Coarse woody habitat as an aggregating structure: hyperstability in a largemouth bass (*Micropterus salmoides*) population

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Abstract

Catch per unit effort (CPUE) is often used as a predictor of population abundance in fisheries management. However, the concept of hyperstability suggests that this may not be an accurate means of assessing fish stocks, as CPUE may remain high even as populations decline. While this has been studied in several open-ocean fisheries, the occurrence of hyperstability in freshwater systems is not as extensively understood. In northern temperate lakes, coarse woody habitat (CWH) is thought to act as an aggregating structure for largemouth bass, causing them to be disproportionately distributed in areas with an abundance of CWH. This study specifically sought to evaluate the ability of CWH to act as an aggregating structure promoting hyperstability. This was accomplished by repeatedly angling on areas of CWH after continuously lowering the population density of largemouth bass in the East basin of Long Lake. Regression analysis revealed a non-significant relationship between catchability and population density, indicating the absence of hyperstability in the East Long basin.

Keywords: coarse woody habitat (CWH), catch per unit effort (CPUE), catchability, largemouth bass, hyperstability, population density, Long Lake

Introduction

In recreational fisheries, catch per unit effort (CPUE) is often used to monitor stock abundance. It is often assumed that CPUE is directly proportional to population size, and can therefore serve as an indicator of overall stock abundance and the general stability of fish populations (Hilborn and Walters 1992; Hangsleben et al. 2013). This linear relationship is most commonly observed in hook-and-line fishing, or angling, and some forms of net fishing. However, this assumption is dependent on randomized fishing effort (Hilborn and Walters 1992). In recreational fisheries, where angling is the primary form of fishing, fishing effort can become concentrated in select areas where CPUE is known to be high (Ward et al. 2013).

The concept of hyperstability suggests that CPUE may not be an accurate reflection of population size and should be used with caution. Hyperstability predicts that CPUE will remain high even as the overall fish population declines. CPUE is defined as the total catch (C) per unit effort (E), which is equivalent to the catchability (q) multiplied by the overall abundance of a population (N) (Hangsleben et al 2013):

$$CPUE = C / E = q \times N \tag{1}$$

As this relationship shows, the ability of CPUE to serve as an indicator of abundance is dependent on maintaining a constant catchability coefficient. Under conditions of hyperstability, catchability increases to compensate for decreasing abundance. Therefore, catchability can be used as a response variable to detect the occurrence of hyperstability. When rearranged algebraically, Equation 1 can be expressed in terms of catchability (Hangsleben et al. 2013):

$$q = \frac{(C / N)}{E} \tag{2}$$

Hyperstability has been observed in several studies of open-ocean fisheries (Rose and Kulka 1999; Mulazzani et al. 2014; Erisman et al. 2011). One of the most notable examples of hyperstability occurred in the commercial fisheries of northern cod (*Gadus morhua*), where overall stock abundance declined fivefold as CPUE increased on the local level (Rose and Kulka 1999). Hyperstability is thought to have various behavioral causes, including spawning and migratory behavior, that result in seasonal changes in the spatial distributions of fish populations (Rose and Kulka 1999; Erisman et al. 2011). However, the occurrence of hyperstability in freshwater systems has been less extensively studied.

In northern temperate lakes, aggregating structures such as coarse woody habitat (CWH) are thought to produce hyperstability by causing high densities of fish to congregate in areas of preferred habitat. The aggregating potential of CWH can be inferred from a study by Rogers and Bergersen (1999) that installed artificial structures in lakes lacking large habitat structures and topographically complex beds, which showed the ability of tree-like structures to cause the aggregation of adult largemouth bass. These tree-like structures accounted for 2/3 of the bass caught during the study period, but only made up 40% of the installed structures (Rogers and Bergersen 1999). CWH is defined as partially or fully submerged trees, logs, and branches originating from riparian trees along the shores of lakes and streams (Czarnecka 2015). This aggregating behavior can result in consistently high catch rates despite significant stock size reduction, as fish from the remaining population continue to move into the areas around aggregating structures to take the places of those removed by angling (Ward et al. 2013). This is important because CWH is not always accounted for in management plans for recreational fisheries. If CWH does serve as an aggregating structure and it is not taken into consideration, hyperstability may mask population decline and lead to overfishing, eventually resulting in the collapse of entire fish populations (Erisman et al. 2011; Ward et al. 2013).

CWH is specifically predicted to act as an aggregating structure for largemouth bass (*Micropterus salmoides*), a popular sport-fishing species. Due to its status as preferred habitat, the abundance of CWH has been shown to influence their spatial distribution, home range sizes, and feeding behavior (Ahrenstorff et al. 2009, Sass et al. 2006). In areas rich with CWH, largemouth bass were found to spend more time in the shallow regions of the littoral zone and to have smaller, less expansive home ranges. In areas lacking abundant CWH, bass spent less time in the littoral zone and exhibited greater range of movement (Ahrenstorff et al. 2009). Largemouth bass are a piscivorous species, meaning they prey on other fish. CWH likely aggregates largemouth bass because it serves as a refuge to prey species such as yellow perch (*Perca flavescens*) and bluegill (*Lepomis macrochirus*), resulting in more frequent predator-prey interactions at the edge of the littoral zone (Sass et al. 2006). After the whole-lake removal of

CWH, Sass et al. (2006) showed that largemouth bass began to rely heavily on terrestrial prey to supplement their diets, with only 14% of their diet consisting of perch in comparison to 81% of their diet in the presence of CWH. Furthermore, CWH is the preferred spawning substrate for largemouth bass, which create nests under or near areas of abundant CWH (Sass 2009; Lawson et al. 2011). This is important to making informed fisheries management and restoration decisions, as lakeshore development is known to reduce the recruitment of new, structurally complex CWH in the littoral zone of lakes (Lawson et al. 2011). Although hyperstability can have negative implications by masking population decline, it can also be used to enhance angling in recreational catch-and-release fisheries.

This study specifically aimed to determine the ability of CWH to act as an aggregating structure that promotes hyperstability. This was accomplished by focusing angling efforts on areas of CWH while continuously reducing the population density of largemouth bass in the east basin of a northern temperate lake. We hypothesized that CWH would serve as an aggregating structure, causing catchability to increase and CPUE to remain constant as the population density of largemouth bass in the east basin decreased, indicating the occurrence of hyperstability. Furthermore, we predicted that catchability would remain constant in the west basin, where population density was kept constant.

Materials and Methods

Study Site

This study was carried out in Long Lake, a northern temperate lake at the University of Notre Dame Environmental Research Center (UNDERC) in Gogebic County, Michigan. The surrounding forest is largely dominated by conifers, which line the shore and contribute to the abundance of CWH in the lake's littoral zone. Long Lake is a restricted access lake used for non-commercial purposes, including research and recreational angling. This is ideal for assessing hyperstability due to aggregating structures in recreational fisheries, which is relatively undocumented. The shape and bathymetry of Long Lake allows for its easy division into a treatment and reference basin. The two basins are connected by a narrow, shallow stretch of water, which facilitated the permanent division of Long Lake by a curtain (Figure 1). The unique physical characteristics of Long Lake allowed for the experimental manipulation of the largemouth bass population on one side of the lake while keeping the other side as an unaltered control. For this study, East Long served as the treatment basin and West Long served as the reference basin.

Timeline

To test for the occurrence of hyperstability, the population density of largemouth bass in East Long was continuously reduced every four days over of a 16-day period, allowing for a total of four manipulations of population density. Meanwhile, the population density of West Long was kept constant throughout the entire study. The 16-day study period occurred during the summer of 2017, from July 4th to July 19th.

Population Density Manipulations

Prior to any manipulations of population density, baseline catch rate data was obtained by angling in both the East Long and West Long basins. In West Long, all bass were released after being scanned to check for the presence of a Passive Integrated Transponder (PIT) tag. Both East Long and West Long have a subset of individuals with PIT tags as part of a long-term monitoring study. By only using fish with PIT tags, catchability could be more accurately calculated, as the exact number of tagged fish was known for each side of the lake. East Long had a subset of 356 tagged individuals, while West Long had 461. In East Long, all tagged fish caught during the angling period were retained and moved into the bass holding pen as part of the population reduction for the following manipulation. These techniques remained the same during each subsequent angling period.

After the baseline catch rate data was collected, the population density of East Long was reduced for the first manipulation. This involved the removal of 29 tagged largemouth bass from the main basin into the holding pen. Three days were allowed to pass before catch rate data was collected again at a given population density, giving the system time to recover after being heavily fished. The three-day recovery period was implemented to reduce the possibility of biased catch rate data, as bass may be less likely to bite if they were caught the day before and are repeatedly subjected to intense angling (Askey et al. 2006).

The following numbers of individuals were kept in the bass holding pen during each manipulation: 29, 54, 70, and 85. Only tagged bass were moved into the holding pen to lower the population density of East Long since catch rates were calculated in terms of tagged fish caught per hour of angling. Up to 85 of the 356 tagged individuals in East Long were removed over the course of this study, which constituted a maximum reduction of about 24 percent in the total tagged population of largemouth bass in the East Long basin. The population in West Long remained constant at 461 tagged individuals for the duration of the study.

Bass Holding Pen

All largemouth bass removed from East Long during the reduction of population density were placed in a small bay off East Long. The mouth of the bay was blocked off by a 50-meter-long net to create a holding pen (Figure 1). The bottom of the net was lined with chain and the top was fixed with floats to keep the net upright and lying flat across the bottom of the bay.

Data Collection

Three days after each manipulation, angling occurred on both East and West Long. Angling efforts in both basins were focused on pre-marked areas of shoreline. In each basin, seven sections of shoreline were marked with flagging tape. Each section of shoreline was 15 meters long, with all seven sections being evenly spaced around the shoreline of each basin (Figure 1). Due to its larger size, each 15-meter section of shoreline was spaced 135 meters apart on West Long and only 90 meters apart on East Long. Because the placement of each section was not dependent on the amount of CWH, each section had variable amounts of CWH. A standard angling period of 2.5 hours per basin was chosen for the duration of the study, allowing for about 20 minutes of angling per section of shoreline. Standard fishing rods were used, with plastic YUM Dinger® worms as bait.

Data Analysis

Due to the difficult nature of population estimates in fisheries, only tagged fish were used in this study. Because the exact number of tagged fish was known for both study populations, there was less uncertainty in catchability calculations due to inaccurate fish abundances. And to account for the different sizes of the two lake basins used in this study, surface area was incorporated into the catchability equation. With these study-specific modifications, catchability (q_i) was ultimately defined as:

$$q_i = \frac{(C_i \text{ x } A_i)}{(N_i \text{ x } E_i)} \quad (3)$$

where C_i = the number of tagged fish caught, A_i = the surface area of the basin being angled on, N_i = the total number of tagged fish available in each basin, and E_i = total angling effort in hours.

On the data from East Long, two least squares regressions were performed to test for significance in the relationship between the population density of tagged bass and catchability during the 16-day study period. Two more least squares regressions were run to include two extra sampling events prior to the 16-day study period, testing the relationship between sampling event and catchability. Due to issues with the net used to block off the bay, a majority of fish were escaping from the bass holding pen and the population density of East Long was not confidently known for the two sampling events prior to the official study period. In addition, two least squares regressions were run to test the relationship between sampling event and catchability on West Long; one on the data from the 16-day study period (after the net was fixed), and one including the two extra sampling events prior to the net being fixed.

Finally, four Analysis of Covariance (ANCOVA) tests were performed to test for a significant difference between the slopes of the regression lines relating catchability to sampling event for East and West Long, using basin (East or West) as a covariate impacting catchability. Like the least squares regressions, the ANCOVA tests were performed with and without the two extra data points prior to the 16-day study period. All statistical analyses were performed in R (R Core Team 2016).

Results

The least squares regression relating the population density of largemouth bass in East Long to catchability was not significant (R^2 = 0.4354, df = 3, p-value = 0.2256), indicating that there was no inverse linear relationship as predicted (Figure 2). When the outlier point (total pop.

= 286, q = 216.38) was excluded, the regression was still not significant (R^2 = 0.7613, df = 2, p-value = 0.1275). However, excluding the outlier resulted in a trend towards a significant, direct linear relationship and explained a greater degree of variance. The slightly negative slope of the regression line can therefore be predominately attributed to natural variation in catchability. Regression analysis on the data that included the two sampling events of uncertain population density on East Long also indicated a non-significant relationship (R^2 = 0.2926, df= 5, p-value = 0.2099) between sampling event and catchability, assuming that population density decreased with each sampling event (Figure 3). When the same outlier point (sampling event = 5, q = 216.38) was excluded, the relationship remained non-significant. However, excluding the outlier again resulted in a trend towards a direct linear relationship between sampling event and catchability while also explaining a greater degree of variance (R^2 = 0.457, df = 4, p-value = 0.1405).

Regression analysis on the data from West Long led us to conclude that there was not a significant relationship between sampling event and catchability (R^2 = 0.03144, df = 3, p-value = 0.7754), assuming that population density was constant at each sampling event (Figure 4). This implies that the slope of the regression line was not significantly different from a zero slope, which supported our prediction that catchability would remain constant on West Long throughout the course of this study. However, only 3.144% of the variance is explained by the regression line. Since problems with fish escaping from the bass holding pen on East Long did not affect the population density of West Long, a regression was run to include the two sampling events prior to the official 16-day study period. As predicted, the relationship between catchability and sampling event was still not significant (R^2 = 0.2534, df = 5, p-value = 0.2495), further supporting the prediction of constant catchability on West Long. (Figure 5)

An ANCOVA test run on the pooled data from the 16-day study period revealed that there was no significant difference between East Long and West Long in catchability over sampling events, assuming that time progressed with each sampling event (p-value = 0.3775; Table 1). Sampling event was found to have no significant effect on catchability (p-value = 0.6816), however, a significant difference in catchability between East and West Long (p-value = 0.0049) was observed (Table 1). When the outlier point from East Long (sampling event = 5, q = 216.38) was excluded, a non-significant difference still existed between East Long and West Long in catchability over sampling events (p = 0.3461; Table 1). Again, sampling event was found to have no significant effect on catchability (p-value = 0.5454), and a significant difference in catchability between East and West Long (p-value = 0.0052) was still observed (Table 1).

When the two sampling events prior to fixing the net and starting the official 16-day study period were included in the pooled data, ANCOVA tests generated the same patterns of significance in each type of interaction. When the same outlier point was retained in the data set, there was no significant difference between East Long and West Long in catchability over sampling events, assuming that time progressed with each sampling event (p-value = 0.0851; Table 1). As in the previous tests, sampling event was found to have no significant effect on catchability (p-value = 0.8854) while a significant difference in catchability was observed between East and West Long (p-value = 0.0003; Table 1). When the outlier point from East Long (sampling event = 5, q = 216.38) was excluded, a non-significant difference still existed between East Long and West Long in catchability over sampling events (p = 0.0647; Table 1). However, including the extra sampling events and removing the outlier revealed a trend towards significance in the difference in catchability over sampling events between East and West Long.

Again, sampling event was found to have no significant effect on catchability (p-value = 0.4047), and a significant difference in catchability between East and West Long (p-value = 0.0006) was still observed (Table 1).

Discussion

The absence of a significant, inverse relationship between population density and catchability (Figure 2), as well as sampling event and catchability (Figure 3), implies that hyperstability did not occur as the population density was reduced in East Long Lake. From the ANCOVA tests that were run, we determined that there was not a significant difference in catchability over sampling events between East and West Long. This means that the slope of the regression line relating catchability to sampling event on East Long (Figure 3) was not statistically different from the regression line relating these same variables on West Long (Figure 5). This difference was even more pronounced when the catchability of East Long with declining population density (Figure 2) was compared to the catchability off West Long over sampling events (Figure 4). A significant difference between these regression lines would have implied that hyperstability was occurring, as the catchability on East Long was predicted to increase with each sampling event while catchability on West Long was predicted to stay constant. Therefore, the lack of significance further supported the conclusion that hyperstability was not occurring in East Long Lake. This could mean that CWH is not serving as an aggregating structure for largemouth bass as we predicted.

A possible explanation for the absence of hyperstability could lie in the physical characteristics of the CWH in Long Lake. In a study that quantified CWH in a northern temperate lake, Newbrey et al. (2005) found that largemouth bass showed a preference for CWH with higher structural complexity values. Complexity values were assigned by scoring the level of branching on each log, where logs with more branching, especially fine branching, received higher complexity values. While newly fallen trees tend to exhibit high levels of branching, the natural breakdown of wood in water reduces branching over time (Czarnecka 2015). From observation, some of the most prominent areas of CWH in Long Lake have little to no branching. If largemouth bass really favor structural complexity in CWH, a lack of branching may affect the success of CWH as an aggregating structure.

Another reason for the absence of hyperstability may be the time between manipulations of population density and angling on CWH. Three days may not have been enough time for new fish to occupy the newly vacated areas around CWH. A study that tracked the movement of largemouth bass in two Florida lakes found that bass home ranges varied in size from 0.01 to 5.16 hectares, with 36% of a tagged bass population spending up to 25% of their time over 10 meters away from shore (Mesing and Wicker 1986). Another movement study found that largemouth bass made up to 7 day excursions away from their home range before returning (Winter 1977). Given these parameters, 3 days may not have been enough time to allow bass to aggregate around newly available CWH.

The slightly negative slopes of the regression lines (Figures 2 and 3) suggest a weakly declining catchability with each progressive sampling event on East Long, assuming that population density declined with each progressive sampling event. Because regression analyses revealed that neither of these relationships were significant, the observable decline in catchability was likely due, in part, to natural variation. From this we can conclude that CPUE can tentatively be used as an indicator of abundance for largemouth bass in Long Lake. However, it is important to understand the factors possibly affecting catchability since the utility and accuracy of CPUE as an estimate of abundance is dependent on a constant catchability coefficient (Hangsleben et al. 2013).

The observable variation in results can be interpreted in a number of ways. One possible explanation for the slight decline in catchability is varying levels of susceptibility to angling in the largemouth bass population of East Long. Originally proposed by Martin (1958), fish populations are hypothesized to contain a subset of fish that are highly susceptible to angling (Askey et al. 2006). Vulnerability to angling is thought to be a heritable trait in largemouth bass. In a selective breeding experiment performed on largemouth bass, high vulnerability was shown to correlate with more aggressive behavior and greater reproductive success (Philip et al. 2015). When these fish are removed due to harvest, a higher proportion of less susceptible fish are left, causing a reduction in catchability (Askey et al. 2006). In Long Lake, where angling has occurred for several years, it is reasonable to suspect that a subset of more vulnerable bass exists. As more bass were removed from East Long with each subsequent manipulation, a natural decline in catchability may have occurred.

This can also manifest as acquired hook avoidance. A study by Askey at al. (2006) suggested that, in catch-and-release fisheries, catchability may still decline even though the highly vulnerable fish are not being removed. Within 7-10 days of implementing daily angling efforts, they observed a dramatic drop in catch rates: from 16 tagged fish/boat day to 5 tagged fish/boat day. This was attributed to learning of the fly fishing patterns used in the study by the highly susceptible individuals. East Long was fished repeatedly before the 16-day study period, during which there were frequent incidences where fish that had escaped from the holding pen were recaptured multiple times. By the time the net blocking off the bay was fixed and the final 16-day study had begun, the more vulnerable population of bass may have become acclimated to the plastic YUM Dinger® worm that was being used as sole type of bait for almost 8 weeks of intensive angling. This same decline in catchability was not observed in West Long, seemingly discounting the possibility of acquired hook avoidance. However, West Long was not fished as heavily as East Long prior to the 16-day study period. The holding pen was filled with largemouth bass from East Long three times before the net was successfully fixed to prevent fish from escaping. During these extra angling periods in which fish were obtained to refill the holding pen, corresponding angling periods did not occur on West Long. As a result, the largemouth bass population of East Long was subjected to greater angling pressure before the 16-day study period, which may have facilitated acquired hook avoidance in the East Long, but not West Long, population.

As expected, there was not a significant linear relationship between catchability and sampling event when population density was kept constant in West Long. (Figures 4 and 5). This suggested that catchability remained relatively constant over the course of this study. The slightly positive slope observable in the regression line of Figure 5 can be mainly attributed to natural fluctuations in catchability. This slight increase in catchability over time was likely due, in part, to the development of angler experience. Prior to this study, I did not have much personal experience with fishing of any type. Due to the nature of this study, I fished anywhere from 5 to 8 hours a week, and quickly improved in casting technique and ability to land fish.

CPUE data has been a disputable part of both freshwater and marine fisheries management plans for decades. However, its viability as an indicator of overall stock abundance has been called into question by the concept of hyperstability, which predicts that CPUE will remain high even as fish populations decrease. Although this study did not find CWH to be an aggregating structure for largemouth bass, more repetition is necessary to definitively rule it out as a possible cause of hyperstability. Allowing for greater periods of time between population density manipulations would ensure that new fish have enough time to move into the areas now open due to the removal of the largemouth bass that previously occupied those areas. Regardless of the nature of these results, there are several important implications for sustainable fisheries management. By discounting CWH as an aggregating structure, CPUE can be used with greater confidence to make decisions about harvest limits and catch-and-release regulations based on abundance and stability of largemouth bass populations.

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Figures and Tables

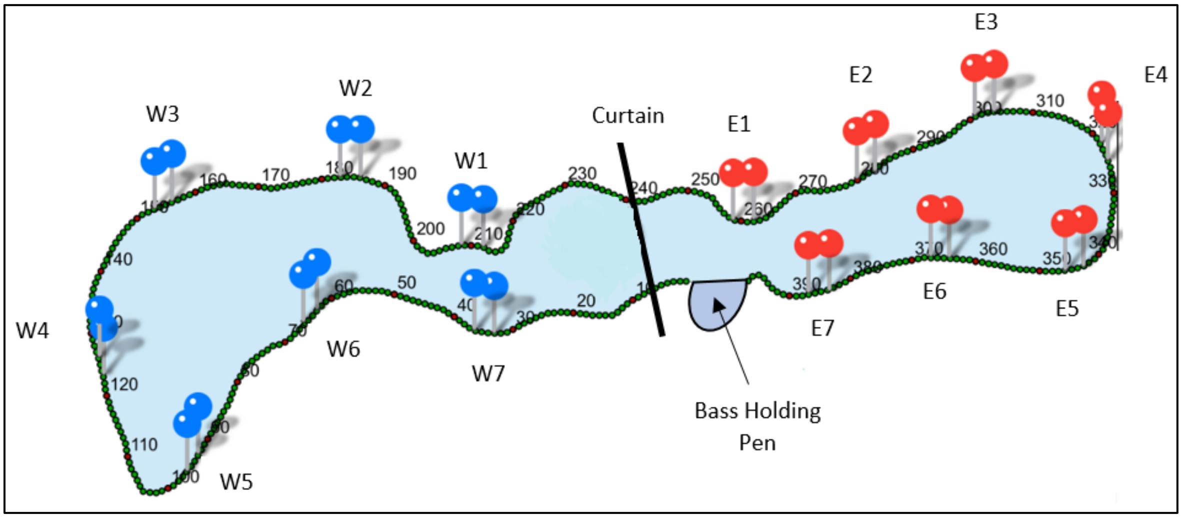

Figure 1. The above figure presents the experimental setup for this study. The division of Long Lake into its West (reference) basin and East (treatment) basin is noted by the thick black line. The location of this study's bass holding pen is indicated by the arrow. The sections of shoreline where angling was focused in each basin are denoted by paired pins.

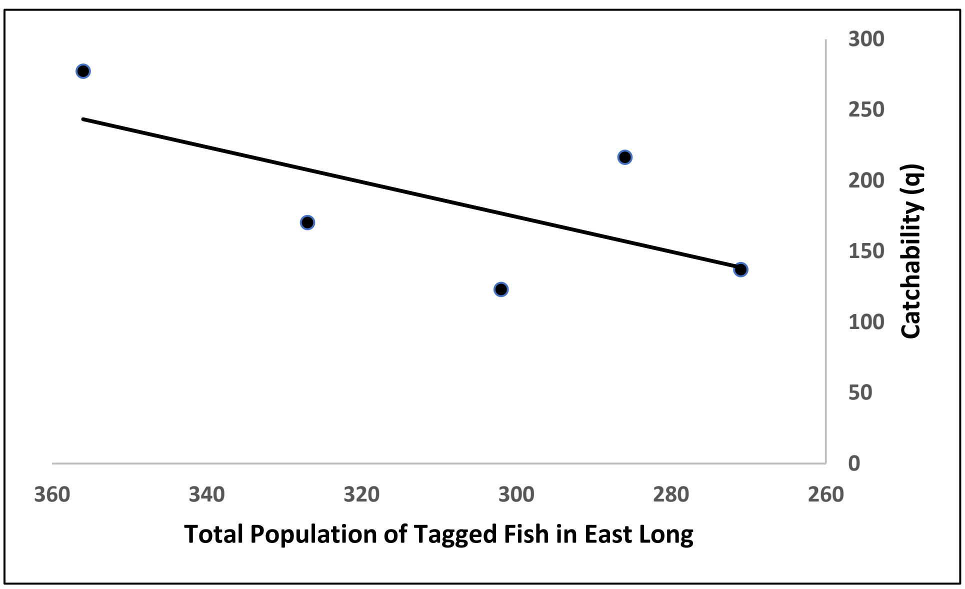

Figure 2. Relationship between catchability and population density of tagged fish on East Long. Least squares regression did not detect a significant linear relationship between declining population density of largemouth bass and catchability, indicating that hyperstability was not occurring in East Long (R^2 = 0.4354, df = 3, p-value = 0.2256).

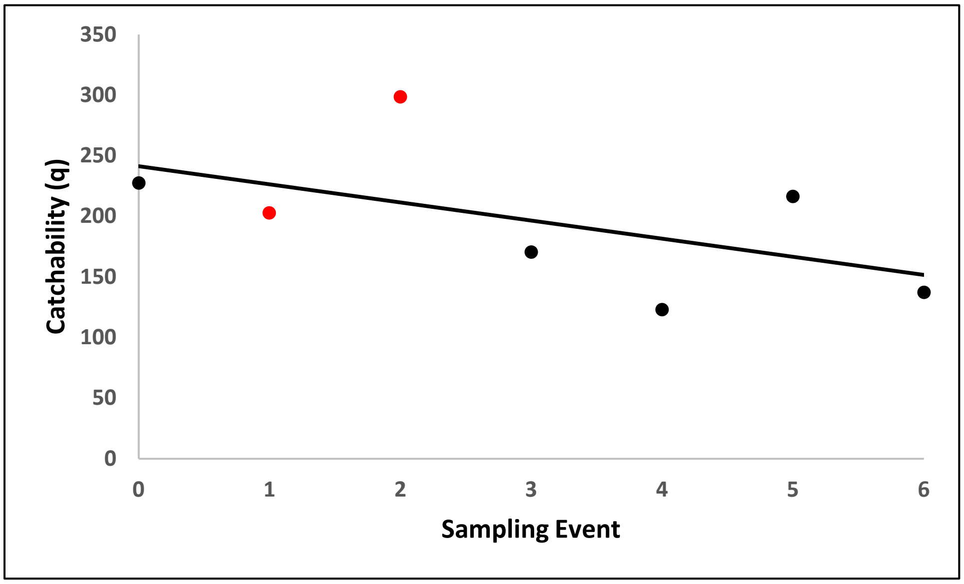

Figure 3. Relationship between catchability and sampling event on East Long. Least squares regression did not detect a significant linear relationship between sampling event and catchability when the two sampling events at uncertain population density (in red) were included, further indicating that hyperstability was not occurring in East Long (R^2 = 0.2926, df= 5, p-value = 0.2099).

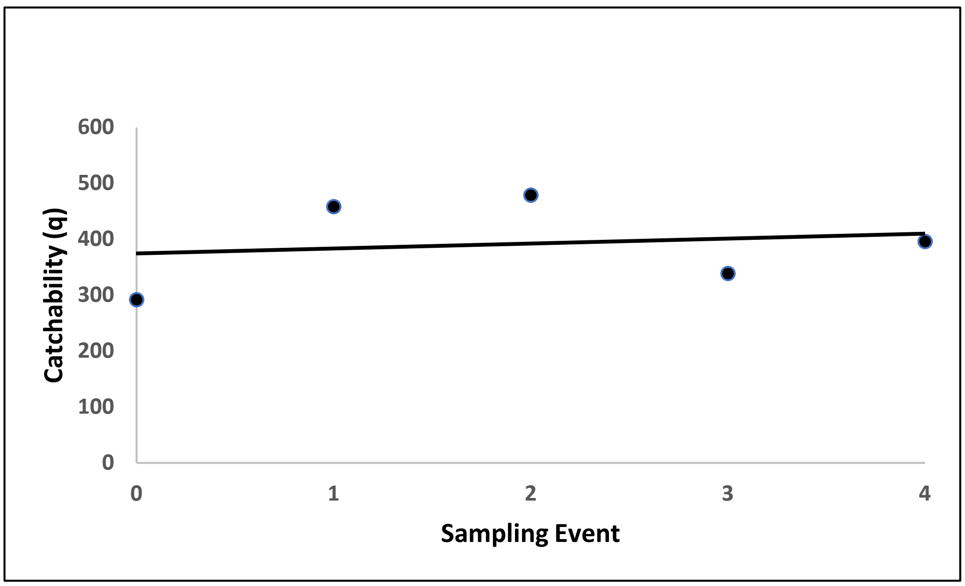

Figure 4. Relationship between catchability and sampling event on West Long. Least squares regression did not detect a significant linear relationship between sampling event and catchability, indicating that catchability remained relatively constant over the course of the study (R^2 = 0.03144, df = 3, p-value = 0.7754).

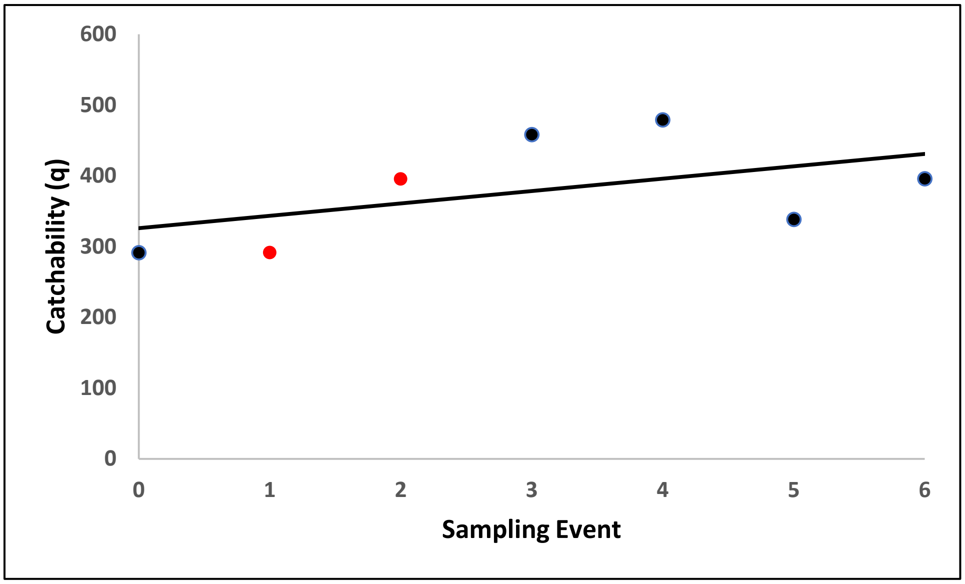

Figure 5. Relationship between catchability and sampling event on West Long. Including the two sampling events prior to the 16-day study period. Least squares regression did not detect a significant linear relationship between sampling event and catchability when the two sampling events prior to the 16-day study period (in red) were included, further indicating that catchability remained relatively constant over time (R^2 = 0.2534, df = 5, p-value = 0.2495).

Table 1. Results of ANCOVA tests. Four Analysis of Covariance (ANCOVA) tests were run on the pooled catchability data from East and West Long. These were performed to test for a significant difference between the slopes of the regression lines relating catchability to sampling event for East and West Long, using basin (East or West) as a covariate impacting catchability.

	Degrees of Freedom	F- value	p- value
Interaction type	**16-day study period**		
Sampling Event and Catchability	1	0.1857	0.6816
Basin and Catchability	1	18.7417	0.0049
Sampling Event and Catchability by Basin	1	0.9078	0.3775
Interaction type	**16-day study period- no outlier**		
Sampling Event and Catchability	1	0.4203	0.5454
Basin and Catchability	1	22.2840	0.0052
Sampling Event and Catchability by Basin	1	1.0812	0.3461
Interaction type	**Including data points prior to fixing net**		
Sampling Event and Catchability	1	0.0219	0.8854
Basin and Catchability	1	28.7317	0.0003
Sampling Event and Catchability by Basin	1	3.6511	0.0851
Interaction Type	**Including data points prior to fixing net- no outlier**		
Sampling Event and Catchability	1	0.7642	0.4047
Basin and Catchability	1	26.5728	0.0006
Sampling Event and Catchability by Basin	1	4.4264	0.0647