employing mark-recapture population estimates from selective in-river fisheries have proven successful and economically superior to traditional stock assessment methods (Link and Peterman 1998).

CONCLUSION

The Kitlope experience suggests that large, undeveloped watersheds are necessary but not sufficient to ensure long-term sustainability of wild salmon. The adoption of a salmon stronghold strategy (Rahr and Augerot 2006) will likely foster resilience in North American salmon populations by guaranteeing an array of sustained, diverse, and abundant habitat in freshwater. However, the strategy is flawed without holistic, risk-averse management that identifies and protects against external “precariousness” factors, such as overfishing and competition and genetic introgression from artificially cultured stocks. Rigorous and routine evaluation of watershed ecosystem condition, including stock status and diversity, will

help in both the development of this resilience-based management strategy, and in understanding the success of the stronghold strategy.

We expect that resilient salmon river ecosystems will be characterized by a high degree of hydrologic and biogeochemical connectedness, a great diversity of locally adapted stocks, high egg-to-spawner survival, and generous transfer of marine nutrients to the riverine food web. Of course, achieving this will require that we prevent or minimize harmful human interventions such as overharvest, salmon culture operations, flow alterations, and other damage to habitat, and it will require that we uphold wild salmon as icons of social and ecological well-being.

Responses to this article can be read online at:
<http://www.ecologyandsociety.org/vol15/iss2/art20/responses/>

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