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Species differences, but not habitat, influence catch rate hyperstability across a recreational fishery landscape

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ABSTRACT

In commercial and recreational fisheries, catch rate is often assumed to be proportional to stock size and is used by managers and fishers as an indicator of fishery sustainability. If catch rate is proportional to stock size, it can signal a decline of stocks and managers can impose restrictive harvest policies or recreational anglers can move to a new system and allow the over-exploited system to rebound. A growing literature has documented catch rates remaining high even as fish stocks decline (i.e., hyperstability of catch rates) leading to delayed management intervention and overexploitation. Although recent evidence has indicated the presence of hyperstability of catch rates in recreational fisheries, whether hyperstability differs across species or system types remains unknown. To investigate whether catch rate hyperstability varies amongst species or systems, we first tested whether electrofishing catch per unit effort (efCPUE) was an appropriate proxy for true abundance. We then compared the relationship between angler catch rate and fish abundance for common freshwater sport fishes across gradients of habitat availability. We found significant differences in the strength of hyperstability amongst species. We did not identify a consistent influence of habitat on hyperstability of catch rates. Angler preferences and behavior may explain some of the variance in non-proportional catch rates. Future research investigating angler behavior, population size structure, and population dynamics in these systems may identify key interactions that create differences in vulnerability to population collapse.

1. Introduction

Sustainable management of recreational fishery landscapes is challenging as a result of complex interactions between biotic factors (e.g., competition, predation, habitat) and social dynamics, including variation in angler avidity, skill level, and desires (Hickley and Tompkins, 1998; Arlinghaus et al., 2002; Post et al., 2002; Carpenter and Brock, 2004; Lewin et al., 2006; Johnston et al., 2010; Dedual et al., 2013; Post, 2013; Ward et al., 2016; Embke et al., 2019; Solomon et al., 2020). One major challenge for managers of recreational fisheries is the relationship between fish abundance and angler catch rates. In the simplest scenario, angler catch rates and fish abundance are proportional leading to self-regulating fisheries when catch rates drive angler decision making. If catch rates are proportional to fish abundance, declines in catch rates would signal declines in abundance to anglers who may subsequently move to other waterbodies (if available) where catch rates are expected to be higher; with reduced effort, fish abundance is expected to rebound through natural recruitment and reduced fishing mortality. However, if catch rates are hyperstable and do not decline proportionally with abundance, anglers may continue to catch fish at a high rate despite low abundances and over-exploit, or even collapse, the fishery (Harley et al., 2001; Post et al., 2002; Ward et al., 2013).

Although hyperstable catch rates have been known to exist in temperate marine commercial fisheries for decades (Creco and Overholtz, 1990; Hilborn and Walters, 1992; Harley et al., 2001), documentation of these patterns and the mechanisms underpinning hyperstability of catch rates in recreational fisheries has only emerged over the last twenty years (Hansen et al., 2005; Erisman et al., 2011;

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Ward et. al, 2013; Maggs et al., 2016; Mrnak et al., 2018; Dassow et al., 2020; Feiner et al., 2020). To this point, three distinct mechanisms have been invoked as drivers of hyperstability in recreational fisheries. First, targeting of aggregated fish is a well-known mechanism that can cause hyperstable catch rates. For example, aggregation during spawning was thought to drive hyperstable catch rates in two species of marine bass (*Paralabrax* spp., Erisman et al., 2011) and angler targeting of preferred habitat was thought to explain hyperstable catch rates in largemouth bass (*Micropterus salmoides*, Dassow et al., 2020). Second, low-skill anglers can leave a fishery as their success declines with fish abundance leaving high-skill anglers that maintain high catch rates even at low fish abundance. This second mechanism is referred to as "effort sorting" and has been identified as a driver of hyperstable catch rates in recreational fisheries targeting rainbow trout (*Oncorhynchus mykiss*) in British Columbia (Ward et al., 2013; van Poorten et al., 2016). Finally, advancements in angler technology have also been shown to produce hyperstable catch rates in recreational fisheries over longer time scales, as was observed in the competitive shoreline fishery for leerfish (*Lichia amia*) in South Africa (Maggs et al., 2016).

Because catch, and consequently hyperstability, arises from interactions between fish, habitat, and fishers, it might be expected that species identity and habitat characteristics influence the strength of hyperstability. Differences in average abundance, body size, habitat preferences, and foraging behavior amongst recreationally targeted fish species could likely generate inter-specific variance in recreational angler catch rates. In addition, differences in behavior, skill, or investment in technology of anglers targeting different fishes may alter the degree to which catch rates are hyperstable amongst species. Contrary to this expectation, Harley et al. (2001) found that the strength of hyperstability was largely similar among ten species in multiple North Atlantic marine commercial fishery regions. Beyond the research of Harley et al. (2001), few studies have attempted to quantify hyperstability in more than one fishery at a time (Erisman et al., 2011; Ward et al., 2013; Maggs et al., 2016; Mrnak et al., 2018; Dassow et al., 2020, but see Feiner et al., 2020). As a result, we hypothesized that, consistent with the findings of Harley et al. (2001), we would not observe differences in the strength of hyperstability amongst species in inland lake recreational fisheries.

Given the prominence of aggregation as a mechanism underpinning hyperstability of catch rates and the influence of habitat on fish behavior, we expect habitat availability to be a likely driver of variation in hyperstability among lakes. However, research investigating the roles of habitat preference and aggregation as mediators of hyperstability has yet to quantify the strength or spatial scale of aggregation required to generate hyperstable catch rates (Erisman et al., 2011; Dassow et al., 2020). Therefore, variation in habitat at multiple spatial scales could modify the strength of hyperstability. For example, lake surface area may influence the strength of hyperstability because small lakes allow anglers to more easily target and capture individuals. Conversely in large lakes, aggregations of fish may be harder to locate at low fish abundances leading to lower catch rates and thus a less hyperstable, and more proportional, relationship between catch rates and fish abundance. In addition, for certain species the availability of shoreline habitat might drive proportional or non-linear changes in the strength of hyperstability. Finally, availability of coarse woody habitat for refuge and ambush sites may alter fish aggregation and angler behavior at fine spatial scales and modify the strength of hyperstability across lakes (Sass et al., 2006a; Pine et al., 2009; Ziegler et al., 2019). Given the importance of habitat for fish behavior, growth, and reproduction (Schindler et al., 2000; Sass et al., 2006b; Gaeta et al., 2011, 2014), we hypothesized that habitat, at one or more spatial scales, would be a strong modifier of the strength of hyperstability across lakes in a recreational fishery landscape. Specifically, we predicted that at low habitat availability fish would aggregate most strongly and produce the most hyperstable angler catch rates.

To test whether differences in species' ecology or lake-to-lake variation in habitat availability influences the magnitude of recreational angler catch rate hyperstability, we used a comparative approach that leveraged long-term, regional fish relative abundance and recreational angler catch rate data for six sport fishes in Wisconsin lakes. Previous research has used the exponent of a power-law relationship between catch rates and fish abundance (β) to quantify the strength of hyperstability of catch rates (Ward et al., 2013). We extended this approach by testing whether β varies as a function of species or indicators of lake habitat availability (e.g., lake surface area, shoreline complexity) using a multiple model comparison framework. If models that include species identity or information about habitat outperform the traditional power-law model, we would infer that these factors modify the magnitude of catch rate hyperstability amongst fisheries. A better understanding of what factors influence catch rate hyperstability could then enhance our ability to model fishery dynamics and our ability to manage these systems.

2. Methods

2.1. Overview

We combined angler catch rate (i.e., creel survey) and electrofishing survey data collected across Wisconsin, USA to test for relationships between fish abundance and mean annual angler catch rates for six North American sport fish. We first evaluated the suitability of the widely available relative abundance data (electrofishing catch per unit effort, efCPUE) to serve as a proxy for fish population density by comparing efCPUE to mark-recapture population estimates in a subset of lakes for largemouth bass and walleye (*Sander vitreus*). We then used average annual angler catch rates from season-long Wisconsin Department of Natural Resources (WDNR) creel surveys and WDNR efCPUE data to quantify the strength of hyperstability in catch rates across the recreational fishery landscape in Wisconsin. We used a multiple model comparison approach to test hypotheses about differences in the strength of hyperstability of catch rates among the six focal species and across gradients of habitat availability.

The six sport fish considered here included four centrarchid - largemouth and smallmouth bass (*Micropterus dolomieu*), black crappie (*Pomoxis nigromaculatus*), and bluegill (*Lepomis macrochirus*) - and two percid species - yellow perch (*Perca flavescens*) and walleye. These species are commonly sought by recreational anglers and often co-occur in temperate lake habitats (Gaeta et al., 2013). Despite co-occurring, centrarchids and percids differ in their preferred water temperature and general habitat preferences. Percid optimal water temperatures are cooler than centrarchids, and therefore percids often reside in cooler and deeper waters and do not rely heavily on the littoral zone or nearshore areas outside of spawning (Becker, 2001).

2.2. Fish collection

Our metric of fish relative abundance was efCPUE, which is routinely collected for a number of lakes across Wisconsin each year by WDNR. Alternating-current, boom electrofishing is used to conduct these fishery-independent, standardized fish surveys, which evaluate species presence and relative abundance. Our survey observations spanned 1995–2016. For largemouth and smallmouth bass, black crappie, bluegill, and yellow perch, the shoreline (including islands) of a sampled lake is subsampled in 0.8 km (1/2-mile) segments, with the number of segments dictated by total shoreline length. Walleye spring electrofishing is done in conjunction with mark-recapture population estimates for adult walleye. When possible, the entire shoreline (including islands) is sampled in a single night, or at a minimum, half of the shoreline is sampled using randomly selected 3.2 km (2-mile) sub-samples.

2.3. Validating efCPUE as an index of abundance

Although efCPUE for a species would be expected to be related to abundance of that species, we confirmed this relationship by comparing efCPUE with abundances as estimated by mark-recapture population estimates. We tested for an efCPUE correlation to mark-recapture-based population estimates of walleye and largemouth bass in a subset of the lakes studied to determine whether efCPUE was a reasonable proxy for true abundance. A significant correlation between efCPUE and population abundance for these key recreational species in both families of fishes (i.e., centrarchids and percids) allowed us to complete our analysis of angling CPUE and efCPUE relative abundances with confidence. For walleye population estimates, the WDNR collected and marked adult walleye using fyke nets, deployed for at least 24 h, immediately after ice off, usually during mid-April to mid-May. Fish were measured for total length and marked with either fin clips or anchor tags. Because day-time electrofishing in Wisconsin lakes has resulted in low catchability of fish, night-time, alternating-current boat electrofishing was used for recapture events 1– 2 d after marking during peak walleye spawning (Rogers et al., 2003; Hansen et al., 2000). Because WDNR does not generate mark-recapture-based population estimates for largemouth and smallmouth bass and panfish (bluegill, black crappie, and yellow perch), our research group completed mark-recapture population estimates of largemouth bass in 13 lakes over the summers of 2018 and 2019. Our largemouth bass mark-recapture population estimates were completed with protocols similar to those used by WDNR but substituted angling for fyke netting due to low catch rates of largemouth bass in fyke nets. In each of our largemouth bass mark-recapture experiments, repeated alternating-current boat electrofishing of whole-lake shorelines was supplemented with angling to mark and recapture adult largemouth bass. Captured fish were marked with anal fin clips. On average, four electrofishing samples and 35 angler-hours per lake were used to generate largemouth bass population estimates (Table S1). For both bass species, mark-recapture population estimates were generated using the Chapman-modified, continuous Schnabel method and all available recapture events in a given year were included (Ricker, 1975).

To test the assumption that efCPUE was a reasonable proxy for fish density, we tested whether mark-recapture population estimates correlated significantly with efCPUE for lakes where we had access to both measures. We conducted separate analyses for walleye and largemouth bass. To control for lake surface area, we expressed mark-recapture-based population estimates as density (fish/km shoreline) and compared this to efCPUE (fish caught/km shoreline). Because 29 lakes in the WDNR walleye data set had multiple years (two to six) with matched population estimates and efCPUE observations, we used a mixed-effects regression with lake as a random effect to avoid pseudoreplication. We used the null hypothesis of no relationship between efCPUE and population density ($\alpha = 0.05$). We tested our hypothesis using a likelihood ratio test to compare the mixed-effects regression to an intercept-only, null model that included the random lake effect for walleye data. We also tested whether electrofishing catch rates were hyperstable relative to PE-based densities using similar methods to those described in subsection *2.5 Data analysis* below.

2.4. Data sets

Our angler catch rate observations were derived from WDNR standardized angler-intercept creel surveys. Angler-intercept creel surveys are performed on a randomized sample of anglers for 40 h a week during open water periods during the first Saturday in May (opening day) to October 31. Angler-intercept creel surveys are stratified by weekday AM and PM shifts in addition to all weekends and holidays. Many catch- and harvest-related metrics are collected, but we used species-specific catch counts and trip length to calculate recreational angler catch per unit effort (CPUE). The Wisconsin DNR standardized creel surveys measure directed (species-specific) and overall (general) effort. The percentage of creel survey respondents that were targeting a single species (directed effort anglers) varied by species from 50% directed for smallmouth bass to 85% directed for walleye. Because average annual angler CPUE for general and directed effort were highly correlated (0.90–0.99), we used all angler creel data available for our target species in our analyses (Fig. S1). Unfortunately, more detailed information on angler avidity, skill-level, or use of technology is not collected as a part of these standardized surveys. For additional detail on the design and implementation of WDNR angler-intercept creel surveys, please see the Wisconsin DNR Creel manual (Gilbert et al., 2013).

Our data set for assessing hyperstability of angler catch rates came from lake-year combinations where angler catch rates from creel surveys and efCPUE were both available for a given species. When multiple observations of either angler catch rates or efCPUE were available for a given lake-year, we used the average of all observations. Therefore, our unit of observation for angler catch rates and efCPUE was lake-year, and not individual anglers nor nights of electrofishing. The number of observations of angler catch rates per lake-year combination varied from 2 to 4511, with 99% of lake-years having more than 10 observations. Only 6% of lake-year-species combinations had multiple observations of efCPUE and < 1% had more than two efCPUE observations, with a maximum of seven observations. After filtering annual mean angler catch rates and efCPUE data for matching lake-year pairs, we were left with 872 lake-year observations from 210 lakes across 21 counties in Wisconsin collected during 1995–2016 (Table 1). There was some variability in the number of lake-year observations across species, with walleye observations being most numerous ($N = 302$) and black crappie being the least ($N = 66$). More detailed information on the distribution of observations across lakes and years (Fig. S2), as well as a power analysis for detecting catch rate hyperstability, are available in Supplementary Materials.

To test for the influence of habitat on the magnitude of hyperstability at different spatial scales, we used three proxies derived from data provided by Hansen et al. (2015). Direct observations of habitat availability would have been preferred (e.g. coarse woody habitat density, variation in water temperature and dissolved oxygen with depth, spawning substrate availability), but these observations were not available for the hundreds of lakes for which we have angler catch rates and efCPUE data. We selected lake surface area as an overall metric of habitat availability and search area for anglers. We $\log_{10}$-transformed lake surface area (m^2) for all analyses because lake areas in our data set varied by four orders of magnitude. Shoreline complexity, which is the ratio of actual lake shoreline length to the shoreline length of a lake of the same area, but with the shape of a perfect circle (commonly referred to as shoreline development index) was used as a proxy for overall littoral habitat availability. We used riparian building density, which

Table 1
Number of observations for relative abundance (electrofishing) and recreational angler catch rates (creel survey) from the Wisconsin Department of Natural Resources data used for hyperstability analyses. We used a total of 872 lake-year observations spanning the six species and years of 1995–2016.

Species	Data	Years	Lakes	Lake-years
largemouth bass	creel	22	242	395
	electrofishing	21	617	948
	both	**21**	**120**	**172**
smallmouth bass	creel	22	249	396
	electrofishing	21	310	554
	both	**21**	**102**	**155**
bluegill	creel	22	253	411
	electrofishing	20	578	780
	both	**16**	**68**	**89**
black crappie	creel	22	242	391
	electrofishing	19	479	649
	both	**15**	**51**	**66**
yellow perch	creel	22	253	412
	electrofishing	20	538	716
	both	**16**	**69**	**88**
walleye	creel	22	254	421
	electrofishing	22	439	724
	both	**22**	**201**	**302**

has repeatedly been shown to be inversely related to the amount of coarse woody habitat available in the littoral zone of lakes, as our proxy for habitat at the finest spatial scale (Christensen et al., 1996; Marburg et al., 2006; Lawson et al., 2011). These habitat proxies were calculated using ArcGIS, online databases (https://lter.limnology.wisc.edu/dataset/wisconsin-lake-historical-limnological-parameters-1925-–2009, http://lakesat.org/), and the Wisconsin DNR monitoring database. Habitat proxies were available for all lakes where average angler catch rates and efCPUE data were also available (Table 1).

2.5. Data analysis

To quantify the strength of hyperstability, we used the exponent of a power function relating CPUE to fish relative abundance, for which we used efCPUE (Ward et al., 2013):

$$CPUE_i = qN_i^{\beta} \tag{1}$$

where $CPUE_i$ is angler catch per unit effort in lake i, q is a catchability coefficient that scales with population abundance (N_i, efCPUE in our analyses), and β dictates the degree of non-linearity in the relationship between N and $CPUE$. As β becomes increasingly less than one, the strength of hyperstability of catch rates increases.

To test the hypothesis that species identity does not significantly influence the magnitude of hyperstability, we considered a more complex model that included species-specific effects:

$$CPUE_{i,S} = q_S N_{i,S}^{\beta_o + \beta_S S} \tag{2}$$

where $CPUE$ in lake i for species S is predicted by a species-specific β for the reference species (β_o), a vector of coefficients representing the difference of all other species from the reference species (β_S), a design matrix that encodes what $CPUE$'s and N's are derived from which species (S), and a species-specific catchability (q_S).

To test for effects of habitat on catch rate hyperstability, we also considered models that included habitat effects. We considered habitat effects on catch rates of each species individually and therefore did not include any species subscripts. To consider habitat availability, we included one of three of our continuous habitat proxies (H_x - lake surface area, shoreline complexity, riparian building density).

$$CPUE_i = qN_i^{\beta_o + \beta_x H_{i,x}} \tag{3}$$

Because it seemed plausible that the strength of hyperstability could be maximized or minimized at extreme values of habitat proxies, we also considered a quadratic influence of H_x on β.

$$CPUE_i = qN_i^{\beta_o + \beta_x H_{i,x} + \beta_{x^2} H_{i,x}^2} \tag{4}$$

To evaluate the statistical significance of species or habitat effects, we compared the full models (Eqs. 2–4) to null models that lacked those terms. Because null models were subsets of the more complex model, we used likelihood ratio tests to compare each null-alternative model pair (Table 2). By log-transforming our independent (efCPUE) and dependent (angler CPUE) variables, all model parameters could be estimated using linear mixed-effect regression. As a result, β from Eq. 1 is represented by the slope estimated when regressing log(CPUE) as a function of log(efCPUE) and the intercept would be the log of the catchability coefficient (q). Coefficients from models described in Eqs. 2–4 can be determined in a similar manner (Table 2). We included a random effect of lake in all models, including null models, to account for multiple observations being derived from a single lake, but different years. Because an effect of species or habitat on β is represented by an interaction term in the regression model, when assessing whether habitat altered the strength of hyperstability, we compared the full model to a null model that included a direct effect (intercept) of species or a habitat proxy (H_x) on log(CPUE), but no interaction term between log(efCPUE) and the habitat covariate ($\beta_{I,x}$) (Table 2). When considering a quadratic effect of a habitat covariate, the null model included direct effects of the habitat covariate and squared habitat covariate (H_x, H_x^2) on log(CPUE), but no interaction terms between log(efCPUE) and the habitat covariate or squared habitat covariate ($\beta_{i,x}, \beta_{i,x^2}$).

Table 2
Linear mixed-effect models used to estimate hyperstability parameters and test for effects of species-identity or habitat. Likelihood ratio tests were used to compare null-alternative model pairs between bold lines in the table (row 1 vs. 2, row 3 vs. 4, and row 5 vs. 6). Note that data were subset for a single species when investigating potential habitat effects.

Model	Regression formula
null species	log(CPUE)~log(efCPUE)+species+ (1|lake)
species effect (Eq. 2)	log(CPUE)~log(efCPUE)+species+log(efCPUE):species+ (1|lake)
null linear habitat	log(CPUE)~log(efCPUE)+habitat+ (1|lake)
linear habitat (Eq. 3)	log(CPUE)~log(efCPUE)+habitat+log(efCPUE):habitat+ (1|lake)
null quadratic habitat	log(CPUE)~log(efCPUE)+habitat+habitat^2 + (1|lake)
quadratic habitat (Eq. 4)	log(CPUE)~log(efCPUE)+habitat+log(efCPUE):habitat+habitat^2 +log(efCPUE):habitat^2 + (1|lake)

If the linear and quadratic habitat covariate models outperformed their null models, we used a third likelihood ratio test to determine whether the linear or quadratic effect was more likely given the observations. For assessing habitat effects, we fit models for each habitat variable (N = 3) as a linear and quadratic model (N = 2) for each species (N = 6) individually. We used a Bonferroni correction to control for the large number of likelihood ratio tests used to compare models; our adjusted α was 0.05/(3 *2 *6) = 0.0014. All model fits were generated using the lme4 package in R.

Uncertainty in independent variables is known to generate biased estimates of regression parameters (Kendall and Stuart, 1967). This statistical effect has been previously considered in the context of density-dependent catch rates, and methods for bias correction have been developed (Shardlow et al., 1985; Hansen et al., 2004, 2005). We used a Monte Carlo approach for bias correcting our estimates of β (Hansen et al., 2004) and extended this approach to our assessment of species and habitat effects using alternative-null model pairs and likelihood ratio tests.

To account for measurement error in efCPUE, we generated 1000 log-normally distributed random efCPUE values for each lake-year. We used the observed efCPUE as the mean of the log-normal distribution and a σ of 0.57, which was the average measurement error for the boat electrofishing we conducted as a part of this study. For each of the 1000 Monte Carlo simulated efCPUEs, we used the observed covariate (species and habitat proxies) and dependent variable (average annual angler CPUE) to fit the null and alternative models described above (Table 2). This means that for each model comparison, we generated 1000 likelihood ratio test p-values (one for each Monte Carlo data set). In our results, we report the proportion of p-values falling below α = 0.05 and the median p-value from the 1000 Monte Carlo data sets (Table 2). We also used the Monte Carlo parameter estimates to calculate bias-corrected β's and 95% confidence intervals for β's according to Hansen et al. (2004):

$$\beta_{bc} = \beta_{obs} + (\beta_{obs} - \beta_{mc}),$$

where β_{bc} are the 1000 bias-corrected β's, β_{obs} is the single β estimated using the observed efCPUE values for each lake-year, and β_{bc} are the 1000 biased β's estimated from the Monte Carlo simulated efCPUE data. All data and code used in our analyses are available on Zenodo (R Core Team, 2020).

3. Results

3.1. Electrofishing CPUE as a proxy for abundance

Electrofishing catch per unit effort (efCPUE) was a good proxy for abundance. Walleye data from WDNR and largemouth bass observations from the electrofishing surveys showed significant relationships between mark-recapture based population densities (shoreline and areal) and night-time efCPUE (Fig. 1). The large amount of available walleye data from WDNR ($N = 159$) generated significant linear relationships between shoreline walleye density and efCPUE (fish per km shoreline; $p = 1.6e^{-8}$), as well as areal walleye density and efCPUE (fish per km^2; $p = 5.9e^{-15}$). However, the correlation between efCPUE and areal walleye density (Pearson's $r = 0.54$) was stronger than between efCPUE and shoreline walleye density (Pearson's $r = 0.40$). We also observed that walleye efCPUE was hyperstable ($\beta = 0.78$ and 0.66 for shoreline and areal densities, respectively). However, a simulation experiment demonstrated that our estimates of walleye angling hyperstability were likely conservative, as hyperstable efCPUE caused overestimation of β (Fig. S3). Although largemouth bass data was much more limited ($N = 13$), a significant correlation between mark-recapture shoreline density and efCPUE (Pearson's $r = 0.84$; $p = 0.0003$) was found. The correlation between areal largemouth bass density and efCPUE was similarly strong. (Pearson's $r = 0.84$; $p = 0.0003$). We did not observe hyperstability in largemouth bass efCPUE ($\beta = 1$ for shoreline and areal density). Although significant relationships between population estimates and efCPUE were observed for both species, there was a large amount of variance in efCPUE around the expected value for a given population abundance (Fig. 1). As a result, we accounted for measurement error in efCPUE in subsequent analyses as described in *2.5 Data Analysis*.

3.2. Inter-specific variation in catch rate hyperstability

Hyperstability in catch rates was observed for all species examined, but species differed significantly in the strength of hyperstability (Table 3). This meant that catch rates were not proportional to abundance and showed relatively little decline until abundances were quite low (Fig. 2). A likelihood ratio test showed strong support for the model that included the species effects (median $p = 2.9e^{-16}$; all Monte Carlo simulations < 0.05). However, examining each species' β and the uncertainty in those estimates revealed variation in pair-wise differences amongst species (Fig. 3a). Yellow perch showed the strongest hyperstability in catch rates and walleye had the weakest (Fig. 3b). The β

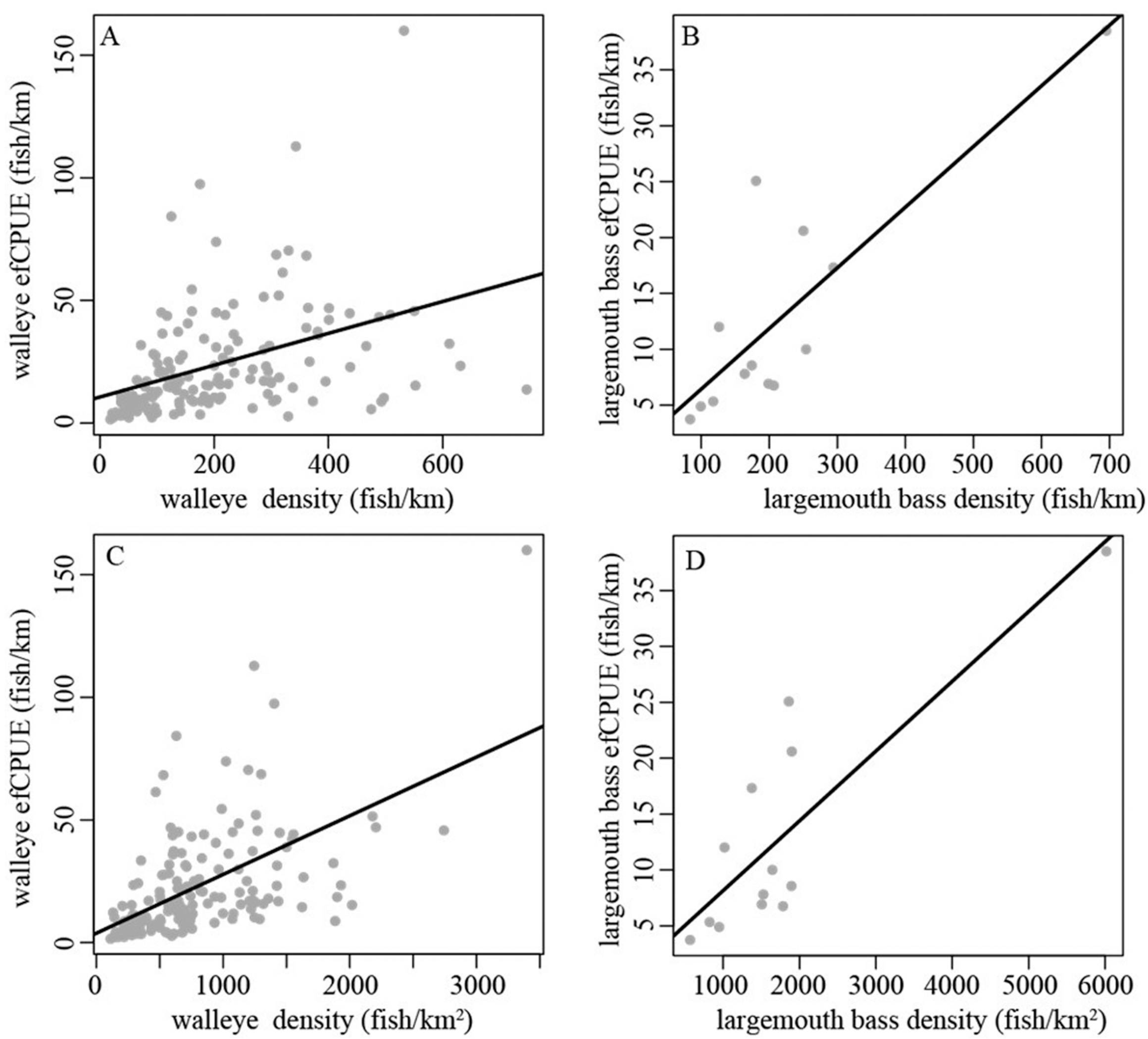

Fig. 1. Electrofishing catch per unit effort (efCPUE) correlated strongly with both shoreline (panels A and B) and areal (panels C and D) population densities from mark-recapture population estimates. Population estimates of walleye from 104 lakes provided by Wisconsin DNR showed a stronger correlation between areal density and efCPUE (Pearson's $r = 0.54$) than shoreline density and efCPUE (Pearson's $r = 0.41$), but efCPUE was hyperstable with β significantly less than one. Largemouth bass population estimates from 13 lakes showed equally strong correlations between density and efCPUE (Pearson's $r = 0.84$ for both), but no hyperstability in efCPUE. Lines are predicted efCPUE as a function of population density.

Table 3
Strength of angler catch rate hyperstability in six north temperate recreational fisheries indicated by the bias-corrected parameter β. As β declines below one, the strength of hyperstability in catch rates increases. Estimates are derived from bias-corrected power function fits relating mean annual angler catch rates, derived from intercept creel surveys, to annual estimates of fish relative abundance, derived from electrofishing surveys (Eq. 2). Values reported are median, 2.5th percentile, and 97.5th percentile from 1000 Monte Carlo simulation that take uncertainty in electrofishing catch per unit effort (efCPUE).

Species	β	2.5th percentile	97.5th percentile
Black Crappie	0.216	0.176	0.252
Bluegill	0.250	0.220	0.277
Yellow Perch	0.063	0.036	0.091
Largemouth Bass	0.442	0.419	0.464
Smallmouth Bass	0.278	0.252	0.303
Walleye	0.762	0.722	0.803

estimates for the centrarchids tended to fall between the two percid species (Fig. 3).

3.3. Habitat as a driver of catch rate hyperstability

Little evidence for an effect of habitat on the strength of hyperstability of catch rates was observed. In fact, after accounting for measurement error in efCPUE, only two of the 36 alternative models (6 species x 3 habitat covariates x 2 linear vs. quadratic) outperformed their corresponding null model frequently enough to be considered significant (Table 4). These two species-habitat proxy combinations showed no Monte Carlo simulations without a significant habitat effect and had median p-values less than our $\alpha = 0.0014$ (Table S2, Fig. S4). Largemouth bass hyperstability showed a quadratic relationship with lake surface area (LRT median $p = 0.0004$), where hyperstability in catch rates was weakest in lakes ~5 km^2 and hyperstability was stronger in smaller and larger lakes. Black crappie hyperstability had a significant quadratic relationship between riparian development and β (LRT median $p = 6.0e^{-6}$). The quadratic model predicted the strongest black crappie hyperstability (lowest β) at around 9% of the riparian zone developed and a rapid decrease in hyperstability (increased β) over the higher range of development observed in our data set (20–40%).

4. Discussion

4.1. Overview

As hyperstability in catch rates has strong implications for sustainable management of exploited fish populations, it is essential to develop a systematic understanding of how the relationship between abundance and angler catch rates varies among fisheries or across ecosystems within a fishery landscape. Indeed, understanding features of recreational fisheries that enhance the strength of hyperstability will allow managers to identify fisheries that are most vulnerable to invisible collapse in order to adopt management strategies that account for this risk (Post et al., 2002). Recent research has documented the presence of hyperstability in diverse recreational fisheries, but we have yet to systematically investigate inter-specific variation in the strength of hyperstability (see Feiner et al., 2020 as a notable exception) nor the role that lake-specific factors, like habitat availability, may play in influencing hyperstability of catch rates (Hansen et al., 2005; Erisman et al., 2011; Ward et al., 2013; Maggs et al., 2016; Mrnak et al., 2018; Dassow et al., 2020; Feiner et al., 2020). Our results reinforce the prevalence of hyperstability across six widely distributed north temperate recreational sport fishes and indicate that differences in fish ecology drive significant variation in the strength of hyperstability of catch rates. Despite demonstrable influences on fish behavior, growth, and reproduction, we found little evidence for habitat effects on hyperstability of catch rates given the habitat proxies we tested. Together, our results demonstrate the difficulties of managing multi-species recreational fisheries and the need to avoid panaceas in management, but also preserve the potential of modern management tools, like habitat restoration and enhancement.

4.2. Implications for habitat management

We expected that habitat availability would influence hyperstability among inland fisheries due to previous research showing the potential for fish aggregation to drive hyperstable catch rates in recreational fisheries (Ward et al., 2013; van Poorten et al., 2016; Dassow et al., 2020). Although we lacked some direct measures of habitat availability, we predicted that lake surface area may influence the strength of hyperstability via its effects on an anglers' ability to find and capture fish. For example, small lakes may allow anglers to more easily target and capture individuals due to a reduced search area. In large lakes, aggregations of fish may be harder to locate at low fish abundances leading to lower catch rates and thus a less hyperstable, and more proportional, relationship between catch rates and fish abundance. We also hypothesized that availability of coarse woody habitat for refuge and ambush sites may alter fish aggregation and angler behavior at fine spatial scales and modify the strength of hyperstability across lakes. Specifically, we predicted that at low habitat availability (high riparian building density), fish would aggregate most strongly and produce the most hyperstable angler catch rates.

Despite aggregation as a potential mechanism for habitat to influence catch rate hyperstability at multiple scales, we did not observe a strong signal of habitat influencing the strength of hyperstability in our data set. Indeed, 34 of the 36 tests we conducted investigating a connection between our habitat proxies and catch rate hyperstability did not show a significant relationship. One potential explanation for limited lake-size effects on an anglers' ability to find and capture fish is that angler effort scales positively with lake surface area in the study region (Trudeau et al., 2021). Therefore, anglers per area of lake, and ability to effectively search an entire lake, may not vary meaningfully across lakes. Additionally, experimental evidence from the study region indicates that hyperstable catch rates can occur when weak habitat preferences combine with angler knowledge of those preferences. This may limit correlation between habitat proxies, at any spatial scale, and estimates of hyperstability (Dassow et al., 2020).

Data availability may have limited our ability to detect meaningful relationships between habitat and angler catch rate hyperstability. A power analysis indicated that despite having fairly large samples sizes (66–306 lake-years for each species) our ability to detect habitat effects would be limited, especially for black crappie and yellow perch, which had the lowest sample sizes (see Power Analysis – Question 4 in supplementary materials). Even doubling our largest sample size would still have relatively low statistical power if habitat effects were weak. In addition, the habitat proxies available for our lakes were quite coarse and environmental gradient effects appear to be relatively difficult to detect (Supplementary Materials). Perhaps future studies that quantify more biologically relevant habitat variables may detect habitat effects on hyperstability. However, generation of improved habitat metrics coinciding with angler catch rate and efCPUE estimates with larger sample sizes than we had in our study would be a very large undertaking.

The only two candidate species-habitat associations that showed significant effects on angler catch rate hyperstability both related a centrarchid species to a habitat proxy in a non-linear (quadratic) manner. First, lake surface area was correlated with largemouth bass catch rate hyperstability such that hyperstability was strongest in small and large lakes. Given this observed relationship and the assumption that lake surface area is correlated with habitat availability, perhaps catch rates can be consistently high in smaller lakes owing to efficient searching of all habitat by anglers, as we previously hypothesized. In contrast, larger lakes could have stable, but consistently low, catch rates because of long search times for anglers. Intermediate-sized lakes may

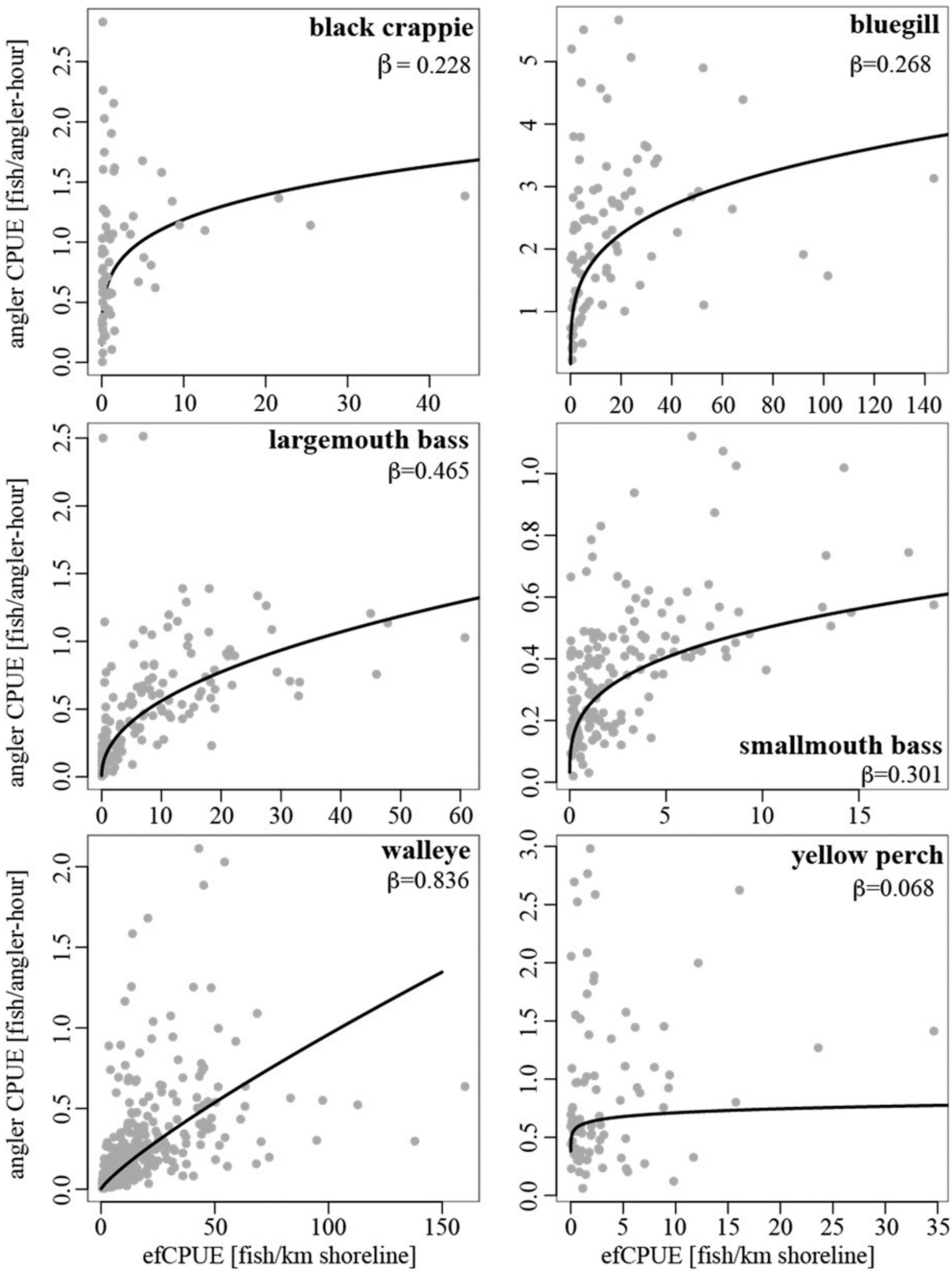

Fig. 2. Species-specific model fits reveal non-linear (hyperstable) relationships between relative abundance, as measured using electrofishing catch per unit effort (efCPUE) and angler catch per unit effort (CPUE) rates in all six of the species we considered. Random lake effects were included in a mixed effect model as repeated observations were available for some lakes but are not considered when displaying the predicted relationship between efCPUE and angler CPUE.

show less hyperstability because they are small enough for anglers to efficiently find fish when abundant, but large enough to make it difficult to find fish as densities decline. Second, hyperstability of black crappie catch rates was strongest at ~9% of riparian shoreline development. Lakes with more or less riparian development showed reduced hyperstability. Perhaps maximized hyperstability at an intermediate level of riparian development makes sense as very low riparian building density would mean homogeneous availability of CWH and high building density would create homogeneous absence of CWH.

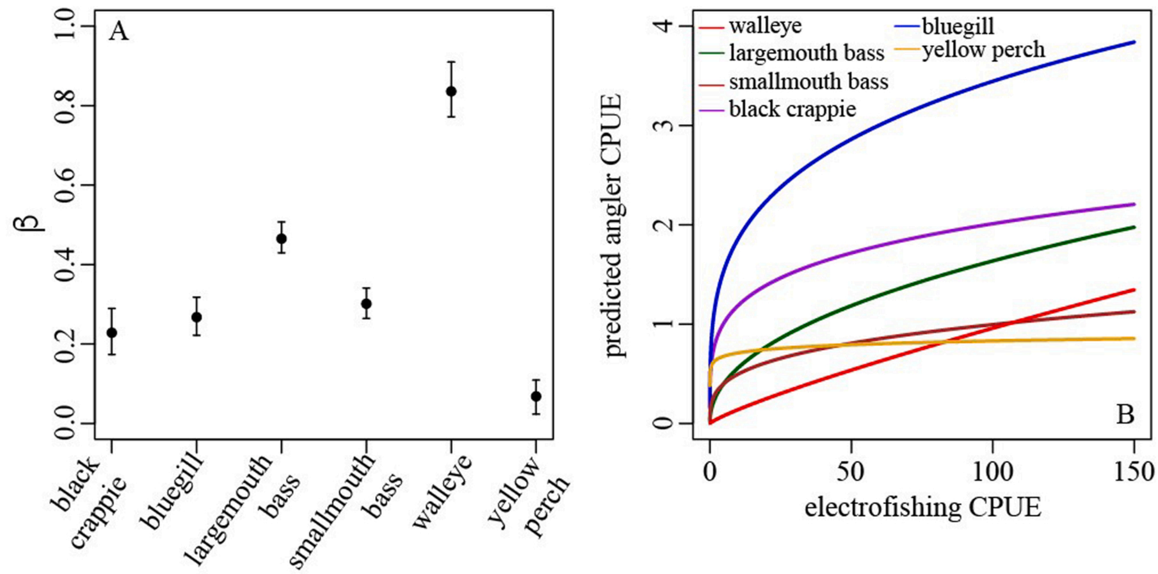

Fig. 3. We observed differences in the strength of angler catch rate hyperstability amongst the six sport fisheries we investigated. A) Bias-corrected estimates of β are indicated by the gray circles and error bars represent 95% confidence intervals of those estimates. B) Differences in β and estimated catchability (q) translate to strikingly different patterns of expected catch per unit effort as abundances decline in each of these fisheries.

Table 4
Results from tests for the influence of habitat on the strength of hyperstability of catch rates. Linear and quadratic effects of habitat, as quantified by three proxies, were considered for each of six recreational sport fishes. Log lake size was considered as an indicator of overall habitat size, shoreline complexity (the ratio of actual shoreline length to shoreline length of a perfectly circular lake with the same lake area) was used as an indicator of littoral habitat availability, and riparian building density is known to be inversely related to coarse woody habitat availability. To take into account uncertainty in electrofishing catch per unit effort, values reported are the proportion of Monte Carlo simulations (N = 1000) that produced a p-value greater than 0.05 from a likelihood ratio test comparing the alternative model (linear or quadratic effect of a habitat proxy) to a null model. Median p-values from the Monte Carlo simulations are reported in Table S2.

	Largemouth bass	Smallmouth bass	Bluegill	Black crappie	Yellow perch	Walleye
Lake size						
linear	0.970	1.000	1.000	0.978	1.000	0.840
quadratic	*0.000*	1.000	1.000	0.866	1.000	0.975
Shoreline complexity						
linear	1.000	0.622	0.998	0.952	1.000	0.956
quadratic	1.000	0.693	1.000	0.978	1.000	0.998
Riparian building density						
linear	0.938	1.000	1.000	0.138	1.000	1.000
quadratic	0.993	0.997	0.423	*0.000*	1.000	0.999

4.3. Interspecific variability in hyperstability

Previous research from our study region using different approaches and data documented hyperstability in most of the species we considered, but our analysis documented clear differences in the strength of hyperstability among these fisheries. For example, our bias-corrected estimate of β for walleye (0.84) is extremely close to a previous estimate from Hansen et al. (2005) (0.83 ± 0.05 standard error) but above a more recent estimate from Mrnak et al. (2018) (0.53, no standard error reported). Further, our estimate of β for largemouth bass (0.47) was the same as a recent estimate derived from experimental manipulation of fish abundances in a single lake (0.47 ± 0.1 standard error; Dassow et al., 2020). In our study, walleye and largemouth bass significantly differed in their strength of hyperstability, but both species displayed much weaker hyperstability than the panfish, as well as smallmouth bass. Our panfish results agree with a recent study showing yellow perch had the strongest hyperstability in catch rates amongst panfish, but our estimate was even lower (0.07, 95% confidence interval 0.02–0.11), but with overlapping uncertainties, compared to their estimate (0.15 ± 0.03 standard error; Feiner et al., 2020).

A deeper understanding of the factors that underpin hyperstable catch rates could provide a more general understanding of catch hyperstability and facilitate improved management of these fisheries. Differences in trophic position, optimal water temperature, adult body size, and angler behaviors among the six fish species we considered could provide opportunities to speculate about the factors mediating differences in the magnitude of hyperstability, but it is not possible at this time to definitively infer mechanism(s) of these interspecific differences in β. If preferred water temperatures, and its effect on habitat use, were an important driver of catch hyperstability, we might have expected β's from cold-water percid species to be like each other and distinct from the warm-water centrarchids. Instead, we found that walleye and yellow perch fell at the extremes of our observed range of β's. The smaller-bodied panfish all tended to show stronger hyperstability, but the larger smallmouth bass fell in this range rather than with other larger-bodied species (largemouth bass and walleye).

Although we assumed that our use of average annual angler catch rates would homogenize likely important angler-to-angler heterogeneity in avidity, skill, and technology use, there is no doubt that angler behavior could play a role in differences in the strength of hyperstability across lakes or species. Previous research in similar regions has shown distinct angler behavioral typologies and that differences in angler skill exist and may be related to hyperstability of recreational angler catch rates (Beardmore et al., 2014; Ward et al., 2013). To the extent that angler behavior and preferences differ amongst targeted fish species, angler behavior may drive divergence in the magnitude of catch hyperstability amongst species that we observed. More research is needed to improve our understanding of the relative importance of angler behavior and fish biology/ecology on catch rate hyperstability.

A striking pattern observed in all species, but especially panfish, was extreme variability in average annual angler catch rates at low relative abundances. If we were considering individual angler catch rates, we would likely expect this pattern owing to differential skill and knowledge amongst anglers (Ward et al., 2013; van Poorten et al., 2016). However, to observe this pattern for average annual angler catch rate is more intriguing. One potential mechanism for this could be variation in size structure of these small populations across lakes and/or years. Due to high inter-annual variance in recruitment and the presence/absence of cannibalism or recruitment depensation, some low-abundance populations could be dominated by small individuals that have not yet recruited to recreational angling gear and other low-abundance populations could be dominated by large, catchable individuals (Henderson and Corps, 1997; Claessen and de Roos, 2003; Ludsin et al., 2014). Populations with, on average, small individuals would show very low catch rates. In contrast, populations dominated by large, catchable individuals might show high catch rates, despite low abundances, and be at extreme risk of invisible collapse (Post et al., 2002). Future investigation into the dynamic relationship between population size structure and annual angler catch rates in these or similar fisheries would be useful for testing this hypothesis.

4.4. Recreational fishery management

Our results provide two important take-aways for the management of recreational fisheries. First, the absence of widespread effects of habitat on the strength of catch hyperstability removes increased catch rate hyperstability as an unintended side effect of habitat restoration or enhancement in recreational fisheries. However, we caution that our conclusion should be tempered by the fact that we only tested for the influence of a few coarse habitat proxies. Second, inter-specific differences in the magnitude of hyperstability suggests a one-size-fits-all approach to recreational fisheries management may not be successful (van Poorten and Camp, 2019).

Previous research has repeatedly demonstrated the role of habitat in regulating behavior of fishes and the dynamics of fish populations, and as a result habitat restoration and enhancement are increasingly used as management tools in recreational fisheries (Sass et al., 2006b, 2017, 2019; Lawson et al., 2011). Because widespread development of lakeshores has eroded the availability of habitat in lakes, many management agencies and conservation groups have invested heavily in habitat modification. Our results indicated that habitat does not strongly influence catch rate hyperstability and managers should not be overly concerned about altering the relationship between population abundance and catch rates when restoring or enhancing habitat.

5. Conclusions

Species-specific differences in the hyperstability of average annual angler catch rates highlights the importance of rejecting a one-size-fits-all approach to fishery management because each fishery may differ in its ability to be self-regulating, which we were surprised to see differ from marine commercial fisheries (Harley et al., 2001). Our results showed that fisheries independent surveys need to be performed to evaluate sustainability because exclusively managing from fisheries-dependent data may not be representative of actual population numbers and fishery status, especially for panfish. Inaccurate assessment of recreationally fished populations could lead to future collapses due to a lack of adequate management intervention amidst continual angler harvest (Carpenter et al., 2017). Our results indicate that species which share many ecological features (e.g. walleye and yellow perch) differ greatly in the degree to which their catch rates are hyperstable. This highlights the need to further understand the interactions between species-specific angler behaviors and the characteristics/behaviors of the species they are targeting. As in other exploited populations, we would expect an improved understanding of the interactions among human behavior, ecological feedbacks, and resource dynamics to facilitate more efficient and targeted management of fisheries.

CRediT authorship contribution statement

Camille L. Mosley: Conceptualization, Formal analysis, Writing – original draft, Writing – review & editing. **Colin J. Dassow**: Conceptualization, Software, Writing – review & editing. **John Caffarelli**: Formal analysis, Writing – original draft. **Alexander J. Ross**: Conceptualization, Data curation, Writing – review & editing. **Greg. G Sass**: Conceptualization, Resources, Validation, Funding acquisition, Writing – review & editing. **Stephanie L. Shaw**: Conceptualization, Validation, Writing – review & editing. **Christopher T. Solomon**: Conceptualization, Supervision, Writing – review & editing, Funding acquisition. **Stuart E. Jones**: Conceptualization, Supervision, Formal analysis, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and code used for analyses described in this study are available on Zenodo (https://zenodo.org/badge/latestdoi/410050601).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2022.106438.

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