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### Experimental demonstration of catch hyperstability from habitat aggregation, not effort sorting, in a recreational fishery

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**Title:** Experimental demonstration of catch hyperstability from habitat aggregation, not effort sorting, in a recreational fishery

**Authors:** Colin J. Dassow, Alexander J. Ross, Olaf P. Jensen, Greg G. Sass, Brett T. van Poorten, Christopher T. Solomon, Stuart E. Jones

**C.J. Dassow** , [cdassow@nd.edu](mailto:cdassow@nd.edu), Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA

**S.E. Jones** [sjones20@nd.edu](mailto:sjones20@nd.edu) Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA

**C.T. Solomon**, [solomonc@caryinstitute.org](mailto:solomonc@caryinstitute.org), Cary Institute of Ecosystem Studies, Millbrook, NY, USA

**A.J. Ross**, Cary Institute of Ecosystem Studies, Millbrook, NY, USA , **Current address:** [aross10@lakeheadu.ca](mailto:aross10@lakeheadu.ca), Natural Resources Management, Lakehead University, Thunder Bay, ON, Canada

**O.P. Jensen**, [ojensen@marine.rutgers.edu](mailto:ojensen@marine.rutgers.edu), Department of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ, USA

**G.G. Sass**, [gregory.sass@wisconsin.gov](mailto:gregory.sass@wisconsin.gov), Escanaba Lake Research Station, Wisconsin Department of Natural Resources, Boulder Junction, WI, USA

**B.T. van Poorten**, [brett.vanpoorten@gov.bc.ca](mailto:brett.vanpoorten@gov.bc.ca), British Columbia Ministry of Environment and Climate Change Strategy, Vancouver, BC, Canada

**Corresponding author** C.J. Dassow, 299A Galvin Life Sciences, University of Notre Dame, Notre Dame, IN, USA 46556, [cdassow@nd.edu](mailto:cdassow@nd.edu), telephone: 1 574 631 5703, fax: 1 574 631 7413

**Abstract:**

The relationship between angler catch rates and fish abundance can contribute to or hinder sustainable exploitation of fisheries depending on whether catch rates are proportional to fish abundance or are hyperstable. We performed a whole-ecosystem experiment where fish abundance was manipulated and paired with weekly angler catch rate estimates from controlled experimental fishing. Catch rates were hyperstable ( $\beta=0.47$ ) in response to changes in fish abundance. By excluding effort sorting (i.e., catch rates remaining high because less-skilled anglers leave the fishery as abundance declines), our experiment isolated the influence of fish aggregation as a driver of hyperstability. Spatial analysis of catch locations did not identify clustering around specific points, suggesting that loose aggregation to preferred habitat at the scale of the entire littoral zone was enough to maintain stable catch rates. In our study, general, non-spawning, habitat preferences created loose aggregations for anglers to target, which was sufficient to generate hyperstability. Habitat preferences are common to nearly all fishes and widely known to anglers, suggesting that many harvest-oriented recreational fisheries can be expected to exhibit hyperstability.

## 46 **Introduction:**

47       The relationship between catch per unit effort (CPUE) and fish abundance plays a critical role in  
48 sustainable exploitation of fisheries. Ideally, CPUE is proportional to abundance, signaling fishers to  
49 reallocate effort as a stock declines. This assumption is often explicit in population models used to  
50 manage fisheries (Hilborn and Walters 1992). Often, however, CPUE remains nearly constant even as  
51 abundance declines considerably (Paloheimo and Dickie 1964; Peterman and Steer 1981; Shuter et al.  
52 1998; Harley et al. 2001; Mrnak et al. 2018). This phenomenon, known as hyperstability, weakens signals  
53 that might feed back to reduce fisher effort and thus increases the vulnerability of fisheries to  
54 overexploitation (Post et al. 2002).

55       Two mechanisms have been proposed to generate hyperstability in CPUE. First, the average skill  
56 (i.e., the catchability coefficient,  $q$ ) of fishers engaged in the fishery may increase concomitantly with the  
57 decrease in fish abundance. This can occur through improvements in fishing technology that augment  
58 fishers' skills and/or because the distribution of active fishers shifts towards those with more skill as less  
59 skilled anglers are quicker to leave the fishery when abundance declines, a process known as effort  
60 sorting (Walters and Martell 2004; Ward et al. 2013; van Poorten et al. 2016; Tidd et al. 2017). Second, if  
61 fish aggregate to preferred habitat at some life history stage, then the density of fish in that habitat may  
62 remain high despite population-level declines in abundance, and fishers may sustain high CPUE by  
63 preferentially targeting the preferred habitat (Myers et al. 1997; Hansen et al. 2005; Erisman et al. 2011;  
64 Sadovy de Mitcheson and Erisman 2012; Mrnak et al. 2018).

65       In recreational fisheries, both the effort sorting and aggregation mechanisms have been  
66 suggested to induce hyperstability, though the evidence is stronger for the former. Perhaps the best  
67 effort to date to resolve hyperstability mechanisms in a recreational fishery is the research by Ward et  
68 al. (2013) on rainbow trout (*Oncorhynchus mykiss*) in British Columbia. Ward et al. (2013) observed

hyperstability across a set of open-access lakes which varied widely in trout density, and showed that angler skill (as measured by the number of days spent fishing annually) was higher in the low-density lakes. They also showed that there was no hyperstability in a set of experimental lakes fished by a single angler. Collectively, these two data sets provided compelling evidence that differences in average angler skill via effort sorting drove hyperstability in these systems. Several other studies have documented hyperstability in recreational fisheries and speculated about the role of effort sorting and aggregation mechanisms as drivers, but other mechanistic examinations are rare (Table 1).

We tested whether hyperstability occurred in a recreational fishery due to fish aggregation to preferred habitat, while controlling for effort sorting. We experimentally manipulated fish abundance in a natural lake, and measured CPUE of a fixed set of anglers at each level of fish abundance. Because our model fish species (largemouth bass, *Micropterus salmoides*), like many fishes in freshwater and marine environments, has strong habitat preferences that anglers recognize and exploit, we hypothesized that the aggregation mechanism alone would be sufficient to generate hyperstability in this system. Because bass potentially aggregate to habitat at multiple scales – the littoral zone within a lake, and patches of cover like coarse woody habitat and macrophytes within the littoral zone (Essington and Kitchell 1999; Ahrenstorff et al. 2009) - we secondarily considered which scale was most important for driving any hyperstability observed. Our study provides a unique experimental test for the mechanisms driving hyperstability in recreational fisheries.

## Methods:

### *Experimental Design and Study Site*

Testing for hyperstability requires estimates of CPUE across a wide range of fish abundance. We measured the CPUE of a set of experimental anglers who repeatedly fished a single lake as we

purposefully manipulated largemouth bass abundance. The same set of experimental anglers also repeatedly fished a similar, nearby, unmanipulated reference lake, allowing us to control for potential variation in CPUE due to seasonal trends, weather anomalies, and/or other factors independent of our abundance manipulation.

Our experiment was conducted on Camp Lake (26.1 ha, 45°59'52.5" N, 89°43'59.7" W), and reference experimental angling was conducted on nearby Little Rock Lake (15.8 ha, 45°59'44.7" N, 89°42'09.0" W). The lakes are within 3 km of one another in the Northern Highlands Lake District of Wisconsin, USA. Largemouth bass are the dominant fish species in both lakes, along with bluegill (*Lepomis macrochirus*) in Camp and yellow perch (*Perca flavescens*) in Little Rock (Sass et al. 2006, 2012; Ahrenstorff et al. 2009). Recreational angler effort on both lakes is limited due to difficult access and motor restrictions (electric motors only allowed on Camp; no motors allowed and gated access on Little Rock). Camp Lake has two distinct basins, connected by a channel that is ~ 30 m long and was less than 6 m wide and 1 m deep during our study (Ahrenstorff et al. 2009; Sass et al. 2012). Previous work, including tagging and radio telemetry studies, indicated minimal movement of bass between basins via this channel (Ahrenstorff et al. 2009; Sass et al. 2012).

We manipulated largemouth bass abundance in the 8.5 ha northern basin of Camp Lake, using the 17.6 ha southern basin as a holding area for bass that we removed from the northern basin. This allowed us to add fish to, as well as remove them from, the manipulated basin and to minimize long-term effects on the population. Because there is some public use of Camp Lake we were not able to physically separate the two basins; instead we used open-population mark-recapture models to account for limited natural movement of fish through the connecting channel and our experimental movement of fish between basins.

We initiated our experiment on 22 May 2018 with a four-night electrofishing mark-recapture experiment to estimate initial abundance of bass in each basin of Camp Lake. One week later, and on a weekly basis for each of the following 12 weeks, we first estimated angler CPUE with daytime angling in the manipulated basin of Camp Lake and in Little Rock Lake, and then electrofished the manipulated basin of Camp Lake that same night to estimate the current abundance and collect fish for removal to the holding basin. When abundance increases for the manipulation basin were desired, we electrofished the holding basin to collect fish to add to the manipulated basin. For many of the early weeks in the experiment, during the initial draw-down of fish abundance, we electrofished again the subsequent night to increase the magnitude of that week's manipulation.

#### *Angler CPUE*

Each week, a set of three anglers was randomly selected from a fixed pool of seven anglers to fish the manipulated basin of Camp Lake and Little Rock Lake using conventional hook-and-line techniques and standardized tackle (Wilde et al. 2003). Each lake was fished for two hours after sunrise and two hours before sunset, alternating weekly which lake was fished first in each morning and evening session. Anglers casted towards shore as they slowly boated along the shore; in each 2-hour sampling period, anglers covered the entire 1.2 km shoreline of the manipulated basin of Camp Lake and about one third of the 3.3 km shoreline of Little Rock Lake. The portion of Little Rock shoreline to be sampled was randomly selected each week. The location of capture of each angled bass in Camp Lake was recorded with a GPS unit to test for patch-scale aggregation (see below). We calculated the mean and variance of angler CPUE for each lake in each week across 6 samples (3 anglers x 2 sessions). We restricted our estimates of angling CPUE, as well as our abundance estimates and manipulations, to "catchable" bass  $\geq 200$  mm total length (TL). All captured bass were checked for tags; untagged bass  $\geq$

200 mm TL were marked by implanting 23 mm Oregon RFID HDX passive integrated transponder (PIT) tags. All captured bass were subsequently released at the point of capture.

#### *Manipulating and estimating abundance*

We used AC boat electrofishing along the entire shoreline to estimate bass abundance and to transfer bass between the two basins of Camp Lake. Abundance estimates were derived from a robust design mark-recapture model implemented in the R package RMark and fit via maximum likelihood (White and Burnham 1999; Laake et al. 2013; R Core Team 2018). The robust design model was well suited for our study because we had a high proportion of the population tagged, a large number of recapture events, and an open population with fish naturally moving or being experimentally moved between the basins of Camp Lake (Pine et al. 2003). The model used individual fish capture histories to estimate fish survival between closed population states, emigration/immigration, encounter probability, and probability of first capture and recapture. We considered model structures in which these parameters were fixed, and structures in which they varied with time or sampling session. We used Akaike's information criterion, corrected for small sample size, to identify the models with the best predictive ability (Cavanaugh 1997).

#### *Testing for hyperstability*

Catch per unit effort (CPUE, or C/E) can be described as a function of catchability ( $q$ ), the abundance of fish ( $N$ ), and a parameter  $\beta$  which describes the degree of non-linearity in catch rate as a function of abundance and therefore distinguishes between hyperstability ( $\beta < 1$ ), proportionality ( $\beta = 1$ ), or hyperdepletion ( $\beta > 1$ ):



$$CPUE = qN^{\beta} \quad (1)$$

(Harley et al. 2001). We estimated  $\beta$  for our paired fish abundance and angler CPUE observations, using simple linear regression of the log-transformed version of Eq. 1 because the precision of our abundance estimates was high (Ward et al. 2013). We included mean angler CPUE from our reference system, Little Rock Lake, as a covariate in the model to account for the potential effects of weather, angler identity, and seasonality on angler CPUE.

#### *Testing for patch-scale aggregation*

If fish aggregation to patch-scale habitat contributes to hyperstability, we would expect the distribution of angling catches to be clustered around specific areas of the littoral zone. We tested this hypothesis by expressing the capture location of each fish as a point on a line representing the shoreline of the manipulation basin, and testing for clustering at a range of spatial scales using Ripley's L test (Fortin and Dale 2005).

#### **Results:**

We successfully manipulated the abundance of largemouth bass in the manipulated basin of Camp Lake over the course of the study, with mark-recapture estimates indicating an order of magnitude decline. Based upon individual recapture histories for 865 fish tagged in both basins of Camp Lake, we fit 351 unique robust design model structures. The top four models had  $\Delta AIC$  values  $< 4$  and very similar structures (Table S1); we used the parameter estimates from the top model to calculate point estimates and confidence intervals for abundance in each week. The abundance of largemouth bass  $\geq 200$ mm TL in the manipulated basin ranged from 352 individuals at the beginning of the experiment to 25 individuals by week 11 (Fig. 1a). Confidence intervals around our weekly estimates

were well constrained, often an order of magnitude less than the estimate itself (Table S2). In generating the population estimates, electrofishing catches accounted for 83% and 63% of the applied and recaptured tags respectively, with the remainder caught by angling.

Dynamics of angler CPUE across our experiment were different in the manipulated basin and reference lake (Fig. 1b, 1c). Angler CPUE ranged from 0.5 to 4 fish per angler hour in the manipulated basin and from 3 to 12 fish per angler hour in the reference lake. Angler catch rates in the manipulated basin were relatively high during the first six weeks of our experiment, then lower for a period of five weeks, and then increased again in the final week of the study (Fig. 1b). Angler CPUE in the reference lake remained relatively constant and high throughout the summer (Fig. 1c).

We identified a strong signal of hyperstability in catch rates in our manipulated basin (Fig. 2). The estimated value of  $\beta$  ( $=0.47$ ) was significantly less than 1.0 ( $df=11$ ,  $p=0.013$ ). Mean angler CPUE in the manipulated basin ranged from about 4 fish per angler hour to 1.5 fish per angler hour across a range of abundances from 350 to 75 individuals. Below about 75 individuals, mean angler CPUE ranged from about 1.5 fish per angler hour to 0.5 fish per angler hour. Mean angler CPUE and fish abundance were positively correlated in models with or without the reference lake CPUE as a covariate ( $\beta=0.42$ ,  $df=11$ ,  $p=0.039$ ; and  $\beta=0.47$ ,  $df=11$ ,  $p=0.013$ , respectively). Including the reference lake CPUE as a covariate provided a significantly better fit than the base model based upon a likelihood ratio test ( $p=0.034$ ).

The distribution of largemouth bass capture locations around the shoreline of our manipulated basin revealed no clustering (Fig. 3a). At all spatial scales we considered, our observed Ripley's L estimates did not exceed the 95% confidence intervals from 1000 Ripley's L calculations based upon random draws from a uniform distribution of possible catch locations (Fig. 3b). When comparing Ripley's

L estimates for catch locations at abundances above and below 75 individuals we saw no evidence of clustering of catch locations at either high or low fish abundance (Fig. 3c & 3d).

## **Discussion:**

Previous research documenting hyperstability in recreational fisheries has rarely tested for the mechanisms driving hyperstable catch rates (Table 1). The few studies that inferred a mechanism have linked hyperstable catch rates to differences in angler skill or spawning aggregations (Erisman et al. 2011; Ward et al. 2013; van Poorten et al. 2016). To our knowledge, no study has experimentally manipulated the abundance of fish over which angler CPUE is estimated, but rather most existing research leverages spatial patterns of fish abundance, effort, and catch rates. Our study used an experimental approach, but also controlled for effort sorting to test whether fish aggregation to preferred habitat was sufficient to drive hyperstability of catch rates in a recreational fishery.

A review of existing studies suggests that hyperstability can occur in diverse recreational fisheries, but experimental or statistical support for underlying mechanisms is limited (Table 1). Most studies discuss potential mechanisms for observed hyperstability in catch rates based on what has been observed in the marine literature or other recreational fisheries hyperstability papers, but few can convincingly point to a specific mechanism (Erisman et al. 2011; Ward et al. 2013). Early studies hypothesized that aggregation underpinned hyperstability of catch rates in recreational fisheries because existing theory and well-known marine examples identified aggregation as a mechanism for increased catchability with declining stock abundance (Paloheimo and Dickie 1964; Peterman and Steer 1981; Hutchings 1996; Erisman et al. 2011; Sadovy de Mitcheson and Erisman 2012). Although only studies investigating intense aggregation during spawning have conclusively identified aggregation as a mechanism for hyperstability of recreational catch rates (Erisman et al. 2011; Sadovy de Mitcheson and

Erismann 2012), general aggregating behaviors such as those exhibited by fish around fish aggregating devices (FADs) in marine systems are also known to promote hyperstability (Hilborn and Walters 1992; Girard et al. 2004; Letessier et al. 2013). Aggregation has also been proposed as one of the mechanisms which kept catch rates in the commercial fishery high even as abundance collapsed in Northwest Atlantic cod (*Gadus morhua*) fisheries (Rose and Kulka 1999). More recent studies in recreational fisheries have identified negative relationships between average angler skill level and population abundance (effort sorting) as the mechanism leading to hyperstability of catch rates (Ward et al. 2013; van Poorten et al. 2016). These authors correctly raise the point that earlier studies that identified hyperstability of catch rates in recreational fisheries did not identify, but could plausibly have been influenced by, effort sorting.

Despite controlling for angler skill and conducting our experiment outside of spawning season, we observed significant hyperstability in angler catch rates of largemouth bass. In our study system, bass home ranges encompassed the entire basin but littoral areas are preferred (Essington and Kitchell 1999; Ahrenstorff et al. 2009). Individual patches of habitat had no effect on the hyperstability observed here given the lack of clustering observed in the spatial distribution of angling capture locations around the entire shoreline of our manipulated basin. Instead, general preferences for littoral areas in our model species were sufficient to produce aggregations that promoted hyperstability. As fish were removed from their preferred littoral areas in our manipulated basin, mixing of fish between pelagic and littoral habitats could have slowed the decline in density, and catch rates, in preferred littoral areas as new fish filled spaces left by the removed fish. This hypothesized mechanism is supported by the combination of consistent catch rates and randomly distributed catch locations along the shoreline of our experimental system even as the population was experimentally reduced (Fig. 1 and 3). These dynamics are analogous to classic foraging arena theory, where in this case sport fish are subject to a risk-resource tradeoff in their preferred, but angler-targeted, habitat (Ahrens et al. 2012; Matthias et al. 2014).

Given that most fishes have preferences for certain habitat types and that only minimal skill may be required for anglers to target these habitats, we would expect that most recreational, harvest-oriented species exhibit hyperstable catch rates independent of heterogeneity in angler skill. However, we might expect the degree of hyperstability to relate to the spatial intensity and temporal extent of aggregation. In this context, spawning for many fishes can be thought of as a spatially intense, but temporally short type of aggregation (Mrnak et al. 2018). In contrast, our results suggest that even moderate spatial intensity of habitat use over a longer temporal extent may lead to hyperstability.

Although non-spawning spatial aggregation appears to be sufficient to generate hyperstable catch rates in a recreational fishery, the effect of angler skill on catch rates is also clear (Ward et al. 2013). Anglers are known to segregate themselves based upon skill across lakes with varying densities of fish, with high skill anglers generally dominating low fish density lakes (Ward et al. 2013). It is likely that these two processes can have additive effects on the response of catchability to population abundance, but could they interact in a non-additive manner? One possibility for non-additive interaction between these two mechanisms would be if knowledge about the location, in space and time, of fish aggregations was related to avidity or skill level. Although many anglers are or become aware of intense spawning aggregations or general preferences for littoral habitat, knowledge of other more subtle or short-lived aggregations may be more limited and linked to differences in angler skill.

Given that aggregation and effort sorting are individually, and likely in combination, sufficient to generate hyperstable catch rates, we would expect widespread hyperstability in recreational fisheries. The apparent cosmopolitan nature of these mechanisms means traditional management strategies may struggle to address complications of management driven by hyperstability of catch rates leaving fisheries vulnerable to overexploitation (Carpenter et al. 2017). Many authors highlight additional control of effort, rather than harvest, as a potentially important management strategy (Camp et al. 2015, 2016; Lynch et al. 2017). Many management agencies impose seasonal closures of fisheries during

known spawning aggregations, in part to limit harvest (as was the case for largemouth bass in northern Wisconsin until recently), but additional spatial or temporal limits on effort, as have been employed in the case of marine protection areas, may be beneficial in attempting to address the effects of aggregation on hyperstability of catch rates (Russ 2002; Roberts et al. 2005). Spatial or temporal closures, though likely to be unpopular with anglers, are being recognized and used by fisheries managers, however the sustainability of a fishery may still be compromised when fish aggregate throughout the season. These non-spawning aggregations in conjunction with effort sorting may require additional measures to be taken by managers.

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**Table Caption**

Table 1. Review of key research exploring hyperstability in recreational fisheries. Two different methods for identifying hyperstability have been used in these studies. The value of the parameter  $\beta$  can be used to identify instances of hyperstability when  $\beta < 1$ . Alternatively, whether or not catchability ( $q$ ) is inversely related to fish density is another method by which researchers can identify hyperstable catch rates.

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## Figure Captions

Figure 1. a) Population estimate for largemouth bass (*Micropterus salmoides*) >200mm TL in the manipulated basin of Camp Lake, Vilas County, Wisconsin over the course of the 12-week hyperstability study in 2018. Error bars are 95% CI. b) Manipulated basin, mean angler largemouth bass catch-per-unit effort (CPUE) over the course of the experiment. Error bars denote 1 standard deviation about the mean. c) Little Rock Lake, Vilas County, Wisconsin (reference system) mean largemouth bass angler CPUE over the course of the experiment. Error bars denote 1 standard deviation about the mean.

Figure 2. Mean angler largemouth bass (*Micropterus salmoides*) CPUE (fish angler<sup>-1</sup> hour<sup>-1</sup>) accounting for potential variation due to seasonal CPUE trends, weather anomalies, and/or other factors independent of abundance manipulations as a function of fish abundance on the manipulated basin of Camp Lake, Vilas County, Wisconsin during 2018.

Figure 3. a) Locations of angling captures of largemouth bass (*Micropterus salmoides*) >200mm TL in two-dimensional space (grey polygon) and one-dimensional space (line segment) on the manipulated basin of Camp Lake, Vilas County, Wisconsin during 2018. Plots of Ripley's L as a function of the number of neighbors within a given distance in meters on either side of a catch location (solid line) for b) all catches during the experiment, c) catches during periods where fish abundance was >75 individuals, and d) catches during periods where fish abundance was <75 fish. Dotted lines represent 95 % CI around Ripley's L for randomly distributed data (dashed line).

Table 1. Review of key research exploring hyperstability in recreational fisheries. Two different methods for identifying hyperstability have been used in these studies. The value of the parameter  $\beta$  can be used to identify instances of hyperstability when  $\beta < 1$ . Alternatively, whether or not catchability ( $q$ ) is inversely related to fish density is another method by which researchers can identify hyperstable catch rates.

Authors	Recreational Fishery	Method	Hyperstability	Mechanism	Beta	q
Peterman & Steer 1981	British Columbia and Oregon Chinook Salmon ( <i>Oncorhynchus tshawytscha</i> )	Estimate catchability from a time series of catch and fish abundance data.	Yes	No mechanism explored. Suggest fish aggregation to easily targeted habitats drives hyperstability.		Negative correlation between q and abundance
Shuter et al. 1998	Ontario Lake Trout ( <i>Salvelinus namaycush</i> )	Describe relationship between estimate of catchability and fish abundance for two lakes through time and 17 lakes spanning a gradient of fish densities.	Yes	No mechanism explored. Suggest the non-random distribution of fish is exploited by anglers who can find these aggregations.		Negative correlation between q and abundance
Hansen et al. 2000	Northern Wisconsin Walleye ( <i>Sander vitreus</i> )	Non-linear models fit to estimates of walleye density and angler/spearfishing catch rates for 118 WI lakes	Spearing -Yes; Angling -No	None explored	Spearing fishery = 0.65	
Hansen et al. 2005	Northern Wisconsin Walleye ( <i>Sander vitreus</i> )	Analysis of data presented in Hansen et al. (2000), this time accounting for measurement error in catch rates and abundance estimates.	Both-Yes	None explored	Spearing = 0.65; Angling = 0.825	

Erisman et al. 2011	Southern California coastal stocks of Barred Sand Bass ( <i>Paralabrax nebulifer</i> ) and Kelp Bass ( <i>Paralabrax clathratus</i> )	Fit a non-linear model to catch rate and fish abundance data	Yes	Overfishing of spawning aggregations	0.44-0.59	
Ward et al. 2013	British Columbia Rainbow Trout ( <i>Oncorhynchus mykiss</i> )	Describe relationship between angler catch rate and fish density in a closed fishery with constant angler skill and an open fishery where angler skill varies.	Yes	Open access fishery exhibited hyperstable catch rates while the closed access fishery did not. Angler skill was strongly predicted by fish density in the open access fishery with high skill anglers targeting low fish density lakes and low skill angler targeting low fish density lakes.	0.42	
vanPoorten et al. 2016	British Columbia Rainbow Trout ( <i>Oncorhynchus mykiss</i> )	Competing models fit to angler CPUE and fish abundance data presented in Ward et al. (2013).	Yes	Best fitting model described hyperstability as purely a function of angler effort sorting. Low skill anglers leave fishery as catch rates decline while high skill anglers remain creating hyperstable average catch rates as high skill anglers continue to catch fish as abundance declines.		Negative correlation between q and abundance

Mrnak et al. 2018	Northern Wisconsin Walleye ( <i>Sander vitreus</i> )	Describe relationship between catch rate and fish abundance from 1990-2015 using the same method as Hansen et al. (2005).	Both-Yes	No mechanism explored. Suggest hyperstable catch rates in spearfishery are due to spawning aggregations while hyperstability in angling fishery is due to effort sorting.	Spearing = 0.41; Angling = 0.53
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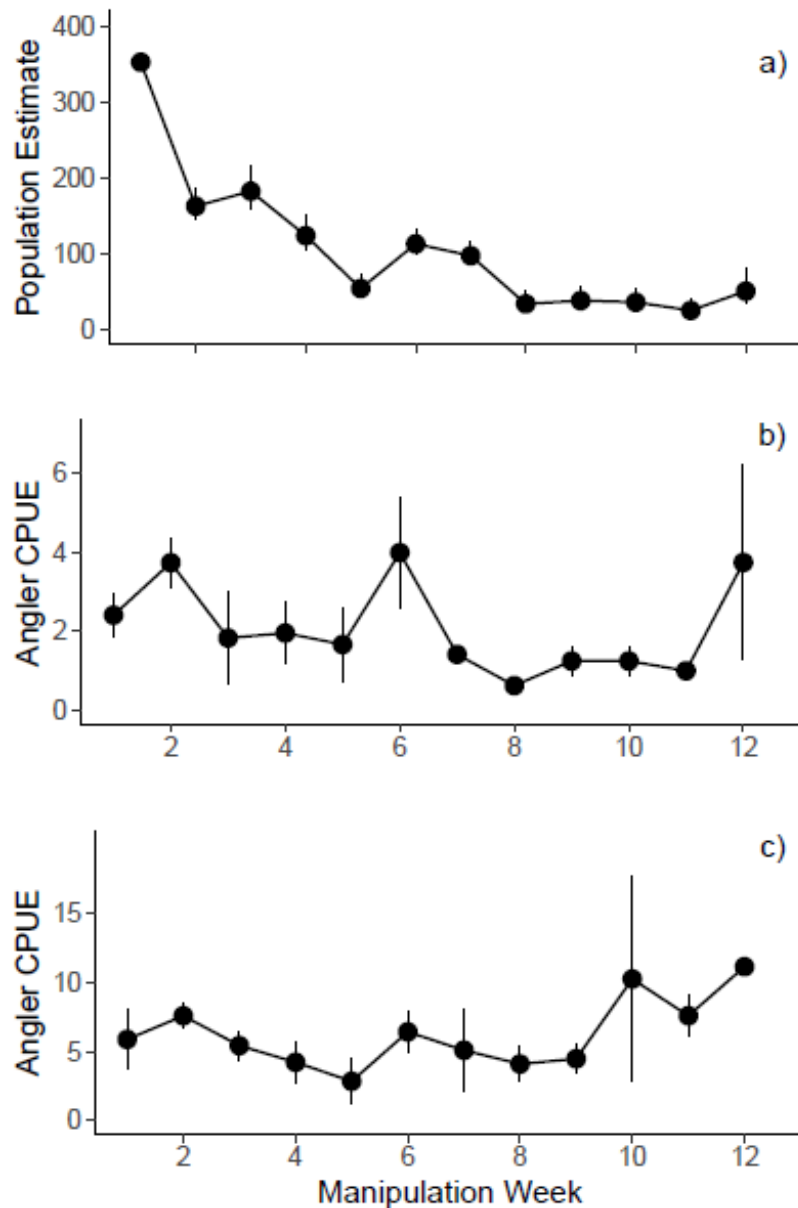


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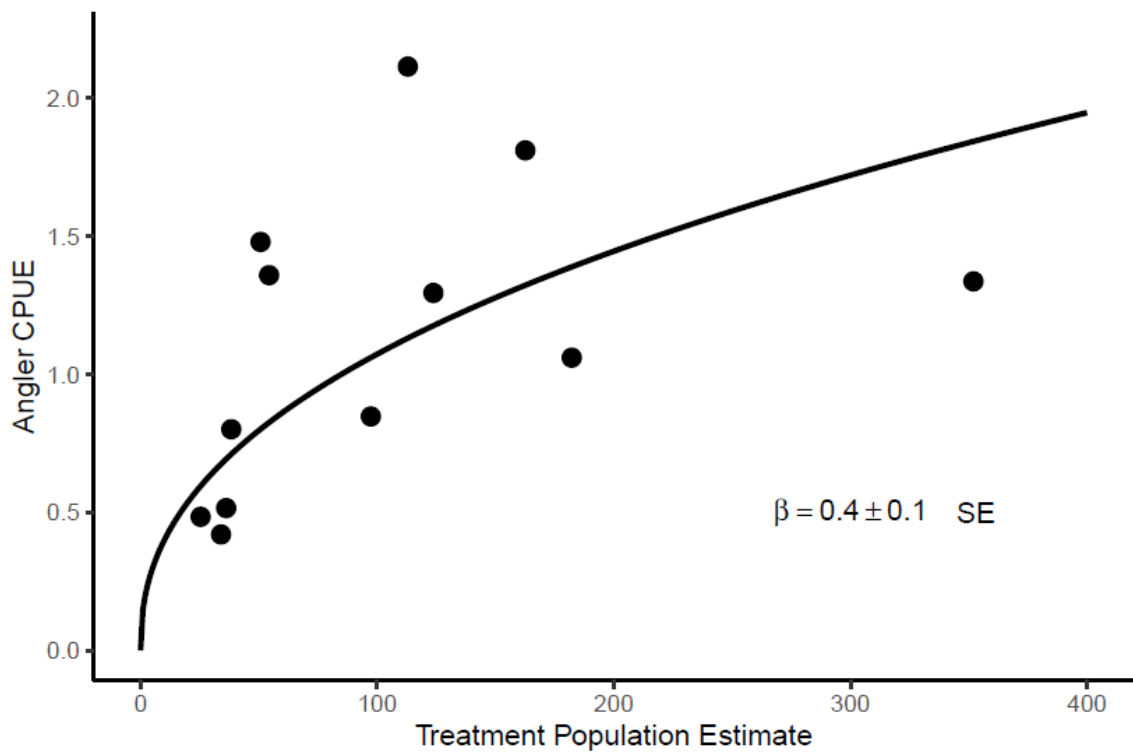


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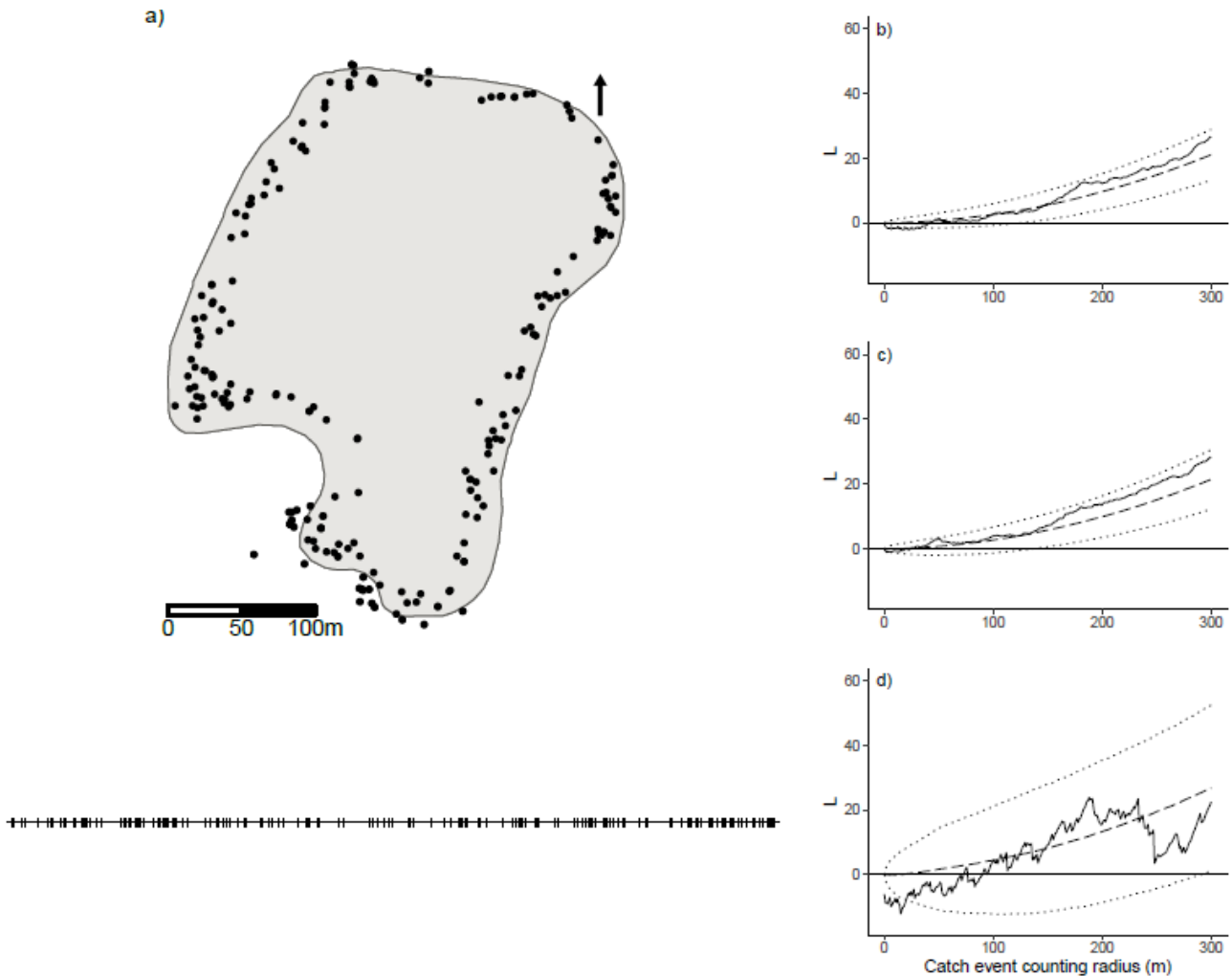


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