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Feature Article

Hyperstability in an inland recreational fishery: Are catch-per-unit-effort data masking the magnitude of steelhead declines?

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ABSTRACT

Objective: Recreational fisheries are complex social–ecological systems, with interactions and feedbacks across local and regional scales and among individual fish, anglers, and managers. Understanding the link between true fish abundance and angler catch per unit effort (CPUE) is crucial to inform management decisions in these systems, especially in the absence of independent monitoring data. For instance, the relationship between fish abundance and CPUE could be linear or nonlinear, such as a hyperstable relationship, which occurs when CPUE remains high even as population abundance declines. We investigated the relationship between fisheries-independent abundance and CPUE in steelhead *Oncorhynchus mykiss* and evaluated the extent to which hyperstability may obscure underlying population declines.

Methods: We analyzed the relationship between steelhead abundance and CPUE in 14 streams across the province of British Columbia, Canada. To explore the impact of hyperstability on our capacity to detect changes in abundance, we simulated three scenarios of steelhead decline, comparing the rate of change in CPUE versus abundance.

Results: Our findings revealed sweeping patterns of hyperstability, indicating that when populations are depressed, CPUE does not decrease as rapidly as abundance. Additionally, we found that the magnitude of CPUE overestimation varied with the extent of population decline. For example, when the population declined by 50%, CPUE decreased by only 40%, representing a 28% overestimation of remaining abundance. This disparity increased in more extreme scenarios of decline.

Conclusions: Our findings underscore that catch data can mask fish population declines and highlight the need for improved fish population monitoring in recreational fisheries.

KEYWORDS: angler behavior, hyperstability, *Oncorhynchus mykiss*, recreational fisheries, socio-ecological systems, steelhead

LAY SUMMARY

Limited fisheries-independent data exist for steelhead; therefore catch data often serve as a key source of information for many stocks. Due to hyperstability, catch rates may remain high even as fish numbers fall, masking true population declines and complicating conservation efforts.

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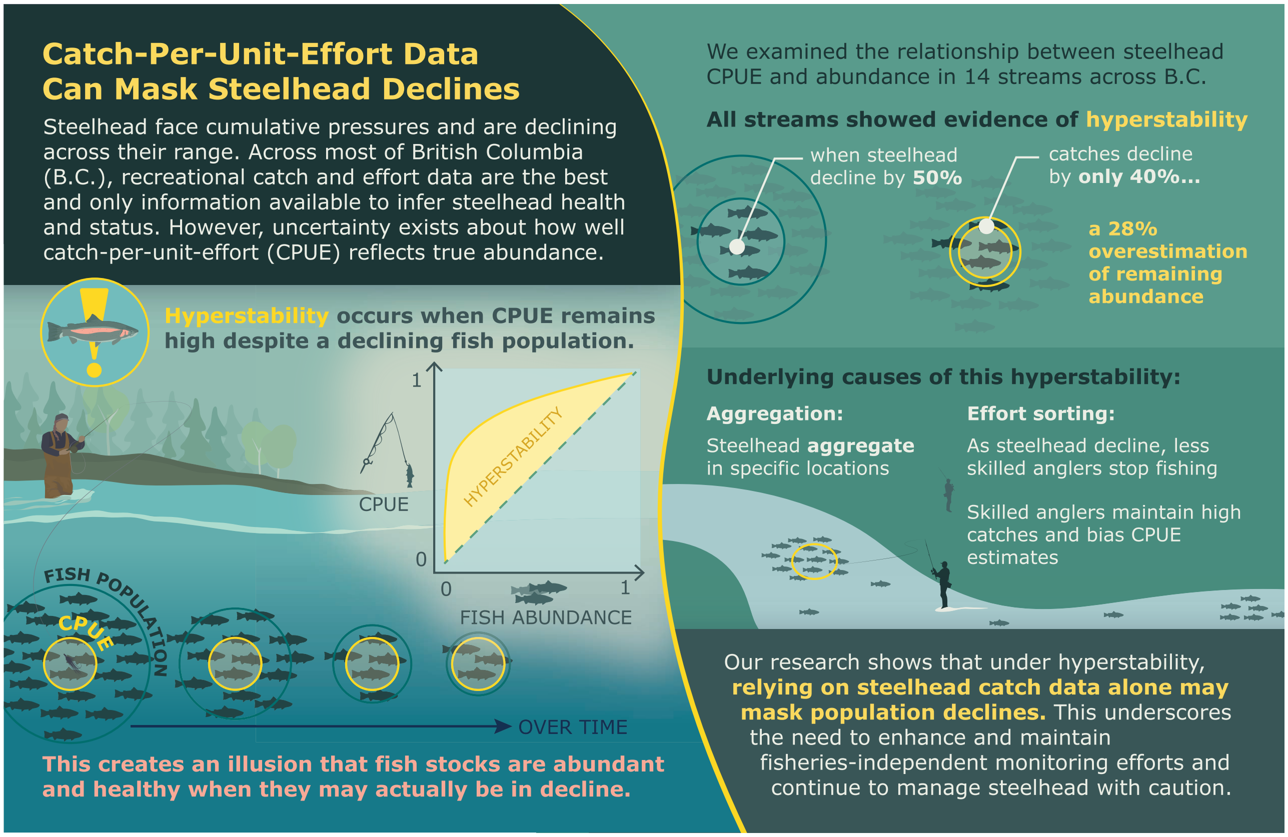
GRAPHICAL ABSTRACT



INTRODUCTION

Recreational fisheries represent complex socio-ecological systems with feedbacks among managers, anglers, fish, and the aquatic environment (Arlinghaus et al., 2017). Understanding the relationship between fish abundance and catch per unit effort (CPUE) is key to managing recreational fisheries, particularly in instances where fisheries-independent monitoring data are limited or nonexistent (Erisman et al., 2011). Although a linear relationship between abundance and CPUE is often assumed (Hilborn & Walters, 1992), this relationship can be nonlinear, reflecting hyperdepletion or hyperstability. Hyperdepletion occurs when CPUE declines more rapidly than abundance, resulting in a decrease in catches that is greater than the proportional reduction in population size (Askey et al., 2006). This can occur when individual fish vary in their susceptibility to capture and fish that are more susceptible are quickly harvested, resulting in a rapidly reduced pool of vulnerable fish and a corresponding decline in CPUE (Cox & Walters, 2002; Young & Hayes, 2004). Alternatively, instances in which CPUE declines less rapidly than abundance are categorized as hyperstable. In this case, catches remain high despite population declines, often due to the tendency for fish to aggregate and become more vulnerable to fisheries as abundance declines (Erisman et al., 2011) and/or the propensity for anglers with higher skill to keep fishing even when fish densities are low (Van Poorten et al., 2016). This creates an "illusion of plenty," where the stock is perceived to be healthy despite a potentially collapsing population (Post et al., 2002).

Relatively few studies have examined the strength of the relationship between wild fish abundance and CPUE in the context of recreational fisheries (Golden et al., 2022). When they have, they often find moderate levels of hyperstability (e.g., Erisman et al., 2011; Hansen et al., 2005; Mrnak et al., 2018; Peterman & Steer, 1981; Shuter et al., 1998; Ward et al., 2013), with comparatively fewer studies finding evidence of a linear relationship (e.g., Giacomini et al., 2020) or hyperdepletion (e.g., Alós et al., 2010; Pierce & Tomcko, 2003). Previous studies have generally focused on single species occupying inland lakes and over short time scales (e.g., 5–20 years or experiments spanning 3–4 months). As a result, numerous gaps remain in our understanding of hyperstability, including the relative strength of hyperstability across species or fisheries (Dassow et al., 2020), potential underlying mechanisms, and how hyperstability may be influenced by biological or fishery characteristics (e.g., different ecotypes; hatchery or wild origin).

Understanding whether fisheries exhibit hyperstability or hyperdepletion is of critical importance for conservation and management for two general reasons. First, this relationship will influence the vulnerability of fish populations to fishing. In systems with hyperstability, fish populations may continue to be exploited to a high degree, even as their populations decrease (Post et al., 2002; Stoeven, 2014). Indeed, while the number of recreational fishers has been increasing steadily in North America, the consequences of this increasing pressure and its impacts on aquatic ecosystems and organisms are still poorly understood in many systems (Post et al., 2008). Second, CPUE from catch and fishing effort data may be used to estimate stock abundance, status, or productivity (Harley et al., 2001). Under hyperstability or hyperdepletion, trends in CPUE could either mask or magnify true trends in abundance, thereby creating the risk of misinformed management.

Steelhead *Oncorhynchus mykiss* (anadromous Rainbow Trout) are among the most recreationally sought-after fish species in temperate western North America, such as in British Columbia (BC), Canada (Wilcove & Wikelski, 2008). While hyperstability has been documented for Rainbow Trout in BC lakes (Askey et al., 2006; Van Poorten & Post, 2005; Ward et al., 2013), little work has been focused on steelhead (Ahrens, 2006; Smith, 1999). In recent decades, shifts in factors impacting steelhead abundance, including marine survival and habitat degradation (Levy & Parkinson, 2014; Solomon et al., 2020), have increasingly threatened the viability of steelhead and their fisheries (Ahrens, 2006). Among the BC steelhead populations that have sufficient data to quantify biological status, 86% (6 of 7) were recently classified as having a "poor" status (Salmon Watersheds Program, 2024), including two populations that were formally assessed as endangered by the Committee on the Status of Endangered Wildlife in Canada (Committee on the Status of Endangered Wildlife in Canada, 2020). Despite these declines, the province of BC continues to attract over 21,000 steelhead anglers annually, and the total annual economic expenditure of freshwater anglers in BC can exceed Can$500 million in revenue (Bailey & Sumaila, 2012).

In the absence of independent monitoring of fish abundance, angler catch and effort data often represent the sole information available to assess the status of recreational fish populations such as steelhead. The province of BC has a large data set of steelhead recreational catch and effort data: the Steelhead Harvest Questionnaire (SHQ), a mail-out survey initiated in 1966/1967. The data set spans 442 steelhead-bearing streams across BC (Hagen et al., 2012), providing a unique opportunity to examine relationships between abundance and CPUE over a long time period and a broad geographic area. Our study of this relationship is timely, given widespread declines in steelhead across their range (Kendall et al., 2017) and their importance for recreational and First Nations fisheries. Changes in hatchery practices, regulations, and angler-related variables (e.g., skill, method, and response bias), coupled with the potential for hyperstability, raise concerns about the use of CPUE as an index (Smith, 1999).

Here, we quantify the relationship between abundance and CPUE in a globally important recreational fishery. Specifically, we quantified the degree of hyperstability or hyperdepletion across 14 streams in BC that support steelhead populations and fisheries. We assessed various factors that contribute to the observed variability in CPUE, such as stocking practices and survey methodologies. Additionally, we investigated how observed patterns of hyperstability affect the ability to detect changes in steelhead abundance by simulating three alternative scenarios of steelhead decline. This work provides insights into the relationship between fisheries-independent abundance and CPUE and reveals sweeping patterns of hyperstability. Collectively, our findings shed light on the expected overestimation of steelhead abundance and the masking of declines if relying solely on catch rate data.

METHODS

Data

Fisheries-independent survey data

Our analyses relied on steelhead abundance estimates for 14 streams across the province of BC (Figure 1), spanning a time series ranging from 1972 to 2019 (Table 1). These data were leveraged from the Pacific Salmon Foundation's Pacific Salmon Explorer platform (Pacific Salmon Foundation, 2024; salmonexplorer.ca). This initiative centralizes and displays the best available data for Pacific salmon *Oncorhynchus* spp. in BC through an interactive, open-access Web-based tool and online data library (data.salmonwatersheds.ca/data-library/). The abundance data available on the Pacific Salmon Explorer were collected by the provincial Fish and Wildlife Branch and First Nations, including the Nisga'a Fisheries and Wildlife Department. The province is responsible for managing freshwater recreational steelhead fisheries and collects these data as part of its monitoring efforts. Abundance estimates are obtained through various methods, including visual surveys (conducted by helicopter or boat), swim surveys, mark–recapture, resistivity counters, and fishway counts. In some cases, a combination of these methods is employed (Table S1 [see online Supplementary Material]).

Fisheries-dependent CPUE data

Since 1966, the province of BC has been collecting angler catch and effort data through the SHQ, a yearly mail-out questionnaire sent out at the end of the angling license year, which spans from April 1 of one year to March 31 of the following year (for an example questionnaire, see Figure S1 [see online Supplementary Material]). The survey is sent to a subset of local and out-of-province licensed anglers who fished for steelhead in BC across five provincial regions: Lower Mainland, Vancouver Island, Thompson, Cariboo, and Skeena. Approximately half of BC resident anglers are surveyed, along with nearly all out-of-province anglers (De Gisi, 1999). The most recent report indicates that on average, the SHQ polls 19% of sport anglers (Ahrens, 2006). Anglers who participate in this survey are requested to report key information, including the name of the stream, the number of days spent fishing, and the counts of both wild and hatchery fish caught or released (where hatchery fish can be distinguished by the lack of an adipose fin).

The responses are stratified based on residency and are adjusted and computationally expanded to provide estimated provincial totals for the annual activity of all anglers targeting BC steelhead (De Gisi, 1999). With the exception of hatchery-supplemented runs (mainly in the south of the province), the fishery currently operates strictly under catch-and-release regulations. For the purposes of this analysis, CPUE estimates, specifically catch per angler-day by year and stream, for the 14 study streams were derived from the most recent SHQ data available (2022), acquired through a request to the BC Fish and Wildlife Branch (Table 1). The first year of the licensing season was selected (e.g., 2018 would be selected for the 2018/2019 season) to facilitate the comparison with the fisheries-independent data.

Figure 1. Map of the study area in British Columbia, including major cities, the streams included in the analysis ($n = 14$), and freshwater fishing management regions.

Table 1. Summary of British Columbia streams included in the analysis, with the associated ecotype (S = summer; W = winter; SW = both summer and winter), management region, time series (TS) properties (first year, last year, and TS length for years with available data), average abundance (*N*), average CPUE (fish/angler-day), average stocking (proportion of hatchery fish in the total catch), and survey score (each year is scored; this table represents the most common survey score in the TS). The Salmon River in reference is situated in region 1 (Vancouver Island).

Stream	Ecotype	Region	Start	End	TS length (years)	Average *N*	Average CPUE	Average stocking	Survey score
Atnarko River	SW	Cariboo	1977	2003	12	187.62	0.5	0.00	5
Bulkley River	S	Skeena	1999	2012	14	23,810.83	1.04	0.02	1
Cheakamus River	W	Lower Mainland	1996	2020	24	421.45	0.28	0.06	3
Chilcotin River	S	Cariboo	1972	2016	49	918.83	0.68	0.02	1
Englishman River	W	Vancouver Island	1982	2019	39	449.17	0.4	0.24	3
Gold River	SW	Vancouver Island	1975	2020	49	252.36	1.11	0.02	5
Gordon River	SW	Vancouver Island	1985	2018	25	300.09	1.2	0.06	5
Heber River	S	Vancouver Island	1975	2020	46	252.25	1.29	0.02	5
Keogh River	W	Vancouver Island	1976	2011	45	668.5	1.03	0.33	2
Kloiya River	W	Skeena	2006	2016	10	67	0.5	0.02	2
Meziadin River	S	Skeena	1994	2020	27	26.96	1.32	0.01	1
Salmon River	SW	Vancouver Island	1999	2019	19	120.41	0.36	0.02	5
Thompson River	S	Thompson–Nicola	1978	2020	43	1,518.62	0.44	0.04	1
Tsitika River	SW	Vancouver Island	1976	2018	43	179.26	1.37	0.00	5

Statistical analyses

Empirical evidence for hyperstability

The relationship between abundance and CPUE can be described as a power function (Hilborn & Walters, 1992):

$$\mathrm{CPUE}_t = \alpha N_t^{\beta}, \tag{1}$$

where CPUE is a function of abundance N at time t, multiplied by the catchability coefficient α, which describes the extent to which the stock is susceptible to fishing, and β is a shape parameter that allows for both linear (proportional) relationships ($\beta = 1$) and nonlinear relationships ($\beta < 1$ indicates hyperstability; $\beta > 1$ indicates hyperdepletion). Hyperstability indicates that CPUE increases more quickly than N at low abundances, which can mask declines in true abundance. On the other hand, hyperdepletion occurs when CPUE increases more quickly than N at high abundances.

To quantify the shape and strength of the relationship between N and CPUE, the natural logarithm was taken for both sides of Equation 1,

$$\log_e(\mathrm{CPUE}_t) = \log_e(\alpha) + \beta \cdot \log_e(N_t), \tag{2}$$

where α becomes the intercept and β is the slope. To increase clarity and follow standard convention, the notation "$\log_e(\alpha)$" will be referred to as β_0. Here, we wanted to estimate the relationship between N and CPUE for all 14 streams as well as the global and system-specific parameters affecting the relationship, which we accomplished with a linear mixed-effects model:

$$\begin{aligned}\log_e(\mathrm{CPUE}_t) &= \beta_0 + \beta_1 \cdot \log_e(N_t) + \beta_2\,\mathrm{Survey} \\ &+ \beta_3\,\mathrm{Stocking} + \mu_{0,\mathrm{Stream}_i} + \mu_{1,\mathrm{Stream}_i} \cdot \log_e(N) + \eta_{\mathrm{Year}} + \varepsilon_t,\end{aligned} \tag{3}$$

where the influences of the fisheries-independent survey quality (i.e., survey score) and stocking (proportion of hatchery fish composition in the total catch from the SHQ) were represented as fixed-effect predictors. We incorporated a random intercept μ_0 to capture baseline differences in $\log_e(\mathrm{CPUE}_t)$ among streams and a random slope $\mu_1 \cdot \log_e(N)$ to account for variability in the effect of $\log_e(N_t)$ on $\log_e(\mathrm{CPUE}_t)$ across streams. Additionally, a random intercept by year was included (η_{Year}) to capture interannual differences in CPUE common to all streams. The errors in the model were assumed to be normally distributed with a mean of zero and constant variance, and the random effects were assumed to follow a multivariate normal distribution. The most parsimonious model was selected based on Akaike's information criterion corrected for small sample size (Akaike, 1974). Finally, the parameter estimates were back-transformed to facilitate comparisons of unstandardized effect sizes in their original measurement units.

One might consider that steelhead density could serve as a more suitable measure to test for hyperstability or hyperdepletion with our independent data. However, an exploratory analysis in which fisheries-independent steelhead abundance was scaled by stream area (km^2) produced quantitatively similar results. Consequently, we opted to use absolute steelhead abundance for ease of interpretation. We also conducted a sensitivity analysis excluding years and streams with the lowest survey score (i.e., 1) to ensure that lower quality data and differences within and among fisheries-independent surveys were not unduly affecting the results. Preliminary analyses with other candidate fixed effects were considered, such as ecotype (summer- and winter-run fish) and management area, but they were highly correlated with other variables, as evidenced by a high variance inflation factor, and thus were not included.

Simulation

To investigate how hyperstability would affect our ability to detect changes in steelhead abundance, we simulated three hypothetical scenarios of steelhead decline. Each time series spanned 30 years, starting with an initial abundance of 1,000 fish. We felt that this was representative of the 14 streams examined in the first part of the analysis (Table 1) because the maximum historical abundances—excluding the Bulkley River due to its disproportionately high numbers—resulted in a mean population size of 1,226. The final abundance was dictated by the rate of decline: a 30, 50, or 90% decline. Random interannual variability was added to the deterministic trends in each time step by taking a random draw from a normal distribution with a mean of zero and a standard deviation equal to the value estimated in the empirical analysis (Equation 3). Each scenario was simulated 1,000 times, resulting in a total of 3,000 time series across three scenarios. Next, we used the global slope and intercept (i.e., estimates obtained when all other predictors are zero) from the model in Equation 3 to simulate CPUE. Error was introduced from the variance–covariance matrix of the fixed effects, and a linear regression (log abundance as a function of year) was fitted to the CPUE estimates to quantify annual decline rates for every scenario.

This simulation approach allowed us to assess the contrast between the magnitude of decline in abundance and the magnitude of decline in CPUE. We expected that under hyperstability, the magnitude of CPUE decline would be lower than that of true abundance. All analyses were implemented in R version 4.3.0 (R Core Team, 2021); the model in Equation 3 was fitted using the lme4 package (Bates et al., 2015).

RESULTS

Empirical evidence for hyperstability

Our analysis revealed that overall, there was a significant positive relationship between fisheries-independent estimates of abundance from the surveys and CPUE from the recreational fishery. As expected, higher steelhead abundance was generally associated with higher catches. However, for the streams examined in this analysis, the relationship was strongly hyperstable, with a global β less than 1 ($\beta = 0.23$, SE = 0.05; Figures 2, 3; Table 2). There was considerable variation in the relationship between abundance and CPUE among streams, as captured by the random slope of stream ($\sigma = 0.12$). There was no obvious discernable geographic pattern in the degree of hyperstability. For instance, the Meziadin River, a tributary of the Nass River, exhibited the highest level of hyperstability ($\beta = 0.09$), followed by the Chilcotin River in the Cariboo region ($\beta = 0.13$). On the northeast side of Vancouver Island, the Tsitika River had a β value of 0.16, while the Englishman River in the southeastern

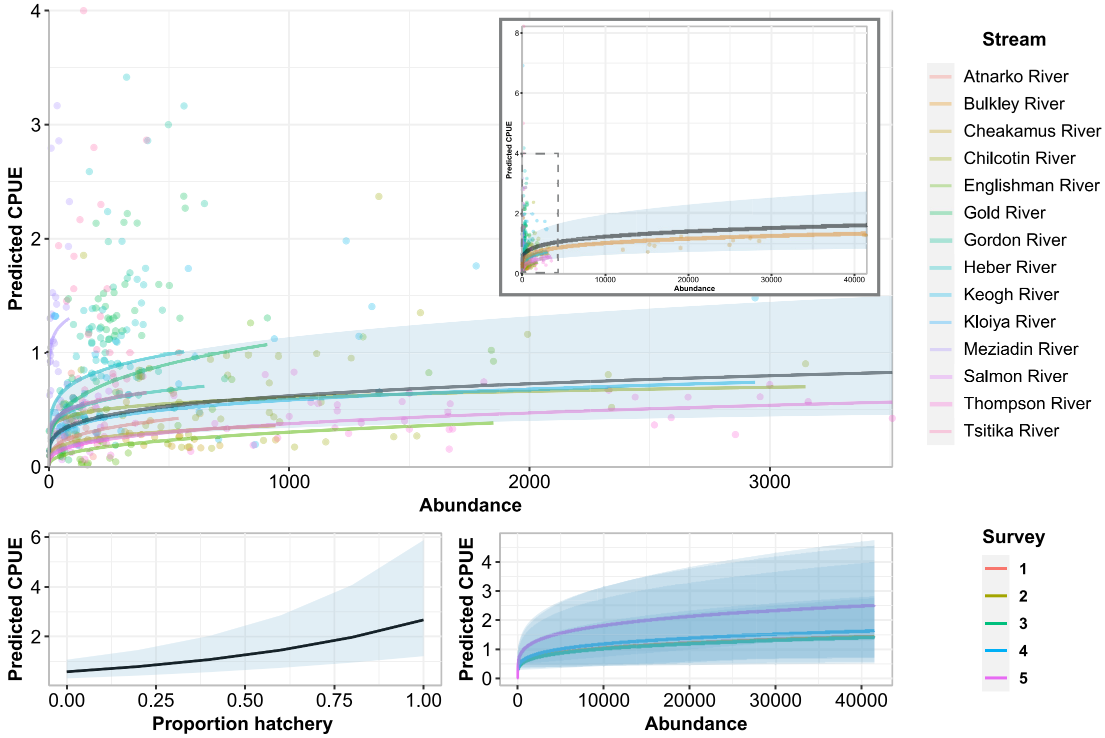


Figure 2. Estimated relationship between steelhead CPUE (fish/angler-day) and abundance, color coded by stream, with raw data superimposed. A subset of all streams is included in the top panel, with the main panel excluding the Bulkley River, to facilitate a comparison among streams. Fixed-effect predictors of the proportion hatchery fish and survey score are shown in the bottom left and bottom right panels, respectively. The 95% confidence intervals are included and shaded in blue.

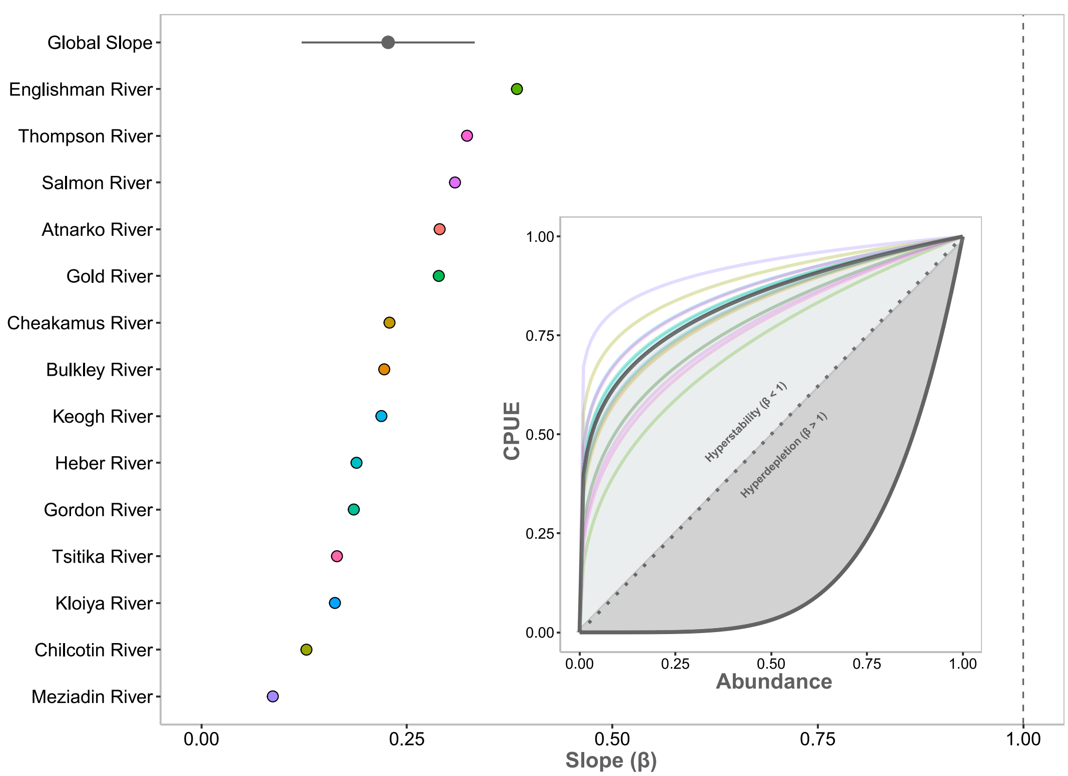


Figure 3. Stream-specific beta (β) values estimated from the random intercept of stream included in the linear mixed-effects model. The global β value of 0.23 is included as a reference (gray). The dotted line represents the cutoff for proportionality ($\beta = 1$), where everything to the left is categorized as hyperstable ($\beta < 1$). For reference, an inset is included where the top curve represents $\beta = 0.23$, the dotted line represents $\beta = 1$, and the bottom curve represents $\beta = 5$, with color-coded stream-specific β values (CPUE is given in fish/angler-day). In this case, the area of hyperstability is shaded in light gray and the area of hyperdepletion is shaded in dark gray.

Table 2. Fixed-effect estimates and 95% confidence intervals (CIs) from the linear mixed-effects model (Equation 3). Estimated coefficients are shown for predictors, including the intercept, log(N), stocking, and survey score (baseline survey score is 1). Random-effect estimates for the variance of year and stream as well as the correlation between stream and log(N) are provided.

Predictor	Estimate	CI	P-value
Fixed effects			
Intercept	−2.14	−3.16 to −1.12	<0.001
log(N)	0.23	0.12 to 0.33	<0.001
Stocking	1.51	0.99 to 2.03	<0.001
Survey score 2	−0.01	−1.12 to 1.09	0.983
Survey score 3	−0.03	−0.81 to 0.75	0.94
Survey score 4	0.12	−0.99 to 1.24	0.83
Survey score 5	0.55	−0.21 to 1.31	0.159
Random effects			
σ^2	0.4		
$\tau_{00,\mathrm{Year}}$	0.03		
$\tau_{00,\mathrm{Stream}}$	1.37		
$\tau_{11,\mathrm{Stream.log}(N)}$	0.01		
$\rho_{01,\mathrm{Stream}}$	−0.89		

Table 3. Summary of the beta (β) values estimated from the random intercept of stream in the linear mixed-effects analysis.

Stream	β
Atnarko River	0.29
Bulkley River	0.22
Cheakamus River	0.23
Chilcotin River	0.13
Englishman River	0.38
Gold River	0.29
Gordon River	0.19
Heber River	0.19
Keogh River	0.22
Kloiya River	0.16
Meziadin River	0.09
Salmon River	0.31
Thompson River	0.32
Tsitika River	0.16

part of the island ranked as least hyperstable among the 14 streams, with a β value of 0.38. Indeed, all 14 streams fell into the "hyperstable" category (Table 3; Figure 4). Thus, as abundance decreased, CPUE decreased less dramatically, which could result in an overestimation of steelhead abundance and obscure actual declines in the population.

Hatchery influence, as indexed by the proportion of hatchery fish in the total catch, was associated with higher CPUEs (estimate = 1.51, SE = 0.26; Figures 2, 3). Thus, anglers tended to have higher catch rates when there were more hatchery fish, independent of true abundance. The proportion of hatchery fish in the total catch exhibited variation across the 14 focal streams. In the Vancouver Island region, hatchery fish comprised 9% of the total catch, while in the Lower Mainland and Thompson–Nicola regions, the proportions were 6% and 4%, respectively (Table 1). Lower rates of hatchery fish were found in the Cariboo (1%) and Skeena (2%) regions (Table 1).

Additionally, we examined the differences among survey methodologies reflected by survey score, a benchmark developed by the Pacific Salmon Foundation to rank the quality of the data on a sliding scale of low to high (1–5). The criteria used to generate this index take into account the spawner survey method, spawner survey coverage, spawner survey execution, juvenile survey method, run timing quality, catch estimation method, and stock ID (Pacific Salmon Foundation, 2024; Salmon Watersheds Program, 2024). Although there were no statistically significant differences among survey scores, scores 2 and 3 had lower estimates relative to other survey categories. This suggests that angler CPUE was reduced for the years and streams associated with those scores. Conversely, there was a positive relationship for the higher ranked surveys with scores 4 and 5 (Figures 2, 3).

Variation in CPUE and abundance among streams

Both CPUE and abundance varied among streams (Table 1). The Vancouver Island streams ($n = 7$), and the Skeena region streams ($n = 3$) had similar average CPUE values of 1.00 and 1.05 fish per angler-day, respectively. In contrast, the Cariboo ($n = 2$) and Thompson–Nicola ($n = 1$) regions had lower average CPUEs of 0.61 and 0.43 fish per angler-day, respectively. The stream with the lowest average CPUE was in the Lower Mainland region ($n = 1$) at 0.28 fish/angler-day. The focal populations also ranged in their total estimated population abundance. For example, the Bulkley River in the Skeena region reached an estimated maximum of 41,428 fish in the time series within this large catchment. In contrast, steelhead populations that were enumerated in other areas of the province generally ranged in the hundreds. For example, the average abundance for the seven Vancouver Island streams was 292 fish. The data presented in this study emphasize the variability in both abundance and catch rates among different steelhead populations, highlighting the intricate dynamics at play across different streams and regions.

Simulation

Our simulations examining three scenarios of steelhead abundance decline illustrated how the observed hyperstability could mask the magnitude of true declines. The proportional differences between the magnitudes of decline in abundance and CPUE varied across scenarios, where the difference was larger for scenarios with steeper true declines, which is consistent with the nonlinear relationship between population decline and catch rates (Figure 4). For example, when abundance declined by 30%, CPUE only declined by an average of 22%, representing an 11% overestimation of abundance. Similarly, when abundance declined by 50%, CPUE only declined by an average of 40%, representing a 28% overestimation of abundance. Finally, when abundance declined by 90%, CPUE only declined by an average of 77%. Therefore, if catches were assumed to be linearly proportional to abundance, this would represent a 109% overestimation of abundance. Consequently, depending on the magnitude of a hypothetical population decline, the observed hyperstability of steelhead populations would lead to relatively small declines in catch rates that could mask population declines.

DISCUSSION

Here, we uncovered consistent evidence of strong hyperstability in a globally important recreational fishery: the steelhead

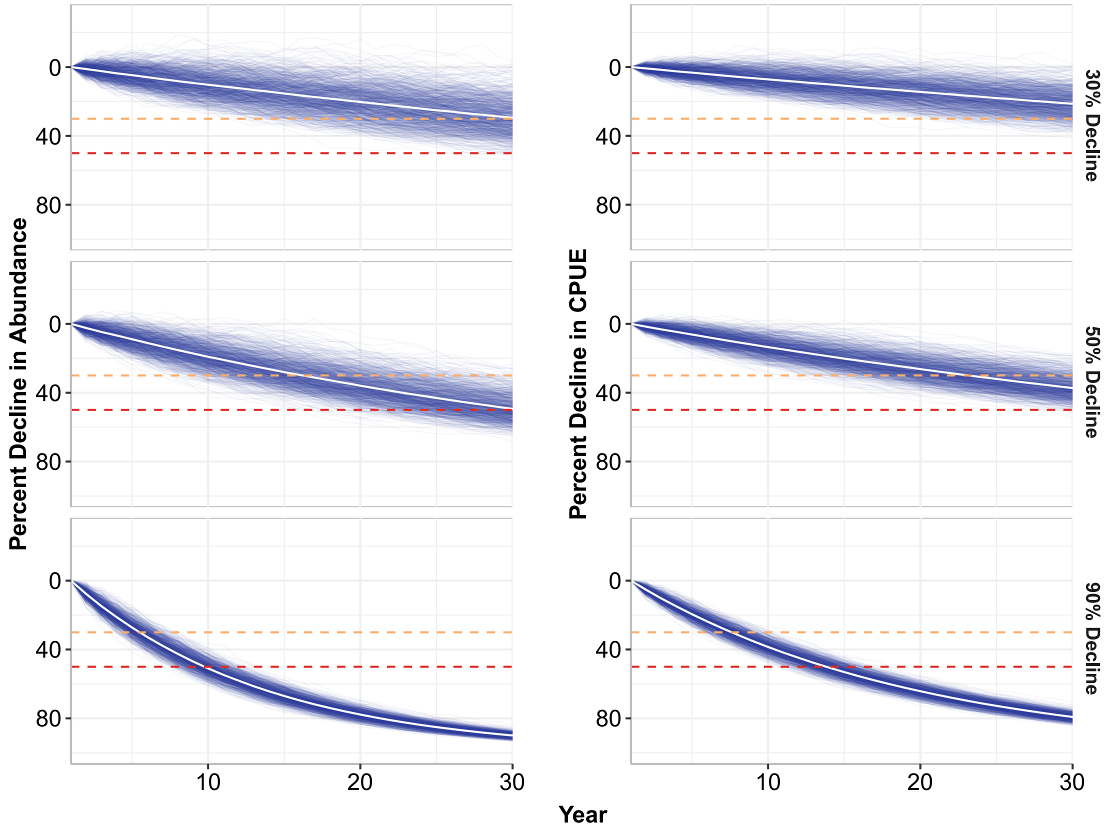


Figure 4. Percent declines of simulated steelhead abundance and estimated CPUE across three scenarios of decline (30, 50, and 90%). Individual lines represent each simulation, which was conducted 1,000 times for each scenario, and the average is illustrated in white. Benchmarks at 30% and 50% have been added as orange and yellow dotted lines, respectively. These are intended to represent endangered and threatened thresholds under the A2 framework of the Committee on the Status of Endangered Wildlife in Canada, which uses these thresholds to assess species risk based on declining population trends over the past 10 years or three generations.

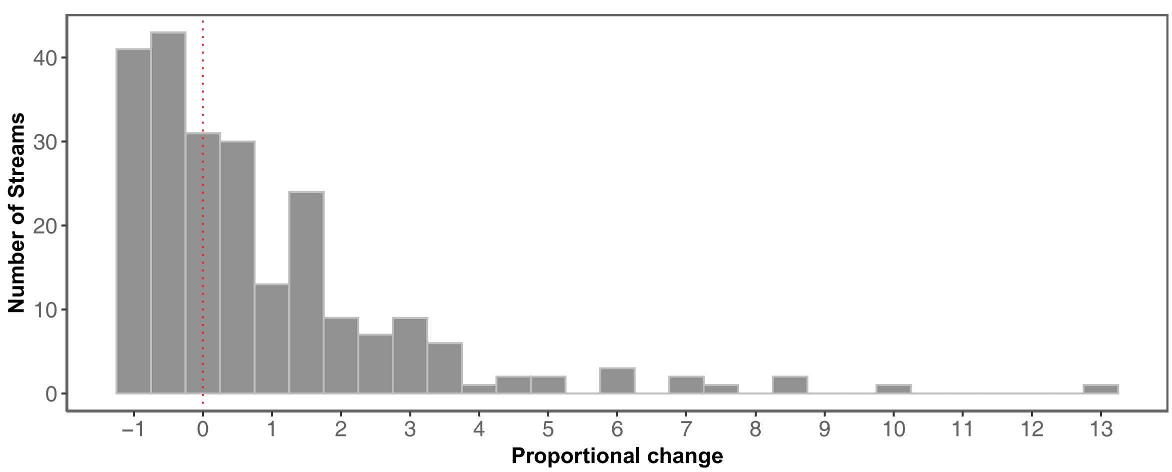


Figure 5. Frequency distribution of the proportional change in steelhead CPUE from the broader Steelhead Harvest Questionnaire data for British Columbia streams with at least 20 years of data ($n = 228$, 14 of which were included in the present analysis). The proportional change is calculated by subtracting the average CPUE for the first 10 years from that for the past 10 years and then dividing by the average CPUE for the first 10 years.

fishery in BC, Canada. While hyperstability has been well documented in marine fisheries (Dickie & Paloheimo, 1965; Sadovy de Mitcheson & Erisman, 2012), its study in the context of recreational fisheries has been comparatively limited (Ward et al., 2013). Not surprisingly, there was a positive relationship between fisheries-independent abundance and CPUE for steelhead in BC, although the strength of this relationship varied considerably depending on the stream ($\beta = 0.13–0.39$; Table 3).

Notably, all 14 streams showed evidence of hyperstability, indicating that catches remain high despite declines in abundance, leading to an overestimation of abundance if CPUE is interpreted as a linear index of abundance. For example, if a population is depleted by 50%, catches would only decline by 40%, resulting in a potential 28% overestimation of abundance. These findings emphasize the importance of exercising caution and considering nonlinearities when relying on recreational catch and effort data alone to infer steelhead status.

Hyperstability: Potential underlying mechanisms

The patterns that we observed likely emerge from some combination of two main mechanisms: aggregation and effort sorting. First, fish may aggregate for foraging, spawning, or general habitat preferences (Clark, 2001; Erisman et al., 2011; Harley et al., 2001; Rose & Kulka, 1999), enabling anglers to exploit these aggregations and maintain high catch rates even as abundances decrease. For example, a recent experimental study by Dassow et al. (2020) manipulated Largemouth Bass *Micropterus nigricans* abundance in a Wisconsin lake and found that anglers had comparable CPUE whether there were 350 bass or as few as 50 in the lake. This hyperstability likely arose because anglers targeted aggregations of fish in preferred littoral habitat. There is widespread evidence that aggregation causes hyperstability, particularly in marine commercial and sport fisheries (Dickie & Paloheimo, 1965; Erisman et al., 2011; Peterman & Steer, 1981; Sadovy de Mitcheson & Erisman, 2012). It seems possible that steelhead aggregation could contribute to the patterns of hyperstability observed in our study. For winter steelhead, fish may aggregate in holding pools or during spawning. Conversely, low flows in summer may constrain summer steelhead to refuge pools and thus contribute to patterns of hyperstability. Inland recreational fisheries for steelhead target the fish in freshwaters while they are not actively feeding, and many different factors could affect the degree of aggregation and their susceptibility to capture during this phase.

A second proposed mechanism leading to hyperstability involves effort sorting, and this concept also has empirical support within the realm of recreational fisheries. Effort sorting operates on the premise that angler skill can greatly impact catch outcomes (Monk & Arlinghaus, 2017; Ruttan, 2003; Ward et al., 2013). As abundance decreases, less-skilled anglers may exit the fishery, leaving behind skilled anglers who can sustain heightened average catch rates (Van Poorten et al., 2016). In a BC Rainbow Trout fishery, Ward et al. (2013) observed that hyperstability in catch rates was associated with fish density in open-access settings, with effort sorting identified as the underlying mechanism (Van Poorten et al., 2016). Effort sorting likely also contributes to the observed patterns of hyperstability in BC's steelhead recreational fishery given the wide range of angler skill levels present. It is quite possible that either or both of these two processes (i.e., effort sorting and aggregation) are contributing to the observed patterns of hyperstability in BC recreational steelhead fisheries. Over longer time scales, improvements to local knowledge and technology have also been proposed to produce hyperstable catch rates. This effect was observed in a South African shoreline Leerfish *Lichia amia* fishery (Maggs et al., 2016). However, comparatively less research has investigated this potential mechanism (Feiner et al., 2020).

Other factors influencing catch rates in BC recreational steelhead fisheries

We found that streams characterized by a higher proportion of hatchery fish had significantly higher CPUE, irrespective of fish abundance. We suggest that there are at least three potential mechanisms for this pattern. First, differences in fishing gear in hatchery versus wild steelhead fisheries may contribute to higher catch rates in systems with proportionally more hatchery fish. While detailed information on system-specific gear restrictions and management interventions was not readily available, the allowance of bait such as salmon or trout roe sacs and beads (gear mimicking roe) for steelhead hatchery runs in BC may play a role. These gear types are associated with higher success rates compared to flies and single-hook lures, which are mandated in many systems with predominantly wild steelhead (e.g., Skeena–Nass regions; Hooton, 2001). Potential disparities in habitat use and behavior between hatchery and wild-type fish may also contribute to higher CPUE. A study of the Vedder–Chilliwack River found distinct spawning locations between wild and hatchery fish; wild fish were dispersed, whereas hatchery fish were concentrated near their release point (Nelson et al., 2005). They also found behavioral differences between wild and hatchery fish, as hatchery fish were recaptured at twice the rate of their wild counterparts. This could be a result of elevated levels of aggression that have been observed in salmonids raised in hatcheries (Weber & Fausch, 2003), differences in early rearing conditions, or unintentional selection for aggressive fish during angling-based broodstock collection (Nelson et al., 2005). On the other hand, the introduction of hatchery steelhead in Oregon streams has been found to unintentionally increase the catch rates of wild stocks, where differences in catchability are hypothesized to increase encounter rates with wild fish (Seals et al., 2024). In any case, there are likely variations in behavior and habitat use among wild and hatchery-type fish across the province.

More generally, other factors that are difficult to quantify likely affect CPUE and abundance. First, the fisheries-independent and fisheries-dependent data are measured with error, and our model only accounts for error in the dependent variable (CPUE). However, we note that error-in-variables bias, when present, tends to result in slope estimates that are biased high (e.g., Freckleton et al., 2006), which in our case would affect the slope of the relationship between abundance and CPUE. As a result, failing to account for error in variables makes our test of hyperstability conservative, and the fact that we find strong evidence for it is even more compelling. There are also many potential biases surrounding the collection of recreational data, some of which were discussed by De Gisi (1999). For example, sampling errors may arise from the exclusion of certain angler groups, such as individuals under 16 years of age, ceremonial fishers, and those who do not purchase a license. Response errors can occur due to recall bias (memory lapses), rounding bias (rounding up to the nearest even digit), prestige bias (inflating responses), or intentional deception. Finally, nonresponse bias is potentially the greatest shortcoming of the SHQ survey, as nonrespondents are often less active or successful, which may lead to an overestimation of catch rates resulting from an increased contribution of successful anglers.

Although survey score, a proxy indicating the precision of abundance estimation, was not found to be a significant predictor of CPUE in this study, steelhead abundance estimates in BC are collected in a number of different ways. These methods include helicopter surveys, snorkel surveys, counting fences, and sometimes a mixture of approaches that vary annually and affect the quality of the abundance data. Additionally, the SHQ spans the angling license year (April 1 of one year to March 31 of the following year; e.g., indicated as 2000/2001). To facilitate a comparison with the survey data, we selected the earlier year in the season (e.g., 2000), creating a slight mismatch between the abundance data and the SHQ data. Other aspects, such as the "fishable" length within a river, vary considerably depending on the area, access, and whether anglers have access to boats and guides. There are also different spatiotemporal regulations for provincial versus out-of-province anglers, particularly in areas with classified waters (Hooton, 2001). For instance, nonresidents (i.e., international anglers) fishing the Dean River on the Central Coast of BC are restricted to a maximum allocation of eight fishing days. The Dean River is one of 52 productive trout streams in the province that are designated as classified waters, requiring a specific license that includes a conservation surcharge. The presence of highly skilled guides in these classified waters could potentially inflate CPUE regardless of steelhead abundance, thus impacting hyperstability. All of these factors—including measurement error, biases in data collection, and varying regulations for anglers—complicate the degree and detection of hyperstability and impact the reliability of the catch data as a proxy for abundance.

Implications for detecting changes in abundance

Some of the most notorious examples of fishery collapses have been linked to hyperstability, where catches were maintained at a relatively high level until the population reached critically low levels. This was the case with the 500-year-old Atlantic Cod (also known as Northern Cod) *Gadus morhua* fishery, where abundance declined by over 90% over a 30-year period and has yet to recover (Atkinson et al., 1997; Hutchings, 2022; Hutchings & Myers, 1994). Extreme hyperstability observed in the CPUE–abundance relationship was attributed to an aggregation of Atlantic Cod in the Bonavista corridor, contributing to the overestimation of stock size and unsustainable fishing practices (Rose & Kulka, 1999). While this example focuses on a commercial fishery, the ability to accurately detect changes in abundance has considerable implications for monitoring population health, determining status, and implementing necessary conservation measures within recreational fisheries. This can be challenging, as recreational fisheries receive less fisheries-independent monitoring compared to commercial fisheries (Cooke & Cowx, 2006). In many cases, such as with steelhead in BC, catch and effort data constitute the primary and often sole source of information for the majority of systems (Ahrens, 2006). Of the estimated 426 steelhead-bearing streams in the province of BC, less than 5% have fisheries-independent indices of abundance (Salmon Watersheds Program, 2024). Catch rate trends across the broader SHQ data set, consisting of streams with over 20 years of data ($n = 228$, 14 of which were included in our analysis) exhibit considerable variability. When the average CPUE over the first 10 years of the time series was compared to the subsequent 10-year averages for each stream, 57% showed increases, while 43% showed decreases (Figure 5). This indicates that CPUE may only begin to accurately reflect abundance when populations are severely depressed and nearing zero. If hyperstability is as prevalent across the province as suggested by this analysis, then the observed declines in catch rates could be associated with substantial declines in true abundance.

Moreover, underestimating abundance may affect our ability to characterize risk for steelhead and impede timely conservation or management actions. One of the key metrics used by assessment bodies such as COSEWIC or the International Union for the Conservation of Nature when assessing extinction risk is the decline of mature individuals over time; under some criteria, a 50% reduction over the past 10 years (or three generations) can lead to an "endangered" designation and a 30% reduction can lead to a "threatened" designation (or "vulnerable" under the International Union for the Conservation of Nature; COSEWIC, 2021; Standards and Petitions Committee, 2022). Based on our simulations, a 50% decline in abundance was associated with only an 40% decline in CPUE (28% underestimation). If catch rate data alone without consideration of nonlinearities were used as a proxy for abundance, then in this illustrative case steelhead would not be considered at risk, which could hinder conservation action. To date, only interior Fraser River steelhead populations in the Thompson and Chilcotin rivers have been assessed, both of which have fisheries-independent records of abundance (COSEWIC, 2020). Other populations may be facing similar declines yet lack fisheries-independent monitoring.

Implications for conservation

Hyperstability in CPUE can destabilize recreational fishery socio-ecological systems by weakening the expected self-regulation of fishing effort in response to population declines (Stoeven, 2014). Recreational fisheries were traditionally expected to self-regulate through a feedback loop, with recreational anglers decreasing their fishing effort in response to population declines (Beard et al., 2003; Post et al., 2002). However, hyperstability in CPUE has the potential to weaken this self-regulatory process because of two linked processes. First, catch rates can stay high even at low abundances if effort stays consistent. Second, if angler satisfaction is positively related to catch rate, as was previously observed for BC steelhead (Pitman et al., 2019), then patterns of hyperstability could incentivize sustained or even increased angling effort despite declining populations. That being said, angler satisfaction is influenced by more than just catch rates. Factors such as access, travel distance, and crowding (Birdsong et al., 2021; Post et al., 2008) also play a role in determining whether anglers continue to fish. Thus, hyperstability in CPUE, combined with these non-catch-related factors influencing angler satisfaction, can destabilize the self-regulating feedback loops. This destabilization can, in turn, affect the sustainability of recreational fisheries. However, other management measures, such as limits on fishing effort, seasonal closures, and gear restrictions, can help to mitigate these risks.

It is important to emphasize that wild steelhead fisheries in BC are subject to catch-and-release measures, and thus, catch does not equate to harvest. Nonetheless, catch-and-release angling can still have some level of impact. Sublethal effects are associated with angling and handling (Arlinghaus et al., 2007); for example, a study conducted by Twardek et al. (2018) in the Bulkley River found a general stress response among caught summer-run steelhead, as indicated by elevated blood lactate levels. Another study based in BC tagged winter steelhead in the Vedder–Chilliwack River between 1999 and 2000, finding that catch-and-release angling resulted in an average mortality of 3.6% (Nelson et al., 2005). However, those authors estimated that mortality was likely lower, as it was confounded with tag loss. Key knowledge gaps remain in understanding the short-term sublethal effects of capture, such as acute stress response; however, these effects may lead to long-term consequences, affecting growth, reproduction, and individual fitness (Papatheodoulou et al., 2024; Richard et al., 2013; S. M. Wilson et al., 2014). Additionally, these impacts are anticipated to worsen with climate change, as rising water temperatures are found to intensify the stress responses and mortality rates in captured and released fish (Gale et al., 2011; Meka & McCormick, 2005). Therefore, even in fisheries that operate under catch and release, it is important to consider that if effort is not restricted and is maintained at high levels, catch rates could remain elevated due to hyperstability and contribute incrementally to declines and mask true trends in at-risk populations. Outside of the recreational fishery and bycatch interception in commercial salmon fisheries (English et al., 2023), steelhead face many challenges arising from cumulative pressures that have led to decreased freshwater and marine productivity (K. L. Wilson et al., 2021).

More broadly, inland fisheries across North America are facing cumulative threats, which in some instances could result in dramatic population declines, which may be undetected due to a lack of baseline monitoring data (Jelks et al., 2008). This is particularly challenging for species that are not commercially targeted, as managers may rely heavily on recreational catch and effort data to infer population health and status, and the successful management of such species hinges on balancing a complicated interplay of ecological, social, and economic dimensions (Arlinghaus et al., 2017; Cooke & Cowx, 2006). The tendency for many fish species to aggregate and the dynamic interplay between fish abundance and angler effort could make many recreational fisheries vulnerable to hyperstability. In the context of steelhead in BC, if hyperstability is as prevalent as suggested by our study, the interpretation of catch rate data from the recreational fishery alone must consider the intrinsic nonlinearity of this relationship when assessing stock health and status. This underscores the need to enhance fisheries-independent monitoring efforts to accurately track population abundance and implement proactive measures to safeguard at-risk populations.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Transactions of the American Fisheries Society* online.

DATA AVAILABILITY

The fisheries-independent abundance data supporting the findings of this study are accessible via the Pacific Salmon Explorer platform, an initiative by the Pacific Salmon Foundation. This platform serves as a centralized repository for the best available data on Pacific salmon in BC and can be accessed through an interactive, open-access Web tool and online data library (data.salmonwatersheds.ca/data-library/). The abundance data featured on the Pacific Salmon Explorer were primarily collected by the BC Fish and Wildlife Branch, which manages the SHQ data (available upon request).

ETHICS STATEMENT

There were no ethical guidelines applicable to this study.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

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