NRC Research Press

ARTICLE

A mechanistic understanding of hyperstability in catch per unit effort and density-dependent catchability in a multistock recreational fishery

Hillary G.M. Ward, Paul J. Askey, and John R. Post

Abstract: Mechanisms resulting in hyperstability (where catch per unit effort (CPUE) remains high as fish density declines) in recreational fisheries are poorly understood owing to a lack of experimental data. We collected data on angler CPUE and fish density to determine whether hyperstability exists in the rainbow trout (*Onchorhynchus mykiss*) lake fishery of British Columbia. We contrasted the relationship between CPUE and fish density in an open-access recreational fishery with an experimental fishery (a set of lakes that had restricted access, standardized fishing methods, and no heterogeneity in angler experience) to assess the mechanistic cause of hyperstability. We detected no evidence of hyperstability in the experimental fishery, but significant hyperstability in the open-access fishery. In the open-access fishery, the composition of the angler population varied among lakes: anglers who fished at low-density lakes were more experienced than anglers fishing at high-density lakes. This segregation of angler experience across lakes appeared to explain the observed hyperstability in this fishery. Our results provide a mechanistic understanding of hyperstability in an open-access recreational fishery and suggest that CPUE data be used in conjunction with data on angler experience when assessing the status of a fishery.

Résumé : Les mécanismes dont découle l'hyperstabilité (où les captures par unité d'effort, ou CPUE, demeurent élevées malgré une diminution de la densité de poissons) dans les pêches sportives sont mal compris en raison d'un manque de données expérimentales. Nous avons recueilli des données sur les CPUE de pêcheurs sportifs et la densité de poissons afin d'établir s'il y a ou non hyperstabilité dans la pêche à la truite arc-en-ciel (*Oncorhynchus mykiss*) en lac en Colombie-Britannique. Nous avons comparé le lien entre les CPUE et la densité de poissons dans une pêche sportive à accès libre et dans une pêche expérimentale (ensemble de lacs à accès restreint, méthodes de pêche standardisées et absence d'hétérogénéité dans l'expérience des pêcheurs) afin d'évaluer les mécanismes causant l'hyperstabilité. Aucun indice d'hyperstabilité n'a été observé dans la pêche expérimentale, alors qu'une hyperstabilité significative était présente dans la pêche à accès libre. Dans cette dernière, la composition de la population de pêcheurs variait selon le lac; les pêcheurs qui pêchaient dans des lacs de faible densité avaient plus d'expérience que les pêcheurs pêchant dans des lacs de forte densité. Cette ségrégation de l'expérience des pêcheurs selon le lac semble expliquer l'hyperstabilité observée dans cette pêche. Nos résultats fournissent une compréhension mécaniste de l'hyperstabilité dans une pêche sportive à accès libre et suggèrent que les données sur des CPUE devraient être utilisées de concert avec des données sur l'expérience des pêcheurs dans l'évaluation de l'état d'une pêche. [Traduit par la Rédaction]

Introduction

Catch per unit effort (CPUE) data are commonly used in both recreational and commercial fisheries to assess the status of fish populations under the assumption that the catch from a fishing vessel is proportional to stock size (Hilborn and Walters 1992; Quinn and Deriso 1999). CPUE is commonly assumed to be a linear function of fish density, where CPUE is linked to fish density (N) using the model

$$\text{(1)} \qquad \text{CPUE} = qN$$

where q is a catchability coefficient. However, it has been recognized for more than 50 years that changes in CPUE may not accurately reflect changes in fish abundance (Beverton and Holt 1957). Many nonlinear versions of this model have been suggested, the simplest being a power function

$$\text{(2)} \qquad \text{CPUE} = aN^{\beta}$$

so that when $\beta \neq 1$, CPUE is not linearly related to fish density, and α is an estimate of q when CPUE and N are near the origin. A CPUE index is defined to be hyperstable when $\beta < 1$ and hyperdeplete when $\beta > 1$ (Hilborn and Walters 1992). Dividing eq. 2 by N demonstrates the relationship between catchability (q) and fish density

$$\text{(3)} \qquad q = \frac{\text{CPUE}}{N} = aN^{(\beta-1)}$$

where catchability is constant across fish density when $\beta = 1$ and density dependent when $\beta \neq 1$ (catchability decreases with fish density when $\beta < 1$ and increases with fish density when $\beta > 1$).

Hyperstability in CPUE has been documented in many commercial fisheries and a few recreational fisheries (Shuter et al. 1998; Rose and Kulka 1999; Erisman et al. 2011). Processes that are responsible for hyperstability in commercial fisheries include gear improvements, technological advances, and fish aggregation (Crecco and Overholtz 1990; Rose and Kulka 1999). However, in open-access recreational fisheries, mechanisms resulting in hyperstability remain largely unknown. Hyperstability results in the "illusion of plenty", where the stock is presumed to be abundant as a result of high CPUE, and no management action is taken until

Received 14 May 2013. Accepted 1 August 2013.

Paper handled by Associate Editor Kenneth Rose.

H.G.M. Ward and J.R. Post. Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, AB T2N 1N4, Canada.
P.J. Askey. British Columbia Ministry of Forests, Lands and Natural Resource Operations, 102 Industrial Place, Penticton, BC V2A 7C8, Canada.
Corresponding author: Hillary G.M. Ward (e-mail: hward@ucalgary.ca).

both the fishery and fish population collapses (Post et al. 2002; Erisman et al. 2011). Therefore, catchability is a key variable driving the dynamic interaction between angler effort and fish density, and the need to better understand catchability in recreational fisheries is well recognized (Hunt et al. 2011*a*; Fenichel et al. 2013; Post 2013).

Three competing mechanisms have been proposed to explain the observed patterns of hyperstability in recreational fisheries. First, it is hypothesized that behavioural aggregations or heterogeneity in habitat quality results in nonuniform distributions of fish and creates areas with high catch rates. If fish continually move into areas of preferred fish habitat as other fish are removed through harvest, CPUE will remain high as stock size declines and exhibit hyperstability (Shuter et al. 1998; Post et al. 2002; Post 2013). This mechanism that results in hyperstability has been documented in a few commercial and recreational fisheries and is especially prevalent in species that form spawning aggregations (Clark 2001; Harley et al. 2001; Erisman et al. 2011). In fact, this mechanism is presumed to be one of the main processes that led to the collapse of the Atlantic cod (*Gadus morhua*) fishery off eastern Canada (Hutchings 1996; Rose and Kulka 1999). The second mechanism that may result in hyperstability is variation in angler behaviour. Less experienced anglers (who have lower proficiency in capturing fish, resulting in lower individual catchability) may abandon low-density fisheries that do not produce sufficient CPUE to satisfy their expectations (Post 2013). Conversely, human dimensions research has suggested that experienced anglers may actually be attracted to low-density fisheries because low-density fisheries are often correlated with more restrictive regulations and larger fish size (Chipman and Helfrich 1988; Hutt and Bettoli 2007). Therefore, as the composition of anglers shifts to more experienced anglers in low-density fisheries, the net catchability of anglers' is higher than would be expected if angler experience was independent of fish density, leading to hyperstability in CPUE. Third, hyperstability may arise owing to the interaction between angler effort density and fish behaviour at the individual level. This hypothesis postulates that the fish community is composed of individuals that vary in their vulnerability to anglers, and as fish are caught, the most vulnerable individuals are removed or enter an invulnerable state (if fish are caught and released) for a certain period of time (Cox and Walters 2002; Askey et al. 2006). As angler effort increases, the number of fish that are vulnerable to anglers at any given time is reduced, and catchability (measured as a function of the total stock size rather than the vulnerable stock size) will decrease with increases in fish density and result in hyperstability.

Separating the mechanisms that result in hyperstability in open-access recreational fisheries is difficult, since density-dependent mechanisms related to fish and angler behaviour are confounded. Furthermore, it is well recognized that inappropriate statistical methods are expected to falsely detect hyperstability (Shardlow et al. 1985; Richards and Schnute 1986). We evaluated the relationship between angler CPUE and fish density to determine whether hyperstability exists in the rainbow trout (*Onchorhynchus mykiss*) lake fishery of British Columbia. We contrasted the relationship between CPUE and fish density in an open-access recreational fishery with an experimental fishery (a set of lakes that had restricted access, standardized fishing methods, and no heterogeneity in angler experience) to test whether hyperstability is primarily a function of fish or angler behaviour.

Materials and methods

Study design and species information

To separate mechanisms hypothesized to produce density-dependent catchability in recreational fisheries, we gathered CPUE data and assessed fish population densities in two separate fisheries using 28 lake-years of data, derived from 24 individual lakes across 4 individual years (Table 1). We examined the relationship between angler CPUE and fish density in two contrasting situations: (*i*) an experimental fishery (with standardized angling methods, restricted public access, and no heterogeneity in angler experience) and (*ii*) an open-access recreational fishery.

The experimental and open-access fisheries were part of the large multistock, spatially structured rainbow trout fishery of the south-central region of British Columbia, Canada. All study lakes in the experimental and open-access fisheries were monocultures of rainbow trout, except Kentucky Lake, which also contained a population of redside shiner (*Richardsonius balteatus*). The lakes in the experimental fishery were feral hatchery populations (with supplemental stocking), whereas the lakes in the open-access fishery were stocked annually with age-0 or age-1 hatchery fish and had no known natural recruitment.

Experimental fishery

Since it is suspected that heterogeneity in angler skill level can result in density-dependent catchability, we controlled for the effects of angler heterogeneity on angling catch rates by experimentally fishing six lakes (in total 10 lake-years of data across 3 years) (Table 1). The experimental lakes were located on the Bonaparte Plateau, north of Kamloops, British Columbia, at 51°09′01″N, 120°21′54″W. These lakes were part of a long-term study on fish population dynamics and have restricted public access (and are considered to be in an unfished state). Experimental angling followed methods in Askey et al. (2006), with angling occurring over a standardized period between 10 and 17 August 2004, 2005, and 2011. A single angler fished all lake-years using two fly patterns from Askey et al. 2006 (black leech and general green nymph on size 14 hooks). The angler was considered to be an expert angler (fished an average of 20 days per year) and was instructed to behave as would a normal angler by focusing efforts on areas and habitats where catch rates and size of fish would be maximized. Time spent fishing and the number of landed fish were recorded. Fish population densities were estimated in each lake-year using mark–recapture techniques (sampling details are described in Askey et al. 2007). A large number of marked hatchery fish (range 417–726) of various sizes (range 50–400 mm) were released into each of the lakes approximately 1 week prior to recapture. Additional fish were marked in each lake using beach seines or fyke nets. Fish were recaptured over 5 consecutive nights of gillnetting. This sample design is highly effective, as ~40% of the population is captured in the gillnets (Askey et al. 2007), and therefore the population estimates for these experimental lakes are precise (mean coefficient of variation for abundance estimates of fish >150 mm = 0.03). Size-dependent vulnerability to angling was estimated in these lakes for the specific fly pattern and hook size as shown in Askey et al. (2006), and fish density estimates for fully recruited fish were adjusted accordingly. Although several of the lakes were experimentally fished in multiple years, the lakes are treated as independent samples, as fish densities were altered among years as a result of stocking and depletion–removal experiments.

Open-access fishery

We conducted creel censuses at open-access recreational fishing lakes (18 lakes) in the south-central region of British Columbia, Canada (Table 1). The lakes ranged from 5.7 to 44.7 ha in surface area and varied in harvest and gear regulations and angler effort (Table 1). These particular lakes were selected for creel censuses from a large recreational fishery to maximize contrasts across lakes in fish density and angler effort.

Angler surveys were conducted at each lake from 1000 to 1800 h from the first ice-free date to 15 September 2010 or 2011 (sampling details are further described in Ward et al. 2013). Survey days were randomly stratified among lakes between weekends and weekdays, and more intense survey effort occurred in the spring. All

Table 1. Physical characteristics, sampling details, and angling regulations for the study lakes.

Lake	Area (ha)	Years sampled	Bag limit	Gear restrictions
Open-access recreational fishery				
Burnell	12.7	2011	0	Artificial fly, bait ban, single barbless hook
Crown	7.6	2010	5	None
Doreen	44.7	2011	5	Artificial fly only, bait ban
Flyfish	29.2	2011	5	None
Gypsum	14.0	2010	5	None
Idleback	11.6	2011	1	Bait ban, single barbless hook
Jackpine	42.9	2011	5	None
Kentucky	36.0	2011	5	None
Kidd	18.8	2011	0	Artificial fly, bait ban, single barbless hook
Leonard	11.9	2011	2	Bait ban, single barbless hook
Loon	8.5	2011	5	None
McConnell	32.4	2011	5	None
Ripley	5.7	2011	5	None
Six Mile	8.1	2011	2	Bait ban, single barbless hook
Stake	23.1	2011	5	None
Turquoise	6.5	2010	5	None
Tyner	18.1	2010	5	None
Vinson	20.5	2011	1	Bait ban, single barbless hook
Experimental fishery				
Big Pantano	2.1	2004	5	None
Spook	4.4	2004, 2005	5	None
Stubby	6.2	2004, 2011	5	None
Today	6.5	2004, 2005, 2011	5	None
No Fish	13	2005	5	None
Pantano	3.2	2011	5	None

study lakes had single access points and no private housing, ensuring that all anglers fishing within the survey day were interviewed. Upon trip completion, all anglers were asked to report on catch, harvest, and hours fished, and the fork length of harvested fish was recorded. Since we hypothesize that angler skill level could explain the hyperstability in the relationship between CPUE and fish density, we also asked anglers to estimate the number of days they spent fishing in the previous calendar year as an approximation of angler skill level. Several studies in human dimensions research have concluded that angler avidity is a useful measure for fishing specialization: anglers who fished more frequently corresponded to high levels of skill and greater resource dependency (Graefe 1980; Ditton et al. 1992).

Across a fishing season, it is well known that angler CPUE is affected by seasonality (van Poorten and Post 2005; Askey et al. 2006). Therefore, to standardize differential survey effort across lakes (some lakes had more survey effort in the spring, when CPUE is typically highest), we expressed CPUE (and similarly, angler experience) as a seasonal mean. CPUE is calculated per month j for lake i as

$$\text{(4)} \qquad \text{CPUE}_{i,j} = \frac{\sum c_{i,j}}{\sum E_{i,j}}$$

and then averaged across n months of survey data

$$\text{(5)} \qquad \overline{\text{CPUE}_i} = \frac{\sum \text{CPUE}_{i,j}}{n}$$

In the open-access recreational fishing lakes, fish density was estimated in 16 of the 18 lakes using mark–recapture techniques and a standard gillnet sampling protocol in the fall following the angler survey (sampling details are described in detail in Ward et al. 2012). Hatchery populations of marked rainbow trout (adipose fin-clipped) were released into each lake approximately 1 week prior to gillnetting. Fish were recaptured using one floating and one sinking gang of multimesh gillnets that were set overnight in the littoral and pelagic habitat of each lake. Marked fish were assumed to be fully recruited to the sampling gear, but not to anglers. This gillnet design is highly size-selective against small fish and essentially non-size-selective for larger fish (Askey et al. 2007). Two of the study lakes (Kidd and Burnell) were considered "trophy fisheries", and owing to the low fish density, fish populations were assessed using mark–recapture techniques rather than gillnets. In these two lakes, fish were captured via angling and then adipose fin-clipped. Approximately 2 weeks later, fish were recaptured (and released alive) using multiple short sets (10 min) of multimesh floating gillnets with the same net mesh configuration as that in Ward et al. (2012).

Estimates of fish density per 10 mm length-bin (l) from the gillnet sample ($N_{G,l}$) were adjusted for angling vulnerability (except for Kidd and Burnell Lakes, where the population estimate includes only the fish vulnerable to anglers, as fish were marked via angling). Vulnerability at length to angling (V_l) was calculated assuming logistic selectivity

$$\text{(6)} \qquad V_l = \frac{l^m}{l^m + L_{50}^m}$$

where L_{50} is the length at 50% vulnerability, m is the steepness of the curve at L_{50}, and l is the midpoint of the length bin. Cox (2000) calculated m = 7 for similar rainbow trout fisheries in British Columbia, so this value is used in the analysis. Estimates of L_{50} varied by lake and were reflective of the size distribution of the population (Appendix A).

The vulnerable density of fish in the fall following the angler survey (N_T) was calculated as

$$N_T = \sum_l^L (N_{G,l} V_l) \tag{7}$$

and initial fish density (N_0) was back-calculated from the fall density estimate (N_T) using the observed harvest per unit effort (HPUE) per lake across the full season and total angler effort (E)

$$N_0 = N_T + \text{HPUE} \times E \tag{8}$$

Angler effort (E) was measured using time-lapse cameras in conjunction with ground-based counts (Appendix B). To account for in-season changes in fish density as a result of harvest, a mean fish density (between the estimated spring and fall densities) was calculated and used to explore trends in the mean CPUE for the entire fishing season.

Statistical analysis

Hyperstability in CPUE is commonly assessed by log-transforming eq. 2 (Ricker 1975)

$$\log(\text{CPUE}) = \log(\alpha) + (\beta - 1)\log(N) \tag{9}$$

and estimating the slope (β) and intercept, $\log(\alpha)$, of the relationship between the log-transformed CPUE and fish density. Similarly, catchability q can be estimated by log-transforming eq. 3, where

$$\log(q) = \log\left(\frac{\text{CPUE}}{N}\right) = \log(\alpha) + \beta\log(N) \tag{10}$$

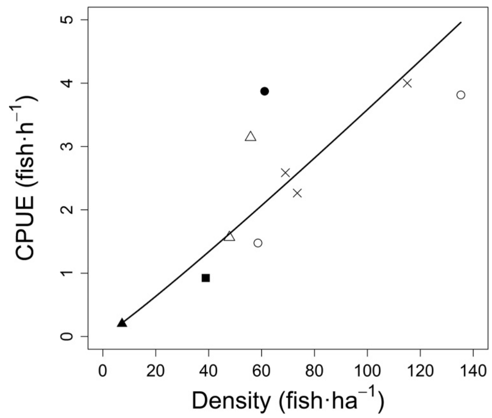
A linear regression analysis relies on the assumption that the dependent variable (fish density) is measured without error, and previous research has shown that erroneous statistical approaches to estimating the slope and intercept of eq. 9 can lead to false detection of hyperstability (Shardlow et al. 1985; Richards and Schnute 1986). Therefore, a standard linear regression analysis (ordinary least squares) is usually not appropriate to estimate parameters. However, since fish densities in the experimental fishery were measured with a high degree of precision and the error in the estimate of fish density was less than one-third of the error in CPUE, a standard linear regression was used to estimate parameters in eq. 9, as recommended by McArdle (1988). For the open-access recreational fishery, fish densities were measured with less precision, and therefore we used a reduced major axis (RMA) regression to estimate parameters in eq. 9. An RMA regression is the recommended method for estimating regression parameters when error is suspected in both the independent and dependent variable (Ricker 1973; McArdle 1988), and this method has been used to detect hyperstability (Erisman et al. 2011). The RMA regression minimizes the product of the dependent (x) and independent (y) deviations from the fitted line and was implemented using the lmodel2 package in R (version 2.13.2).

Angler characteristics and mechanisms of density-dependent catchability

If catchability is not constant (i.e., $\beta \neq 1$) in the open-access fishery, it is hypothesized that catchability might be positively related to the mean angler skill level on an individual lake (Post 2013). Therefore, we examined the relationship between catchability and angler skill level and fit the data using an RMA regression, since error is suspected in both the dependent and independent variables.

It has also been proposed that density-dependent catchability may arise owing to the effects of fish learning and angler effort on fish vulnerability resulting from an angler effort response to fish density (Cox and Walters 2002; Askey et al. 2006). Since the open-access recreational fishing lakes surveyed in this study varied in harvest regulations, fish density, and angler effort, we tested for a relationship between angler effort density (angler hours·ha^{-1}), exploitation rate, proportion of the fish population captured (capture rate), and fish density. Exploitation rate was calculated as the ratio between the total number of harvested fish (HPUE × E) and fish density, and capture rate was calculated as the ratio between the total number of caught fish (CPUE × E) and fish density. Since the potential for fish learning is affected by the proportion of fish that are released by anglers (which is a function of the daily bag limit and angler effort density), we tested for a relationship between angler catchability and angler effort density, proportion of released fish, and daily bag limit. If this hypothesis is correct, it is expected that catchability should be negatively related to both angler effort density and proportion of fish released. We tested for significant relationships by fitting a linear model to the variables and used a t test to determine whether the slope was significantly different than zero.

Fig. 1. Catch per unit effort (CPUE) as a function of fish density in the experimental fishery. The solid line is the regression fit to the log-transformed data. Lakes with multiple years of data are shown with the same plot symbol. Key to point markers: solid circle, Big Pantano; open circle, Spooke; open triangle, Stubby; cross, Today; solid triangle, No Fish; solid square, Pantano.



Results

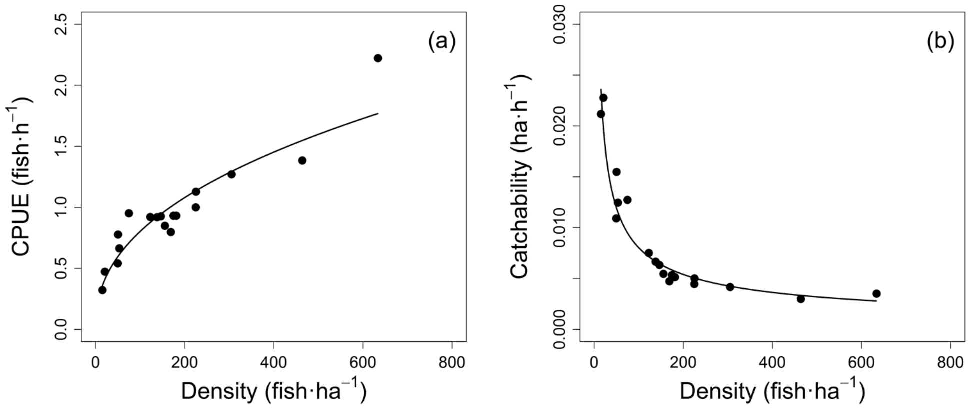
Experimental fishery

Fish density and CPUE varied by approximately 20-fold over the 10 lake-years of data in the experimental fishery (Fig. 1). Fish density ranged from 7.24 to 135.4 fish·ha^{-1}, and CPUE ranged from 0.20 to 4.00 fish·h^{-1}. The relationship between CPUE and fish density for an individual angler was linear and therefore showed no evidence of hyperstability. The parameter estimates for β and α were 1.075 (standard error = 0.1417) and 0.02535 ha·h^{-1} (standard error = 0.5754) respectively. The lack of hyperstability in the relationship between CPUE and fish density resulted in little variation in catchability q among lakes. Estimates of catchability ranged from 2.372×10^{-2} to 6.330×10^{-2} ha·h^{-1}. At a fish density of 100 fish·ha^{-1}, CPUE in the previously unfished experimental angling lakes was approximately 2.5 times higher than the CPUE of expert anglers (defined as anglers who fished more than 20 days per year) in the open-access recreational fishery.

Open-access fishery

The lakes in the open-access recreational fishery exhibited large variation in both fish density and angler CPUE: mid-season estimates of fish density varied ~40-fold (range 15.2–633.7 fish·ha^{-1}), whereas seasonal-averaged CPUE varied 7-fold between 0.32 and 2.22 fish·h^{-1}. An RMA regression detected evidence of hyperstability (p < 0.05) in the CPUE data (Fig. 2). The parameter

Fig. 2. (*a*) CPUE and (*b*) catchability as a function of fish density in the open-access fishery. Solid line is the reduced major axis regression fit to log-transformed CPUE and density data.



estimates for β and α were 0.4276 (95% confidence interval (CI): $0.3562 < \mu < 0.5134$) and 0.1120 ha·h^{-1} (95% CI: $0.07425 < \mu < 0.1578$), respectively. Catchability q varied approximately 10-fold across lakes and ranged from 2.982×10^{-3} to 2.276×10^{-2} ha·h^{-1}. The relationship between CPUE and fish density for fish densities in the same range as the experimental lakes (<135.4 fish·ha^{-1}) was also hyperstable: the estimate of β = 0.5447 (95% CI: $0.3571 < \mu < 0.8310$).

Angler characteristics and mechanisms of density-dependent catchability in the open-access fishery

A total of 1765 anglers were interviewed across both survey years (226 anglers were interviewed in 2010, and 1539 in 2011). Angler experience (measured by the mean number of days fished per year) varied across the interviewed anglers and ranged between 0 to 250 days fished per year (Fig. 3*a*). Mean angler experience decreased as fish density increased across lakes, and the relationship between mean angler experience and fish density was best described by the power function (Fig. 3*b*; r^2 = 0.77)

$$\text{(11)} \qquad \text{Mean days fished per year} = (92.62)N^{-0.3007}$$

Similarly, mean angler experience was positively related to the mean size of harvested fish in each lake (r^2 = 0.51; $t_{1,16}$ = 4.31; $p < 0.05$) (Fig. 3*c*).

We examined several covariates to help identify the mechanistic cause of the observed density-dependent catchability in the open-access fishery. Angler catchability was positively related to angler experience (mean days fished per year, D) across lakes, and the following function best described the relationship (r^2 = 0.83) (Fig. 4*a*):

$$\text{(12)} \qquad q = (1.077 \times 10^{-3})1.086^{D}$$

An increase in bag limits corresponded to a decrease in catchability across lakes (r^2 = 0.33; $t_{1,16}$ = −3.039; $p < 0.05$) (Fig. 4*b*). There was no evidence that angler catchability was related to angler effort density (Fig. 4*c*; r^2 = −0.06; $t_{1,16}$ = −0.135; p = 0.8944), and the relationship between angler catchability and proportion of fish released by anglers was slightly positive (Fig. 4*d*; r^2 = 0.28; $t_{1,16}$ = 2.743; $p < 0.05$). Similarly, there was a lack of support for a relationship between angler effort density and fish density (r^2 = −0.02; $t_{1,16}$ = 0.7950; p = 0.4382), exploitation rate and fish density (r^2 = −0.06; $t_{1,16}$ = 0.2740; p = 0.7872), or capture rate and fish density (r^2 = 0.06; $t_{1,16}$ = −1.433; p = 0.1710) (Fig. B1). Our data also suggests no evidence of a relationship between catchability adjusted for variation in angler skill level (the residuals from eq. 12 and angler effort density (r^2 = −0.06; $t_{1,16}$ = −0.0920; p = 0.9280) or the proportion of fish released (r^2 = 0.03; $t_{1,16}$ = 1.226; p = 0.2380).

Discussion

We detected significant hyperstability and density-dependent catchability for the multistock, spatially structured rainbow trout fishery of British Columbia, and this result complements those of several other studies that have estimated the catchability coefficient for open-access recreational fisheries (Shuter et al. 1998; Hansen et al. 2005; Erisman et al. 2011). We observed a linear relationship between CPUE and fish density in the experimental fishery, within which we controlled for heterogeneity in angler skill level, and a hyperstable relationship in the open-access fishery. Although fish densities in the experimental lakes had a lower range of densities compared with that of the open-access lakes (as a result of the productive limits of these higher altitude lakes), observations of CPUE at low fish densities provide the most information on hyperstability. The truncated density range of the experimental lakes does not impact the results, as we detected hyperstability in the open-access fishery for the same range of fish densities as the experimental fishery. The observed nonlinear relationship between fish density and CPUE needs to be accounted for if measures of CPUE are used to infer stock size or angling quality.

Our results provide no evidence to support the hypothesis that changes in fish behaviour with declines in fish density produced the apparent hyperstability in the open-access fishery. In the open-access fishery, the observed density-dependent catchability was best described by a segregation of angler experience levels among lakes. Across lakes, declines in fish density corresponded to an increase in the average experience of the anglers. Several studies have noted that experienced anglers prefer "trophy" fisheries characterized by large fish (Chipman and Helfrich 1988; Hutt and Bettoli 2007), and we found that angler experience increased as the size of harvested fish increased across lakes. Therefore, since low-density lakes (that have large fish sizes) attracted experienced anglers, we found a positive relationship between the observed catchability and the average experience of the angler population. This suggests that as fish density declines, the composition of the angler population shifts towards experienced anglers (who have higher individual catchabilities) and produces a net increase in catchability.

Variation in anglers' impacts on stocks has been previously noted (Baccante 1995; Jones et al. 1995), and it is well understood that angler experience varies across the population of anglers (Bannerot and Austin 1983; Fisher 1997; Ward et al. 2013). Across a multistock, spatially structured fishery, anglers choose where to

Fig. 3. (*a*) Frequency distribution of angler experience (days fished per year). The *x* axis is on a log scale, and the axis labels have been back-transformed for interpretation. (*b*) Mean angler experience (days fished per year) as a function of fish density. (*c*) Mean angler experience as a function of the mean size of harvested fish. Error bars represent 95% confidence intervals.

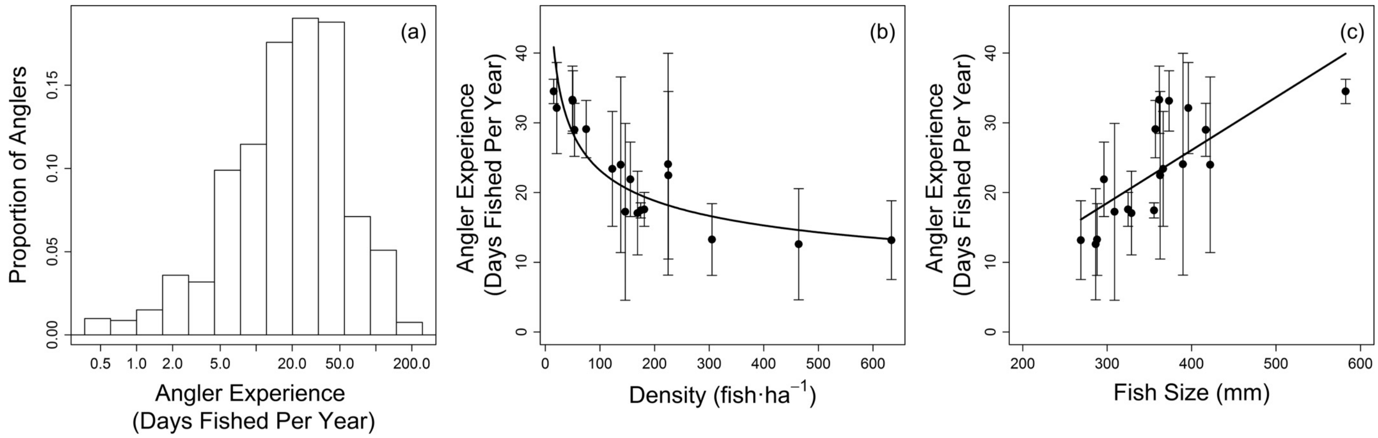
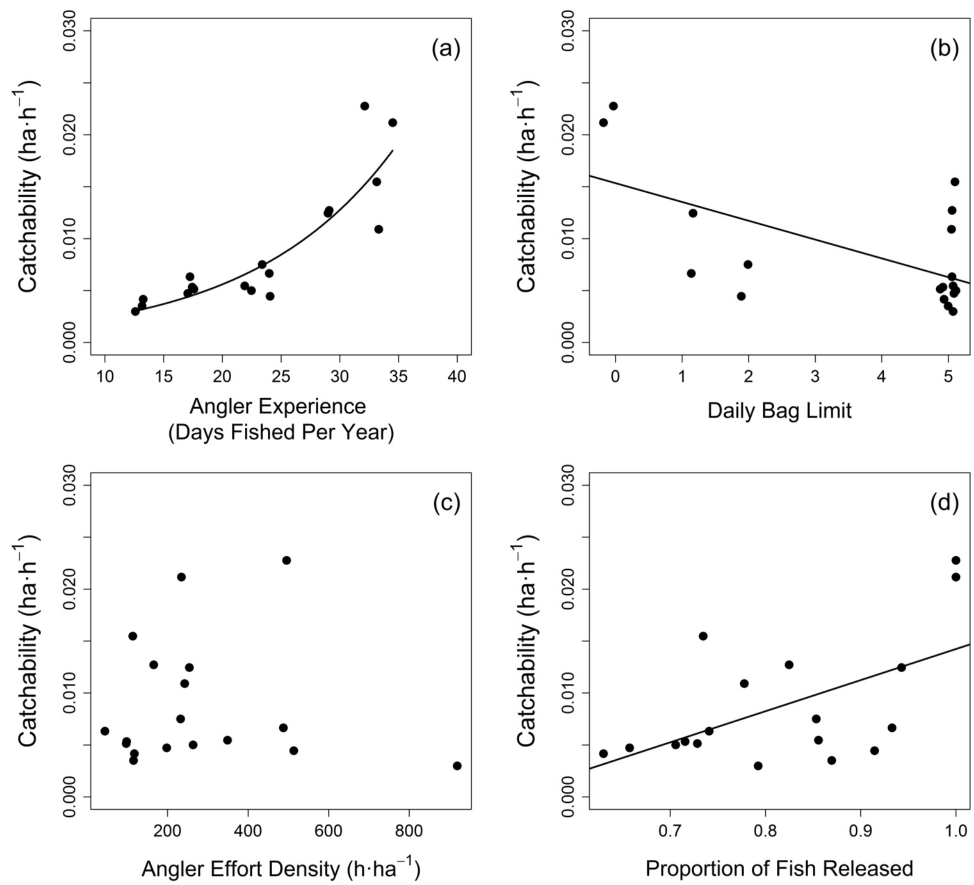


Fig. 4. (*a*) Catchability as a function of angler experience (mean days fished per year). (*b*) Catchability as a function of the daily bag limit (points have been jittered for interpretation). (*c*) Catchability as a function of angler effort density and (*d*) the proportion of fish released by anglers.



fish based on their perceptions of catch and noncatch related angling quality, commonly termed "utility" in economics and human dimensions literature (Carpenter and Brock 2004; Hunt 2005). Taken together, variation in skill level and factors influencing site choice among anglers are likely to produce density-dependent catchability, as more experienced anglers (with higher individual catchabilities) will derive greater utility from fishing low-density stocks in comparison with less skilled anglers (Chipman and Helfrich 1988; Hutt and Bettoli 2007). Therefore, the observed correlation between catchability and the composition of the angler population for the multistock spatially structured rainbow trout fishery of British Columbia is not surprising.

In the open-access fishery, catchability varied approximately 10-fold and was positively related to angler experience. The large variation in angler skill level across lakes (and the relationship between angler skill and catchability) suggests that the observed hyperstability in the open-access fishery is a result of variation in the composition of anglers among lakes, rather than interactions between fish behaviour and catchability. Previous work (Cox and Walters 2002; Askey et al. 2006) predicts that lakes with high effort (and (or) a high proportion of released fish) would have low catchabilities owing to the effects of learned hook avoidance and fish behaviour that leads to invulnerability to angling. We observed no relationship between angler catchability and effort or the proportion of fish released, and thus it appears that fish behaviour has a smaller impact on catchability than angler behaviour (sorting of experience levels among lakes) once fisheries are established. However, CPUE in the experimental fishery was approximately 2.5 times higher than that in the open-access fishery at the same fish density. The seasonal timing of the experimental fishery was mid-August, which is a below-average catchability period for those lakes (Askey et al. 2006) and other rainbow trout lakes (Cox 2000; van Poorten and Post 2005), and there are no obvious reasons why catchability should be inherently higher in the experimental lakes. Differential vulnerability of fish to angling has been repeatedly studied, and it is well known that intrinsically aggressive (catchable) fish are captured first by anglers (Askey et al. 2006; Biro and Post 2008). Therefore, the high catch rates in the experimental fishery may be a reflection of the unfished conditions of these lakes, and even the lowest effort observed in open-access fisheries is sufficient to rapidly condition fish to a lowered (density-independent) catchability.

Catchability represents a fundamental component of the functional response within the predator–prey dynamics of anglers and fish (Hunt et al. 2011*a*; Post 2013). However, the numerical response of anglers to fish abundance is equally important in understanding whether the interaction between fish abundance and harvest is likely to be sustainable (Schueller et al. 2012; Allen et al. 2013; Askey et al. 2013). Typically there is a positive relationship between fish abundance and angler effort (e.g., Post et al. 2008; Schueller et al. 2012), yet we observed no significant relationship in this study. It is not clear why there is a lack of correlation in our study, but it could be partially due to differential access or travel costs between lakes (Post et al. 2008). The lack of a relationship between angler effort and fish abundance can be a concern for the sustainability of wild stock fisheries (Walters and Martell 2004; Schueller et al. 2012; Allen et al. 2013), although the lakes in this study are maintained by stocking. If angler effort does not respond to changes in fish abundance, then the possibility for overfishing exists if angler effort remains high as fish abundance declines.

Exploitation in recreational fisheries results from not only the intensity of angling effort, but also the efficiency of the effort. Since catchability is the key variable that describes the dynamic interaction between angler effort and fish density, several authors have emphasized the importance of understanding the relationship between catchability and fish density (Johnston et al. 2010; Hunt et al. 2011*a*; Fenichel et al. 2013). However, the more fundamental role of catchability in recreational fisheries is that it dictates an angler's perception of a fishery and influences angler behaviour (relating to choice of fishing site). For the rainbow trout fishery in British Columbia, variation in site choice among anglers led to more experienced anglers choosing to fish at low-density lakes (that have large fish). The large variation in angler skill level among lakes and relationship between angler skill level and catchability suggests that any management action that alters the composition of the population of anglers at a lake (either through catch or noncatch related factors) may have substantial impacts on catch statistics and harvest rates. From a management perspective, our results suggest that restrictive regulations may not be effective at controlling exploitation rates (except catch-and-release regulations), as these restrictive bag limits tend to create trophy fisheries (low density, high fish size) that favor experienced anglers. Since experienced anglers have high individual catchabilities, our results suggest that these anglers are attracted to low-density fisheries (characterized by large fish size). Low-density fisheries are often sustained using restrictive regulations, but if effort and catchability are high in low-density fisheries with restrictive bag limits, the possibility for overfishing exists. In the stocked lake system where we collected our data, sustainability is not a concern, but in a wild fishery, the impact of increasing angler efficiency with decreases in bag limits could have counter-intuitive effects on harvest rates, where exploitation rates could increase with more restrictive regulations.

Hyperstability has been documented in a few recreational fisheries (Peterman and Steer 1981; Shuter et al. 1998; Hansen et al. 2005; Erisman et al. 2011). In contrast with our observation that the apparent hyperstability in the multistock spatially structure rainbow trout fishery of British Columbia was caused by a segregation of angler experience levels among lakes, Erisman et al. (2011) and Shuter et al. (1998) suggested that density-dependent catchability in recreational fisheries can also result from variation in fish behaviour. Specifically, Erisman et al. (2011) demonstrated that fisheries that selectively targeted spawning aggregations of barred sand bass (*Paralabrax nebulifer*) and kelp bass (*Paralabrax clathratus*) in southern California, USA, exhibited hyperstable CPUE. Similarly, Shuter et al. (1998) suggested that the observed density-dependent catchability of lake trout (*Salvelinus namaycush*) in several lakes in Ontario is related to anglers selectively targeting spatial aggregations of fish associated with spatial heterogeneity in habitat quality. However, neither of these studies measured angler experience, and therefore it remains unknown how variation in angler experience with fish density relates to the observed hyperstability in these studies. The potential variation in the processes producing hyperstability across fisheries suggests that the mechanistic cause of hyperstability is likely fishery specific owing to variation in fish behaviour across species and angler behaviour across multistock, spatiallystructured fisheries.

The increasingly common occurrence of hyperstability in recreational fisheries suggests that fishery-independent surveys are necessary to estimate stock abundance. If fishery-independent surveys are unavailable, fisheries managers should assume that catchability is density dependent until data can be collected to suggest otherwise. Assuming density-dependent catchability is precautionary, as it results in a lower (and more conservative) population estimate than would be predicted by the traditional linear relationship. In fact, several theoretical and empirical studies of capture processes in fisheries suggest that density-dependent catchability should be expected (Rose and Kulka 1999; Erisman et al. 2011), and when explicitly tested for, the majority of studies demonstrate the presence of density-dependent catchability.

We have witnessed the collapse of approximately 10% of the world's commercially fished stocks (Branch et al. 2011), and increasing evidence suggests that similar outcomes could be seen for recreational fisheries (Coleman et al. 2004; Lewin et al. 2006; Hilborn and Hilborn 2012). In recreational fisheries, population and fishery collapse are often termed "invisible", in part owing to hypothesized hyperstability. Recreational fisheries are often viewed as self-sustaining entities, since fishing effort is expected to decrease with decreases in fish abundance (Carpenter et al. 1994). However, hyperstability results in an "invisible collapse" in both the fishery and fish population, since CPUE remains high as fish abundance declines, and therefore, fishing effort does not respond to a decline in abundance (Post et al 2002; Erisman et al. 2011).

We demonstrate that the observed hyperstability in the rainbow trout fishery in British Columbia is related to a variation in angler skill level among lakes. Quantifying the strength of hyperstability and understanding the mechanistic cause has important impacts for resource managers. Given this information, resource managers can better use fishery data (CPUE and angler skill level) to estimate stock abundance and develop management strategies for the sustainability of fish populations. The large variation in angler skill level across this fishery suggests that CPUE is not indicative of angling quality for the average angler and that heterogeneity in angler skill level must be quantified to optimize management strategies across open-access fisheries. Our results add to the growing body of knowledge that the management of recreational fisheries needs to include both a social and ecological component, and developing quantitative models of how social and ecological processes impact fish populations will improve the management of a fishery.

Acknowledgements

This study was funded by Discovery and Collaborative Research and Development Grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Freshwater Fisheries Society of British Columbia (FFSBC) to John R. Post. We recognize the Habitat Conservation Trust Foundation (HCTF) and anglers, hunters, trappers, and guides who contribute to the Trust, for making a substantial financial contribution to support this project. Hillary Ward was supported by an Industrial NSERC Post-Graduate Scholarship. We thank the staff of FFSBC and the BC Ministry of Environment for the outstanding support they have provided for this project. This research was granted ethical approval by the Conjoint Faculties Research Ethics Board (Certification 6546) and approved by the Canadian Council on Animal Care (Protocol BI08R-21) at the University of Calgary. Field support was provided by Ryan Ashley, Kyera Cook, Travis Desy, Jon Fearns, Brian France, Thamara Hendricks, Collin Middleton, Tabatha Nedokus, Eric Newton, Michelle Phillips, and Daniel Swainson.

References

Allen, M.S., Ahrens, R.N.M., Hansen, M.J., and Arlinghaus, R. 2013. Dynamic angling effort influences the value of minimum-length limits to prevent recruitment overfishing. Fish. Manage. Ecol. **20**(2–3): 247–257. doi:10.1111/j.1365-2400.2012.00871.x.

Askey, P.J., Richards, S.A., Post, J.R., and Parkinson, E.A. 2006. Linking angling catch rates and fish learning under catch-and-release regulations. N. Am. J. Fish. Manage. **26**(4): 1020–1029. doi:10.1577/M06-035.1.

Askey, P.J., Post, J.R., Parkinson, E.A., Rivot, E., Paul, A.J., and Biro, P.A. 2007. Estimation of gillnet efficiency and selectivity across multiple sampling units: a hierarchical Bayesian analysis using mark–recapture data. Fish. Res. **83**(2–3): 162–174. doi:10.1016/j.fishres.2006.09.009.

Askey, P.J., Parkinson, E.A., and Post, J.R. 2013. Linking fish and angler dynamics to assess stocking strategies for hatchery-dependent, open-access recreational fisheries. N. Am. J. Fish. Manage. **33**(3): 557–568. doi:10.1080/02755947.2013.785996.

Baccante, D. 1995. Assessing catch inequality in walleye angling fisheries. N. Am. J. Fish. Manage. **15**(3): 661–665. doi:10.1577/1548-8675(1995)015<0661:ACIIWA>2.3.CO;2.

Bannerot, S.P., and Austin, C.B. 1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. Trans. Am. Fish. Soc. **112**(5): 608–617. doi:10.1577/1548-8659(1983)112<608:UFDOCP>2.0.CO;2.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fisheries Investment Series 2, Vol. 19. UK Ministry of Agriculture and Fisheries, London, UK.

Biro, P.A., and Post, J.R. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. Proc. Natl. Acad. Sci. **105**(8): 2919–2922. doi:10.1073/pnas.0708159105. PMID:18299567.

Branch, T.A., Jensen, O.P., Ricard, D., Ye, Y., and Hilborn, R. 2011. Contrasting global trends in marine fishery status obtained from catches and from stock assessments. Conserv. Biol. **25**(4):777–786. doi:10.1111/j.1523-1739.2011.01687.x. PMID:21535149.

Carpenter, S., and Brock, W. 2004. Spatial complexity, resilience, and policy diversity: fishing on lake-rich landscapes [online]. Ecol. Soc. **9**(1): 8. Available from http://www.ecologyandsociety.org/vol9/iss1/art8/ [accessed 11 December 2012].

Carpenter, S.R., Muñoz-del-Rio, A., Newman, S., Rasmussen, P.W., and Johnson, B.M. 1994. Interactions of anglers and walleyes in Escanaba Lake, Wisconsin. Ecol. Appl. **4**(4): 822–832. doi:10.2307/1942011.

Chipman, B.D., and Helfrich, L.A. 1988. Recreational specialization and motivations of Virginia River anglers. N. Am. J. Fish. Manage. **8**(4): 390–398. doi:10.1577/1548-8675(1988)008<0390:RSAMOV>2.3.CO;2.

Clark, M. 2001. Are deepwater fisheries sustainable? The example of orange roughy (*Hoplostethus atlanticus*) in New Zealand. Fish. Res. **51**(2–3): 125–135. doi:10.1016/S0165-7836(01)00240-5.

Coleman, F.C., Figueira, W.F., Ueland, J.S., and Crowder, L.B. 2004. The impact of United States recreational fisheries on marine fish populations. Science, **305**(5692): 1958–1960. doi:10.1126/science.1100397. PMID:15331771.

Cox, S. 2000. Angling quality, effort response and exploitation in recreational fisheries: field and modelling studies on British Columbia rainbow trout (*Oncorhynchus mykiss*) lakes. Ph.D. thesis, The University of British Columbia, Vancouver.

Cox, S.P., and Walters, C.J. 2002. Modeling exploitation in recreational fisheries and implications for effort management on British Columbia rainbow trout lakes. N. Am. J. Fish. Manage. **22**(1): 21–34. doi:10.1577/1548-8675(2002)022<0021:MEIRFA>2.0.CO;2.

Crecco, V., and Overholtz, W.J. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. **47**(2): 385–394. doi:10.1139/f90-040.

Ditton, R.B., Loomis, D.K., and Choi, S. 1992. Re-conceptualization from a social worlds perspective. J. Leisure Res. **24**(1): 33–51.

Erisman, B., Allen, L.G., Claisse, J.T., Pondella, D.J., II, Miller, E.F., and Murray, J.H. 2011. The illusion of plenty: hyperstability masks collapses in two recreational fisheries that target fish spawning aggregations. Can. J. Fish. Aquat. Sci. **68**(10): 1705–1716. doi:10.1139/f2011-090.

Fenichel, E.P., Abbott, J.K., and Huang, B. 2013. Modelling angler behaviour as a part of the management system: synthesizing a multi-disciplinary literature. Fish Fish. **14**(2): 137–157. doi:10.1111/j.1467-2979.2012.00456.x.

Fisher, M.R. 1997. Segmentation of the angler population by catch preference, participation, and experience: a management-oriented application of recreation specialization. N. Am. J. Fish. Manage. **17**(1): 1–10. doi:10.1577/1548-8675(1997)017<0001:SOTAPB>2.3.CO;2.

Graefe, A.R. 1980. The relationship between level of participation and selected aspects of specialization in recreational fishing. Doctoral dissertation, Texas A&M University, College Station, Texas.

Greenberg, S., and Godin, T. 2012. Timelapse Image Analysis Manual [online]. Technical Report 2012-1028-11, Department of Computer Science, University of Calgary, Alta., Canada. March 15. Software and other documentation available from http://grouplab.cpsc.ucalgary.ca/cookbook/index.php/Demos/TimelapseCoder.

Hansen, M.J., Jr., Beard, T.D., and Hewett, S.W. 2005. Effect of measurement error on tests of density dependence of catchability for walleyes in northern Wisconsin angling and spearing fisheries. N. Am. J. Fish. Manage. **25**(3): 1010–1015. doi:10.1577/M04-153.1.

Harley, S.J., Myers, R.A., and Dunn, A. 2001. Is catch-per-unit-effort proportional to abundance? Can. J. Fish. Aquat. Sci. **58**(9): 1760–1772. doi:10.1139/f01-112.

Hilborn, R., and Hilborn, U. 2012. Overfishing: what everyone needs to know. Oxford University Press, New York.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.

Hunt, L.M. 2005. Recreational fishing site choice models: insights and future opportunities. Hum. Dimens. Wildl. **10**(3): 153–172. doi:10.1080/10871200591003409.

Hunt, L.M., Arlinghaus, R., Lester, N., and Kushneriuk, R. 2011. The effects of regional angling effort, angler behavior, and harvesting efficiency on landscape patterns of overfishing. Ecol. Appl. **21**(7): 2555–2575. doi:10.1890/10-1237.1. PMID:22073644.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**(5): 943–962. doi:10.1139/f96-097.

Hutt, C.P., and Bettoli, P.W. 2007. Preferences, specialization, and management attitudes of trout anglers fishing in Tennessee tailwaters. N. Am. J. Fish. Manage. **27**(4): 1257–1267. doi:10.1577/M05-215.1.

Johnston, F.D., Arlinghaus, R., and Dieckmann, U. 2010. Diversity and complexity of angler behaviour drive socially optimal input and output regulations in a bioeconomic recreational-fisheries model. Can. J. Fish. Aquat. Sci. **67**(9): 1507–1531. doi:10.1139/F10-046.

Jones, C.M., Robson, D.S., Lakkis, H.D., and Kressel, J. 1995. Properties of catch rates used in analysis of angler surveys. Trans. Am. Fish. Soc. **124**(6): 911–928. doi:10.1577/1548-8659(1995)124<0911:POCRUI>2.3.CO;2.

Lewin, W., Arlinghaus, R., and Mehner, T. 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev. Fish. Sci. **14**(4): 305–367. doi:10.1080/10641260600886455.

McArdle, B.H. 1988. The structural relationship: regression in biology. Can. J. Zool. **66**(11): 2329–2339. doi:10.1139/z88-348.

Peterman, R.M., and Steer, G.J. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Trans. Am. Fish. Soc. **110**(5): 585–593. doi:10.1577/1548-8659(1981)110<585:RBSCCA>2.0.CO;2.

Post, J.R. 2013. Resilient recreational fisheries or prone to collapse? A decade of research on the science and management of recreational fisheries. Fish. Manage. Ecol. **20**(2–3): 99–110. doi:10.1111/fme.12008.

Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L., and Shuter, B.J. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries, **27**(1): 6–17. doi:10.1577/1548-8446(2002)027<0006:CRF>2.0.CO;2.

Post, J.R., Persson, L., Parkinson, E.A., and van Kooten, T. 2008. Angler numerical response across landscapes and the collapse of freshwater fisheries. Ecol. Appl. **18**(4): 1038–1049. doi:10.1890/07-0465.1. PMID:18536261.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Richards, L.J., and Schnute, J.T. 1986. An experimental and statistical approach to the question: is CPUE an index of abundance? Can. J. Fish. Aquat. Sci. **43**(6): 1214–1227. doi:10.1139/f86-151.

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. **30**(3): 409–434. doi:10.1139/f73-072.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. Bull. 191.

Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Can. J. Fish. Aquat. Sci. **56**(S1): 118–127. doi:10.1139/f99-207.

Schueller, A.M., Fayram, A.H., and Hansen, M.J. 2012. Simulated equilibrium walleye population density under static and dynamic recreational angling effort. N. Am. J. Fish. Manage. **32**(5): 894–904. doi:10.1080/02755947.2012.705258.

Shardlow, T., Hilborn, R., Peterman, R.M., Steer, G.J., and Bradford, M.J. 1985. Density-dependent catchability coefficients. Trans. Am. Fish. Soc. **114**(3): 436–440. doi:10.1577/1548-8659(1985)114<436:DCC>2.0.CO;2.

Shuter, B.J., Jones, M.L., Korver, R.M., and Lester, N.P. 1998. A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. Can. J. Fish. Aquat. Sci. **55**(9): 2161–2177. doi:10.1139/f98-055.

Smallwood, C.B., Pollock, K.H., Wise, B.S., Hall, N.G., and Gaughan, D.J. 2011. Quantifying recreational fishing catch and effort: a pilot study of shore-based fishers in the Perth Metropolitan area. Fisheries Research Report No. 216. Final NRM Report - Project No. 09040. Department of Fisheries, Western Australia.

Sunger, N., Teske, S.S., Nappier, S., and Haas, C.N. 2012. Recreational use assessment of water-based activities, using time-lapse construction cameras. J. Expo. Sci. Environ. Epidemiol. **22**: 281–290. doi:10.1038/jes.2012.4. PMID: 22354175.

van Poorten, B.T., and Post, J.R. 2005. Seasonal fishery dynamics of a previously unexploited rainbow trout population with contrasts to established fisheries. N. Am. J. Fish. Manage. **25**(1): 329–345. doi:10.1577/M03-225.1.

Walters, C.J., and Martell, S.J.D. 2004. Fisheries ecology and management. Princeton University Press, Princeton, N.J.

Ward, H.G.M., Askey, P.J., Post, J.R., Varkey, D., and McAllister, M. 2012. Basin characteristics and temperature improve abundance estimates from standard index netting of rainbow trout (*Oncorhynchus mykiss*) in small lakes. Fish. Res. **131–133**: 52–59. doi:10.1016/j.fishres.2012.07.011.

Ward, H.G.M., Quinn, M.S., and Post, J.R. 2013. Angler characteristics and management implications in a large multi-stock spatially structured recreational fishery. N. Am. J. Fish. Manage. **33**(3): 576–584. doi:10.1080/02755947.2013.785991.

Appendix A

It is hypothesized that anglers change their methods of fishing to relate to the expected size composition of the population to increase their catch rates (Cox 2000). As a result, length at vulnerability to angling should vary with the length composition of the population. Cox (2000) assessed angling vulnerability for rainbow trout in lakes in British Columbia and demonstrated that the ratio between length at 50% vulnerability (L_{50}) and the maximum asymptotic size (L_∞) is constant across populations, and this ratio was measured to be 0.433 (σ = 0.052). Vulnerability at length (v_l) was calculated using this ratio and an estimated L_∞ from fall gillnet samples.

Lapilli otoliths were collected from all nonclipped fish in the fall gillnet sample and aged (certain year classes in some lakes had unique adipose or ventral clips). A von Bertalanffy growth model was fit to the length-at-age data, L_a:

$$L_a = L_\infty[1 - e^{-K(A-t_0)}] \tag{A.1}$$

where K is a metabolic growth coefficient, A is the age in years, and t_0 is the predicted length at t = 0. Equation A.1 was fit to the observed length-at-age data assuming normally distributed residuals using optim in R, and the lake-specific parameter estimate for L_∞ was used to calculated L_{50} for each lake.

Appendix B

Angler effort was assessed using time-lapse cameras in combination with ground-based counts. Several other authors have used time-lapse cameras to assess water-based recreational activities (Smallwood et al. 2011; Sunger et al. 2012). Cuddeback (Expert Model) cameras were installed at each lake on a tree at the shoreline. The cameras were programmed to take a picture of the lake every hour. The number of anglers in each picture was counted manually using the program Time-Lapse (Greenberg and Godin 2012).

To account for anglers not seen by the camera, ground-based creel counts occurred at the same time. The total number of anglers seen by the camera at time t ($A_{\mathrm{Cam},t}$) can be described by the binomial distribution

$$A_{\mathrm{Cam},t} \sim d\mathrm{Bin}(p, A_{\mathrm{Creel},t}) \tag{B.1}$$

where p is the proportion of anglers seen and $A_{\mathrm{Creel},t}$ is the number of anglers recorded in the ground-based count at time t. The number of anglers missed by the camera (A_{Missed}) is described by the negative binomial distribution

$$A_{\mathrm{Missed}} = d\mathrm{negbin}(p, A_{\mathrm{T}}) \tag{B.2}$$

where A_{T} is the total number of anglers for all camera counts. Therefore, the total annual effort from all anglers is

$$N = A_{\mathrm{Missed}} + A_{\mathrm{T}} \tag{B.3}$$

N and p were estimated in OpenBUGS. A β distribution was used to describe the prior for p with shape parameters (1, 1).

Fig. B1. (*a*) Angler effort density, (*b*) exploitation rate, and (*c*) capture rate as a function of fish density. Exploitation rate is the ratio between the total number of harvested fish and fish density, and capture rate is the ratio between the total number of fish caught (both harvested and released) and fish density. The *y* axis in panel (*c*) is on a log scale, and the axis labels have been back-transformed for interpretation.