

RESEARCH ARTICLE

Synchrony – An emergent property of recreational fisheries

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Abstract

1. Recreational fisheries are traditionally managed at local scales, but more effective management could be achieved using a cross-scale approach. To do this, we must first understand how local processes scale up to influence landscape patterns between anglers and resources. We highlight how population-based synchrony methods, used in conjunction with a complex-adaptive-systems framework, can reveal emergent spatial properties within social-ecological systems such as recreational fisheries.
2. Herein, we quantified the level of spatial synchrony in angler behaviour, defined the relationship between angler synchrony and distance among waterbodies, and highlighted social-ecological attributes contributing to these patterns. We leveraged a 111 waterbody-year (34 waterbodies, 5-year collection period) recreational fisheries dataset from Nebraska, USA to address these objectives.
3. Intra-annual patterns in angler behaviour were moderately synchronous across large spatial scales and predominately unrelated to distance among waterbodies. Large-scale synchronous patterns in angler behaviour emerged from local-scale interactions between angler heterogeneity and waterbody diversity.
4. Spatial synchrony in angler behaviour is an emergent property that resulted from local-level processes that scaled up to form large-scale patterns. We posit that angler utility in combination with waterbodies sharing these desired utility components caused spatial synchrony among anglers with similar preferences or specializations. The level of spatial synchrony in angler behaviour will therefore depend on the degree of angler heterogeneity and waterbody diversity on the landscape, with high or low levels of both leading to low and high levels of spatial synchrony respectively.
5. *Synthesis and applications.* Synchrony-based methods proved useful for unveiling an emergent property in recreational fisheries that is beneficial for effective cross-scale management. It may not be appropriate to extrapolate information and apply uniform management actions among local waterbodies because angler behaviour was not synchronous at small scales. Rather, anglers respond uniquely to waterbody diversity and therefore substitute waterbodies may be dispersed throughout the landscape. Creating boat access, for example could yield unintended consequences for a particular angler group and cause local and regional shifts in angler behaviour. Evaluating appropriate management options will

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require a cross-scale monitoring approach that captures angler heterogeneity and waterbody diversity at multiple scales.

Keywords

complex adaptive systems, cross-scale interactions, emergent properties, fisheries, social-ecological systems, spatial and temporal dynamics, synchrony, waterbody and angler diversity

1 | INTRODUCTION

Major advancements have been made in our understanding of population dynamics by evaluating spatial population synchrony (Bjørnstad, Ims, & Lambin, 1999). Spatial population synchrony or spatial covariation describes how populations fluctuate through time and space (Bjørnstad et al., 1999; Liebhold, Koenig, & Bjørnstad, 2004). Populations may fluctuate simultaneously across a large geographic area or may fluctuate independently within a localized area (Ranta, Kaitala, Lindstrom, & Linden, 1995). Identifying the level of population synchrony and the relationship of these patterns to spatial distance can afford insights on the cross-scale mechanisms driving population dynamics (i.e. local to metapopulation scale). For example, snowshoe hare *Lepus americanus* and Canada lynx *Lynx canadensis* populations exhibit synchrony throughout their range, corresponding to interactions between highly mobile predators and local food supplies (Krebs, Boonstra, Boutin, & Sinclair, 2001). This level of insight was only gained by examining multiple populations through space and time, yielding further appreciation for local and widespread mechanisms that act on populations (Liebhold et al., 2004).

Undoubtedly, recognizing and understanding population synchrony has made large contributions to ecology, but can we extend this concept to social-ecological systems within a complex-adaptive-systems framework? Particularly, understanding synchrony of social behaviour and social dynamics across spatial and temporal scales, in relation to ecological components, could be of tremendous value. Understanding how patterns change through time and space is a hallmark of methods used to understand population synchrony (Bjørnstad et al., 1999). Social-ecological systems represent complex adaptive systems (Levin et al., 2013); these systems are exemplified by higher level patterns that result from localized processes (Levin, 1998; Rammel, Stagl, & Wilfing, 2007). Recreational fisheries demonstrate characteristic features of both social-ecological systems and complex adaptive systems (Arlinghaus et al., 2017). The management of recreational fisheries is challenging because complex feedbacks between people and the natural environment (Ward et al., 2016) are often inextricably linked through space and time (Post & Parkinson, 2012). It is therefore essential to describe the relationship between angler behaviour at local scales and how this translates to larger spatial scales (Ward et al., 2016). Social-ecological systems, such as recreational fisheries, are best managed by taking into account these cross-scale interactions (Arlinghaus

et al., 2017; Gunderson, 2001; Walker, Holling, Carpenter, & Kinzig, 2004). Developing a broad-scale or landscape approach to manage recreational fisheries requires insight from multiple spatial and temporal scales (Lester, Marshall, Armstrong, Dunlop, & Ritchie, 2003). Local-level interactions and management efforts may form unique emergent properties at larger spatial scales that will change the way we view and manage recreational fisheries (Arlinghaus et al., 2017).

Local-level utility-based choice models used in conjunction with a complex-adaptive-systems framework offer insight as to how angler behaviour may scale up to the regional level (Arlinghaus et al., 2017; Hunt, Arlinghaus, Lester, & Kushneriuk, 2011; Matsumura, Beardmore, Haider, Dieckmann, & Arlinghaus, 2017). Total utility describes the social welfare or benefits that a recreational fishery offers to society (Dorow, Beardmore, Haider, & Arlinghaus, 2010; Malvestuto & Hudgins, 1996). Site choice models assume an angler will select a fishing site that provides the greatest utility, often derived from specific waterbody attributes and the cost of accessing that site (Hunt, 2005). Specifically, fishing costs, fishing quality, environmental quality, facility development, encounters with other anglers, and regulations have been related to angler site choice (Hunt, 2005; Scrogin, Boyle, Parsons, & Plantinga, 2004). Angler specialization, or the range in interest and skill level among anglers, should also be considered in this context (Bryan, 1977; Ditton, Loomis, & Choi, 1992). Therefore, the degree of angler heterogeneity and waterbody diversity throughout a landscape will likely influence angler behaviour at a larger spatial scale (Arlinghaus et al., 2017; Hunt et al., 2011; Matsumura et al., 2017).

To date, few studies have attempted to link local-level interactions to large-scale emergent properties within recreational fisheries (Hunt et al., 2011). Based on a latent class and utility model, Matsumura et al. (2017) predicted that emergent properties within recreational fisheries should occur as a function of local-level processes. Specifically, local-level interactions among residential patterns (i.e. urban or rural), the angler population residing in these areas, and waterbody diversity or resource quality should predict these emergent properties (Matsumura et al., 2017). Therefore, regional synchrony in angler behaviour could be an important emergent property of recreational fisheries, stemming from these local-level interactions among anglers and ecological resources. The level of regional synchrony may depend on the proximity of anglers to these waterbodies, leading to localized synchrony but not widespread synchrony. For example, waterbodies within urban centres may attract anglers with similar motivations and preferences,

whereas waterbodies positioned more distantly may attract a different set of anglers (Arlinghaus & Mehner, 2004) yielding strong local synchrony in angler behaviour that dissipates across the landscape. The same pattern could emerge from a set of similar waterbodies (i.e. attracting similar anglers) that are in close proximity but are ecologically much different than outlying waterbodies.

Herein, we use population synchrony methods within a complex-adaptive-systems framework to understand angler behaviour in a regional recreational fishery. We leveraged a 111 waterbody-year (34 waterbodies, 5-year collection period) recreational fisheries dataset from Nebraska, USA to address our objectives. Specifically, we evaluate (a) the level of synchrony in angler behaviour by measuring angling effort (hours spent fishing) across a network of waterbodies, (b) how synchrony in angler behaviour is related to distance among waterbodies and (c) which social-ecological attributes explain patterns of synchrony in angler behaviour. This insight should provide cross-scale direction for managing social-ecological systems such as recreational fisheries.

2 | MATERIALS AND METHODS

2.1 | Study sites

Angler behaviour and characteristics were collected at 34 Nebraska, USA waterbodies during 2009–2013 from April to October, resulting in 111 waterbody-years (Table S1 in Appendix S1). Waterbodies were diverse, ranging from large reservoirs (used for hydropower or irrigation storage) to small groundwater-filled lakes created by sand-pit mining. Distance between waterbodies was also variable with nearly 500 km separating the furthest two waterbodies and included a complex of spatially close (<4.5 km) waterbodies (Figure S1 in Appendix S1). Depending on waterbody, anglers could fish for a wide range of species, but primarily targeted black bullhead *Ameiurus melas*, black crappie *Pomoxis nigromaculatus*, bluegill *Lepomis macrochirus*, channel catfish *Ictalurus punctatus*, common carp *Cyprinus carpio*, hybrid striped bass *Morone chrysops* × *Morone saxatilis*, largemouth bass *Micropterus salmoides*, muskellunge *Esox masquinongy*, rainbow trout *Oncorhynchus mykiss*, walleye *Sander vitreus*, white bass *M. chrysops* and white crappie *Pomoxis annularis* (Pope, Chizinski, Wiley, & Martin, 2016).

2.2 | Angler effort and angler interviews

We surveyed anglers onsite at each waterbody using a stratified multistage probability sampling regime (Malvestuto, 1996) to determine sampling days (i.e. subsamples) within each month (i.e. experimental unit). We completed surveys on 10, 12, 20 or 24 days per month at each waterbody, depending on surface area and logistics. Within a month, survey days were stratified into either a week or a weekend day to account for variation in day type (e.g. 14 week days and 6 weekend [including U.S. Federal holiday days] per month). Days were further stratified into a morning (sunrise to 13.30 hr) or afternoon (13.30 hr to sunset) survey period. We conducted instantaneous

counts to estimate daily angler effort and conducted interviews to collect additional social-ecological information (Malvestuto, 1996). Count times were predetermined randomly within a survey period and completed within an hour of starting the count (depending on waterbody surface area and time to survey the entire waterbody).

Absolute monthly angler effort (hours spent fishing) and associated variances were calculated and extrapolated using methods previously outlined (Malvestuto, 1996; Malvestuto, Davies, & Shelton, 1978; Pierce & Bindman, 1994; Pollock, Hoenig, Jones, Robson, & Greene, 1997; Pollock, Jones, & Brown, 1994). Absolute angler effort for each survey day within a given waterbody was calculated by multiplying the mean angler count by the number of hours in the survey period adjusted by the proportion of the daily period (i.e. 0.5 or half of the total daylight hours). Mean daily effort was calculated by day type (i.e. week and weekend days) for each month, and these two means within each month were weighted by the proportion of day types sampled per month to generate a mean estimate of angler effort for a typical day during the month. The typical daily effort estimate for a month was multiplied by the number of days in that month to obtain a monthly estimate of absolute angler effort for each waterbody.

Anglers were predominately interviewed at boat ramps and by roving the shoreline at access points around the waterbody. Boat angler interviews were mostly complete trips, whereas bank interviews comprised both incomplete and complete trips. All interviews were conducted at the party level where one angler (i.e. the representative of the party) completed the survey. During the interview, clerks identified and counted harvested fish and recorded the number of anglers in the party, time spent fishing, and the numbers and taxa of fish released. Angler catch was the sum of fish harvested and fish released.

Social-ecological characteristics for each waterbody were used to further understand relationships contributing to patterns observed in angler effort. Absolute angler effort was converted to effort density by dividing monthly absolute angler effort by waterbody surface area (i.e. hours spent fishing per ha). Effort density served as a proxy for the intensity of effort each waterbody received (i.e. standardized effort). Party size included the number of anglers that traveled together for the purpose of fishing and is related to social dynamics (Choi, Loomis, & Ditton, 1994; Hunt & Ditton, 1997). Catch rate (number of fish caught per person per hour) was estimated by dividing the total number of fish caught (harvested and released) by the number of anglers within each party and by the time spent fishing as a standard measure of catch rate (Jones, Robson, Lakkis, & Kressel, 1995). Fish stocking was characterized by the number of fish species stocked annually. Angler access was characterized by the number of boat-launch sites at each waterbody. Catch richness described the number of different fish species caught (harvested and released) for each angling party interviewed. Angler type reported the proportion of boat anglers and was estimated by dividing boat angler effort by the total effort (boat and bank angler effort); the composition of angler type (boat vs. bank anglers) was indicative of fishing strategies, and could reflect different skill levels, financial

investment in fishing gear and social aspects (Arlinghaus & Mehner, 2004). Monthly means were calculated for party size, catch rate and catch richness for each waterbody.

2.3 | Data analyses

2.3.1 | Synchrony in angler effort and relation to distance

We quantified and evaluated patterns in angler behaviour by estimating the level of intra-annual synchrony in absolute angler effort among waterbodies. In other words, we assessed the degree of correlation or similarity among a network of waterbodies with respect to changes in angler effort through time. Intra-annual synchrony patterns in angler effort were assessed across waterbodies within each year ($N = 5$ years). Monthly angler effort was transformed ($\ln + 1$) and the mean annual cross-correlation was estimated using the R package “ncf” (see Bjørnstad et al., 1999 for specific details and equations). We used Pearson’s product moment correlation and bootstrapped with resampling 1,000 times to provide confidence intervals around synchrony estimates. We also explored the relationship between synchrony estimates in absolute angler effort and distance using empirical variograms, which allowed us to test if the local synchrony value within each lag distance was different from the regional mean. This technique allowed us to identify local and regional patterns in synchrony. Variograms were constructed using Pearson’s product moment correlation within the R package “synchrony” (Gouhier & Guichard, 2014) whereby statistical significance at each lag distance was assessed via 999 Monte Carlo randomizations (Bjørnstad & Falck, 2001; Bjørnstad et al., 1999; Fortin & Dale, 2005). The number of lag distances evaluated each year was proportional to the number of waterbodies sampled.

2.3.2 | Grouping waterbody-year patterns in angler effort

Intra-annual patterns (April–October) in absolute angler effort were further explored to allow us to group waterbody-years according to similar temporal trends in effort. That is, waterbody-years ($N = 111$) were grouped according to similar patterns in angler effort that reflect putative similarities in social-ecological attributes (Aukema et al., 2006). This approach also facilitated the detection of both spatial (i.e. waterbody) and temporal (i.e. annual) changes in absolute angler effort. For example, an individual waterbody sampled 3 years may exhibit the same intra-annual patterns in effort across all years leading to placement in a single group. Alternatively, an individual waterbody sampled 3 years may exhibit different intra-annual patterns in effort across all years leading to placement in three different groups. Essentially, the degree of similarity in intra-annual angler effort patterns was high within a group and low across groups. We used time-series clustering within the R package “dtwclust” (Sarda-Espinosa, 2016) to explore both partitional (K-means) and hierarchical (dendrogram) method types for selecting the number of clusters

or groups (Hastie, Tibshirani, & Friedman, 2009). Both methods produced the same number of groups, using Ward’s minimum variance as the measure of proximity between groups (Aukema et al., 2006). Thus, we only report the results from the hierarchical method to identify which waterbody-year combinations ($N = 111$) were assigned to each group (hereafter referred to as angler-effort groups). We then compared the amount of absolute effort among the angler-effort groups using a one-way analysis of variance (ANOVA) in the same way social-ecological attributes were compared (further details below).

2.3.3 | Social-ecological attributes of angler-effort groups

Social-ecological attributes were compared across the angler-effort groups identified in the time-series clustering analysis. Specific attribute estimates were calculated for each waterbody-year within each angler-effort group. Attribute estimates were averaged across the 7 months for each waterbody-year. Furthermore, we conservatively averaged each attribute across multiple years for individual waterbodies represented multiple times (i.e. multiple waterbody-years) in a single angler-effort group. For example, an individual waterbody sampled 3 years and subsequently all three waterbody-years placed in a single angler-effort group would result in a single estimate of each attribute within that angler-effort group. Alternatively, an individual waterbody sampled 3 years and subsequently each waterbody-year placed in three different angler-effort groups would result in estimates of each attribute within each of the three angler-effort groups. Attributes for each waterbody-year included effort density, waterbody size, party size, catch rate, boat launches, species stocked, catch richness and the proportion of boat anglers. We compared these social-ecological attributes across angler-effort groups using a one-way multivariate analysis of variance (MANOVA). The MANOVA was followed by performing separate one-way ANOVA’s and Tukey’s HSD tests for each attribute. The relationships among angler-effort groups and associated attributes were also visually assessed using nonmetric multidimensional scaling. An ordination plot was created from attribute data for each angler-effort group with Bray–Curtis distance measure using the R package “vegan” (Oksanen et al., 2011). We fit 95% confidence interval ellipses for each angler-effort group and plotted the direction and strength of each attribute, using the *envfit* function, as a visual representation of the differences among groups. Variables were transformed (\ln or $\ln + 1$), if necessary, to meet statistical assumptions for each respective statistical technique.

3 | RESULTS

3.1 | Synchrony in angler effort and relation to distance

Absolute angler effort was moderately synchronous among waterbodies (5-year cross-correlation mean = 0.58; Figure 1) and this

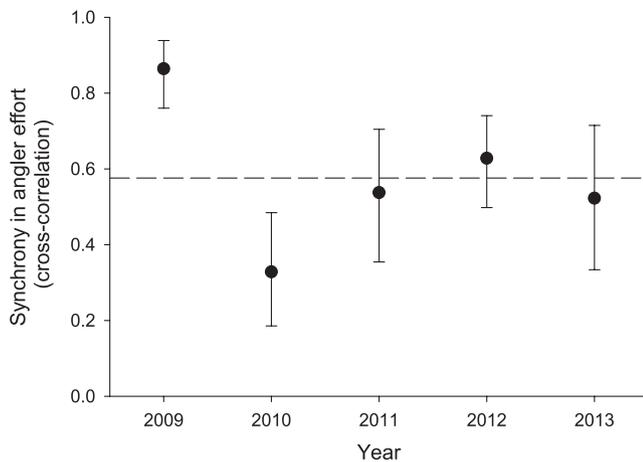


FIGURE 1 Synchrony cross-correlation scores (r ; ± 95 CI) among Nebraska waterbodies, indicating the level of intra-annual synchrony in absolute angler effort from 2009 through 2013. Horizontal dashed line represents mean region-wide synchrony across all years

synchrony varied among years (range in cross-correlation = 0.33–0.86). In general, there was no relationship between distance and the level of synchrony (Figure 2); the only exception was in 2009 where synchrony dissipated after 250 km. Therefore, synchrony in absolute angler effort was generally moderate and widespread (>500 km) across the diversity of waterbodies, demonstrating little evidence for localized synchrony.

3.2 | Grouping waterbody-year patterns in angler effort

Our time-series cluster analysis revealed three distinct intra-annual temporal patterns in absolute angler effort among the waterbody-year combinations (Figure 3). In addition, these three distinct intra-annual temporal patterns differed in the amount of absolute angler effort (ANOVA; $F_{2,37} = 152.3$, $p < 0.001$). The combination of different intra-annual temporal patterns in angler effort and the amount of absolute angler effort received formed high, moderate and low absolute angler-effort groups (hereafter referred to as high, moderate and low angler-effort groups; Figure 3). The intra-annual pattern for the high angler-effort group was characterized by a bell shaped curve, whereas the moderate angler-effort group exhibited somewhat constant effort, and the low angler-effort group exhibited decreasing effort from April to October. Most years for an individual waterbody were represented in a single angler-effort group. However, six individual waterbodies exhibited different intra-annual patterns in angler-effort across years and therefore were represented in two angler-effort groups. All of these waterbodies were represented in adjacent angler-effort groups (i.e. high and moderate or moderate and low) with no individual waterbody represented in both the high and low angler-effort groups (Table S1 in Appendix S1).

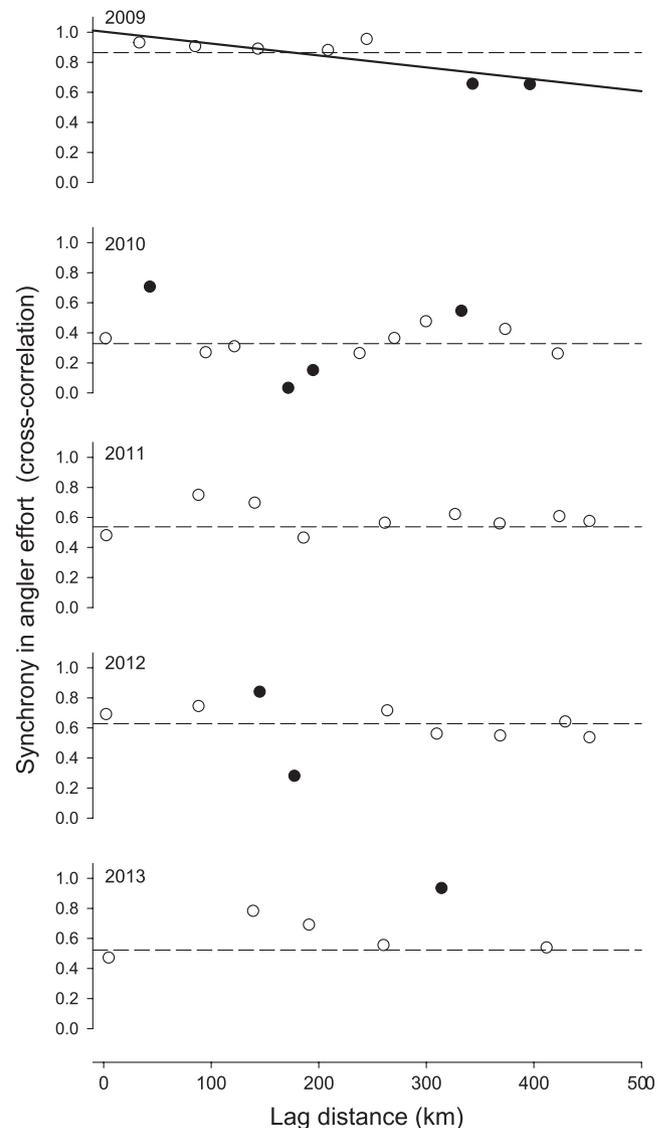


FIGURE 2 Empirical variograms of absolute angler effort among Nebraska waterbodies from 2009 to 2013 (top to bottom). Horizontal dashed line indicates mean region-wide synchrony (Pearson's product moment correlation), filled circles represent statistically significant levels of synchrony from the region-wide level at each lag distance (based on 999 Monte Carlo randomizations and a two-tailed test) and the solid line indicates a significant relationship between synchrony levels across lag distances

3.3 | Social-ecological attributes of angler-effort groups

Social-ecological attributes differed greatly across the angler-effort groups (Table 1). Separate one-way univariate ANOVA's for all attributes were significant across angler-effort groups, which varied in the magnitude and direction among the angler-effort groups (Table 1; Figure 4). The high angler-effort group had the least effort density, consisted of the largest waterbodies, contained the largest party sizes comprised primarily of boat anglers, offered the most boat launches for anglers, received more fish species through stocking

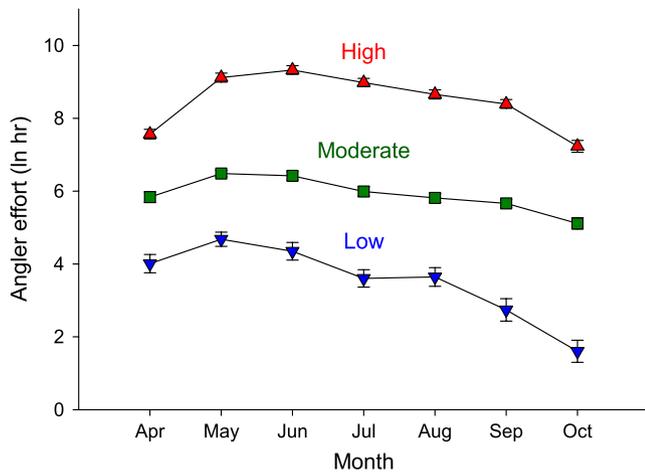


FIGURE 3 Absolute angler effort (ln transformed hours; ±SE) patterns among the three different angler-effort groups (high = ▲, moderate = ■, low = ▼) identified using time-series cluster analysis. The graph depicts effort patterns for each group from April to October

efforts, had the greatest species richness in catch and had the lowest catch rate (Figures 4 and 5). In contrast, the low angler-effort group had an intermediate effort density, consisted of smaller waterbodies, contained smaller party sizes comprised primarily of bank anglers, offered fewer boat launches for anglers, received fewer fish species through stocking efforts, had the lowest species richness in catch and had a higher catch rate (Figures 4 and 5).

4 | DISCUSSION

There is a growing need and recognition for cross-scale management within social-ecological systems and complex adaptive systems,

such as recreational fisheries (Arlinghaus et al., 2017). Our study highlights the utility of synchrony-based methods within a complex-adaptive-systems framework to understand how local-scale processes scale up to create large-scale patterns in a social-ecological system, ultimately revealing important emergent properties such as synchrony in angler behaviour among recreational fisheries. Utility-based angler choice models developed at local scales proved useful for making predictions about large-scale spatial and temporal patterns in angler behaviour (Hunt et al., 2011). The level of regional synchrony appeared to be a function of waterbody attributes and angler preferences, with angler-effort groups sharing similar utility components exhibiting similar patterns in absolute angler effort (Hunt, 2005). Essentially, these angler-effort groups were able to attract similar types of anglers and absorb angler effort on the landscape in a similar temporal fashion. Building on the work of Matsumura et al. (2017), we predict that the level of regional synchrony will depend on both the degree and location of angler and ecological heterogeneity on the landscape (Figure 6). High angler heterogeneity paired with high waterbody diversity will likely result in low levels of angler synchrony. Likewise, low angler heterogeneity paired with low waterbody diversity could result in high levels of angler synchrony. In our study, we identified a moderate level of synchrony, suggesting there was at least some homogeneity among waterbodies or anglers.

Patterns in spatial synchrony are often further explored in relation to distance (Bjørnstad et al., 1999). In general, synchrony in angler effort was unrelated to distance, but exhibited social-ecological relationships and dependencies. We postulate that this could result from a heterogeneous population of anglers on the landscape that respond uniquely to distance. For example, Ward, Quinn, and Post (2013) identified four distinct angler groups that varied with how

TABLE 1 Multivariate analysis of variance (MANOVA) and univariate analysis for the effect of angler-effort group (high, moderate, low) on effort density, waterbody size, party size, catch rate, boat launches, species stocked, catch richness and angler type (i.e. proportion of boat anglers)

Source	Wilk's λ	df	MS	F	p
MANOVA	0.05	16, 60		13.77	<0.0001
Effort density		2	19.51	24.83	<0.0001
Error		37	0.79		
Waterbody size		2	127.28	90.10	<0.0001
Error		37	1.41		
Party size		2	0.44	8.40	<0.001
Error		37	0.05		
Catch rate		2	0.43	7.03	<0.01
Error		37	0.06		
Boat launches		2	2.96	14.82	<0.0001
Error		37	0.20		
Species stocked		2	0.99	4.55	<0.05
Error		37	0.22		
Catch richness		2	4.35	72.87	<0.0001
Error		37	0.06		
Angler type		2	0.64	36.13	<0.0001
Error		37	0.02		

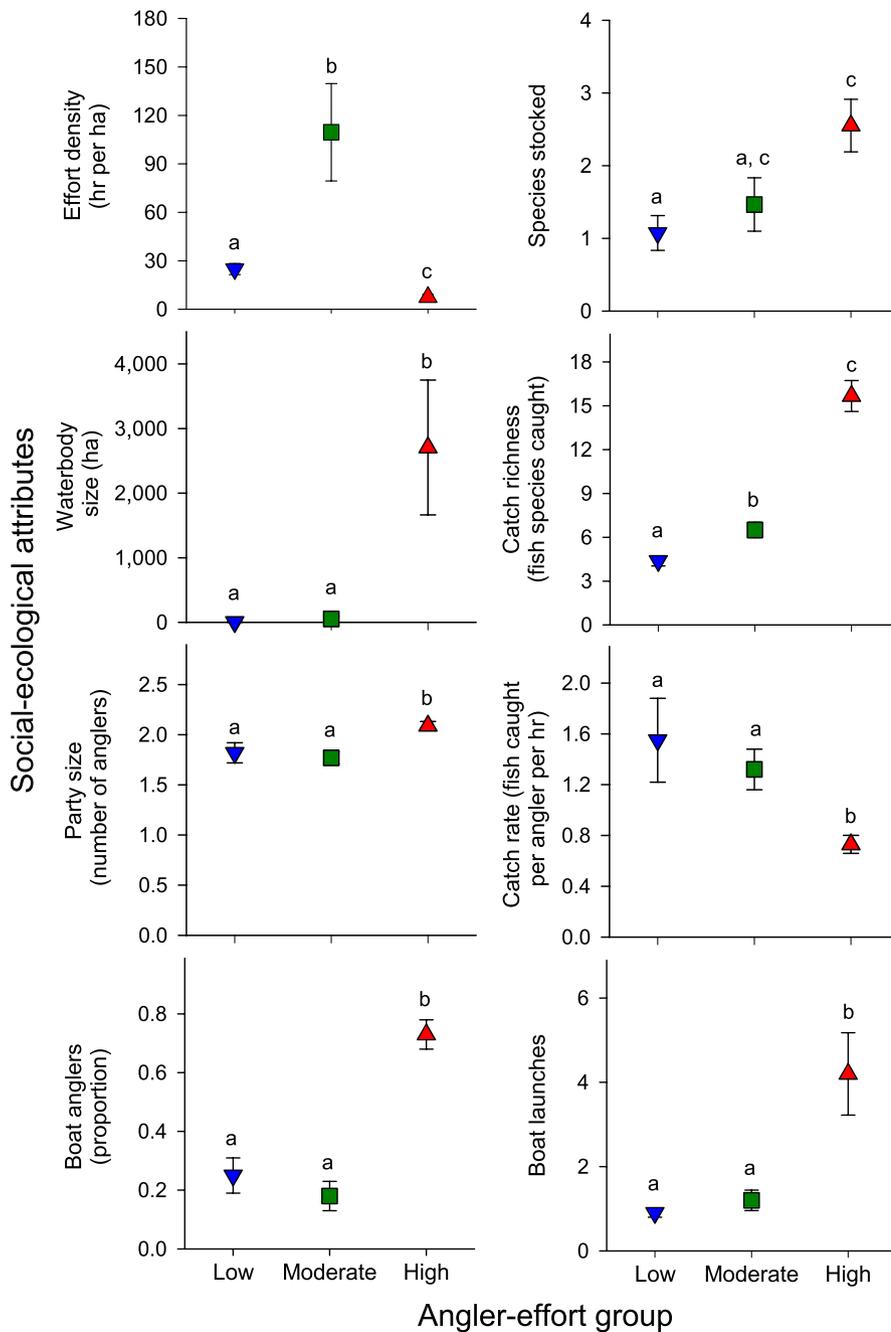


FIGURE 4 Social-ecological attribute differences (\pm SE) among angler-effort groups (high = \blacktriangle , moderate = \blacksquare , low = \blacktriangledown) that included effort density, waterbody size, party size, boat anglers, species stocked, catch richness, catch rate and boat launches. Different letters indicate significant differences among angler-effort groups for each attribute as indicated by separate univariate ANOVA's and post hoc Tukey HSD tests (conversely same letters = no significant difference)

they interacted with a fishery, including their spatial distribution and distance traveled. The most specialized anglers were willing to travel a greater distance than the least specialized anglers (Ward et al., 2013). Therefore, regional synchrony in angler behaviour may depend on the residency (or location) of different types of anglers on the landscape in relation to these ecological resources (Matsumura et al., 2017). Localized processes could be important for shaping the decisions of the least specialized anglers, whereas highly specialized anglers are more likely to shape their decisions at a much broader spatial scale, leading to cross-scale behaviours and resultant regional synchrony.

Grouping waterbody-year patterns in angler effort revealed unique and potential underlying factors responsible for shaping

these recreational fisheries. Angler-effort groups not only differed in their intra-annual temporal patterns but also differed in the absolute angler effort received, ultimately creating high, moderate and low angler-effort groups. These angler-effort groups were further typified by differences in social-ecological attributes. Though we did not explicitly evaluate angler specializations in our study, the differences observed among the angler-effort groups suggest that our angler population was heterogeneous. Discrete angler groups likely responded uniquely to the diversity of waterbodies on the landscape, revealing consistent patterns in these coupled social-ecological systems. For example, the high angler-effort group was comprised of the largest waterbodies and experienced the least effort density. These larger waterbodies were stocked

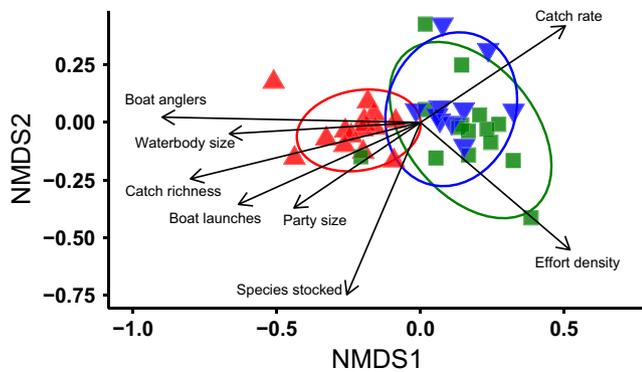


FIGURE 5 Nonmetric multidimensional scaling (NMDS) plot of angler-effort groups (high = ▲, moderate = ■, low = ▼) and associated 95% confidence intervals (ellipses). Arrows represent the direction and strength of each attribute when compared across angler-effort groups

annually with more fish species and provided more boat-launch sites than the smaller waterbodies. Anglers sampled at these larger waterbodies fished primarily from a boat in larger parties and experienced lower catch rates with greater catch species richness. Utility-based choice models predict that fishing quality (e.g. catch rate and species richness), facility development (e.g. boat launches), management actions (e.g. species stocked), encounters with other anglers (e.g. effort density) and other factors should lead to different waterbody selections among a heterogeneous group of anglers (Hunt, 2005). Though we did not measure or account for other social-ecological attributes at these waterbodies, such as water visibility and algal blooms (that vary among natural lakes in Nebraska; Jolley, Albin, Kaemingk, & Willis, 2013), and residential waterbody properties and regulation differences, it is probable that these factors also contributed to the angler effort patterns we observed (Johnston, Arlinghaus, & Dieckmann, 2010; Roberts, Boyer, & Lusk, 2008).

Local-scale interactions between a heterogeneous angler population and a diverse set of waterbodies created the emergent property of large-scale synchrony in angling effort. Our study only included reservoirs within the US state of Nebraska; thus, we wonder how spatial patterns in angler synchrony may change by increasing the spatial scale (e.g. other US states or countries), increasing waterbody diversity (e.g. natural lakes, rivers, streams) and including greater angler heterogeneity. The total number of annual fishing permit sales for Nebraska was relatively stable throughout our study period (3% increase; U.S. Fish and Wildlife Service, 2017). Including other regions with more dynamic angler populations should affect regional-level patterns, such as angler synchrony (Matsumura et al., 2017). Our conceptual framework would predict that angler synchrony at larger spatial scales that includes greater waterbody diversity and angler heterogeneity would be lower than the moderate amount of synchrony we observed (Figure 6). It is also plausible that localized levels of synchrony may be higher (than the regional estimate) but that levels of angler synchrony decay at larger spatial scales. Identifying where the spatial threshold exists could expose

elements of angler behaviour, waterbody diversity and governance (i.e. state specific) aspects that shape angler behaviour at national and international levels. This information would be incredibly useful for global management of important social-ecological systems, such as freshwater fisheries (Arlinghaus, Cooke, & Potts, 2013). Recognizing how and why local patterns may or may not scale up to larger spatial scales is critical. For these reasons, we encourage other studies to examine spatial and temporal patterns in social-ecological systems using synchrony-based methods within a complex-adaptive-systems framework.

5 | CONCLUSIONS

Local and regional management options exist within social-ecological components of recreational fisheries that can be manipulated to reach a desired management outcome. However, management actions at a local waterbody or focused on a regional angler group could lead to unintended consequences at both local and regional scales. Typically we consider how management actions at one waterbody may influence other nearby substitute waterbodies, but are less likely to consider how this may impact regional dynamics. Synchrony in angler behaviour on public waterbodies in Nebraska was not related to distance. Therefore, extending similar management actions (and extrapolating information) across a set of local waterbodies may not be appropriate. Substitute waterbodies may not have any geographic relationship but rather share similar social-ecological properties (i.e. waterbody size, angler types), such as our angler-effort groups. From a resiliency standpoint having a network of substitute waterbodies spread out across the landscape could afford additional management options at both local and regional levels (Martin, Shizuka, Chizinski, & Pope, 2017). This insight has implications for establishing sampling designs and monitoring programs; sampling waterbodies randomly throughout the landscape may yield more insight than following a spatially explicit design. A spatially randomized approach should more adequately capture the diversity of anglers and waterbodies on the landscape, leading to better cross-scale management of these complex adaptive systems.

Recognizing emergent properties, such as regional synchrony in angler behaviour, sheds light on potential cross-scale management options and consequences. We can begin to understand how local-level actions may extend to regional-level consequences if we consider our three identified angler-effort groups and how reducing boat launch access (as an example) could influence cross-scale angler behaviour. In our study, Red Willow Reservoir followed intra-annual patterns in angler effort reflective of the high angler-effort group, but then conformed to the moderate angler-effort group. During our study, Red Willow Reservoir required an emergency decrease in water level after cracking was observed in the earthen dam. Water-drawdown shifted the composition of anglers from primarily boat anglers to primarily bank anglers, corresponding to the shift we observed from our high angler-effort group dominated by boat anglers to our moderate angler-effort group dominated by bank anglers (Chizinski, Martin,

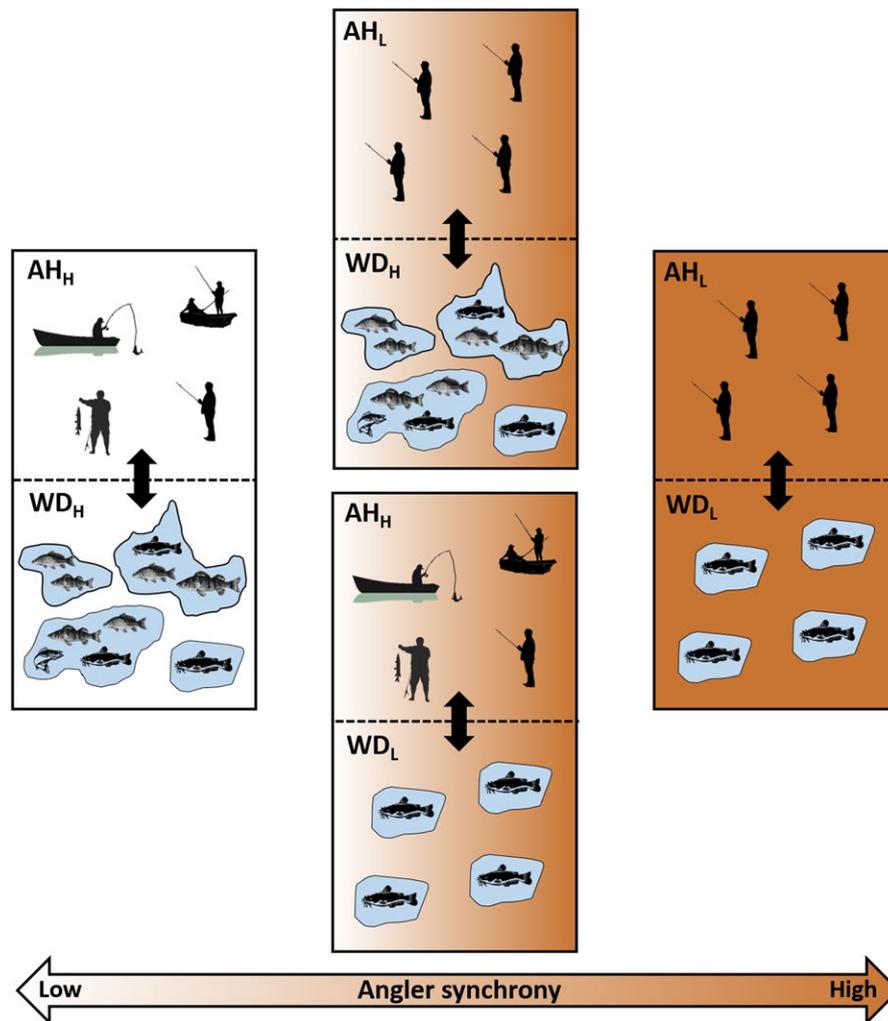


FIGURE 6 A conceptual predictive model illustrating the relationship between angler behaviour and waterbody attributes along a synchrony gradient at a regional or landscape scale. High angler heterogeneity (AH_H) paired with high waterbody diversity (WD_H) would result in low angler synchrony (left panel). In contrast, low angler heterogeneity (AH_L) paired with low waterbody diversity (WD_L) would result in high angler synchrony (right panel). Intermediate levels of angler synchrony would result from a combination of low angler heterogeneity paired with high waterbody diversity (upper middle panel) or high angler heterogeneity paired with low waterbody diversity (lower middle panel)

Huber, & Pope, 2014). We suspect that these boat anglers were displaced and found a waterbody-year substitute, which may not have been local. If correct, then this management action likely influenced spatial and temporal dynamics of anglers at multiple scales.

We suggest that changes made at the local scale will influence large-scale patterns in angler behaviour that either reinforce synchrony or diminish synchrony. Outlining specific management goals and understanding the best way to implement a desirable change, while considering subsequent cascading consequences through space and time, will be necessary for successful management of these social-ecological systems. Traditional recreational fisheries management techniques applied to the waterbody level, such as designated fishing seasons, species-specific size and length limits, and fish stockings could also be balanced by taking a watershed-scale approach (Mee et al., 2016; Nguyen et al., 2016; Wilson et al., 2016). We suggest that cross-scale management that includes an

understanding of how angler and resource heterogeneity interact through space and time will be most effective for maximizing ecosystem services within these recreational fisheries (Arlinghaus et al., 2017; Ward et al., 2016).

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AUTHORS' CONTRIBUTIONS

M.A.K. conceived the initial idea and received substantial input for improving the study design from C.J.C., K.L.H. and K.L.P. C.J.C., K.L.H. and K.L.P. provided oversight of data collection. M.A.K. analysed the data and wrote the initial draft of the manuscript. All four authors contributed critically by editing drafts of the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the University of Nebraska-Lincoln Data Repository <https://doi.org/10.13014/k22v2d92> (Kaemingk, Chizinski, Hurley, & Pope, 2018).

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SUPPORTING INFORMATION

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