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Predicting changes in the catchability coefficient through effort sorting as less skilled fishers exit the fishery during stock declines

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ABSTRACT

Effort sorting is a process in fisheries where fishers of various skill levels sort according to fish density so that the mean catchability of remaining fishers increases as stock size declines. The resulting hyperstability in catch rates masks declining density, sometimes until fish populations have effectively collapsed. Effort sorting as a potential mechanism leading to hyperstability has been known for a while, but the ability to detect it using existing fisheries data has been limited. We present a way to detect effort sorting in fisheries and evaluate it using published recreational fisheries data. Specifically, we propose that catchability among anglers is log-normally distributed, but the anglers remaining fishing on any particular lake will have catchabilities high enough to exceed a minimum acceptable catch rate given available stock size. It is then possible to discern between hypotheses about causes of hyperstability, namely effort sorting or range contraction. However, the fitted model cannot reliably be used to predict fish density from catch-per-unit effort (CPUE) data, reiterating the importance of fishery-independent data, and serving as a warning against using CPUE as an index of density in management.

1. Introduction

Catchability is a measure of the fishing efficiency per fish density or the fishing mortality rate per unit of fishing effort (Arreguin-Sanchez, 1996). Catchability is a function both of fish behavior (e.g., activity, aggregation, naiveté; Arreguin-Sanchez, 1996; Askey et al., 2006; Kuparinen et al., 2010; Alos et al., 2012) and fisher behavior (e.g., skill in finding and capturing fish; Jones et al., 1995; Gaertner et al., 1999; Ruttan, 2003; Salas and Gaertner, 2004). It is commonly assumed that catchability is constant across a wide range of fish densities, implying that catch-per-unit effort (CPUE) is directly proportional to density. Assuming constant catchability is important because in the absence of fishery-independent data CPUE is commonly used as an index of density (Hilborn and Walters, 1992; Quinn and Deriso, 1999). However, catchability in many (particularly recreational) fisheries is density-dependent and most often hyperstable (Erisman et al., 2011; Shuter et al., 1998; Ward et al., 2013a), meaning catchability increases as density declines. Density dependent catchability is problematic for managers monitoring catch rates because density declines more quickly than catch rates, masking potential fishery collapses (Hilborn and Walters, 1992; Post et al., 2002). Understanding the range of conditions under which catchability may vary is important for fisheries management and conservation (Fenichel et al., 2013; Hunt et al., 2011), especially in situations where fisheries-independent data are sparse or absent.

It is typical for the skill of recreational anglers to vary considerably (Abrahams and Healey, 1990; Baccante, 1995; Ruttan, 2003; Ward et al., 2013b), often seen as catch inequality across individuals. If there is a minimum success rate that anglers are willing to tolerate, then less skilled anglers will exit the fishery (or seek other recreational opportunities) before more skilled individuals during periods of stock decline (Post, 2013; Walters and Martell, 2004). This "effort sorting" process (Walters and Martell, 2004) will lead in turn to increases in the average catchability coefficient of the subset of anglers still actively participating. Such a perceived increase in average catchability coefficient can cause fishing morality rate to remain high despite effort decreases and cause CPUE to exhibit hyperstability even when other mechanisms that typically cause hyperstability (handling time, range contraction) are absent. Obviously, this process will also depend on the dynamics of other fishing opportunities, making direct observation difficult. The notion of effort sorting is not new, but the ability to detect it as a mechanism has been limited. The effort sorting mechanism is not specific to recreational fisheries. For example, commercial fisheries experi-

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ence effort sorting near the end of a fishing season as less efficient boats leave early to balance revenue against costs. Vessel buyback programs are also more likely to attract less efficient skippers and owners. While the relative influence of effort sorting in different fisheries has not been evaluated, it seems likely that this mechanism is particularly strong in recreational fisheries, where skill and experience vary widely (Walters and Martell, 2004).

We propose a framework for predicting how the average catchability coefficient, i.e., the fishing mortality rate if effort is known, will change under the assumption that anglers have similar constraints that result in similar catch rates at which they cease fishing. Within this framework, we explore alternative hypotheses for variation in catchability. Namely, we suggest that effort sorting may occur due to one or more of the following mechanisms: 1) the basic effort sorting mechanism outlined above; 2) effort sorting exacerbated by tolerance for low catch rates being related to catchability, so skilled anglers will also accept lower catch rates than less skilled anglers due to factors such as increases in maximum fish size; or 3) effort sorting exacerbated by hyperstability in catchability due to spatial contraction of fish at low densities. We evaluate these models against catch rate data presented in Ward et al. (2013a) on freshwater recreational fisheries in British Columbia.

2. Characterizing change in catchability as less-skilled anglers leave the fishery

Anglers will only continue to fish if they believe there is a positive benefit. Suppose that catching fish is the primary motivation for fishing, and the catch rate at which anglers exit the fishery is c_o. An angler i, who has catchability coefficient q_i, will seek other options (either fishing elsewhere or not at all) when stock density N is low enough so that catch rate q_iN is less than c_0, or equivalently when that individual's q_i satisfies:

$$q_i < c_0/N. \tag{1}$$

Next, suppose that the distribution of q_i's over the population of anglers is approximately log-normal (or the distribution of $q_i{}^* = \log_e(q_i)$ is normally distributed), with mean μ_q and standard deviation σ_q. That is, suppose that 50% of anglers will exit the fishery, so that effort drops below half its maximum value, when$q_i{}^* = \log_e(c_0) - \log_e(N) < \mu_q$. Highly heterogeneous angler populations are represented by high σ_q (Walters and Martell, 2004), potentially resulting in a few very skilled anglers. For the constant-catchability case (Eq. (1)), a normal distribution of $q_i{}^*$'s over anglers implies that the effort response (number of anglers fishing) to increasing N will have a sigmoidal shape, i.e., will be a cumulative log-normal distribution with cumulative probability 0.5 at the density for which catch rate is equal to c_0.

Given a density N, we can then predict the mean catchability coefficient of the anglers that will continue to fish at that density as the back-transformed mean of the truncated normal distribution with lower truncation limit q_{min} given by Eq. (1). That mean is given by (Greene, 2003)

$$q_e = \exp\left(\mu_q + \sigma_q \frac{n(d)}{1 - N(d)}\right) \tag{2}$$

where q_e is the mean of the remaining anglers with individual q_i's, $n(d)$ is the standard normal density function (mean 0, standard deviation 1.0) evaluated at the deviate

$$d = \frac{\left(\log_e(q_{min}) - \mu_q\right)}{\sigma_q} \tag{3}$$

using q_{min} equal to the q_i from Eq. (1) and $N(d)$ is the cumulative standard normal distribution function evaluated at standard deviate d.

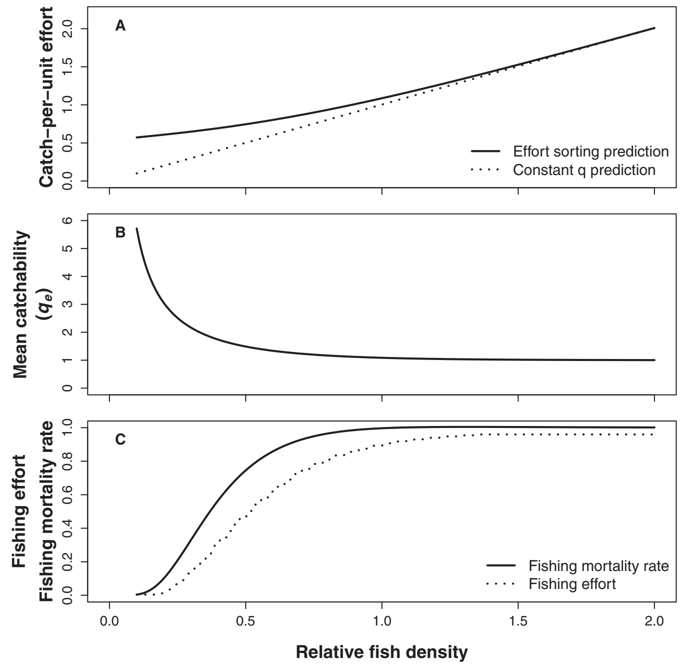

Fig. 1. (A) Hyperstability in CPUE caused by increases in mean q_i at low stock size due to effort sorting even assuming CPUE = qN, where q is catchability and N is fish density; (B) change in catchability as density declines due to effort sorting; (C) change in fishing mortality rate and fishing effort as fish density declines.

For illustrative purposes, when N changes from 0.0 to 2.0, $\mu_q = 0$, $\sigma_q = 0.25$ and $c_0 = 0.5$, effort sorting leads to differences in CPUE at low stock sizes (Fig. 1A) and increases in q_e at low stock sizes (Fig. 1B). However, fishing mortality, calculated as $F = q_e \times$ effort, does not increase at low stock sizes due to decreases in fishing effort (Fig. 1C). Note that the outcome of this process is that CPUE for this example would display dangerous hyperstability for stock sizes below 0.75.

It should not be difficult to obtain reasonable estimates of c_0 from observations of catch rates at which anglers exit the fishery and from economic analysis of the costs of fishing relative to catch per effort (Cinner et al., 2008; Daw et al., 2012). The catchability distribution parameters μ_q and σ_q are much more difficult to estimate. One possibility is to examine how observed CPUE changes with density estimates from various assessment methods (e.g. Fig. 1). Another possibility is to conduct experimental fishing with standardized q and to compare a standardized q to changes in mean q measured over the heterogeneous angler population as Ward et al. (2013a) did for recreational trout fishing in British Columbia.

Note that the q distribution cannot be estimated just by examining short term variation in catch rates among anglers; many factors contribute to that variation, especially chance variation in encounter rates (Ruttan, 2003). For example, in recreational fisheries we typically see Poisson or negative binomial distributions of catch rates across anglers over short sample periods (Seekell, 2011). This variation does not mean that catchability varies among anglers, or that the distribution of catchability among anglers is Poisson or negative binomial; rather, it means only that luck varies for every angler and "real" or persistent variation in catchability among anglers can only be seen by comparing average catch rates across anglers over long time periods (fishing seasons, years; Deriso and Parma, 1987). Over longer periods, we expect q_i for any given angler to increase with experience (Ward et al., 2013a,b) and accumulated information about best fishing sites and practices, then decrease with angler age for those old enough to have difficulty handling the physical rigors of fishing. An obvious statistical approach is to use a hierarchical modeling approach such as is commonly used in "standardizing" CPUE, with year effects representing density change and angler effects representing the "hyperdistribution" of q_i values. This analysis would need to be conducted on CPUE data collected over periods short enough for such cumulative learning effects to be negligible. Ward et al. (2013a) used this approach in a cross-lake comparison, where more experienced (presumably higher q_i) anglers were typically found to fish on lakes with lower fish densities. In the next section, we use this data to estimate parameters of our model and test several assumptions regarding the cause of hyperstability seen in their data.

3. Application to recreational fishery data from a landscape of lakes

While we argue that effort sorting is a potentially important mechanism driving variation in catchability and hyperstability in many fisheries, there are other competing mechanisms that will likely occur in concert. We propose three variations of related mechanisms that may explain effort distribution in BC lakes, as reported in Ward et al. (2013a). The base model (Model 1) supposes that effort sorting occurs due to anglers with lower catchability leaving as densities decline, as outlined above. Model 2 assumes that anglers with higher q_i's may also have lower fishing costs (or tolerance for low CPUE for various reasons, such as larger average fish size when density is low; Beardmore et al., 2015). This can be incorporated into the model structure by assuming a linear decrease in the cost of exiting the fishery with increasing q, i.e.:

$$c_{exit,i} = c_0 - c_1 q_i, \tag{4}$$

which changes the calculation of q_{min} for Eq. (1) from c_0/N to

$$q_{min} = c_0/(N + c_1). \tag{5}$$

The variable c_1 represents the rate at which the cost of exiting the fishery changes across anglers as individual q_i changes. Model 3 assumes there is density dependence in catchability and/or a search-handling time effect on catchability (e.g. $CPUE = \frac{q_i N}{1+hN}$; Appendix A), so the condition where anglers exit the fishery becomes

$$q_{min} = c_0 \frac{(1 + hN)}{N}. \tag{6}$$

Note that density dependent catchability implies density must be lower by a factor determined by the handling time or range contraction parameter h before an individual will exit the fishery.

We evaluated each of the assumptions regarding the behaviors that lead to CPUE patterns (Models 1–3) using the data presented in Ward et al. (2013a). CPUE in the 18 lakes was assessed using a seasonally and weekly stratified creel survey where anglers were asked catch and effort upon trip completion. Fish densities were estimated in 16 of 18 lakes using a standardized gill net protocol (Ward et al., 2012). In the remaining two lakes, fish densities were estimated using a mark-recapture method (see details in Ward et al. (2013a)).

Each of the three proposed mechanistic models were fit to the CPUE data from Ward et al. (2013a) (Table 1). Prior probability distribution functions (PDF) for each of the estimated parameters were assumed uniform except for precision (τ), which was assumed to be gamma distributed. CPUE data were assumed normally distributed with estimated precision τ. Posterior distributions for each model were calculated from 100,000 Markov chain Monte Carlo iterations after an initial burn-in of 4,900,000 iterations and further thinned to provide a final sample of 1000 iterations from each of four chains (using JAGS 3.4.0; Plummer, 2003). Burn-in length and associated convergence were evaluated iteratively through examination of trace plots and using the Gelman-Rubin diagnostic for each parameter. Model parsimony and selection was determined

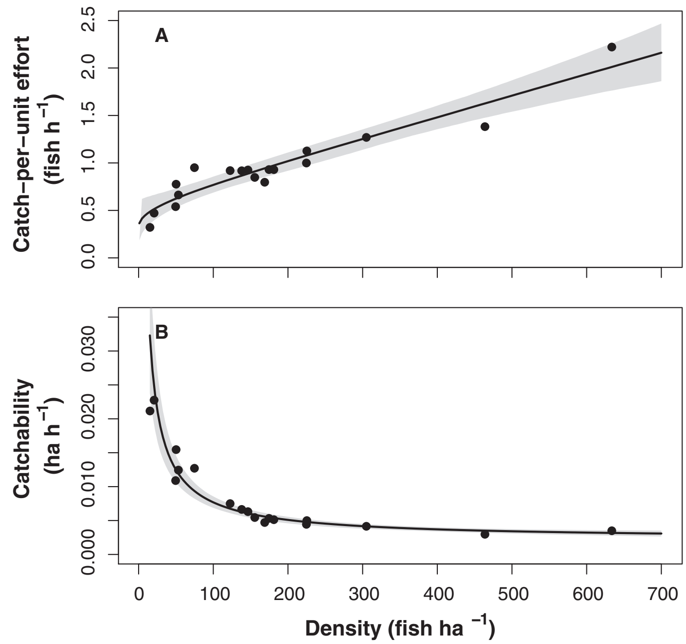

Fig. 2. Hyperstability in catch per effort caused by increases in mean catchability (q) at low stock size (N) due to effort sorting assuming CPUE = qN. Observations are shown as dots; median and 95% credible intervals from posterior prediction of Model 1 are shown as solid lines and shaded areas, respectively; Expectation given constant catchability shown as dotted line. Panel (A) shows observed and predicted catch per effort in BC lakes from Ward et al. (2013a). Panel (B) shows observed and predicted catchability of anglers fishing on the same lakes.

using the Deviance Information Criterion (DIC; Spiegelhalter et al., 2002).

Fitting each of the three models to the data from Ward et al. (2013a) showed that the simplest model, which assumed hyperstability in CPUE occurred solely due to effort sorting as a function of fish density (Model 1) was selected using DIC (Table 2). Model 2, which accounted for increased tolerance for low CPUE as densities decline, was strongly rejected; Model 3, which accounts for density dependent catchability or handling time was also rejected based on the relative DIC values. (Burnham and Anderson, 2002). This suggests two things: first that the effort sorting mechanism proposed is appropriate for the data, as argued in Ward et al. (2013a); second is that including density dependent catchability or handling time does not help explain the data. The results of Model 1 explain the overall pattern in CPUE (Fig. 2A) and catchability (Fig. 2B) across the range of fish observed in the data from Ward et al. (2013a). Note that the fitted model shows that catchability in anglers remaining on low-density lakes must dramatically increase to account for the observed pattern in lake-wide catchability of anglers.

4. How can predicting effort sorting help us manage fisheries?

Unfortunately, knowing the shape of the CPUE-density relationship does not directly help us manage the fishery. First, the parameters of the model must be known before it can be used, i.e., there has to be spatial or temporal fish density data as well as CPUE data to 'calibrate' the function. This may take several years to accomplish and there is no guarantee that estimated parameters are stable over time. Second, there is no analytical solution to back-calculate fish density from observed CPUE using the model described above. This can be overcome using Bayes' theorem

Table 1
Prior and posterior probability distribution functions (PDF) for parameters of the three models fit to the Ward et al. (2013a) data when catchability among anglers is assumed to follow a log-normal distribution. Uniform distributions are denoted with U and gamma distributions are noted with G. Posterior probability distribution functions are described with means and 95% credible intervals.

Parameter	Prior PDF	Posterior PDF		
		Model 1	Model 2	Model 3
μ_q	U(0,10)	0.71 (−0.66,1.24)	0.62 (−6.75,1.28)	1.19 (−0.11,2.07)
σ_q	U(0,10)	1.65 (0.57,3.82)	0.71 (0.23,3.38)	1.28 (0.26,3.31)
c_o	U(0.01,10)	0.26 (0.03,0.57)	0.86 (0.14,1.82)	0.31 (0.04,0.64)
c_1	U(0,10)	–	0.05 (0.00,0.31)	–
h	U(0,10)	–	–	0.72 (0.01,2.91)
τ	G(0.001,0.001)	51.50 (22.17,94.50)	65.46 (15.14,130.61)	45.36 (18.41,85.53)

Table 2
Results of the three models fit to the Ward et al. (2013a) data, each model differentiated by the q^*_{min}. Here, catchability among anglers is assumed to follow a log-normal distribution. Models differ in the effective number of parameters (p_D), the deviance information critierion (DIC) and the relative difference between each DIC and the minimum DIC among tested models (ΔDIC).

Model	q^*_{min}	p_D	ΔDIC
1	$\log_e(c_o) - \log_e(N)$	5.0	0
2	$\log_e(c_o) - \log_e(N + c_1)$	30.7	21.8
3	$\log_e(c_o) - \log_e\left(\frac{N}{1+hN}\right)$	8.4	5.7

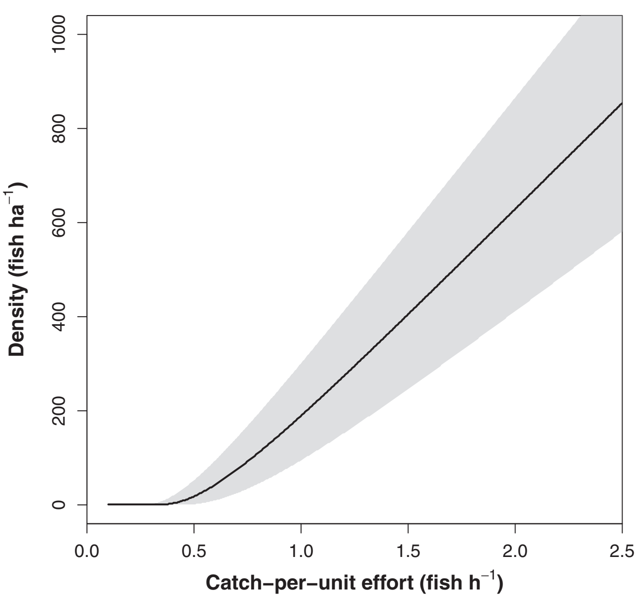

Fig. 3. Prediction of fish density given observed catch-per-unit effort as predicted using fitted Model 1. Dark line represents median predictions; shaded area represents 95% credible intervals. Dashed line represents prediction given constant catchability.

(Hilborn and Mangel, 1997), where a prediction of the distribution of density (N) given observed CPUE is given by

$$P(N|CPUE) = \frac{P(N)P(CPUE|N)}{\int P(N)P(CPUE|N)} \quad (7)$$

where $P(CPUE|N)$ is given by Eq. (3) and $P(N)$ is the prior probability density function in fish density.

Fish density on BC lakes similar to those evaluated in Ward et al. (2013a) was predicted by numerically integrating Eq. (7) using a uniform prior probability distribution for N ranging from 0 to 700 fish/ha. The resulting relationship (Fig. 3) shows that as with all fisheries with hyperstable CPUE, there is an range of fish density for which CPUE is relatively invariant to N and is hence uninformative (Hilborn and Walters, 1992). For instance, a CPUE of one fish per hour on BC lakes could mean a density ranging from 92 to 320 fish/ha; a 3-fold range. CPUE between 0.75 and 1.25 represents a wide range of fish density, while a similar range in CPUE from 0.25 to 0.50 indicates extremely low fish density and may signal near-collapse conditions (Fig. 3). Therefore, estimating the strength and mechanism of hyperstability, as we have done here for BC lakes, should not be used as a means to provide management recommendations. Rather, detecting hyperstability should be used as a signal that fishery independent data must be used to assess and monitor fisheries and make management decisions.

5. Discussion

The model framework presented here is intended to help interpret CPUE data collected over relatively short time periods during which density does not appreciably change. For prediction of average CPUE over longer time scales, e.g., over fishing seasons during which there is a substantial decrease in density due to high fishing effort, the mean CPUE will need to be calculated for a series of shorter time steps using the average density present during each of the steps. At this point, other sources of variation in catchability may need to be considered. Several authors have noted a seasonal pattern in fish catchability (Askey et al., 2006; Gordoa et al., 2000; Stoner, 2004; van Poorten and Post, 2005) primarily due to environmentally-driven variation in fish behavior. As finer time steps are considered, more detail on how catchability may change will likely be required.

One warning from this framework is that it does not predict observed changes in fishing effort (number of anglers fishing) across lakes. Our models assume effort declines as fish density declines because less skilled anglers drop out, yet, there is no pattern in observed fishing effort across the BC lakes in Ward et al. (2013a). There are several reasons for this, which the data are not able to appropriately discriminate. The first is that skilled anglers avoid lakes with many unskilled anglers. This may be strictly to avoid interference competition, whereby skilled anglers understand the biology and likely areas of fish concentrations but unskilled anglers may encroach on those areas by chance yet not have the skill to capitalize on their location. The implication here is that the distribution of individual q_i's is bimodal rather than lognormal. In this case, as fish density declines across lakes, total effort will remain relatively constant. Therefore, as catchability of remaining anglers increases across lakes, fishing mortality rate may actually increase: a type of "super-depensation". This will almost certainly lead to collapse in unregulated fisheries. Initial work showed this alternate model to fit equally well to the CPUE data, though the proportion of skilled anglers (the upper mode in the bimodal catchability distribution) could not be estimated without use of a strongly informative prior probability distribution function.

The second, more likely, reason why our model does not fit the observed effort pattern across lakes is that while anglers are attracted to catch rates, their primary motivations for fishing low density lakes becomes increasingly diverse. The BC lakes modeled here are both stocked (no natural reproduction) and regulated so as to specifically create particular fishing experiences (trophy – large maximum sizes; family – high densities; and regional regulations – average size and numbers). It may well be that anglers fishing on low density lakes are actually attracted to particular fishing regulations (Cook et al., 2001) and the expected fishing experience they will provide. The intention of these lake classifications is to attract particular angler typologies so it is not surprising that our theory breaks down for low density lakes that are intended to attract specific subsets of anglers. Moreover, because of the restrictive regulations on some lakes, high catchability combined with high effort will not necessarily lead to high fishing mortality, unless release mortality is particularly high (Coggins et al., 2007). Obviously our interpretation of fisheries dynamics integrates over several catch-related factors (through c_0, c_1 and h) that may drive decisions on where and when to fish. More importantly, this analysis assumes equal costs among anglers. For the recreational fishery examined here, costs are generally described among human-dimensions researchers as non-catch related motivations and constraints (Fedler and Ditton, 1994; Holland and Ditton, 1992). The most obvious non-catch related factors in recreational fisheries are travel distance and fishing regulations or quotas, which may restrict where and when anglers fish and, therefore, shape aspects of the fishing experience (Beard et al., 2003; Cook et al., 2001; Post et al., 2008; Radomski et al., 2001). Several authors have shown that regulations in recreational fisheries not only limit angler fishing behavior, but also directly influence where people fish by establishing expectations (Aas, 1995; Beard et al., 2003; Cook et al., 2001; Salas and Gaertner, 2004). For example, Cook et al. (2001) suggested that setting a high bag limit may signal to anglers that there are many fish to catch, thereby attracting anglers motivated by catch rates. Harvestable size limits send similar messages about the general size structure of fish populations. These additional sources of variation may somewhat obscure the true relationship between CPUE and fish density and serve to reinforce the unreliability of CPUE in driving management decisions.

Determining angler preferences and skill using angler interview data or surveys is difficult and prone to errors. Ward et al. (2013a) pointed out that it may be useful to collect ancillary information that can be correlated with angler skill as a means of detecting whether effort sorting is occurring in a fishery. This collection poses its own challenges, as there are no consistently accurate covariates of angler skill or preferences (Beardmore et al., 2013; Ward et al., 2013b). In some fisheries, it may be possible to examine relative fishing effort across space or time. However, this assumes costs are relatively equal across anglers. Because costs are rarely equal across anglers, there is a need to carefully consider and incorporate multivariate utility functions that mimic angler decision making when creating predictive models of angler effort and catch. The obvious overlap between the natural and social sciences in recreational fisheries management calls for a re-examination of how we view anglers and assess fisheries.

Fisheries are complex social-ecological systems made up of interacting fish populations and the anglers that affect them directly through harvest and indirectly through release mortality and the subtler physiological and behavioral consequences of capture and release (Arlinghaus et al., 2009; Camp et al., 2015; Carpenter and Brock, 2004; Johnson and Carpenter, 1994). Fisheries management is evolving from a field focused on fish population dynamics to one actively attempting to understand the primary motivations behind effort distribution and behavior. This is not a simple task: most fisheries managers are trained as biologists and much of the human dimensions behind fleet dynamics and angler satisfaction are difficult to grasp (Carpenter et al., 1994). Relatively simple mechanistic models that integrate over a variety of phenomenological sub-processes are necessary to help make management decisions that are robust to uncertainty about the details of human behavior (Fenichel et al., 2013). The model presented here should help managers recognize the extent to which hyperstability may be undermining their ability to sustainably manage fisheries and encourage thought on alternative monitoring activities with which to base decisions (Lester et al., 2003; Post et al., 2002; Shuter et al., 1998).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2016.06.023.

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