NRC Research Press

ARTICLE

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

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

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 in which 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.

Résumé : La relation entre les taux de prise de pêcheurs à la ligne et l'abondance de poissons peut contribuer à l'exploitation durable de ressources halieutiques ou lui faire entrave, selon que les taux de prise sont proportionnels à l'abondance de poissons ou hyperstables. Nous avons mené une expérience à l'échelle écosystémique dans laquelle l'abondance de poissons a été manipulée et jumelée à des estimations des taux de prise hebdomadaires des pêcheurs pour des pêches expérimentales contrôlées. Les taux de prise étaient hyperstables ($\beta = 0{,}47$) en réponse à des changements de l'abondance de poissons. En excluant le tri de l'effort (c.-à-d. des taux de prise demeurant élevés parce que les pêcheurs moins compétents délaissent la pêche quand l'abondance baisse), l'expérience a isolé l'influence du regroupement de poissons comme facteur d'hyperstabilité. L'analyse spatiale de l'emplacement des prises n'a pas relevé de concentrations autour de lieux précis, ce qui indiquerait qu'un regroupement lâche autour des habitats de prédilection à l'échelle de toute la zone littorale suffit pour maintenir des taux de prise stables. Dans l'étude, les préférences générales en matière d'habitat, autres que pour le frai, créaient des regroupements lâches pouvant être ciblés par les pêcheurs, ce qui suffisait pour produire une hyperstabilité. Presque tous les poissons montrent des préférences en matière d'habitat, que les pêcheurs généralement, ce qui donne à penser que de nombreuses pêches récréatives axées sur la capture devraient présenter une hyperstabilité. [Traduit par la Rédaction]

Introduction

The relationship between catch per unit effort (CPUE) and fish abundance plays a critical role in sustainable exploitation of fisheries. Ideally, CPUE is proportional to abundance, signaling fishers to reallocate effort as a stock declines. This assumption is often explicit in population models used to manage fisheries (Hilborn and Walters 1992). When CPUE is not proportional to abundance, it is often described as either hyperdeplete or hyperstable. A hyperdeplete relationship between angler CPUE and fish abundance describes a scenario in which catch rates decline rapidly with very little decline in actual fish abundance, often giving the impression that fish populations have declined when in fact fish have reduced vulnerability to capture (Askey et al. 2006; Alós et al. 2019). In contrast, especially in harvested systems, CPUE can remain nearly constant even as abundance declines considerably (Paloheimo and Dickie 1964; Peterman and Steer 1981; Shuter et al. 1998; Harley et al. 2001; Mrnak et al. 2018). This phenomenon, known as hyperstability, weakens signals that might feed back to reduce fisher effort and thus increases the vulnerability of fisheries to overexploitation (Post et al. 2002).

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

Received 18 July 2019. Accepted 15 November 2019.

C.J. Dassow and S.E. Jones. Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA.
A.J. Ross* and C.T. Solomon. Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA.
O.P. Jensen. Department of Marine and Coastal Sciences, Rutgers University, New Brunswick, NJ 08901-8520, USA.
G.G. Sass. Escanaba Lake Research Station, Wisconsin Department of Natural Resources, Boulder Junction, WI 54512, USA.
B.T. van Poorten. British Columbia Ministry of Environment and Climate Change Strategy, Vancouver, BC V8W 9M2, Canada.
Corresponding author: Colin J. Dassow (email: cdassow@nd.edu).
*Current address: Natural Resources Management, Lakehead University, Thunder Bay, ON P7B 5E1, Canada.

2005; Erisman et al. 2011; Sadovy de Mitcheson and Erisman 2012; Mrnak et al. 2018).

In recreational fisheries, both effort sorting and aggregation mechanisms have been suggested to induce hyperstability, though the evidence is stronger for the former. Perhaps the best effort to date to resolve hyperstability mechanisms in a recreational fishery is the research by Ward et al. (2013) on rainbow trout (*Oncorhynchus mykiss*) in British Columbia. Ward et al. (2013) observed hyperstability across a set of open-access lakes that 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 the skill of the average angler 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 the effects of effort sorting. We experimentally manipulated fish abundance in a natural lake and measured the CPUE of a fixed set of anglers at each level of fish abundance. Because our model's fish species (largemouth bass, *Micropterus salmoides*), as 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 such as 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 Lake and yellow perch (*Perca flavescens*) in Little Rock Lake (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 are allowed on Camp Lake; no motors are allowed on Little Rock Lake and it has gated access). 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 radiotelemetry 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 an open-population mark–recapture model, detailed later, 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 drawdown of fish abundance, we electrofished again the subsequent night to increase the magnitude of that week's manipulation.

Angler CPUE

A set of three anglers was randomly selected each week from a fixed pool of seven anglers with heterogeneous angling experience 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 2 h hours after sunrise and 2 h 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-h 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 (discussed later). We calculated the mean and variance of angler CPUE for each lake in each week across six samples (three anglers × two sessions). We restricted our estimates of angling CPUE, as well as our abundance estimates and manipulations, to "catchable" bass ≥ 200 mm total length (TL). All captured bass were checked for tags, and untagged bass ≥ 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 (version 3.5.3) RMark (version 2.2.5) 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 (AIC_c) to identify the models with the best predictive ability (Cavanaugh 1997).

Table 1. Review of key research exploring hyperstability in recreational fisheries.

Authors	Recreational fishery	Method	Hyperstability	Mechanism	β	q
Peterman and Steer 1981	British Columbia and Oregon Chinook salmon (*Oncorhynchus tshawytscha*)	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 (*Salvelinus namaycush*)	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 nonrandom 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 (*Sander vitreus*)	Nonlinear models fit to estimates of walleye density and angler–spearfishing catch rates for 118 Wiconsin lakes	Spearing — yes; angling — no	None explored	Spearing fishery = 0.65	
Hansen et al. 2005	Northern Wisconsin Walleye (*Sander vitreus*)	Analysis of data presented in Hansen et al. (2000), this time accounting for measurement errors 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 (*Paralabrax nebulifer*) and kelp bass (*Paralabrax clathratus*)	Fit a nonlinear 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 (*Oncorhynchus mykiss*)	Describe relationship between angler catch rate and fish density in a closed fishery with constant angler skill and an open fishery in which 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 highly skilled anglers targeting low fish density lakes and low skilled anglers targeting low fish density lakes	0.42	
van Poorten et al. 2016	British Columbia rainbow trout (*Oncorhynchus mykiss*)	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 skilled anglers leave fishery as catch rates decline while highly skilled anglers remain, creating hyperstable average catch rates as they continue to catch fish as abundance declines		Negative correlation between q and abundance
Mrnak et al. 2018	Northern Wisconsin walleye (*Sander vitreus*)	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	

Note: Two different methods for identifying hyperstability have been used in these studies. The value of the parameter β can be used to identify instances of hyperstabiliy 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.

Testing for hyperstability

Catch per unit effort at time t ($CPUE_t$, or catch per effort) can be described as a function of catchability (q), the abundance of fish at time t (N_t), and a parameter β, which describes the degree of nonlinearity in catch rate as a function of abundance and therefore distinguishes between hyperstability ($\beta < 1$), proportionality ($\beta = 1$), or hyperdepletion ($\beta > 1$):

$$(1) \qquad CPUE_t = qN_t^{\beta}$$

(Harley et al. 2001). Following Ward et al. (2013), we estimated β for our series of fish abundances and angler CPUEs using a simple linear regression of the log-transformed version of eq. 1. We did not include uncertainty in N_t when estimating β because, similar to the experimental fishery in Ward et al. (2013), the precision of our abundance estimates was greater than that of our $CPUE_t$ estimates. 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

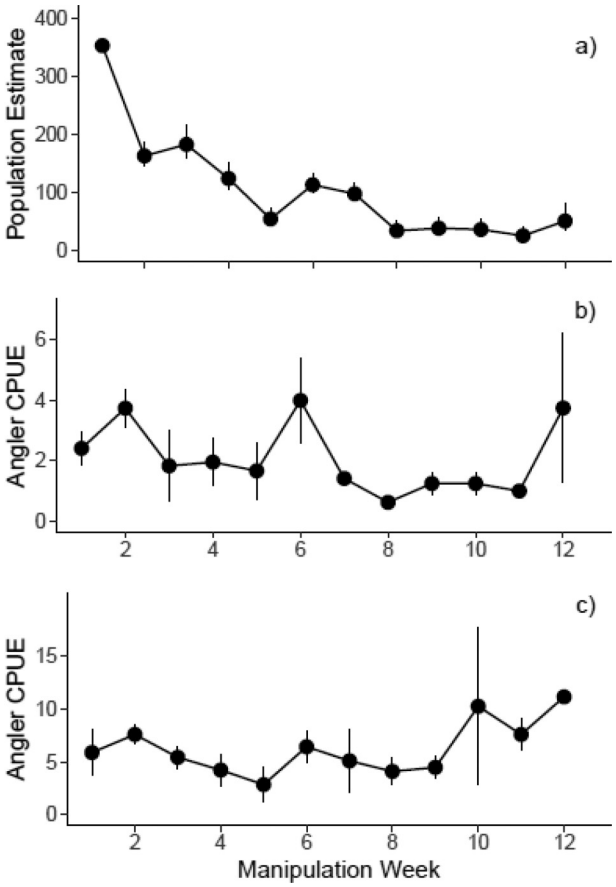
We successfully manipulated the abundance of largemouth bass in the manipulated basin of Camp Lake over the course of the study, with mark–recapture estimates indicating a decline of an order of magnitude. Based on individual recapture histories for 865 fish tagged in both basins of Camp Lake, we fit 351 unique robust design model structures. The top four models had ΔAIC_c values < 4 and very similar structures (Supplementary Table S1);[1] we used the parameter estimates from the top model to calculate point estimates and confidence intervals (CIs) for abundance in each week. The abundance of largemouth bass ≥ 200 mm TL in the manipulated basin ranged from 352 individuals at the beginning of the experiment to 25 individuals by week 11 (Fig. 1*a*). CIs around our weekly estimates were well constrained, often an order of magnitude less than the estimate itself (Supplementary Table S2).[1] 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.

The dynamics of angler CPUE across our experiment were different in the manipulated basin and reference lake (Figs. 1*b*, 1*c*). 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 6 weeks of our experiment, then lower for a period of 5 weeks, and then increased again in the final week of the study (Fig. 1*b*). Angler CPUE in the reference lake remained relatively constant and high throughout the summer (Fig. 1*c*).

We identified a strong signal of hyperstability in catch rates in our manipulated basin (Fig. 2). The estimated value of β (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 and 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 on a likelihood ratio test ($p = 0.034$).

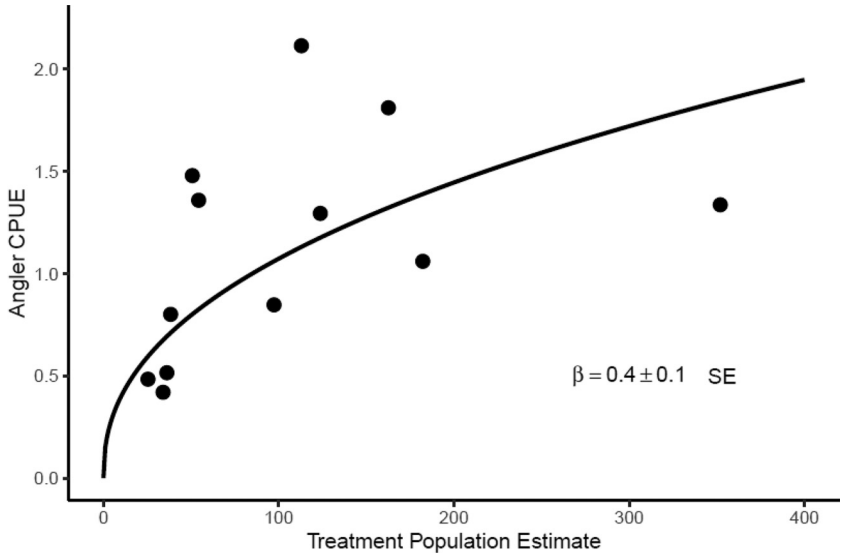
The distribution of largemouth bass capture locations around the shoreline of our manipulated basin revealed no clustering (Fig. 3*a*). At all spatial scales considered, our observed Ripley's L estimates did not exceed the 95% CIs from 1000 Ripley's L calculations based on random draws from a uniform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

Fig. 1. (*a*) Population estimate for largemouth bass (*Micropterus salmoides*) > 200 mm 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.



[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0245.

Fig. 2. Mean angler largemouth bass (*Micropterus salmoides*) CPUE (number of fish per angler per hour) 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 in the manipulated basin of Camp Lake, Vilas County, Wisconsin, during 2018.



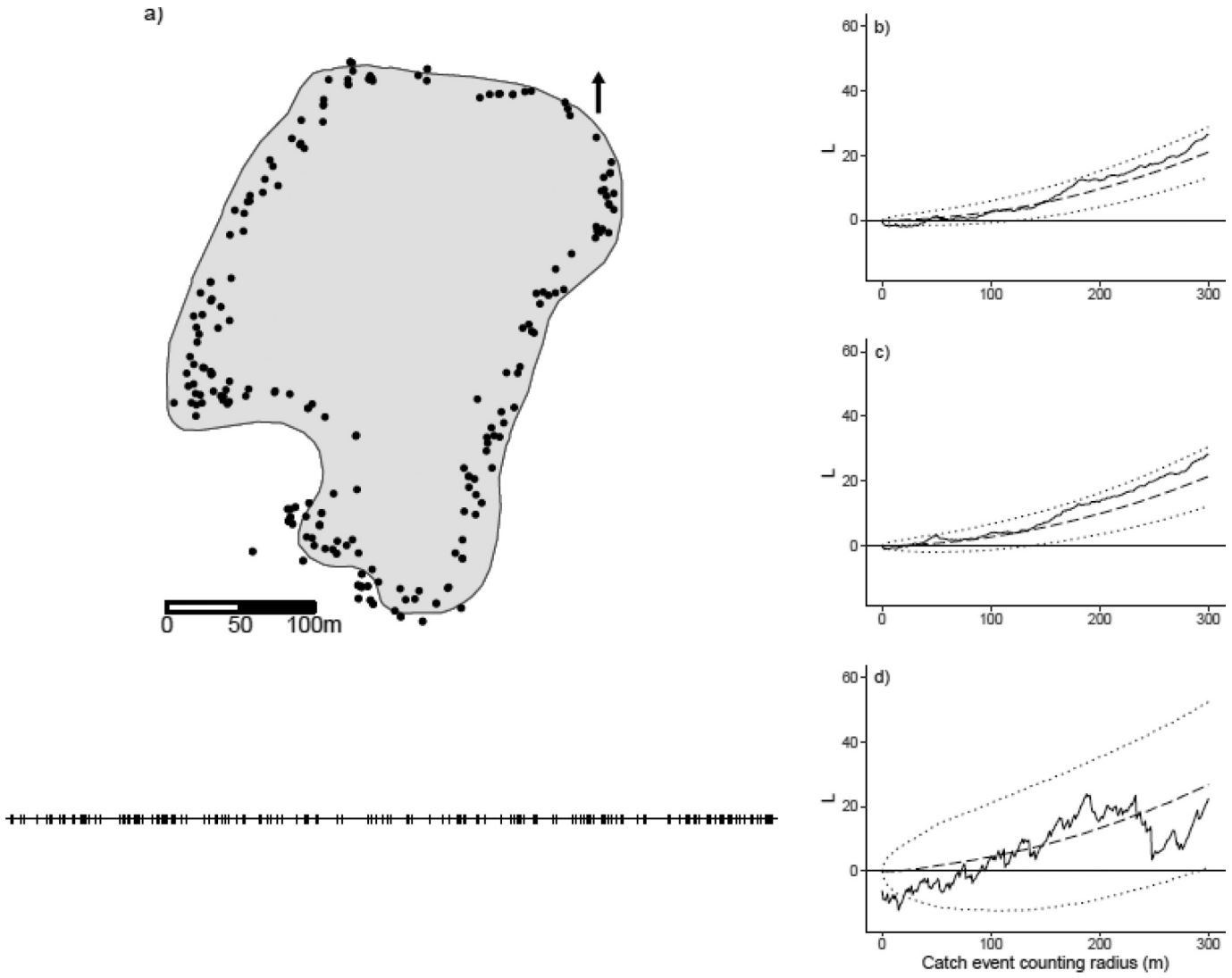
Discussion

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 Erisman 2012), general aggregating behaviors such as those exhibited by fish around fish aggregating devices 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 that 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 the effects of angler skill on catch (Ward et al. 2013; van Poorten et al. 2016). Ward et al. (2013) and van Poorten et al. (2016) identify and describe a 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. Although the findings of these previous studies are consistent with effort sorting, recent work has questioned the role of skill in determining catch rates (Seekell 2011; Monk and Arlinghaus 2018). Monk and Arlinghaus (2018) found that self-reported angler skill did not affect CPUE but did allow higher skilled anglers to be more successful at catching large fish in a system with telemetry-tagged fish and tracked anglers. Furthermore, angler catch by a group of heterogeneously skilled anglers was found to be not significantly different from predictions of a random catch model (Seekell 2011).

Despite controlling for angler skill and conducting our experiment outside the 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. Previous work on our treatment basin tracked largemouth bass home ranges and found that individual fish used both littoral and pelagic habitats nearly equally (Ahrenstorff et al. 2009). Consequently, even though our sampling methods were based around littoral habitats, it is unlikely that a significant proportion of the population was unaccounted for during our sampling because fish were mixing between pelagic and littoral areas. Also, the combination of our observed consistent catch rates and randomly distributed catch locations along the shoreline of our experimental system, even as the population was experimentally reduced further, support this mechanism (Figs. 1, 3). These dynamics are analogous to classic foraging arena theory in which, in this case,

Fig. 3. (*a*) Locations of angling captures of largemouth bass (*Micropterus salmoides*) > 200 mm 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 metres) on either side of a catch location (solid line) for (*b*) all catches during the experiment, (*c*) catches during periods when fish abundance was >75 individuals, and (*d*) catches during periods when fish abundance was <75 fish. Dotted lines represent 95% CI around Ripley's *L* for randomly distributed data (dashed line).



sport fish are subject to a risk-resource trade-off 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 possible (Ward et al. 2013). If angler skill effects do exist, it is likely that fish aggregation and angler skill 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. Van Poorten et al. (2016) suggest that as fish abundance declines, more skilled anglers are able to find remaining fish concentrations and unskilled anglers, instead of exiting the fishery, could encroach on the areas fished by the skilled anglers. In this way, more anglers are fishing the remaining aggregations, resulting in increased fishing mortality, further accelerating fishery decline. This may result in a positive feedback cycle in which, as abundance declines, anglers are further concentrated around the remaining aggregations instead of exiting the fishery, hastening the decline. In this way, though 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 sufficient to generate hyperstable catch rates individually and likely in combination, we would expect widespread hyperstability in recreational

fisheries. The apparent cosmopolitan nature of these mechanisms means that 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). However, one adverse effect of these spatial and temporal closures may be increased reactivity of fish to angling that unintentionally leads to elevated exploitation rates (Koeck et al. 2020). 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, more direct measures to be taken by managers such as issuing of harvest tags for some especially vulnerable species.

Acknowledgements

This work was funded by the U.S. National Science Foundation under grant 1716066. We thank B. Aulino, J. Barron, C. Bishop, A. Fink, S. Phillips, and M. Solokas for assistance in data collection. We also thank the Wisconsin Department of Natural Resources, Mike Vogelsang, and Steve Gilbert for allowing us to use Camp Lake for our experiment. All procedures in this study were approved under permits from the Wisconsin Department of Natural Resources and institutional animal care protocols (Scientific Collectors Permit #SCP-FM-2018-087, State Natural Area Permit #18-14, University of Notre Dame IACUC #18-04-4590).

References

Ahrens, R.N.M., Walters, C.J., and Christensen, V. 2012. Foraging arena theory. Fish Fish. **13**(1): 41–59. doi:10.1111/j.1467-2979.2011.00432.x.

Ahrenstorff, T.D., Sass, G.G., and Helmus, M.R. 2009. The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*). Hydrobiologia, **623**(1): 223–233. doi:10.1007/s10750-008-9660-1.

Alós, J., Campos-Candela, A., and Arlinghaus, R. 2019. A modelling approach to evaluate the impact of fish spatial behavioural types on fisheries stock assessment. ICES J. Mar. Sci. **76**(2): 489–500. doi:10.1093/icesjms/fsy172.

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

Camp, E.V., van Poorten, B.T., and Walters, C.J. 2015. Evaluating short openings as a management tool to maximize catch-related utility in catch-and-release fisheries. North Am. J. Fish. Manage. **35**(6): 1106–1120. doi:10.1080/02755947.2015.1083495.

Camp, E.V., Ahrens, R.N.M., Allen, M.S., and Lorenzen, K. 2016. Relationships between angling effort and fish abundance in recreational marine fisheries. Fish. Manage. Ecol. **23**(3–4): 264–275. doi:10.1111/fme.12168.

Carpenter, S.R., Brock, W.A., Hansen, G.J.A., Hansen, J.F., Hennessy, J.M., Isermann, D.A., et al. 2017. Defining a Safe Operating Space for inland recreational fisheries. Fish Fish. **18**(6): 1150–1160. doi:10.1111/faf.12230.

Cavanaugh, J.E. 1997. Unifying the derivations for the Akaike and corrected Akaike information criteria. Stat. Probab. Lett. **33**(2): 201–208. doi:10.1016/S0167-7152(96)00128-9.

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

Essington, T.E., and Kitchell, J.F. 1999. New perspective in the analysis of fish distributions: a case study on the spatial distribution of largemouth bass (*Micropterus salmoides*). Can. J. Fish. Aquat. Sci. **56**(S1): 52–60. doi:10.1139/f99-213.

Fortin, M.-J., and Dale, M.R.T. 2005. Spatial analysis: a guide for ecologists. *In* Spatial Analysis: A Guide for Ecologists. 2nd edition. Cambridge University Press, Cambridge, U.K. doi:10.1017/CBO9780511542039.003.

Girard, C., Benhamou, S., and Dagorn, L. 2004. FAD: Fish Aggregating Device or Fish Attracting Device? A new analysis of yellowfin tuna movements around floating objects. Anim. Behav. **67**: 319–326. doi:10.1016/j.anbehav.2003.07.007.

Hansen, M.J., Beard, T.D., Jr., and Hewett, S.W. 2000. Catch rates and catchability of walleyes in angling and spearing fisheries in northern Wisconsin lakes. North Am. J. Fish. Manag. **20**(1): 109–118. doi:10.1577/1548-8675(2000)020<0109.

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

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

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

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

Koeck, B., Lovén Wallerius, M., Arlinghaus, R., and Johnsson, J.I. 2020. Behavioural adjustment of fish to temporal variation in fishing pressure affects catchability: an experiment with angled trout. Can. J. Fish. Aquat. Sci. **77**(1): 188–193. doi:10.1139/cjfas-2019-0064.

Laake, J.L., Johnson, D.S., and Conn, P.B. 2013. marked: An R package for maximum likelihood and Markov Chain Monte Carlo analysis of capture–recapture data. Methods Ecol. Evol. **4**(9): 885–890. doi:10.1111/2041-210X.12065.

Letessier, T.B., Meeuwig, J.J., Gollock, M., Groves, L., Bouchet, P.J., Chapuis, L., et al. 2013. Assessing pelagic fish populations: the application of demersal video techniques to the mid-water environment. Methods Oceanogr. **8**: 41–55. doi:10.1016/j.mio.2013.11.003.

Lynch, A.J., Cooke, S.J., Beard, T.D., Jr., Kao, Y., Lorenzen, K., Song, A.M., et al. 2017. Grand challenges in the management and conservation of North American inland fishes and fisheries. Fisheries, **42**(2): 115–124. doi:10.1080/03632415.2017.1259945.

Matthias, B.G., Allen, M.S., Ahrens, R.N.M., Beard, T.D., and Kerns, J.A. 2014. Hide and seek: interplay of fish and anglers influences spatial fisheries management. Fisheries, **39**(6): 261–269. doi:10.1080/03632415.2014.903836.

Monk, C.T., and Arlinghaus, R. 2018. Eurasian perch, *Perca fluviatilis*, spatial behaviour determines vulnerability independent of angler skill in a whole-lake reality mining experiment. Can. J. Fish. Aquat. Sci. **75**(3): 417–428. doi:10.1139/cjfas-2017-0029.

Mrnak, J.T., Shaw, S.L., Eslinger, L.D., Cichosz, T.A., and Sass, G.G. 2018. Characterizing the angling and tribal spearing walleye fisheries in the Ceded Territory of Wisconsin, 1990–2015. North Am. J. Fish. Manage. **38**: 1381–1393. doi:10.1002/nafm.10240.

Myers, R.A., Hutchings, J.A., and Barrowmann, N.J. 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecol. Appl. **7**(1): 91–106. doi:10.1890/1051-0761(1997)007[0091:WDFSCT]2.0.CO;2.

Paloheimo, J.E., and Dickie, L.M. 1964. Abundance and fishing success. Fish. Res. Board Canada. pp. 152–163.

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

Pine, W.E., Pollock, K.H., Hightower, J.E., Kwak, T.J., and Rice, J.A. 2003. A review of tagging methods for estimating fish population size and components of mortality. Fisheries, **28**(10): 10–23. doi:10.1577/1548-8446(2003)28[10:AROTMF]2.0.CO;2.

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

R Core Team. 2018. R: a language and environment for statistical computing. Version 3.5.3. R Foundation for Statistical Computing, Vienna, Austria. Available from www.R-project.org.

Roberts, C.M., Hawkins, J.P., and Gell, F.R. 2005. The role of marine reserves in achieving sustainable fisheries. Philos. Trans. R. Soc. B, **360**(1453). doi:10.1098/rstb.2004.1578.

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

Russ, G.R. 2002. Yet another review of marine reserves as reef fishery management tools. *In* Coral reef fishes: dynamics and diversity in a complex system. *Edited by* P.R. Sale. Academic Press, San Diego, Calif. pp. 421–443.

Sadovy de Mitcheson, Y., and Erisman, B.E. 2012. Fishery and biological implications of fishing spawning aggregations, and the social and economic importance of aggregating fishes. *In* Reef Fish Spawning Aggregations: Biology, Research and Management. *Edited by* Y. Sadovy de Mitcheson and B.E. Erisman. Springer, New York. pp. 225–284. doi:10.1007/978-94-007-1980-4.

Sass, G.G., Kitchell, J.F., Carpenter, S.R., Hrabik, T.R., Marburg, A.E., and Turner, M.G. 2006. Fish community and food web responses to a whole-lake removal of coarse woody habitat. Fisheries, **31**(7): 321–330. doi:10.1577/1548-8446(2006)31[321:FCAFWR]2.0.CO;2.

Sass, G.G., Carpenter, S.R., Gaeta, J.W., Kitchell, J.F., and Ahrenstorff, T.D. 2012.

Whole-lake addition of coarse woody habitat: response of fish populations. Aquat. Sci. **74**: 255–266. doi:10.1007/s00027-011-0219-2.

Seekell, D.A. 2011. Recreational freshwater angler success is not significantly different from a random catch model. North Am. J. Fish. Manage. **31**(2): 203–208. doi:10.1080/02755947.2011.572788.

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

Tidd, A., Brouwer, S., and Pilling, G. 2017. Shooting fish in a barrel? Assessing fisher-driven changes in catchability within tropical tuna purse seine fleets. Fish Fish. **18**(5): 808–820. doi:10.1111/faf.12207.

van Poorten, B.T., Walters, C.J., and Ward, H.G.M. 2016. Predicting changes in the catchability coefficient through effort sorting as less skilled fishers exit the fishery during stock declines. Fish. Res. **183**: 379–384. doi:10.1016/j.fishres.2016.06.023.

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

Ward, H.G.M., Askey, P.J., and Post, J.R. 2013. A mechanistic understanding of hyperstability in catch per unit effort and density-dependent catchability in a multistock recreational fishery. Can. J. Fish. Aquat. Sci. **70**: 1542–1550. doi:10.1139/cjfas-2013-0264.

White, G.C., and Burnham, K.P. 1999. Program mark: survival estimation from populations of marked animals. Bird Study, **46**: S120–S139. doi:10.1080/00063659909477239.

Wilde, G.R., Pope, K.L., and Durham, B.W. 2003. Lure-size restrictions in recreational fisheries. Fisheries, **28**(6): 18–26. doi:10.1577/1548-8446(2003)28[18:LRIRF]2.0.CO;2.