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[Article]

Linking Angling Catch Rates and Fish Learning under Catch-and-Release Regulations

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Abstract.—Many recreational fisheries are subject to varying degrees of catch-and-release fishing through regulations and conservation-minded anglers. Clearly, releasing a proportion of the catch improves conservation of the fishery, yet it is not clear how the released catch contributes to angling quality. If fish change their behavior to lower their individual catchability after they have been caught, then angler catch rates may not be proportional to fish density. Therefore, even catch-and-release fisheries could exhibit poor angling quality if there is sufficiently high angler effort. We tested this idea by experimentally fishing five small lakes that contained rainbow trout *Oncorhynchus mykiss* in the interior of British Columbia. We found that with sustained effort of 8 angler-hours $\cdot$ d^{-1} $\cdot$ ha^{-1} and complete release of the catch, catch rates quickly dropped within 7–10 d. Given the individual capture histories of tagged fish, the most parsimonious catchability model incorporated learning and heterogeneity into intrinsic catchability. The best-fit parameter values suggest that the population contained a group of highly catchable fish that were quickly caught and then learned to avoid hooks. There was a seasonal decrease in catchability that was independent of angling; however, it was not sufficient to explain the data. Our results indicate that catch rates may decline because of high angling effort even when the number of fish remains constant. Therefore, management goals that go beyond conservation issues and attempt to maximize angler satisfaction must account for effort density on a recreational fishery.

Stringent regulations and conservation-minded anglers have made catch-and-release fishing increasingly common in North America (Barnhart 1989; Cooke and Suski 2005). Catch-and-release fisheries are positive for conservation-oriented management goals, because intentional, legal harvest mortality is eliminated. However, managers often must balance conservation issues with angler satisfaction and provide quality angling opportunities. The extent to which angler catch rates are improved by regulations that impose partial or complete catch and release is unclear. If catch rates are directly related to fish density, then angler catch should increase in proportion to the number of fish saved from harvest. However, catch-and-release fisheries differ from harvest fisheries in that the fished population consists of fish that have never been caught as well as fish that have been caught and released. Thus, whether catch per unit effort (CPUE) is proportional to density depends on the intrinsic assumption that the catchability of fish that have been caught before and fish that have never been caught fish is equal.

Biologists have frequently observed seasonal declines in CPUE that supersede the decline in sport fish abundance due to harvest (Aldrich 1939; Beukema 1970; Hackney and Linkous 1978; van Poorten and Post 2005). Catch per unit effort is the product of fish density (number per area) and the capture efficiency of anglers (area swept per angler time); therefore, excessive decrease in CPUE indicates a seasonal decrease in capture efficiency. It has been hypothesized that this pattern may arise because previously caught fish learn to avoid hooks. Decreased catchability of previously captured fish has been tested for several different sport fishes (Beukema 1970; Hackney and Linkous 1978; Tsuboi and Morita 2004; Young and Hayes 2004). The conditioning hypothesis has been supported in most of these experiments. However, some of the tests produced no evidence of learning, and the effect appears to vary depending on species and experimental conditions.

Several other processes have been postulated to cause seasonal decreases in catchability. Martin (1958) hypothesized that a rapid decrease in CPUE was caused by differential vulnerability to capture among individual fish. The more vulnerable fish are rapidly

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TABLE 1.—Physical description of experimental lakes in British Columbia used to assess catchability of rainbow trout, and total angler effort for each lake for the entire open-water season (1 angler-day is 4 angler-hours).

Lake	Area (ha)	Maximum depth (m)	Total effort (angler-days/ha)
Little Pantano	1.1	3	72.2
Big Pantano	2.1	4	2.9
Today	6.5	11	1.5
Stubby	6.2	9	1.4
Spook	4.4	4	1.5

harvested, which leaves a less vulnerable pool of fish and a corresponding decrease in CPUE. Cox and Walters (2002) presented a theoretical framework in which fish populations are composed of two pools of individuals that are defined as vulnerable or invulnerable to angling. In their example, fish may move between these defined states by a behavioral change in reactivity to lures (independent of learned hook avoidance) or by physically moving between shallow, fishable shoals and deepwater, unfishable habitats. They showed theoretically that when an invulnerable pool of fish is present, increasing effort can lead to decreased catch rates, despite a near-constant fish density. Finally, catchability may decrease because of seasonal environmental changes that are independent of angler dynamics (van Poorten and Post 2005). Seasonal changes in temperature and resource availability may affect the feeding behavior of fish and thus their susceptibility to anglers.

Seasonal decreases in catchability are common in recreational fisheries; however, the mechanisms underlying this pattern remain unclear. Evidence is accumulating to suggest that learned hook avoidance is a common behavioral response among sport fishes. However, the most convincing evidence comes from the laboratory or small experimental ponds. How this individual-level behavior scales up to entire recreational fisheries is still poorly understood. In this study, we used several whole-lake experimental fisheries to investigate mechanisms for decreased catchability. We used the individual capture histories of tagged fish to infer the processes leading to changes in observed catchability. These processes were then modeled as time series superimposed against the observed fishery dynamics.

Methods

Experimental lakes.—Our study was conducted on four lakes that contained naturalized populations of rainbow trout *Oncorhynchus mykiss* and were located on the Bonaparte Plateau north of Kamloops, British Columbia (51°9′43.43″N, 120°23′26.34″W; altitude = 1,500 m; Table 1). One of the lakes was divided into two sections, which created a total of five experimental units. Four of the experimental lakes were subjected to low angler effort and used to detect environmental effects on catchability. We subjected one small lake to intensive fishing effort in order to investigate the effects of angling pressure on catchability.

To maximize our data collection regime, it was necessary to create a small, fishable lake that had a high density of catchable-sized fish. This was accomplished by quarantining a 1.1-ha section of the 3.2-ha Pantano Lake. The natural bathymetry of the lake consisted of two basins separated by a narrow (width ≈ 12 m) and shallow (mean depth = 0.5 m) section. To divide the lake, we constructed a fence of rebar and 6-mm mesh wire fencing across the shallow area between the two basins. The small basin was named Little Pantano and the large basin was named Big Pantano. We used Little Pantano, which had no creeks flowing in or out, for the high-effort angling experiment. Fish were captured with fyke nets (hoop diameter = 0.5 m; mesh diameter = 6 mm) from both basins and a nearby lake. We graded the catch for the largest individuals (minimum fork length = 150 mm) to be tagged and measured. The fish were released into Little Pantano after a 24-h recovery period in a net pen. In total, 159 individually tagged fish were released into Little Pantano. In addition, we stocked small size-classes of fish that were batch marked with fin clips as part of a separate study. Specifically, we released three size-classes of fish: 100 small (mean fork length = 80 mm), 79 medium (mean fork length = 117 mm), and 80 large (mean fork length = 147 mm). Use of several size-classes allowed us to assess size selectivity of the angling gear and to observe the rate at which each group was recruited into the fishery.

Between September 29 and October 3, 2004, we used gill nets and fyke nets to sample Little Pantano. Over five nights, the sizes and numbers of gill nets used per hectare were identical to those used by Post et al. (1999) and Askey et al. (in press). This standardized gill-net method has been found to be non-size-selective for taggable-sized fish (>150 mm). We also fished one to three fyke nets per night to capture small fish (<100 mm) as part of a separate study. The efficiency of our netting effort was assessed by the recovery rates for three size-classes of fish that had been stocked 1 week before netting. After making a temporary clip on the upper tip of the caudal fin, we released 60 small (mean fork length = 117 mm), 40 medium (mean fork length = 156 mm), and 45 large (mean fork length = 191 mm) fish into all lakes for the mark–recapture experiment. Furthermore, we used fyke nets to capture fish in each lake in the week before netting; these fish were clipped and released, which added 52 fish to the mark–recapture effort.

Capture efficiency for the gill nets and fyke nets of tagged fish was estimated from the proportion of marked fish recovered (fork lengths of 180–310 mm, equivalent to range in size of tagged fish) as $p = m/n$ where p is the probability of capture, n is the number of marked fish released, and m is the number of marked fish that were recaptured.

Angling procedures.—To standardize our angling treatment as much as possible, we restricted the angling to three individuals who used similar fly-fishing gear. We tested fly patterns on a nearby lake that was not part of the experiment and chose two general patterns, which were used for all angling. The patterns were tied on number 14 hooks; one imitated a general nymph and the other was a leech pattern.

Little Pantano was fished every day for 30 d from June 13 to July 12, 2004. Two anglers fished from a single boat for 4 h daily (presented as 1 boat-day of effort), ending approximately 30 min before dusk. The same lake was then fished for 8 d in early August and 3 d in early September. Captured fish were brought to the boat and held in a large bin that contained a small amount of water; tag and length data were then collected. Fish were placed into a small recovery bin beside the boat; and within an hour, they were moved into one of two large net-pens, where they were kept overnight. This was done to control for delayed hooking mortality.

Big Pantano and three other nearby lakes were subjected to very low angler effort (Table 1). This was done so that we could measure if seasonal changes in catchability had occurred independent of angling pressure. The lakes were fished once per month for a 2-h period by each angler; anglers used the same gear that was used to fish in Little Pantano. These fishing events were organized to coincide with the start and end of the 30-d period on Little Pantano and the August and September visits to that lake. All the lakes in our study were accessible to anglers on foot only, which limited the risk of angling pressure by other parties. During the entire summer, we witnessed only a single hike-in party of two individuals on Lakes Today and Stubby; this observation is included in the Table 1 angler effort.

Analysis of catch data.—The main goal of our experiment was to test for learned hook avoidance by fish in recreational fisheries. However, there are at least three mechanisms that may independently affect catch rates over the fishing season: (1) growth of individuals into more vulnerable size-classes (Cox 2000; Parkinson et al. 2004), (2) environmental and/or ecological factors (e.g., changes in temperature or insect activity) that affect foraging behavior (van Poorten and Post 2005), and (3) apparent mortality, which is the summation of death and tag loss in mark–recaptures. Each of these factors must be incorporated into our experimental design.

We have explicitly incorporated size into the probability of capture, because the size-dependence of vulnerability to angling is well known (Cox 2000; van Poorten and Post 2005). The relative vulnerability (v) is assumed to be a sigmoid function of fish length l, and is expressed as

$$v_l = p_{\max} \frac{l^m}{l^m + {L_{50}}^m}, \qquad (1)$$

where $p_{\max}$ is the maximum vulnerability for large fish, L_{50} is the length at which fish are at 50% of full vulnerability, and m is the slope at that point. To scale v to the relative vulnerability for an individual, $p_{\max}$ is set to 1. The individual vulnerability model was fit to the proportion of marked fish recovered per 1-cm size-group in the first 5 d of the fishing experiment on Little Pantano. These parameters were then fixed for fitting the model to capture histories as described below.

A problem exists where environmental effects on catchability occur simultaneously with learned hook avoidance and their effects may be difficult to separate. We therefore divided our angling experiment into two parts: (1) a set of lightly fished lakes to assess the seasonal trend in catchability and (2) a single, intensely fished lake to assess fish learning. This approach allowed us to first test whether a purely seasonal trend in catchability exists. Existence of such a trend would allow us to incorporate it into the multiple mark–recapture efforts on Little Pantano and to isolate learning effects from environmental effects on catchability.

The effort on our four lightly fished lakes was very low (Table 1), so that a negligible proportion of the fish population had encountered an angling experience at any given time. Thus, any changes in catchability over time were because of temporal changes in environmental or ecological factors. Let δ be a parameter to describe the seasonal environmental influence on catch rates. It could be simply a function of temperature or a function of multiple environmental factors, which can be modeled as a function of time:

$$\delta_t = f(t). \qquad (2)$$

Thus, the expected catch rate EC_{il} for angler i on lake l can be modeled as the seasonal average catch rate for angler i on lake l (μ_{il}) modified by the seasonality parameter:

$$\mathrm{EC}_{il} = \mu\delta_t. \tag{3}$$

The incorporation of the μ parameter puts all lakes on a relative scale, because we are interested in the relative change in catch rates over the season. Our results are not sensitive to differences in absolute catchability, which vary between lakes because of fish density or lake characteristics. This time- or temperature-dependent expected catch rate is incorporated into the Poisson log-likelihood function (LL) of a single observed catch (C) as

$$\mathrm{LL}(C|\mu_{il}, \delta_t) = C\log_e(\mu_{il}\delta_t) - \mu_{il}\delta_t - \sum_{x=1}^{C}\log_e(x). \tag{4}$$

The maximum likelihood for the entire data set of observed catches given a seasonality effect is

$$\mathrm{LL}(\mathrm{data}|\delta) = \sum_{x=1}^{N}\mathrm{LL}(C_x|\mu_x, \delta). \tag{5}$$

We maximized this likelihood for the catch data, where δ was a function of time or temperature. We omitted fish from the catch data that would not have been vulnerable (<150 mm) on day 1 to control for recruitment of catchable fish over the season. Estimates for δ on days not fished was estimated by linear interpolation. As a result, for any given day of the season, the baseline catchability could be adjusted by multiplying by the estimated δ.

Individual catchability analysis.—Suppose I fish are marked on day 0 and released into a lake. On N occasions, the fish are recaptured. The first N-1 recaptures are by angling and the last recapture is by net. The day of recapture n is denoted t_n. Let $x_{i,n} = 1$ if fish i ($i = 1$ to I) is recaptured on day t_n, and $x_{i,n} = 0$ if the fish is not recaptured. Let $\mathbf{X}$ be the N by I matrix describing the recapture data.

Now consider a single fish. Let c_n be the probability the fish is caught during recapture day n (we will consider c_n in more detail below). Let s_n be the probability that the fish survives to time of the nth recapture, given that it was alive at the time of the (n − 1)th recapture. If the fish experiences a time-independent instantaneous mortality rate $m(t)$ at time t, then the survival probabilities can be calculated using

$$s_n = \begin{cases} \exp(-mt_1) & \text{if } n = 1 \\ \exp(-m(t_n - t_{n-1})) & \text{if } n > 1 \end{cases}. \tag{6}$$

The probability of observing the N recapture data associated with a single fish, given the probabilities of recapture and survival, is

$$\Pr(x_1, \ldots x_N | c_1 \ldots c_N, s_1 \ldots s_N)$$
$$= \begin{cases} \prod_{n=1}^{N} s_n[x_n c_n + (1 - x_n)(1 - c_n)] & \text{if } l = N \\ \prod_{n=1}^{l} s_n[x_n c_n + (1 - x_n)(1 - c_n)] & \\ & \text{if } l < N \\ \times\left[\sum_{j=l+1}^{N}(1 - s_j)\prod_{n=l+1}^{j-1}s_n(1 - c_n) + \prod_{n=l+1}^{N}s_n(1 - c_n)\right], & \end{cases} \tag{7}$$

where l is the last recapture (i.e., $x_n = 0$ for all $n > l$). If the fish is never recaught, $l = 0$. Assuming the fish recaptures are independent, the probability of observing all the data $\mathbf{X}$ is the product of the above probability for all fish. The log-likelihood function (LL) is $\log_e[\Pr(\mathbf{X})]$, which is incorporated into our model selection criteria, Akaike's information criterion (AIC), as

$$\mathrm{AIC} = -2\mathrm{LL} + 2k, \tag{8}$$

where k is the number of estimated parameters in the model. Akaike's information criterion values are used to select the most parsimonious model by penalizing the model fit (LL) by the number of parameters used. Thus, the optimal models possess the minimal AIC values and the relative parsimony of other models is evaluated by the differences between AIC values, ΔAIC (Burnham and Anderson 2002; Richards 2005).

We used AIC to test a suite of biologically plausible models that may describe temporal patterns in catch rates. A null model describes catchability as a constant or dependent on environmental factors; however, we incorporated two additional reasons for decreased catch rates: (1) learned hook avoidance and (2) heterogeneity in intrinsic catchability. To incorporate these factors, the probability of capture (c) for a single fish is manipulated. The probability of capture is actually a composite of several factors, expressed as

$$c_n = 1 - e^{-q_n v_n E_n}, \tag{9}$$

where c is the probability of capture on day n, q is the catchability coefficient (area swept per angler per unit time), E is the effort (angler time per area), and v accounts for the size selectivity of fishing gear (equation 1).

For a given effort and length on day t, the probability of capture for an individual depends on the catchability coefficient (q). In the simplest case, catchability is constant:

$$q = q_0. \tag{10}$$

However, q may be dependent on the number of times an individual fish has been captured previously (denoted tc)

$$q = q_{\mathrm{tc}}. \tag{11}$$

A potentially more parsimonious version of this idea is to describe q as a continuous function of times previously caught

$$q = f(\mathrm{tc}). \tag{12}$$

Since catchability cannot be negative, a logical function is the negative exponential,

$$q = q_0[e^{(-\beta\mathrm{tc})}], \tag{13}$$

where q_0 is the catchability for fish that have never been captured and β is a parameter that describes the decline in catchability for an individual fish that has been previously captured. The above models were then substituted into equation (9) for capture probability.

A second possibility is that heterogeneity in q occurs within the population because individual fish are intrinsically more or less catchable regardless of their capture history. This could arise from behavioral differences in foraging activity or diet preference. To model this scenario, we assume the existence of discrete fish classes (Pledger et al. 2003), each with its own catchability parameters. Each individual has an unknown probability π_i of being in class i. We return to equation (7) for the probability of an individual fish capture history and sum the Prob($x_{1...N}|s_{1...N},c_{1...N}$) × Prob(class $= i$) over all possible fish classes. We tested the simple case of two fish classes with unknown proportions (π and $1 - \pi$) in each class, which leaves the following probability:

$$\begin{aligned}&\Pr(x_{1\ldots N}|c_{1\ldots N}, s_{1\ldots N}, \pi)\\&\quad= \pi \times \Pr(x_{1\ldots N}|c_{1\ldots N}, s_{1\ldots N})\\&\qquad+ (1-\pi) \times \Pr(x_{1\ldots N}|c_{1\ldots N}, s_{1\ldots N}).\end{aligned}$$

We tested another set of models that incorporated the existence of two classes of fish and catchability based on capture history.

The final data set for model selection was a matrix of 157 fish (two hooking mortalities were omitted) and 43 capture events with 1 or 0 values. The final capture event was fall gillnetting, which was used to confirm survival for the captured fish and estimate abundance as mentioned above. A second matrix of equal dimensions was created by using individual fish fork lengths. Lengths on days when fish were not measured were estimated using linear interpolation.

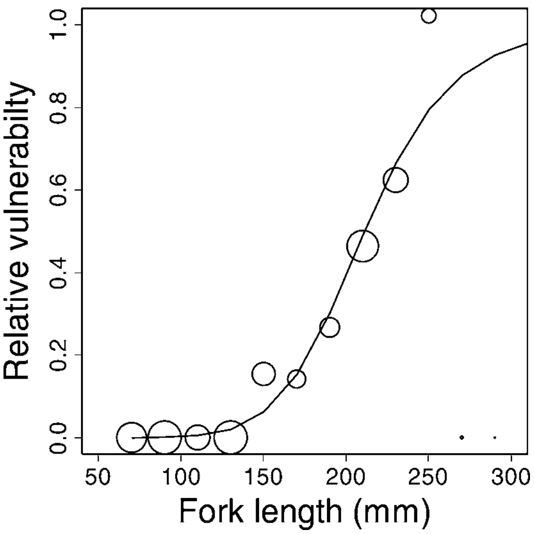

FIGURE 1.—The relationship between rainbow trout fork length and vulnerability to experimental angling in British Columbia lakes during 2004. Size of the points is proportional to number of marked fish within the 10-mm size bin (smallest point = 1; largest point = 57). Solid line is the maximum likelihood fit of equation (1), where data and model have been scaled so that the maximum vulnerability for large fish is 1.

Results

Size Selectivity

The proportion of marked fish captured in the first 5 d of fishing varied with mean length (1-cm size bins). The maximum likelihood fit of the size-selective vulnerability function yielded parameter estimates of $m = 7.95$ and $L_{50} = 211.4$ (Figure 1), which are similar to the parameter values found in other studies of rainbow trout (Cox 2000; van Poorten 2003). The estimated parameters confirmed that all individually tagged fish were vulnerable to angling (minimum size = 150 mm), although they had not reached a fully vulnerable size (i.e., $0 < v < 1$). These parameter estimates were set as constants in the model selection process.

Seasonal Trends in Catch per Unit Effort

On our four control lakes, the catch rates for fish that were vulnerable to capture since day 1 showed a decreasing trend (Figure 2). The trend was not temperature driven; catch rates did not recover in the fall when water temperatures decrease. A temperature-driven model fit the data poorly (LL = −104.75). We chose to describe the trend with a four-parameter, time-dependent model that fit a mean catch rate adjustment for each fishing period (LL = −92.43). The data could be described by a simple linear decrease, but the goal

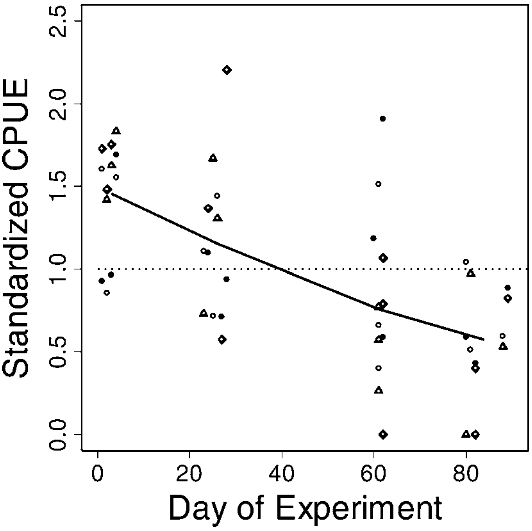

FIGURE 2.—Standardized rainbow trout CPUE (CPUE × mean CPUE^{-1}; CPUE in units of fish per angler-hour) for four lakes in British Columbia subjected to low angling effort over the summer (day 1 = June 13, 2004; black filled circles = Big Pantano Lake, open circles = Lake Today, open triangles = Lake Stubby, diamonds = Spook Lake). The black line is the best-fit model for the seasonal trend (δ).

was to fit the seasonal fluctuations as accurately as possible to create a baseline for the mark–recapture analysis.

Little Pantano Catch per Unit Effort

Catch rates were initially quite high on Little Pantano: approximately 16 tagged fish/boat-day were caught for the first 5 d (Figure 3a). However, the CPUE declined rapidly to approximately 5 tagged fish/boat-day by day 15 and remained low for the rest of the 30-d trial. Catch rates for the tagged fish remained low when fishing resumed after a break of 23 d.

In addition to the tagged fish, the lake also contained fin-clipped fish that were initially too small to be fished but recruited into vulnerable size-classes as they grew. These fish became more prevalent in the catch over time and made up most of the catch in the second half of the summer, after the break (Figure 3b). Continual recruitment throughout the summer of the small, batch-marked fish prevented a dramatic drop in catch rates for the overall population (Figure 3c).

Our mark–recapture data indicated that we recaptured 51.6% of fish larger than 180 mm (all tagged fish were in this size range) after angling had ceased. We used fyke nets and gill nets for the recapture; given the netting efficiency, we estimated 41% of the fish tagged on day 0 remained present with tags at the end of the experiment. There were three processes by which fish were removed from the experiment: (1) hooking mortality, (2) natural mortality, and (3) tag loss. Hooking mortality was estimated based on observation of deaths within the 24-h recovery bins. There were nine mortalities from hooking injuries; however, only 2 were from the 159 fish marked on day 0. Fourteen fish with visible tag scars were captured in gill nets, which gives an estimated tag loss of 30%. These fish are considered mortalities in the data analysis, because no information can be collected from them (post tag loss). Thus "mortality" estimates in model fitting (Table 2) include tag loss and death during the season. Tag loss was not a problem for the fitting of individual capture histories; only seven fish with tag scars were caught, and all such captures occurred from day 54 on.

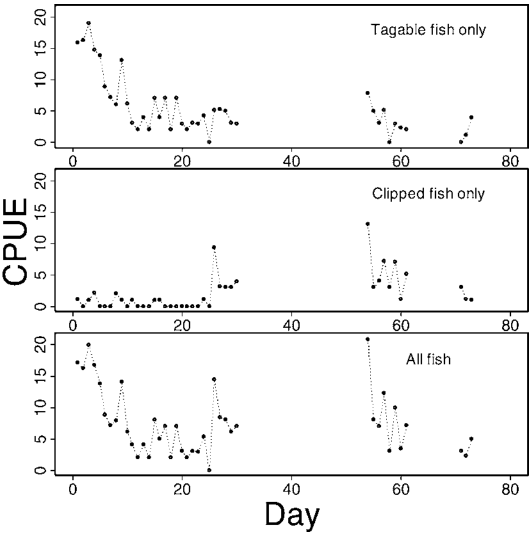

FIGURE 3.—Rainbow trout catch rates (CPUE in fish/boat-day) in Little Pantano Lake, British Columbia, over the entire fishing period (June 13–September 3, 2004). The top panel shows catch rates for fish that were tagable from day 1 (minimum size = 180 mm). The middle panel shows catch rates for batch-clipped fish that were too small to individually tag and that were essentially invulnerable to angling on day 0. These fish recruited into the fishery by growth. The bottom panel shows catch rates for all fish present. One boat-day equals two anglers fishing for 4 h from a single boat.

Individual Catchability and Model Selection

The first set of models that were fit to the data set of individual capture histories, focused on the potential influence of learned hook avoidance by varying catchability with previous capture experience. The ΔAIC values suggested that the abrupt drop in catch rates could not be described by a constant catchability adjusted for seasonal effects (Table 2; Figure 4).

TABLE 2.—Summary of rainbow trout catchability models tested, including associated parameter values and fitting performance. Parameters and abbreviations are as follows: qa = catchability coefficient for class a; qb = catchability coefficient for class b; tc = times caught previously; βa and βb are slope parameters; μ = catch rate; π = probability of being in class i; k = number of estimated parameters; LL = log likelihood; AIC = Akaike's information criterion; ΔAIC = difference in AIC between the given model and the model with the lowest AIC value.

Model specification		
Model number	Equation	Description
1	$q_t = q$	Constant q
2	$q_t = q_{\text{tc}}$	q changes after first capture event
3	$q_t = q_{\text{tc}}$	q changes for capture events 1 and 2
4	$q_t = q_{\text{tc}}$	q changes for capture events 1–3
5	$q_t = q_0 \times e^{(\beta \times \text{tc})}$	q is a continuous function of times caught
6	$q_t = \begin{cases} qa \text{ class} = a \\ qb \text{ class} = b \end{cases}$	Two classes of fish with constant qs
7	$q_t = \begin{cases} qa_0 \times e^{(\beta_1 \times \text{tc})} \text{ class} = a \\ 0 \quad \text{class} = b \end{cases}$	Continuous learning with an invulnerable class
8	$q_t = \begin{cases} qa_0 \times e^{(\beta \times \text{tc})} \text{ class} = a \\ qb_0 \times e^{(\beta \times \text{tc})} \text{ class} = b \end{cases}$	Two classes of fish with continuous learning
9	$q_t = \begin{cases} qa_0 \times e^{(\beta a \times \text{tc})} \text{ class} = a \\ qb_0 \times e^{(\beta b \times \text{tc})} \text{ class} = b \end{cases}$	Two classes with independent learning parameters

Models that incorporated experience-dependent catchability models were found to be more parsimonious (Table 2). The parameter estimates indicated that fish became less catchable if they had been previously captured. Furthermore, when specific catchabilities were fitted to the model for capture history, it was found that fish catchability continued to decrease with additional capture experiences. Model 5 had the optimal fit and depicted catchability as a negative exponential function of times caught. However, none of the models that were based on learned hook avoidance alone were flexible enough to mimic the sharp initial decrease in catch rates seen in the data (Figure 4). All models that were based on a single class of fish underestimated the catch rates seen in the beginning of the angling experiment

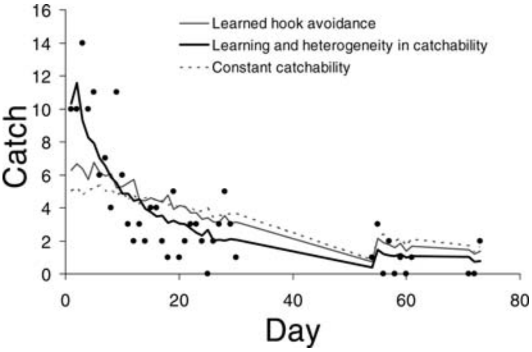

FIGURE 4.—Model fits of empirical rainbow trout catch data for Little Pantano Lake, British Columbia, which contained 157 fish tagged on day 0 of an angling experiment in 2004. The dashed line is model 1 (see Table 2) based on the simple case of constant catchability adjusted for seasonal effects. The solid gray line is model 5, where catchability is a negative exponential function of the number of times a fish has been caught previously. The solid black line is model 8, which incorporates learning and two classes of fish within the population that differ in their intrinsic catchability. Seasonal effects (δ) are incorporated into all models as depicted in Figure 2, and jaggedness of lines represents variability in effort.

Simply dividing the population into two classes (with regards to intrinsic catchability) is not helpful, as model fitting produced equal catchabilities between classes ($q_a = q_b$) or the existence of a single class ($\pi = 1$). However, models that incorporated learning with heterogeneity in catchabilities were able to better fit the trend seen in the catch data. The most parsimonious model separated the population into two classes based on intrinsic catchability and both classes exhibited the same learned hook avoidance function (Table 2; Figure 4). The parameter estimates for this model indicated that about 32% ($\pi = 0.322$) of the entire population were highly catchable fish that quickly learned to avoid hooks. Model fitting suggested that both classes learned at a similar rate; a sixth parameter (β_b) was not justified (ΔAIC = 0.7; Table 2). The change in AIC from the best-fit model to the next best single-class model was greater than 20, which indicates that the model including heterogeneous intrinsic catchability is substantially better than the learning-only model (Burnham and Anderson 2002; Richards 2005).

TABLE 2.—Extended.

Model specification	Parameters										Fit and selection		
Model number	μ	qa_0	qa_1	qa_2	$qa_{>2}$	π	qb	β_a	β_b	k	−LL	AIC	ΔAIC
1	0.011	0.047	0.047	0.047	0.047	1				2	749.2	1,502.3	33.0
2	0.011	0.059	0.037	0.037	0.037	1				3	745.5	1,497.1	27.8
3	0.011	0.059	0.046	0.023	0.023	1				4	742.7	1,493.5	24.2
4	0.011	0.059	0.046	0.024	0.021	1				5	742.7	1,495.5	26.2
5	0.011	0.061				1		−0.375		3	743.0	1,492.0	22.7
6	0.011	0.047				0.500	0.047			4	749.2	1,506.3	37.0
7	0.010	0.101				0.747	0	−0.714		4	737.6	1,483.3	14.0
8	0.009	0.299				0.322	0.030	−1.125	−1.125	5	729.9	1,469.3	0.0
9	0.009	0.382				0.265	0.033	−1.126	−0.550	6	729.0	1,470.0	0.7

Discussion

There have been many hypotheses put forth to explain seasonal decreases in recreational fishery catch rates. Our study shows that, indeed, several components explain this phenomenon, including learned hook avoidance, heterogeneity among individual fish, and environmental factors. The culmination of these components led to a sharp decrease in daily catches from 16 to 4 fish (tagged individuals) within 30 d of intensive catch-and-release angling.

Learned hook avoidance was a key component needed to explain the large data set of individual capture histories. Our study supports previous studies that have reported the potential for learned hook avoidance in fished populations. Similar evidence in studies of other sport fish (Anderson and Heman 1969; Beukema 1970; Hackney and Linkous 1978) indicates that learned hook avoidance is not restricted to rainbow trout. However, only some of the largemouth bass *Micropterus salmoides* experimental groups exhibited learning (Anderson and Heman 1969; Hackney and Linkous 1978). Furthermore, Tsuboi and Morita (2004) found no evidence of learning among whitespotted char *Salvelinus leucomaenis* in a Japanese stream, and cutthroat trout *O. clarkii* in Yellowstone River were estimated to be captured 9.7 times per season (Schill et al. 1986). This suggests that differences in learning and/or habitats may make some species more suited for catch-and-release management than others. Previous work has demonstrated differences in catchability among species and strains owing to variation in behavior (e.g., Brauhn and Kincaid 1982; Dwyer 1990). It seems plausible that conditioning should vary because of species-specific behavioral characteristics as well. The lack of learning behavior demonstrated by whitespotted char in Japan and cutthroat trout in the Yellowstone River could also be a result of the lotic environment. For example, the nature in which food is presented in a stream necessitates a rapid response by the fish or the food will be lost downstream. Therefore, fish cannot examine and potentially reject their prey to the same degree possible in a lake. However, disturbed or angled fish in New Zealand streams were found to exhibit other conditioned behaviors, such as hiding, that would prevent their capture (Young and Hayes 2004).

Learned hook avoidance was only part of the process suggested to explain seasonality in catch rates. It was only possible to fit the sharp initial decline in catch rates if intrinsic differences in fish were also taken into account. It seems plausible that some proportion of fish populations should be less vulnerable to angling because of factors such as highly selective diets. Cox and Walters (2002) proposed that some proportion of the population is unavailable to angling due to spatial distribution in unfishable areas. Our experimental lake was small and relatively shallow so that the entire lake could be fished effectively. However, our data supported a similar hypothesis, whereby, a proportion of the fish are highly susceptible to angling but quickly learn to avoid hooks. Martin (1958) originally proposed that populations may contain a more catchable group of fish that would be quickly harvested. Yet we have shown that even when fish are not harvested, the same decline in CPUE will occur because of a more catchable group that exhibits learning. This result indicates that lakes exposed to fishing for the first time are likely to exhibit a short period of exceptional angling that is rapidly reduced to average catch rates, regardless of bag-limit regulations. Catch rates may continue to decline with continued pressure; however, the decline is much slower after the original "fishdown" period.

The dramatic drop in catch rates of tagged fish seen in our experiment may have been more extreme than would be typical in nature. Our protocol of retaining fish in net pens to control for hooking mortality may also have stressed fish and changed their behavior. Given our data, we cannot separate the relative effect of stress in net pens from the stress incurred during capture. It was also apparent that catch rates were affected by recruitment of fish that had grown over the summer. However, if effort is sustained over the summer, it seems likely that growth recruitment will only prevent further declines after the abrupt fishdown early in the season. We may have exaggerated the learning ability of fish by only using two fly patterns for all angling. Presumably we could have continued to entice strikes if we would have changed to new patterns that the fish had not previously seen. However, fish probably take some cues from characteristics common to all lures (e.g., visible hooks or fishing line). Lastly, a small part of the decline in catch rates was fishery independent; catch rates were found to decline in the lightly fished lakes. Thus, other geographical regions that have different climatic patterns and fish species may experience different seasonal trends.

As angling effort continues to increase in many fishing areas, managers are challenged to produce quality angling opportunities. Trophy fisheries are normally managed by high minimum size limits or catch-and-release regulations. However, as demand and effort on such fisheries increases, even catch-and-release fisheries can produce relatively low catch rates. This result was previously suggested based on hooking mortality and illegal harvest (Post et al. 2002, 2003). However, hooking mortality and illegal harvest are potentially lowered through management actions other than effort control. Low catch rates due to learning limit management strategies to: (1) finding strains of fish that have high catchability, low hooking mortality, and exhibit poor learning ability; or (2) effort control. Managers are faced with the difficult notion that if they are successful in generating license sales, they will not be able to maintain angling quality by simply setting restrictive bag limits, size limits, or even by implementing catch-and-release regulations.

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