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ARTICLE

Bipartite networks improve understanding of effects of waterbody size and angling method on angler–fish interactions

Christopher J. Chizinski, Dustin R. Martin, Daizaburo Shizuka, and Kevin L. Pope

Abstract: Networks used to study interactions could provide insights to fisheries. We compiled data from 27 297 interviews of anglers across waterbodies that ranged in size from 1 to 12 113 ha. Catch rates of fish species among anglers grouped by species targeted generally differed between angling methods (bank or boat). We constructed angler–catch bipartite networks (angling method specific) between anglers and fish and measured several network metrics. There was considerable variation in networks among waterbodies, with multiple metrics influenced by waterbody size. Number of species-targeting angler groups and number of fish species caught increased with increasing waterbody size. Mean number of links for species-targeting angler groups and fish species caught also increased with waterbody size. Connectance (realized proportion of possible links) of angler–catch interaction networks decreased slower for boat anglers than for bank anglers with increasing waterbody size. Network specialization (deviation of number of interactions from expected) was not significantly related to waterbody size or angling methods. Application of bipartite networks in fishery science requires careful interpretation of outputs, especially considering the numerous confounding factors prevalent in recreational fisheries.

Résumé : Les réseaux utilisés pour étudier les interactions pourraient fournir de l'information utile sur les pêches. Nous avons compilé des données de 27 297 entrevues de pêcheurs à la ligne dans différents plans d'eau allant de 1 ha à 12 113 ha. Les taux de prise de différentes espèces de poisson de pêcheurs regroupés selon l'espèce ciblée varient généralement selon la méthode de pêche (de la rive ou d'une embarcation). Nous avons construit des réseaux bipartites pêcheur–prises (selon la méthode de pêche) entre les pêcheurs et les poissons et mesuré plusieurs paramètres de ces réseaux. Il y a des variations considérables des réseaux entre plans d'eau, plusieurs paramètres étant influencés par la taille de ces derniers. Le nombre de groupes de pêcheurs ciblant des espèces précises et le nombre d'espèces de poissons pêchées augmentent avec la taille du plan d'eau. Le nombre moyen de liens pour les groupes de pêcheurs ciblant des espèces et les espèces pêchées augmente également avec la taille du plan d'eau. La connectance (proportion de liens possibles réalisés) des réseaux d'interactions pêcheur–prises diminue plus lentement pour les pêcheurs en embarcation que pour les pêcheurs de la rive pour des plans d'eau de plus en plus grands. La spécialisation des réseaux (écart entre le nombre d'interactions observées et prévues) n'est pas significativement reliée à la taille du plan d'eau ou à la méthode de pêche. L'application de réseaux bipartites aux sciences halieutiques nécessite une interprétation soigneuse des données de sortie, étant donné, notamment, les nombreux facteurs de confusion qui caractérisent les pêches récréatives. [Traduit par la Rédaction]

Introduction

In recreational fisheries, anglers' influence extends beyond the species that they target (Cooke and Cowx 2004, 2006; Lewin et al. 2006). The influence of recreational angling on targeted species is well known and includes decreases in abundance, changes in age structure and size structure, and changes in species composition (Blaber et al. 2000). Anglers tend to prefer certain species because of their value for food and angling challenge (Lewin et al. 2006). However, the angling population is not comprised of a single, homogeneous group but is rather a heterogeneous group made up of numerous subgroups (O'Neill 2001; Arlinghaus et al. 2008; Hutt and Jackson 2008; Beardmore et al. 2015). Each subgroup of anglers can vary in their specialization, motivations, choice of species targeted, angling method, and tackle choices, among a multiplicity of other factors. Thus, during any given period at a waterbody, there is a heterogeneous suite of anglers fishing for a multitude of species (Chizinski et al. 2014*a*, 2014*b*), using various gears and approaches (e.g., angling from a boat or bank). Furthermore, no angling tackle or bait is exclusive to the species being targeted. Anglers' decisions on where and how to fish, along with decisions on tackle choice, create a potential subset of the fish community that could be caught (whether intended or not). Pope et al. (2016) provided evidence that anglers tend to catch and harvest the species being targeted, but there was also considerable recreational bycatch (species caught but not targeted). Further, Pope et al. (2016) indicated that there was a large segment of the angling community that were target generalists (i.e., targeting all species), who tended to have the second greatest catch rate of each species.

Interaction networks are increasingly used to study dynamics within populations, communities, and ecosystems (Montoya et al. 2006; Kéfi et al. 2015). A primary objective of analyzing ecological networks is to provide an understanding of the complexity in the

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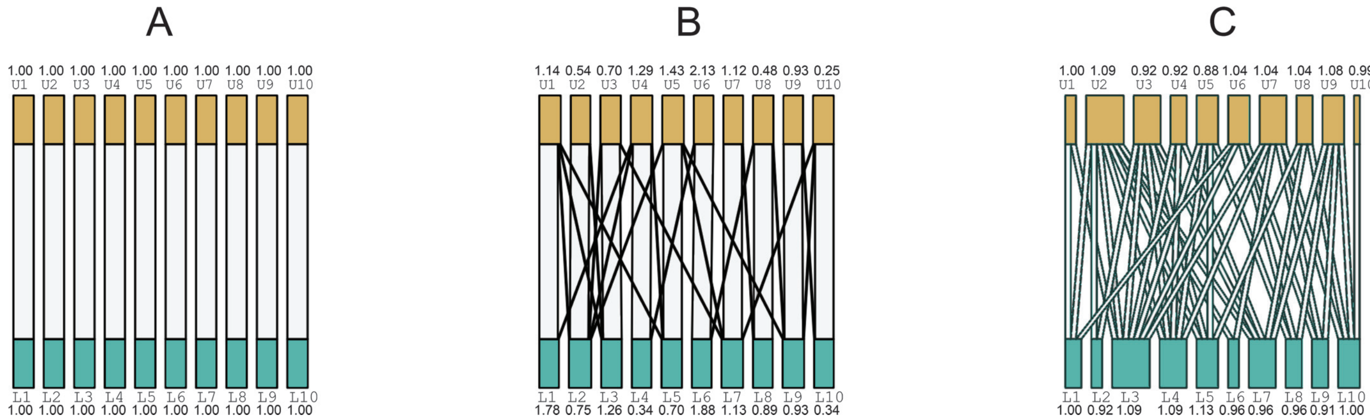
Fig. 1. Examples of weighted angler catch interactions networks displaying the range of possible network structures. (A) A simple network with complete specialization (species-targeting angler groups catch only what is sought), (B) a more complex network with specialization but with some bycatch, and (C) a complex network with low specialization (species-targeting angler groups catch multiple fish species). The orange boxes signify the anglers grouped by species-targeted nodes and blue boxes signify species-caught nodes. The connections between the nodes (edges) are in light gray. Node labels are denoted with a U for upper nodes and L for lower nodes. Node strength is indicated above the node label for the upper nodes and below the node label for the lower nodes. Further details about these example networks are provided in the Materials and methods.



natural world that ultimately affects ecosystem functioning (Ings et al. 2009). Ecological interactions need to be assessed at the community level to draw valid conclusions about the ecological and evolutionary mechanisms underlying these interactions (Vázquez et al. 2007). This understanding is essential in predicting ecological responses to disturbances, habitat loss, climate change, and invasive species (Ings et al. 2009).

Ecological interaction networks are representations of associations (links) between species (nodes). A particular type of ecological network, the bipartite network, describes the interactions between two levels in the community (Vázquez et al. 2007; Eklöf et al. 2013), which include plant–animal interactions, plant–pollinator interactions, and parasite–host interactions. Recreational fisheries, like other complex social–ecological systems (Mitchell 2009), are well suited to assess interactions between anglers and fish because the relationships between anglers and fish are complex and dynamic (Pope et al. 2014; Beardmore et al. 2015; Mee et al. 2016), made further so by multiple angler groups interacting with multiple fish species at any given time. Network analysis could provide unique understanding of the underlying structure of a social–ecological system that could inform detailed mechanistic models and provide managers better information on basic patterns of fishing activity (Martin 2013). Bipartite networks can be extended from an ecological context to investigate the socioecological interaction between anglers grouped by species targeted (i.e., the predator) and captured fish species (i.e., the prey). In theory, this "angler–catch interaction network" could range in structure from relatively simple networks in which anglers grouped by species targeted catch only the species targeted to random networks in which each species-targeting angler group captures a random set of fish species (Fig. 1). As we will show, real networks display complex structure in which each species-targeting angler group catches a mixture of fish species, but to different degrees (Fig. 1). The purpose of this study is threefold: (1) illustrate application of bipartite networks to recreational fisheries, (2) compare angler–catch interaction networks between angling methods (i.e., anglers fishing from the bank versus anglers fishing from a boat), and (3) describe the influence of waterbody size on the angler–catch interaction networks.

The species–area relationship predicts that there would be increasing numbers of species with increasing size of area (Connor and McCoy 1979), and this could have complex effects on the interactions between anglers and fish. As the number of fish species in a waterbody increases with size (Eadie et al. 1986), we expect a greater number of anglers and hence a greater number of targeting groups. With increasing number of groups, we may observe patterns in the interactions associated with waterbody size (i.e., decreased connectivity, greater network complexity) among these groups. Further, with increasing waterbody size, there is often a transition from littoral- to pelagic-dominated fish communities (Mehner et al. 2005) and thus, we might expect differences in the networks (e.g., number of species caught, number of angler targeting groups, network connectance) with waterbody size between anglers that are fishing from the shore and anglers fishing from a boat.

Materials and methods

Angler survey data

We compiled creel surveys from 2009 to 2013 for 42 waterbodies in Nebraska (Table 1). Data were collected through in-person interviews to document angler participation patterns, species targeted, and catch and harvest at reservoirs across Nebraska. Although interviews took place throughout the year, we limited data to interviews that occurred during May–August. One angler, the representative of the party, completed the survey; thus, all data were collected at the party (i.e., a group of individuals travelling together for fishing) level. All complete trips and incomplete trips >30 min were included in the analysis. Bank anglers were defined as those fishing from the shoreline and boat anglers were those using a floating vessel (e.g., kayak, float tube, or motorized boat). A stratified multistage probability-sampling regime (Malvestuto 1996) was used to determine days of interviews. At each waterbody, we calculated the mean catch per unit effort (CPUE) (1 h of fishing) for each species for all species present in the waterbody for each species-targeting angler group. The result was a matrix of CPUE with rows representing each species caught and columns representing the species sought by anglers. For waterbodies that had data for several years, we took the mean across the years.

Similarity between angling methods

Before building the angler–catch networks, we needed to assess the similarity between angling methods (bank or boat) within a waterbody to provide justification on whether the catches by angler groups were different enough to warrant different networks for bank and boat anglers. Strong correlation between the two matrices would indicate similar catches and at similar rates between boat and bank anglers and suggest that a network could be created with catches combined across angling method; lack of

Table 1. Lake names, surface area, number of angler interviews, and mean ± SE proportion of interviews for anglers fishing from the shoreline, species targeted (anglers grouped by species targeted), and species (fish species caught) of greatest importance for bank-angler and boat-angler networks.

				Bank-angler network		Boat-angler network	
Name	Surface area (ha)	Interviews	Bank*	Species targeted	Species	Species targeted	Species
Fremont 5	1.1	262	0.83±0.03	ANY	BLG	CRP	BLG
Fremont 13	1.9	15	0.92±0.08	—	—	—	—
TaHaZouka	2.2	51	1.0	ANY	BLG	—	—
Fremont 17	2.3	252	0.93±0.02	CCF	BLG	—	—
Fremont 11	2.5	221	0.94±0.02	ANY	BLG	CRP	LMB
Fremont 3	2.6	378	0.99±0.00	ANY	BHD	—	—
Fremont 12	2.9	74	0.77±0.05	LMB	BLG	LMB	CCF
Fremont 9	4.3	62	0.95±0.03	ANY	BLG	—	—
Fremont 18	4.5	139	0.95±0.05	CCF	BLG	—	—
Fremont 4	4.8	50	0.95±0.03	LMB	BLG	—	—
Yanney	5.0	121	1.0	ANY	LMB	—	—
Fremont 1	5.1	413	0.92±0.04	CCF	BLG	CRP	LMB
Fremont 7/8	5.1	9	0.88±0.13	—	—	CRP	LMB
Fremont 16	5.4	83	0.92±0.02	ANY	BLG	CRP	BLG
Fremont 2	6.4	557	0.93±0.02	ANY	BLG	ANY	CCF
Cottontail	10.2	36	0.47	ANY	CCF	ANY	BLG
Timber Point	11.7	43	0.72	ANY	LMB	LMB	BLG
Cottonmill	12.2	168	0.92	ANY	LMB	LMB	LMB
Fremont 10	14.8	160	0.92±0.02	ANY	CCF	CCF	CRP
Skyview	16.3	167	0.98	CRP	BLG	ANY	LMB
Fremont 20	18.9	420	0.50±0.07	LMB	CCF	BLG	BLG
Meadowlark	18.9	17	0.71	CRP	BLG	LMB	BLG
Fremont 15	21.7	484	0.97±0.01	ANY	CCF	LMB	CCF
Holmes	39.2	247	0.14±0.05	LMB	BLG	ANY	BLG
Wildwood	45.5	271	0.71±0.03	CCF	BLG	CRP	BLG
Stagecoach	70.3	152	0.54±0.00	ANY	LMB	ANY	BLG
Conestoga	74.7	76	0.45	LMB	CCF	ANY	BLG
Yankee Hill	79.2	123	0.62	ANY	LMB	LMB	BLG
Willow Creek	234.3	235	0.62	ANY	BLG	WAE	CCF
Pawnee	254.3	138	0.26±0.02	WAE	CCP	WAE	BLG
Enders	500.5	817	0.26±0.10	ANY	WHB	ANY	WHB
Box Butte	555.3	794	0.14±0.06	YEP	NOP	ANY	NOP
Medicine Creek	642.5	930	0.41±0.05	WAE	WHB	CRP	WHB
Branched Oak	712.6	467	0.66±0.01	CCF	CCF	CCF	BLG
Johnson	907.6	1872	0.77±0.01	ANY	FWD	CRP	WHB
Merritt	1093.2	3393	0.33±0.05	ANY	BLG	ANY	YEP
Sherman	1173.9	2352	0.60±0.04	ANY	CRP	CRP	CRP
Swanson	1657.3	1219	0.22±0.06	WAE	LMB	ANY	WHB
Calamus	2054.5	2990	0.45±0.05	WAE	WHB	WAE	WHB
Harlan Co.	5544.1	3690	0.21±0.03	ANY	CCF	WAE	WHB
Lewis and Clark	11581.2	1621	0.36±0.04	WAE	CCF	WAE	BLG
McConaughy	12113.0	1728	0.12±0.04	ANY	CCF	WAE	WHB

Note: A dash indicates that the network metrics could not be calculated because of too few interviews or no fish caught by interviewed anglers. Taxa codes are given in Table A1.

*Mean and SE were calculated across years. Lakes without SE presented had one year of data.

correlation would indicate that the catches were different enough that we should construct separate networks for bank and boat anglers. To do this, we scaled and centered by columns (angler targeting groups). Scaling and centering allowed us to determine the relative influence of each fish species by each angler group rather than differences in magnitude in those values. We then used Euclidean distances and Mantel's test to assess the correlation between the two matrices using the ade4 package (Dray and Dufour 2007) in R. Significance of Mantel's *r* was determined from 999 iterations.

Angler–catch interaction networks

We created networks in which fish taxa and angler groups are represented as "nodes" (or vertices) and the reported harvest of a fish taxon by an angler group as an "edge" (or link) that connects these two nodes. This network is considered a "bipartite network" because it only contains edges between two distinct types of nodes ("anglers" and "fish"). Edges in bipartite networks represent interactions or strengths of associations between the two different groups (Michailidis 2008). In the context of an angler–catch interaction network and for the approach we used (i.e., using CPUE), we have the anglers grouped by species targeted as the upper nodes and the fish species caught as the lower nodes (Fig. 1). The width of the node (related to node strength) for an angler group is the relative CPUE for all species caught by that angler group, whereas the width of the node for a fish species caught is the relative CPUE for that species caught by all anglers. The width of an edge (bar connecting the upper and lower nodes) is the proportion of total CPUE for the species-targeting angler group comprised of the individual fish species. The bipartite networks are arranged such that nodes in the middle have more connections (i.e., anglers grouped by species targeted that caught more fish species and fish species caught by more angler groups) and nodes at the periphery have fewer connections. Weighted bipartite networks were created for each lake using the bipartite package (Dormann et al. 2008) in R (R Development Core Team 2015); this bipartite package generates a visualization of the network.

For each network, we extracted several network- (Dormann et al. 2009), group-, and species-level (Dormann et al. 2008) metrics. Network-level metrics describe the entire network structure, group-level metrics describe the properties of upper (i.e., species-targeting groups or predators) and lower (i.e., species caught or prey) nodes, and species-level metrics describe individual nodes in the upper and lower levels. The specific network-level metrics that we examined were connectance, which is the realized proportion of possible links (Dunne et al. 2002), and H2′, which is the network-level measure of specialization that is based on the deviation of a species' realized number of interactions from that expected for each species' total number of interactions (Blüthgen et al. 2006). The H2′ index is scaled such that its values range from 0 in networks with completely random interactions to 1 in networks with complete specialization. The specific group-level metrics that we examined were the number of upper (i.e., anglers grouped by species targeted) and lower (i.e., fish species caught) nodes and the mean number of links per node for the upper and lower levels. For the species-level metrics, we identified the node with the greatest species strength, which is the sum of dependencies of each node (Bascompte et al. 2006), i.e., either the number of fish species that are caught by species-targeting angler groups or the number of species-targeting angler groups that caught a particular fish species.

The above metrics were chosen to describe angler–catch interaction networks for several reasons. Connectance is the most commonly used and simplest metric to describe the density of links between nodes in an interaction network and can be interpreted as the degree of generalization in the system (i.e., high connectance = high generalization) (Blüthgen et al. 2006, 2008). An angler–catch interaction network with a high connectance would indicate that many of the angler groups catch many of the fish species and likewise that many of the fish species are being caught by many of the angler groups. Although similar to connectance in describing a degree of generalization of a network, H2′ is a finer description of the nature of the connectance in an interaction network. As such, H2′ describes specialization in terms of exclusiveness, where H2′ = 1 represents the most nested scenario possible given the frequency distribution and H2′ = 0 describes the greatest deviation from that nested assemblage (i.e., completely random interactions) (Blüthgen et al. 2006, 2008). In the context of the angler–catch interaction network, H2′ describes the degree of specialization (i.e., catching only the species that is being sought) across all the angler groups, where H2′ = 1 indicates a fishery with no recreational bycatch and H2′ = 0 indicates a fishery with extensive recreational bycatch. The species strength focuses on the architecture of the network and provides a measure of the importance of a node from the perspective of the nodes at the opposite level (i.e., the sum of the weight of all interactions of a predator on its prey) (Barrat et al. 2004; Bascompte et al. 2006). In the context of the angler–catch interaction network, at the upper level, a node with the greatest strength would indicate a species-targeting angler group with high CPUE of many fish species, and at the lower level, a node with the greatest strength would indicate a fish species that has a high CPUE among many angler groups.

To illustrate how the metrics described above change with varying network complexity, we will refer to our conceptual networks described previously (Fig. 1). In this conceptualization, all of the simulated networks had 10 upper nodes and 10 lower nodes. The simple network with no interaction (Fig. 1A) has a connectance of 0.10 (10 connections of a possible 100), an H2′ of 1 (complete specialization), a mean number of links of upper nodes of 1, and a mean number of links of lower nodes of 1. In this simple network, species strength was constant across the upper nodes (1 for each node) and the lower nodes (1 for each node), indicating that all nodes were equally influential. The network with intermediate complexity (Fig. 1B) has a connectance of 0.38 (38 connections of a possible 100), an H2′ of 0 (random interactions), a mean number of links of upper nodes of 4.47, and a mean number of links of lower nodes of 4.37. In this intermediate network, species strength varied across the upper nodes and across the lower nodes, indicating that node U6 was the most influential on the upper level and node L6 was the most influential on the lower level. The complex network (Fig. 1C) has a connectance of 0.29 (29 connections of a possible 100), an H2′ of 0.85 (somewhat specialized), a mean number of links of upper nodes of 2.93, and a mean number of links of lower nodes of 2.95. In this network, species strength varied across the upper nodes and across the lower nodes, indicating that node U2 was the most influential on the upper level and node L5 was the most influential on the lower level.

Statistical analyses

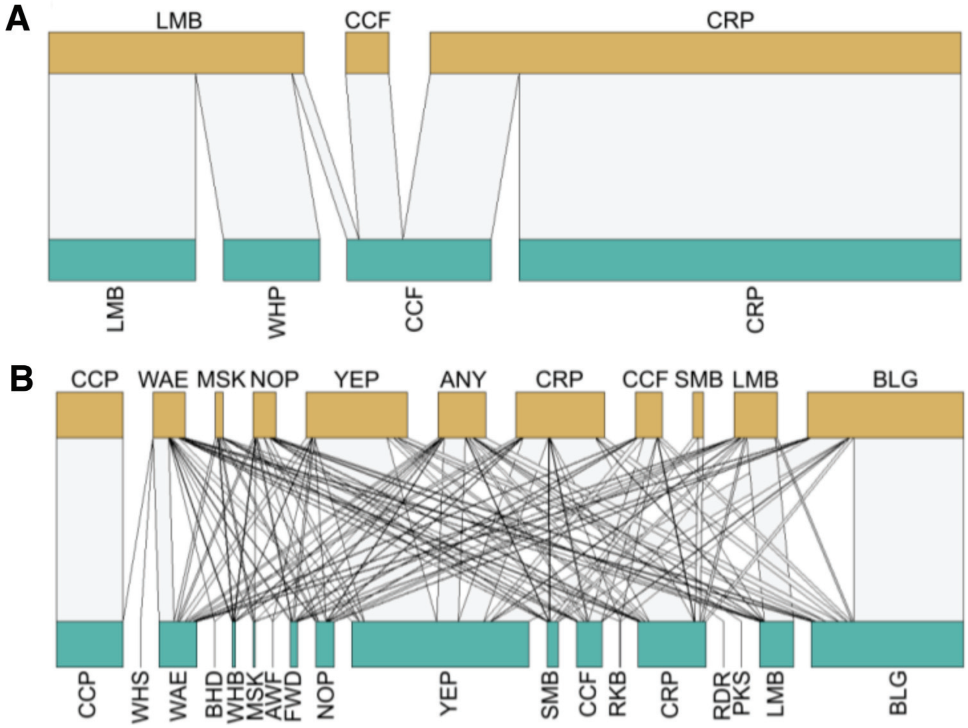
We were interested in how the angler–catch interaction networks varied over waterbody size and angling method. For the network-level and group-level metrics, we assessed the relationship of the metric (dependent) with surface area (log transformed), angling method (bank or boat), and the interaction between surface area and angling method using linear regression. If the interaction term was not significant ($P > 0.05$), we dropped the interaction and ran the model with the main effects only. For each network metric, we present the final model (i.e., with or without the interaction term) following standard nomenclature, including F statistic with model and residual degrees of freedom, model significance, and variance explained (i.e., R^2). In addition, we provide the coefficients for the final linear regression models with coefficient estimate, standard error, t statistic (i.e., coefficient estimate divided by the standard error), and associated P value (i.e., upper-tail probability of achieving a t value from a t distribution with degrees of freedom equal to the residual degrees of freedom from the model). We log transformed surface area to reduce the spread in our surface area (i.e., most lakes were <1000 ha with a few lakes >5000 ha), which qualitatively had no influence on our results. For the influential species metric, we identified the node with the greatest strength for both anglers grouped by species targeted and fish species for both angling methods.

Results

We compiled interview data from 27 297 interviews of angler parties for waterbodies that ranged in size from 1 to 12 113 ha (median size = 19 ha) (Table 1). The across-year mean proportion of bank anglers ranged from 0.12 to 1.00, with lower proportions of bank anglers associated with larger waterbodies.

We assessed the similarity in the angler–catch matrices between bank and boat anglers for 36 of the 42 waterbodies. Six waterbodies had data only for bank anglers; these waterbodies were excluded from the Mantel test. Only four (Fremont Lake 20 (Mantel test $r = 0.977$, $P = 0.003$), Harlan County Reservoir (Mantel test $r = 0.728$, $P = 0.001$), Fremont Lake 11 (Mantel test $r = 0.716$, $P = 0.014$), and Willow Creek Lake (Mantel test $r = 0.592$, $P = 0.050$)) of the 36 waterbodies had a significant correlation between bank and boat anglers grouped by species targeted and fish species caught, which suggests that the angler–catch interaction networks were different between bank and boat anglers and warranted separate analyses. The number of angler groups ranged from 3 to 14 for bank anglers and from 2 to 12 for boat anglers. The number of fish species caught ranged from 3 to 22 for bank anglers and from 2 to 19 for boat anglers. In our assessments, 59% of bank and 71% of the boat angler–catch interaction networks had more fish species caught than were targeted. The most frequently sought fish species among bank anglers were anything (98% of waterbodies), channel catfish (*Ictalurus punctatus*) (93%), and largemouth bass (*Micropterus salmoides*) (88%) and among boat anglers were largemouth bass (97%), anything (86%), and crappie (*Pomoxis* spp.)

Fig. 2. Examples of (A) a simple angler–catch network (Fremont 15) and (B) a complex angler–catch network (Merritt Reservoir) for boat anglers. The width of an edge (bar connecting the upper and lower nodes) is the proportion of total CPUE for the species-targeting angler group comprised of the individual fish species. Taxa codes are given in Table A1.



(83%). There were five fish species (rainbow trout (*Oncorhynchus mykiss*), bullhead (*Ameiurus* spp.), grass pickerel (*Esox americanus vermiculatus*), buffalo (*Ictiobus* spp.), and gizzard shad (*Dorosoma cepedianum*)) sought by bank anglers that were not sought by boat anglers. Conversely, there were four fish species (longnose sucker (*Catostomus catostomus*), tiger muskellunge (*Esox masquinongy* × *Esox lucius*), carp sucker (*Carpiodes carpio*), and rudd (*Scardinius erythrophthalmus*)) sought by boat anglers that were not sought by bank anglers. There were two species (shorthead redhorse (*Moxostoma macrolepidotum*) and smallmouth buffalo (*Ictiobus bubalus*)) caught by bank anglers that were not caught by boat anglers. Conversely, there were eight fish species (redear sunfish (*Lepomis microlophus*), saugeye (*Sander vitreus* × *Sander canadensis*), goldeye (*Hiodon alosoides*), yellow bass (*Morone mississippiensis*), blue sucker (*Cycleptus elongatus*), carp sucker, and grass pickerel) caught by boat anglers that were not caught by bank anglers.

We illustrate the utility of bipartite networks for assessing angler-targeting and catch data using boat angler–catch networks from Fremont Lake 15 (simple network) and Merritt Reservoir (complex network) (Fig. 2). Fremont Lake 15 is a 22 ha waterbody in eastern Nebraska and Merritt Reservoir is a 1093 ha waterbody in north-central Nebraska. At Fremont Lake 15, there were three upper-level (i.e., angler targeting groups) and four lower-level groups (i.e., species caught), a connectance of 0.50, an H2′ of 0.97, a mean number of species caught per species-targeting angler group of 2.26, and a mean number of species-targeting angler groups per species of 1.35. The largemouth bass targeting angler was the most influential upper-level group and channel catfish was the most influential lower-level group on the angler–catch network in Fremont Lake 15. At Merritt Reservoir, there were 12 upper-level and 18 lower-level groups, a connectance of 0.52, an H2′ of 0.50, a mean number of species caught per species-targeting angler group of 9.44, and a mean number of species-targeting angler groups per species of 7.97. The anything-targeting angler group (anglers that indicated they targeted any fish species) was the most influential upper-level group and yellow perch (*Perca flavescens*) was the most influential lower-level group on the angler–catch network in Merritt Reservoir.

The anything-targeting angler group was most frequently (21 of the 40 waterbodies) the angler group of greatest importance to the angler–catch interaction networks, regardless of waterbody size for bank anglers (Table 1). The anything-targeting angler group was also important in the boat angler–catch interaction networks but was less frequently the angler group of greatest importance (10 of 34 waterbodies). The crappie-targeting angler group closely followed the anything-targeting angler group in the boat angler–catch interaction networks (9 of 34 waterbodies). There was a transition in the fish species caught of greatest importance for both bank and boat angler–catch interaction networks with increasing waterbody size (Table 1). At smaller waterbodies (<100 ha), the fish species of greatest importance were littoral-associated species (e.g., bluegill (*Lepomis machrochirus*), crappie, and largemouth bass). In contrast, there was a transition to pelagic species (white bass (*Morone chrysops*) and walleye (*Sander vitreus*)) becoming the fish species of greatest importance at larger (>100 ha) waterbodies.

There was considerable variation in the complexity in the networks among the 42 waterbodies assessed, with multiple metrics influenced by waterbody size, method, and the associated interactions. The model of the number of species-targeting angler groups ($F_{[3,72]} = 37.08$, $P < 0.001$, $R^2 = 0.61$) included log-transformed area, angler type, and the associated interaction. The interaction in this model indicated that the number of angler groups increased with waterbody surface area slower for bank anglers than for boat anglers (Table 2; Fig. 3). The model of the number of species caught ($F_{[2,73]} = 86.50$, $P < 0.001$, $R^2 = 0.70$) included log-transformed area and angler type, with no associated interaction. The lack of significant interaction indicated that the numbers of fish species caught increased significantly with waterbody surface area, but there was no difference between angling methods

Table 2. Coefficients for the linear regression models assessing network metrics to the surface area of the waterbodies.

Coefficient	Estimate	Standard error	*t* statistic	Residual df	*P* value
Number of species-targeting angler groups					
Intercept	4.711	0.468	10.063	72	<0.001
log(Area)	0.575	0.101	5.690	72	<0.001
Method	−2.755	0.756	−3.643	72	0.001
log(Area) × Method	0.449	0.154	2.917	72	0.005
Number of fish species caught					
Intercept	2.623	0.623	4.211	73	<0.001
log(Area)	1.584	0.121	13.144	73	<0.001
Method	−0.682	0.633	−1.078	73	0.285
Mean number of links for species-targeting angler groups					
Intercept	1.971	0.323	6.088	73	<0.001
log(Area)	0.513	0.063	8.187	73	<0.001
Method	0.232	0.328	0.707	73	0.482
Mean number of links for fish species caught					
Intercept	3.398	0.371	9.168	72	<0.001
log(Area)	0.245	0.080	3.056	72	0.003
Method	−2.138	0.589	−3.573	72	<0.001
log(Area) × Method	0.409	0.122	3.357	72	0.001
Connectance					
Intercept	0.578	0.025	23.460	73	<0.001
log(Area)	−0.020	0.005	−4.352	73	<0.001
Method	0.052	0.025	−2.071	73	0.041
H2′					
Intercept	0.625	0.040	15.692	73	<0.001
log(Area)	−0.000	0.007	−0.023	73	0.982
Method	−0.030	0.040	−0.751	73	0.455

Note: Angling method is for bank anglers relative to boat anglers.

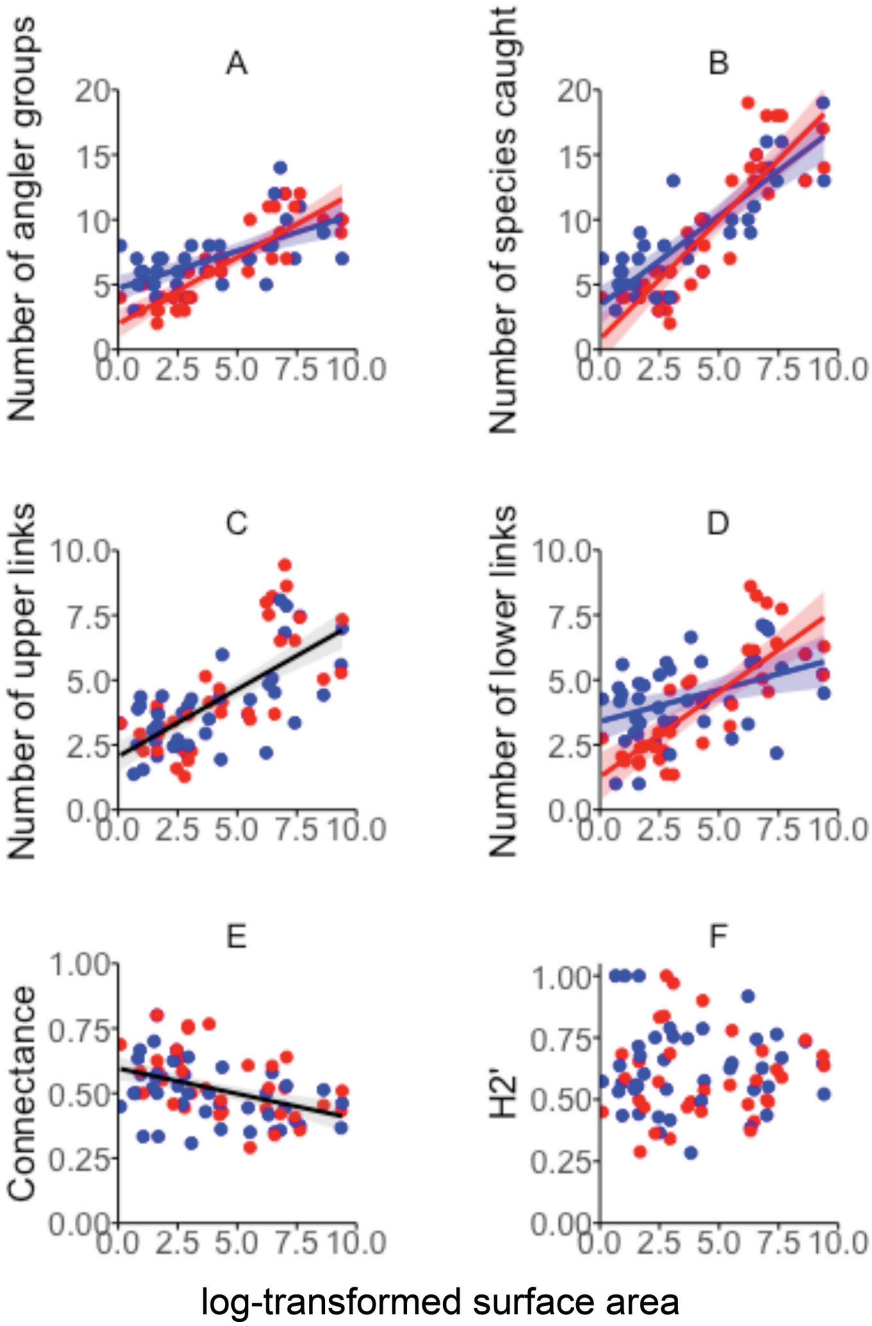
(Table 2; Fig. 3). The model of the mean number of links for species-targeting angler groups ($F_{[2,73]}$ = 34.94, P < 0.001, R^2 = 0.49) included log-transformed area and angler type, with no associated interaction. In contrast, the model predicting the mean number of links for fish species caught ($F_{[3,72]}$ = 20.07, P < 0.001, R^2 = 0.46) included log-transformed area, angler type, and the associated interaction. The inclusion of the interaction in the mean number of links for fish species caught but not for the mean number of links for species-targeting angler groups is opposite from what was observed in the number of angler groups and number of species caught. The interaction in the mean number of links for fish species caught indicated that number of angler groups increased with waterbody surface area slower for bank anglers than for boat anglers (Table 2; Fig. 3). The model of connectance ($F_{[2,73]}$ = 10.70, P < 0.001, R^2 = 0.23) included log-transformed area and angler type, with no associated interaction. Connectance of angler–catch interaction networks decreased slower for boat anglers than for bank anglers with increasing waterbody size (Table 2; Fig. 3). The model of H2′ ($F_{[2,73]}$ = 0.2882, P = 0.750, R^2 = 0.01) included log-transformed area and angler type, with no associated interaction. Unexpectedly, network specialization (H2′) was not significantly related to waterbody size or angling method (Table 2, Fig. 3).

Discussion

Research has highlighted the extent and subsequent effect on the ecosystem of commercial fishing (Cooke and Cowx 2006; Drake and Mandrak 2014), but the influence of recreational fishing is less well known (Arlinghaus et al. 2007). The angler–catch interaction networks from this study indicate that recreational fisheries are complex and extend well beyond a single angler group – fish species relationship. Anglers can potentially affect a great number of fish species beyond the target species. Many fish species are caught and released (Pope et al. 2016) and thus are subject to numerous sublethal and behavioral changes associated with catch and release (Cooke and Cowx 2004, 2006). Further, there is great variation in the number and type of bycatch produced across angler groups that target different fish species. Therefore, angler–fish interactions on any given waterbody can be complex (Pope et al. 2016; Arlinghaus et al. 2017). One can improve understanding of interactions between anglers and fish, whether targeted or not, by examining angler–catch interaction networks; improved understanding could lead to better fisheries management and conservation practices.

We documented a range of complexity in angler–catch interaction networks across waterbodies. For example, the boat angler–catch network in Fremont Lake 15 was relatively simple (Fig. 2A) and illustrated some of the utility of bipartite networks to assess angler groups and fish species. On the upper level of the Fremont Lake 15 angler–catch network, we see that crappie-targeting anglers had the greatest relative catch rates followed by largemouth bass targeting anglers and then channel catfish targeting anglers. On the lower level of the network, we see that the greatest relative catch rates were for crappie (regardless of who sought them) and that relative catch rates for largemouth bass and channel catfish were similar. Angler–catch interaction networks also provide an opportunity to illustrate patterns between species-targeting angler groups and the fish species caught. The Fremont Lake 15 angler–catch interaction network illustrates that largemouth bass targeting anglers were the only anglers to catch largemouth bass. Channel catfish targeting anglers only caught channel catfish, but channel catfish were also caught by largemouth bass and crappie-targeting anglers. In addition to providing an opportunity to identify which fish species are being caught by which angler groups, angler–catch interaction networks also provide the ability to identify which angler groups are potentially catching species of concern (e.g., invasive, nuisance species). White perch (*Morone americana*) is an invasive species in Nebraska (Chizinski et al. 2010) and is the focus of state management efforts to maintain populations below ecologically damaging levels (Stewart 2015). The Fremont Lake 15 angler–catch interaction network illustrates that only largemouth bass targeting anglers are

Fig. 3. Relationship of (A) number of species-targeting angler groups, (B) number of fish species caught, (C) mean number of links for species-targeting angler groups, (D) mean number of links for species caught, (E) connectance, and (F) H2′ to the natural log-transformed surface area. Blue circles, lines, and confidence ribbons are for bank anglers; red circles, lines, and confidence ribbons are for boat anglers. A black line and confidence ribbon indicates a significant relationship between waterbody size and the metric that was unaffected by angling method (bank or boat). No line indicates no significant relationship between waterbody size and the metric. Regression coefficients and associated statistics are given in Table 2.



catching this invasive species; in this system, largemouth bass targeting anglers may be the most likely to potentially remove this species from the system and thus, education material (e.g., signs, pamphlets) could be targeted to this angler group to illustrate the danger of transporting this species.

The boat angler–catch interaction network in Merritt Reservoir was much more complex, in relation to Fremont Lake 15 (Fig. 2B). This network indicates that there is considerable recreational by-catch (although relatively small in some cases) by the species-targeting angler groups in this system. The alignment of the anything-targeting anglers in the middle of the figure illustrates that this angler group had the greatest interactions with the fish species caught, whereas the alignment of the bluegill- and common carp targeting anglers on the sides of the network illustrates that these angler groups had the least interactions with the fish species caught. Anything-targeting anglers at Merritt Reservoir primarily caught yellow perch and bluegill, but also caught 11 other species. Unfortunately, managers and scientists often exclude the anything-targeting angler group from species-specific analyses of angler effort, catch and harvest, and attitudes and opinions (Pope et al. 2016), despite having relatively moderate catch rates and interacting with numerous fish species in the community.

The position of the angler group provides insight for our conceptualization that species targeted influences the recreational bycatch caught. We expect that anglers targeting similar species groups, such as bluegill and redear sunfish, would choose approaches and gears that are similar and hence catch similar fish species; as such, bluegill- and redear sunfish targeting angler groups would be proximate to each other in the network. In the Merritt angler–catch network, muskellunge-, and northern pike (*Esox lucius*) targeting angler groups were proximate to each other, as were smallmouth bass (*Micropterus dolomieui*) and largemouth bass targeting angler groups. The angler–catch interaction network could thus be used to understand and predict the appropriate subset of fish species that are vulnerable to a specific angler group.

We compared angler catch networks between bank and boat anglers and determined that in most cases, there were significant differences in the catch rates of fish species among species-targeting angler groups. Our research focused on differences occurring between bank and boat anglers and not the mechanisms behind those differences. Recent research (Pope et al. 2016) indicated that catch and harvest for bluegill, common carp (*Cyprinus carpio*), and crappie were greater for bank anglers, whereas catch and harvest for channel catfish, walleye, and white bass were greater for boat anglers. Perhaps this is not surprising given that the availability and catchability of a species likely differ among habitat types, especially habitats typical within littoral and limnetic zones. Further, bank anglers are often confined more than boat anglers in their choice of habitat to fish; bank anglers can only fish littoral habitat (with a possible few exceptions), whereas boat anglers can choose to fish littoral or limnetic or both zones. In addition to differences in the environmental factors influencing differences in catch composition between bank and boat anglers, there are motivational differences that could affect species caught and the rates that those species were caught. For example, Hudgins (1984) indicated that bank anglers rated the importance of harvest and privacy greater than did boat anglers, whereas beauty of the landing and trophy fish were more important to boat anglers. Further research is needed to evaluate the mechanisms that may be influencing the difference between bank and boat anglers.

A common generalization in community ecology is that, within a group of islands or other isolated habitats within a restricted latitudinal range, larger areas harbor more species (i.e., species–area relationship) (MacArthur and Wilson 1967; Connor and McCoy 1979). Similar to ecological networks within a temperate region, larger waterbodies are able to support more fish species caught and more species-targeting angler groups. Further, increasing area affects both the number of interactions and network structure in ecological networks (Sugiura 2010). In the 42 angler–catch interaction networks in Nebraska, we observed increasing numbers of species-targeting angler groups with increasing waterbody size, and this rate of increase was lesser for bank anglers than for boat anglers. We also observed increasing numbers of fish species caught by anglers with greater waterbody size, but this rate was not different between bank and boat anglers. Further, there is decreasing connectance (i.e., proportion of links from all those possible) in the angler–catch interaction network with increasing waterbody size. That is, the number of possible links between angler groups and fish species increases with waterbody size faster than the number of fish species that each angler group actually captures. This property of the angler–catch interaction network follows the general rule that connectance decreases with the number of species in ecological networks (Jordano 1987; Sugiura 2010).

There was no relationship between the degree of network specialization or partitioning and waterbody size or angling method when using the H2′ index, which compares the diversity of each node's connections with the null expectation given the network size and connectance. For example, in the two networks illustrated in this manuscript, we observed greater specialization in the small waterbody (i.e., Fremont Lake 15) than we did in the larger waterbody (i.e., Merritt Reservoir). Overall, we see that angler–catch interaction networks become more complicated with waterbody size and that angler–catch interaction networks for boat anglers are more intricate (i.e., contain more species-targeting angler groups and more fish species caught) than angler–catch interaction networks for bank anglers, but we do not necessarily observe increases in network specialization. This may indicate that there is a general rule that governs the degree of network specialization (or generalization) by angler groups that is independent of the number of fish species available. In the case of angler–catch interaction networks, the combination of species-specific fishing strategies (e.g., lure type, habitat choice) is likely to constrain generalization of the fish species they catch, while ecological overlap of fish species may make some degree of bycatch inevitable. Our results suggest that this interplay between anglers and bycatch species may be indirectly related to waterbody size through the effect of waterbody size on species diversity.

Networks in this study were built on mean CPUE between angler groups and fish species caught. Many other angler–fish networks could be investigated to elucidate other patterns in network structure. For example, if we looked at total catch (as opposed to CPUE) by each angler group, we could identify the total influence on the fish community. Unfortunately, we were unable to calculate total fishing pressure by each species-targeting angler group given the manner in which data were collected in our creel surveys and thus unable to predict the total number of fish caught by each species-targeting angler group. Further, these networks likely would appear different if focused on species harvested instead of species caught. If we had investigated angler–harvest interaction networks, we would have observed fewer nodes and decreased connectance as anglers tend to harvest a smaller subset of the species caught (Pope et al. 2016). Two additional caveats of this study have to do with our sampling approach that could influence the interpretation of our results. First, we collected information at the party level and there is the possibility that there may have been subtle decisions at the individual level that may have been masked at the party level, although we primarily generalized across two individuals (mean ± SE party size was 1.80 ± 0.02 anglers for bank anglers and 2.24 ± 0.01 anglers for boat anglers). Second, our survey approach precluded gathering data on multiple target species. If multiple species were specified (other than "anything") by the respondent, the creel clerk was instructed to record the first species specified; thus, bycatch as discussed in this manuscript is likely overstated.

The use of bipartite networks to assess the interactions between anglers and fish provides an important visualization of the inherent complex relationships in recreational fisheries. This application of bipartite networks requires careful interpretation of outputs, especially considering the numerous confounding factors prevalent in recreational fisheries. Effective management of social–ecological systems, like those observed in recreational fisheries, requires an understanding of the complex interactions between people and the environment (Mee et al. 2016). We can describe the interactions between the entities of the system using network theory and illustrate some of the observed emergent properties (e.g., resilience of the system (Pope et al. 2014)) of the entire system. For example, we can assess how the establishment of an invasive species affects the species-targeting angler groups and associated species caught, identifying angler groups and fish species that are resilient to the establishment of the new species. Focusing on and responding to the complexity of these systems will lead to better management of these social–ecological systems (Degnbol et al. 2006; Mee et al. 2016).

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Appendix A

Appendix Table A1 appears on following page.

Table A1. Codes, common names and scientific names for angler targeting groups and taxa caught used in the weighted angler-catch interaction networks.

Code	Common name	Scientific name
ANY	Anything	—
AWF	Alewife	*Alosa pseudoharengus*
BLG	Bluegill	*Lepomis macrochirus*
BHD	Black bullhead	*Ameiurus melas*
CCF	Channel catfish	*Ictalurus punctatus*
CCP	Common carp	*Cyroinus carpio*
CRP	Crappie	*Pomoxis* spp.
FWD	Freshwater drum	*Aplodinotus grunniens*
LMB	Largemouth bass	*Micropterus salmoides*
MSK	Muskellunge	*Esox masquinongy*
NOP	Northern pike	*Esox lucius*
PKS	Pumpkinseed	*Lepomis gibbosus*
RDR	Redear sunfish	*Lepomis microlophus*
RKB	Rock bass	*Ambloplites rupestris*
SMB	Smallmouth bass	*Micropterus dolomieu*
WAE	Walleye	*Sander vitreus*
WHB	White bass	*Morone chrysops*
WHP	White perch	*Morone americana*
WHS	White sucker	*Catostomus commersonii*
YEP	Yellow perch	*Perca flavescens*