Spatial Patterns of Synchrony in Recruitment of Trout Among Streams

Troy Zorn and Jan-Michael Hessenauer

Abstract Synchronous recruitment has been documented among salmonid populations in streams draining mountainous regions, and to a lesser degree in low-gradient, groundwater-fed streams. Relatively little is known about the spatial extent of recruitment synchrony among trout populations in low-gradient streams. We mapped Brook Trout *Salvelinus fontinalis*, Brown Trout *Salmo trutta*, and Rainbow Trout *Oncorhynchus mykiss* populations in low-gradient Michigan, USA streams whose recruitment dynamics were synchronous based on correlations in annual densities of age-0, age-1, and age-2 fish, and used maps of correlated populations to estimate the spatial extent of synchrony. Significant correlations indicative of synchronous recruitment occurred for all three species. The maximum spatial extent of synchronous recruitment observed for each species was greater than in many studies to date. Most Rainbow Trout populations were adfluvial, resulting in our documenting synchrony in steelhead recruitment. The persistence of synchronous patterns in year-class strength among older age groups of trout highlights the importance of recruitment to trends in trout abundance among streams within a region. By controlling for spatial variation among sites through time, use of index sites enables a coherent picture of synchronous patterns in recruitment to emerge at the regional scale and better positions fishery managers to evaluate influences of local-scale factors and larger-scale processes on local stream trout populations.

Keywords Brook trout · Brown trout · Rainbow trout · Steelhead · Recruitment · Synchrony · Rivers · Streamflow

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1 Introduction

Abiotic processes often play a driving role in population dynamics of stream-dwelling salmonids. Recruitment has been found to be synchronous among trout populations in high-gradient streams in many areas of the world, including the United States, Spain, and France (e.g., Strange et al. 1993; Nehring and Anderson 1993; Cattanéo et al. 2002; Lobón-Cerviá and Rincon 2004), with reproductive success negatively affected by high flow conditions that influence eggs and fry in redds or salmonid fry after they emerge from redds. Synchronous recruitment of Brook Trout and Brown Trout in low-gradient, groundwater-fed streams has also been documented the Great Lakes region of North America, being governed by similar mechanisms noted in more mountainous regions (Nuhfer et al. 1994; Zorn and Nuhfer 2007a). As age-0 trout disperse and age, biotic factors may become important (Elliott 1994; Bret et al. 2016), though the initial effects of stochastic factors (e.g., flow or current velocity at fry emergence) often persist even as year-classes reach maturity (Strange et al. 1993; Lobón-Cerviá 2007; Zorn and Nuhfer 2007b; Bret et al. 2016; Kanno et al. 2016).

The spatial extent to which recruitment synchrony occurs among salmonid populations has been described for mountainous regions. Lobón-Cerviá (2004) observed synchrony in Brown Trout recruitment among Spanish stream sites less than 30 km apart and concluded that similarities in streamflow levels among sites during or just after emergence were responsible for synchrony observed in Brown Trout population dynamics. Gowan and Fausch (1996) observed synchronous changes in adult trout abundance among six Colorado streams up to 60 km apart. Copeland and Meyer (2011) noted recruitment synchrony among salmonid populations spaced up to 330 km apart.

Less is known about the spatial extent of synchrony in salmonid population levels in groundwater-fed, low-gradient streams. For low-gradient (e.g., 0.1–0.2% gradient) streams draining glacial drift deposits in Michigan, synchrony in recruitment of Brook Trout and Brown Trout was noted for populations up to 140 km apart (Zorn and Nuhfer 2007a). Zorn and Nuhfer (2007a) observed that peak spawning and estimated swim-up periods for Brown Trout were synchronous among several streams in the northern Lower Peninsula of Michigan and that temporal patterns in average May discharge (associated with fry emergence) were synchronous for streams across much of Michigan, but corresponding biodata to evaluate trout population trends and synchrony were lacking. Likewise, Kanno et al. (2016) highlighted the lack of information characterizing the spatial extent of synchronous population dynamics for wide-ranging species such as Brook Trout.

Initiation of Michigan's statewide inventory program in 2002 resulted in the establishment of over 30 salmonid population index sites throughout the state (Hayes et al. 2003), providing a spatially dispersed network of locations for assessing synchrony in recruitment of stream salmonids. These sampling locations include streams with resident Brook Trout and Brown Trout and reaches hosting naturally reproducing populations of adfluvial or resident Rainbow Trout. Negative effects of

Pacific salmonids on Brook Trout and Brown Trout populations, and of Brown Trout on Brook Trout, have been documented in Michigan and elsewhere (e.g., Waters 1983; Nuhfer et al. 2014; Zorn et al. 2020), and the extent to which such effects might obscure synchrony was unknown.

The goal of this study was to describe and better understand synchrony in Brook Trout, Brown Trout, and Rainbow Trout recruitment in low-gradient cold-water streams in the Great Lakes region of North America using data collected at these index sites in Michigan since 2002. Our specific objectives were twofold. First, we conducted a landscape-scale evaluation of whether synchrony in trout recruitment was greater for streams within a region than among regions by comparing correlations in density of trout age-classes. Second, we identified and mapped locations of trout populations whose recruitment dynamics appeared to be synchronous based on correlations between annual densities of age-0, age-1, and age-2 fish at sites, and used mapped patterns of synchronous recruitment to estimate the potential spatial extent of synchrony of recruitment in Michigan streams.

2 Methods

2.1 Study Area

Michigan, in the Great Lakes region of North America (Fig. 1), has an estimated 47,535 km of stream reaches capable of supporting salmonids (Zorn et al. 2018). Streams in this relatively flat region of North America support trout populations year-round due to high inflows of groundwater entering stream channels located downslope of coarse-textured glacial moraines and outwash features (Wiley et al. 1997; Zorn et al. 2002, 2020).

Michigan streams host an array of trout and salmon species, most of which are not native to the state (Zorn et al. 2018). Resident stream trout populations are largely self-sustaining, consisting of Brown Trout and Brook Trout. Brown Trout was first introduced into Michigan (and North America) in 1884, while Brook Trout is native to Michigan's Upper Peninsula and the northern tip of the Lower Peninsula (Zorn et al. 2020). Both species were widely stocked into Lower Peninsula streams during the late 1800s, resulting in widespread establishment of Brown Trout and substantial range expansion for Brook Trout (Zorn et al. 2020). Both species spawn in fall, with data from several Michigan streams indicating synchrony in periods when peak spawning and fry emergence occur (Zorn and Nuhfer 2007a).

Adfluvial populations of Rainbow Trout became established in Michigan within 20 years of the species introduction in 1876 (Michigan Department of Natural Resources (MDNR) 1974). Chinook Salmon and Coho Salmon were initially introduced in 1966 and 1967 to reduce nuisance-level populations of invasive Alewife *Alosa pseudoharengus* (Zorn et al. 2020). Adfluvial populations of these three species in the Great Lakes represent a combination of naturally reproduced and hatchery fish, with the contributions from each source varying by location (Zorn et al. 2020).

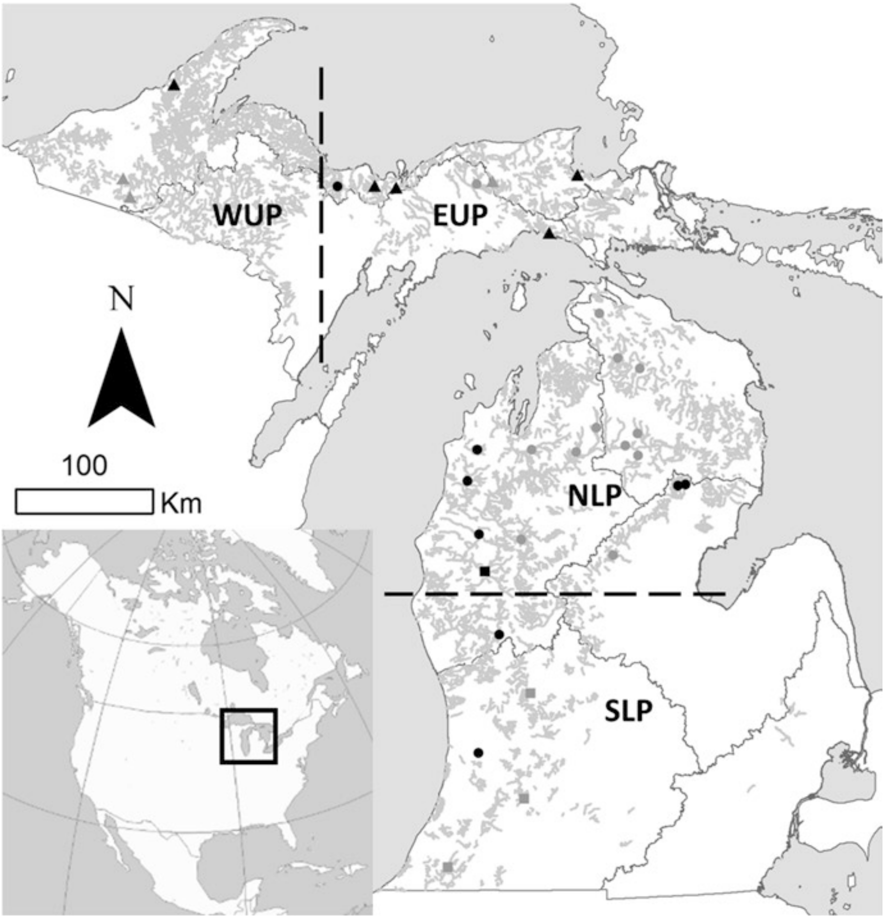

Fig. 1 Locations of index reaches on cold-water streams (gray lines) in Michigan, indicating Great Lakes accessibility and resident trout species present. Sites accessible to Pacific salmonid species are black and inaccessible (land locked) sites are gray. Possible combinations of resident trout species at sites were both Brook Trout and Brown Trout (circles), only Brook Trout (triangles), and only Brown Trout (squares). Dashed lines separate study regions Eastern and Western Upper Peninsula (EUP and WUP), and the Northern and Southern Lower Peninsula (NLP and SLP)

Fish population data were obtained from 32 long-term population index reaches (fixed sites) sampled from 2002 to 2019 under MDNR Fisheries Division's Status and Trends Program (Hayes et al. 2003). Fixed sites are geographically representative, providing a range of sizes, with some having Great Lakes access and others not (Table 1; Fig. 1). Most fixed sites were established at the initiation of the Status and Trends Program in 2002, with a few sites being added or discontinued since (Zorn et al. 2020). Trout populations in each stream are sustained entirely by natural reproduction and are representative of quality trout waters in that area of the state (Zorn et al. 2020).

Table 1 Attributes of study reach including region, stream name, site coordinates, trout species present indicated by "X" (BKT = Brook Trout, BNT = Brown Trout, RBT = Rainbow Trout), sampling rotation (1 or 2), with Great Lakes accessible (G Lks) reaches indicated with "Y". List is sorted by region (Fig. 1) and latitude of the reach sampled on a river (R) or creek (Cr)

Region	Stream	Latitude	Longitude	BKT	BNT	RBT	Rotation	G Lks
WUP	Elm R	47.02689	−88.85787	X		X	2	Y
WUP	Two Mile Cr	46.39431	−89.31069	X			2	
WUP	Middle Branch Ontonagon R	46.27693	−89.23872	X			1	
EUP	Naomikong Cr	46.46127	−84.98575	X		X	2	Y
EUP	Tahquamenon R	46.42391	−85.79789	X			1	
EUP	East Branch Fox R	46.40467	−85.94731	X	X		1	
EUP	Rock R	46.39078	−86.91258	X		X	1	Y
EUP	Chocolay R	46.38406	−87.26437	X	X	X	1	Y
EUP	North Branch Valley Spur	46.38060	−86.70893	X		X	2	Y
EUP	Davenport Cr	46.08248	−85.26009	X		X	2	Y
NLP	West Branch Maple R	45.55113	−84.79639	X	X	X	2	
NLP	West Branch Sturgeon R	45.25537	−84.63091	X	X	X	2	
NLP	Pigeon R	45.18495	−84.42838	X	X	X	1	
NLP	Manistee R	44.80001	−84.84069	X	X		1	
NLP	North Branch Au Sable R	44.75737	−84.45760	X	X		2	
NLP	Au Sable R	44.67992	−84.57599	X	X	X	1	
NLP	Platte R	44.65955	−85.94386	X	X	X	1	Y
NLP	Boardman R	44.65733	−85.43771	X	X		1	
NLP	North Branch Manistee R	44.64122	−85.02698	X	X		1	
NLP	South Branch Au Sable R	44.61379	−84.45641	X	X		1	
NLP	Bear Cr	44.45612	−86.03139	X	X	X	2	Y
NLP	Gamble Cr	44.41485	−84.02862	X	X	X	2	Y
NLP	Houghton Cr	44.40824	−84.09631	X	X	X	1	Y
NLP	Little Manistee R	44.10448	−85.92491	X	X	X	1	Y
NLP	Pine R	44.06974	−85.54030	X	X	X	2	
NLP	North Branch Tobacco R	43.95969	−84.70352	X	X		1	
NLP	Pere Marquette R	43.86023	−85.87194		X	X	1	Y
SLP	Bigelow Cr	43.44592	−85.74408	X	X	X	2	Y
SLP	Bear Cr	43.05770	−85.46510		X		2	
SLP	Silver Cr	42.66847	−85.93237	X	X	X	1	Y
SLP	Spring Brook	42.36344	−85.52986		X		1	
SLP	Pokagon Cr	41.91440	−86.20560		X		1	

2.2 Sampling Methods

Fish populations at fixed sites were sampled during 2002–2019. Fixed sites are generally sampled in 3 years on 3 years off rotations which enables broader spatial coverage (for a fixed level of sampling effort) of Michigan while allowing estimation of annual survival of resident trout age-classes in 2 of the 3 survey years at a site (Wills et al. 2006; Zorn et al. 2020). About 90% of electrofishing reaches were 305 m, with longer or shorter survey reaches (from 229 to 488 m in length) occurring for some sites to match reaches historically sampled prior to 2002 (Zorn et al. 2020).

Population estimate surveys were typically conducted at the same time of year for an individual reach, with the low-flow month of August being the target period for surveys across all fixed sites in Michigan (Zorn et al. 2020). Salmonid population estimates were made via mark–and–recapture electrofishing (without block nets) using 240-volt DC tow-barge or backpack electrofishing units. The number of anodes used ranged from one to three across all survey locations, varying with stream size, but was consistent through time at each survey reach (Zorn et al. 2020). Fish sampling began at the downstream end of the study area and proceeded upstream. Resident trout and Pacific salmonids captured on the marking run received a small caudal fin clip to identify them on the recapture run; clips were regenerated between years (Zorn et al. 2020). Recapture collections were typically made 1–2 days after marking. Population estimates were computed for 25-mm length groups of resident trout using the Chapman modification of the Petersen mark–recapture method (Ricker 1975). Scales were taken from up to 10 trout per 25-mm length group and the aging results were used to apportion population estimates by length groups into estimates by age-class (Zorn et al. 2020). Additional detail on field and population estimation methods occurs in Wills et al. (2006) and Zorn et al. (2020).

Population estimates were reasonably precise with the standard deviation about non-zero estimates for age-0, age-1, and age-2 trout being within 18.5%, 13.4%, and 19.1% of the estimate value, based on 550, 530, and 276 population estimate surveys, respectively (Zorn and Hessenauer, unpublished data). Field survey measurements, scale aging data, and population estimates from all surveys are stored in a centralized database. We queried species and age-class-specific population estimates for each fixed site survey from this database for our analysis.

2.3 Statistical Analysis

Synchrony within regions vs. between regions—We expected synchrony to be greater among populations within a region than populations between regions, so tested the hypothesis that mean correlations for pairs of sites within a region would be more positive than those based on pairings of sites among regions. We divided the state into four regions (Fig. 1) having similar spatial extent and watershed-based boundaries generally corresponding to existing MDNR fisheries management units, the Southern Lower Peninsula (SLP), Northern Lower Peninsula (NLP), Eastern Upper Peninsula (EUP), and Western Upper Peninsula (WUP). We focused on age-0, age-1, and age-2 Brown Trout, Brook Trout, and Rainbow Trout, analyzing each age-species combination separately and combining results for the two sampling rotations. For each species-age combination, we obtained Pearson correlations for all pairs of sites within the region and did the same for all pairs of sites representing each combination of regions. We then calculated the mean and standard error for all correlations within and between regions. We did not report values for regions where there were insufficient pairs of sites for computing a standard error value. These criteria eliminated WUP sites from the analysis.

Identifying pairs of synchronous populations—We examined correlations among age-class densities to identify pairs of sites where trout populations appeared to be synchronous, restricting our selection of potentially synchronous sites as follows. For sites having at least 5 years of paired population estimates, we identified pairs of sites whose Pearson correlation coefficients for a given species and age-class were positive and significant at $P < 0.05$. We limited our selection to pairs of sites having at least 5 years of observations to minimize the likelihood of spurious correlations due to low sample sizes and excluded significant correlations for pairs of sites when zeros made up the large majority (e.g., all but one or two) of the density estimate values for a location.

For each species and age-class studied, pairs of sites showing synchrony were mapped using lines to connect significantly correlated sites. Visual analysis of spatial patterns in significant correlations provided insight into the potential spatial extent of synchronous recruitment patterns for each species in Michigan.

3 Results

Synchrony within regions vs. between regions—Summary of 923 correlation coefficients indicated synchrony in age-class densities was generally greater among streams within a region than between streams in neighboring regions for Brown Trout and Brook Trout, but not Rainbow Trout (Table 2). For each age-class of Brown Trout, mean correlation coefficients from all pairings of sites within the NLP and SLP were higher than mean correlation values when NLP and SLP sites were paired, though considerable variation occurred around each mean value (Table 2). The same was true for Brook Trout, except that the mean correlation coefficient for age-1 brook trout in NLP stream pairings was lower than that from NLP-EUP pairings. For Rainbow Trout, mean correlation coefficient values from between region pairings of sites were greater than those from within region pairings of sites, except for age-1 fish in the EUP (Table 2). Several regions were not included due to limited occurrence of a species (e.g., Brown Trout in EUP and WUP; Brook Trout in SLP)

Table 2 Mean, standard error, and number (*n*) of Pearson correlations by fish species and age-class (1, 2, or 3) within and between different regions of Michigan. Regions are Northern Lower Peninsula (NLP), Southern Lower Peninsula (SLP), and Eastern Upper Peninsula (EUP). Region category with "-" between regions represents correlations for pairs of sites where one site was in each of the regions shown

	Mean correlation			SE			*n*		
Region	0	1	2	0	1	2	0	1	2
Brown trout									
NLP	0.119	0.147	0.274	0.051	0.045	0.039	70	81	81
NLP-SLP	−0.134	−0.040	−0.106	0.057	0.068	0.063	45	48	48
SLP	−0.040	0.018	0.125	0.320	0.157	0.094	4	4	4
Brook trout									
EUP	0.014	0.176	0.355	0.154	0.148	0.100	9	9	9
EUP-NLP	−0.035	0.170	−0.039	0.061	0.057	0.062	50	59	50
NLP	0.053	0.035	0.009	0.070	0.054	0.065	43	69	43
Rainbow trout									
EUP	0.023	0.444	−0.356	0.115	0.061	0.138	2	2	2
EUP-NLP	0.063	0.314	0.090	0.073	0.072	0.079	24	27	25
NLP	0.013	0.200	−0.117	0.059	0.074	0.059	32	46	37

or a lack of sites or sites within a rotation needed for calculating within region standard errors (e.g., all species in WUP; Rainbow Trout in WUP and SLP).

Identifying pairs of synchronous populations—We identified 66 significant positive correlations indicative of synchrony in recruitment between pairs of stream sites from 1252 correlations examined. Significant positive correlations in fish density occurred for age-0 Brook Trout at 9 pairs of sites, age-1 fish at 10 pairs of sites, and age-2 fish at 8 pairs of sites (Fig. 2). Correlated sites were up to 430 km apart (based on straight-line distance between sites), often spanning Great Lakes drainage divides and sometimes the Upper and Lower peninsulas of Michigan.

Brown Trout year-classes showed considerable synchrony at age-0 and as year-classes aged. Significant positive correlations in fish density occurred for age-0 Brown Trout at 8 pairs of sites, age-1 fish at 10 pairs of sites, and age-2 fish at 10 pairs of sites (Fig. 3). An additional 8 pairs of sites were approaching significance, having P values <0.10. Significant positive correlations in density occurred for sites that were up to 350 km apart.

The extent of synchrony in Rainbow Trout densities among streams seemed to differ with the age-class examined. Significant positive correlations in age-0 Rainbow Trout density occurred for only one pair of sites, but significant positive correlations occurred for 10 pairs of sites when analyzing age-1 fish, with an additional 4 pairs of sites approaching significance having P values <0.10 (Fig. 4). No pairs of sites had significant positive correlations in density of age-2 Rainbow Trout. Rainbow Trout in nearly all study reaches were from adfluvial populations, so age-2 fish may often have out-migrated to the Great Lakes prior to sampling, confounding

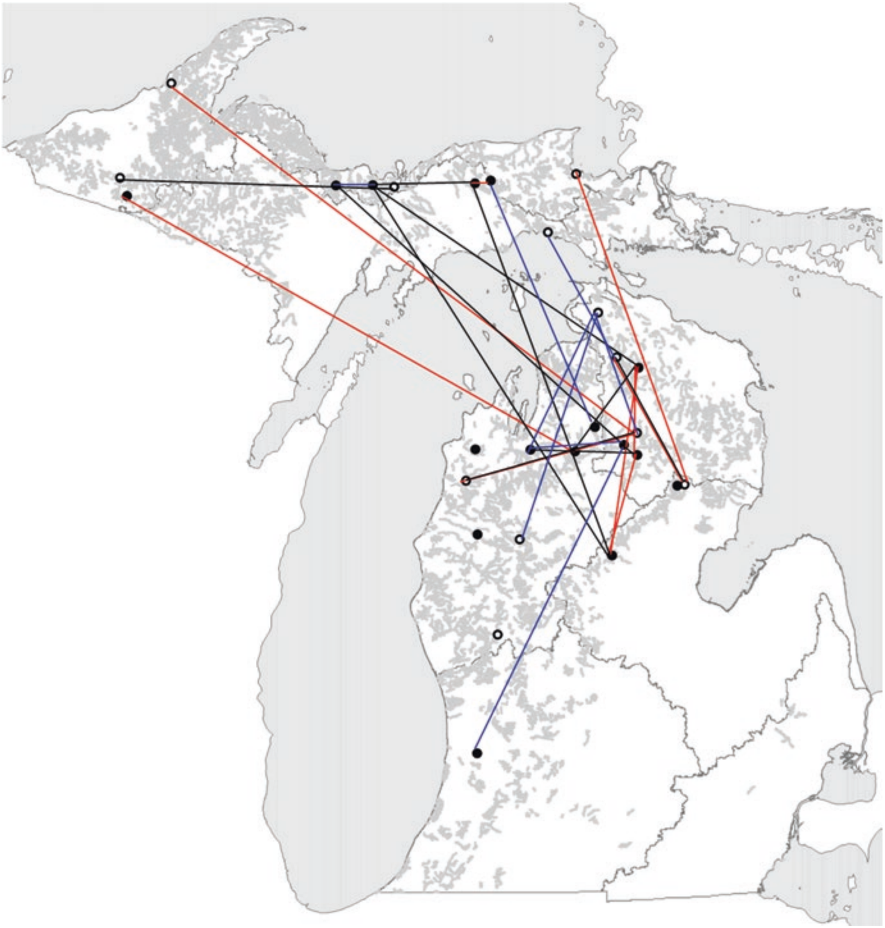

Fig. 2 Map of index sites on Michigan streams showing sampling rotation (open vs. closed circles) with lines connecting sites where densities of age-0 (red lines), age-1 (black lines), or age-2 (blue lines) Brook Trout were significantly correlated ($P < 0.05$) over time. Correlations could not be calculated between sites in different sampling rotations

detection of year-class synchrony at age-2. For sites where Rainbow Trout occurred, 54% of age-2 density values were zero while only 30% of age-0 density values were zero. Of the three species studied, age-class density values of zero occurred most often for Rainbow Trout (34% of values), followed by Brook Trout (22%) and Brown Trout (6%). Significant positive correlations in density of Rainbow Trout occurred for sites up to 260 km apart.

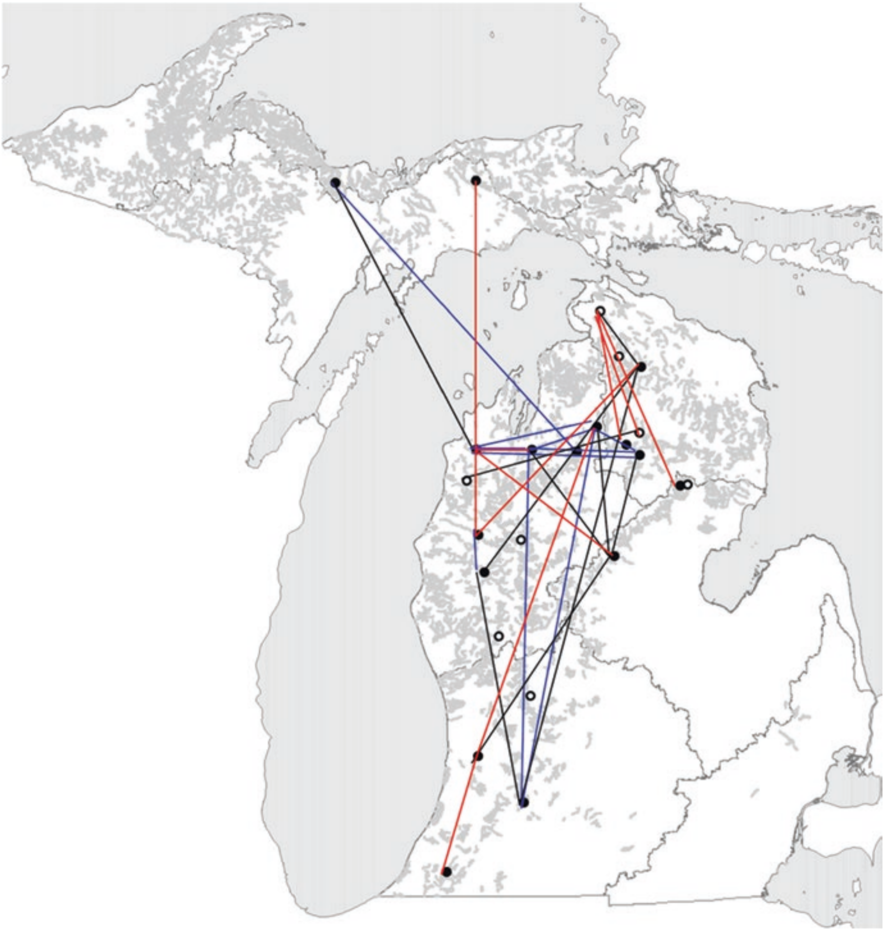

Fig. 3 Map of index sites on Michigan streams showing sampling rotation (open vs. closed circles) with lines connecting sites where densities of age-0 (red lines), age-1 (black lines), or age-2 (blue lines) Brown Trout were significantly correlated ($P < 0.05$) over time. Correlations could not be calculated between sites in different sampling rotations

4 Discussion

Our findings of stronger patterns of synchronous recruitment of Brown Trout and Brook Trout within regions compared to between regions were consistent with previous studies highlighting synchronous recruitment at relatively small spatial scales. For example, Gowan and Fausch (1996) observed synchrony in abundance of adult Brown Trout, Brook Trout, and Rainbow Trout across a 60-km area, Lobón-Cerviá (2004) noted synchrony among Brown Trout in Spanish streams less than 30 km apart, and Myers et al. (1997) suggested a scale of less than 50 km for freshwater

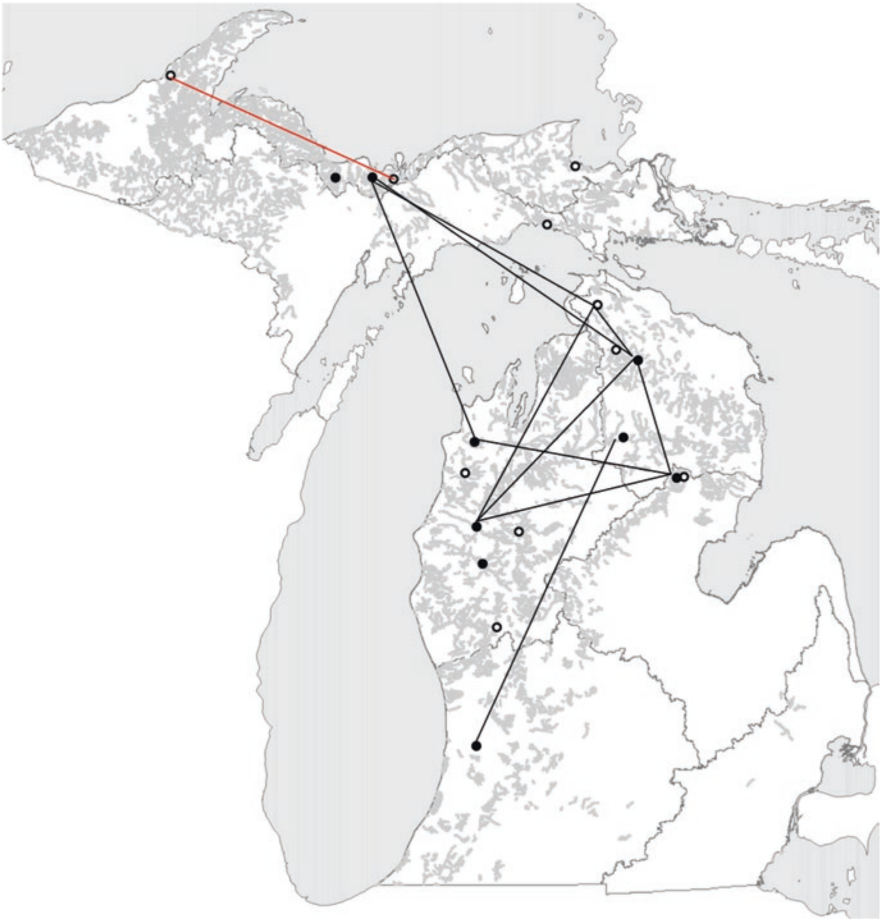

Fig. 4 Map of index sites on Michigan streams showing sampling rotation (open vs. closed circles) with lines connecting sites where densities of age-0 (red lines), age-1 (black lines), or age-2 (blue lines) Rainbow Trout were significantly correlated ($P < 0.05$) over time. Correlations could not be calculated between sites in different sampling rotations

fish. Consistent with our findings, Bergerot et al. (2019) found that synchrony among Brown Trout populations in France did not occur across the entire country but was more localized and likely to occur among streams whose streamflow patterns were synchronous, especially during periods critical for trout reproduction.

The maximum spatial extent of synchronous population dynamics we noted (430 km for Brook Trout, 350 km for Brown Trout, and 260 km for Rainbow Trout) was greater than estimates in most studies to date. Copeland and Meyer (2011) noted synchrony of six salmonid species, including steelhead and Brook Trout, across a 330 km region of Idaho. Bret et al. (2016) noted strong synchrony in Brown Trout year-classes for streams less than 75 km apart and strong synchrony in flows at emergence across distances over 200 km. The broader spatial extent of synchrony we noted likely relates to the greater sampling extent of our study and similarities in seasonal stream discharge patterns among streams in the Great Lakes region due to its relatively flat topography and uniform climate (Albert 1995). For example, Zorn and Nuhfer (2007a) documented significant correlations in May discharge among Michigan streams spanning several 100 km, many of which support trout and were included in this study.

Correlations in fish densities observed among fixed sites during 2002–2019 were consistent with findings of analyses of long-term trout population data from seven Michigan streams (Zorn and Nuhfer 2007a). As in their study, we saw significant correlations in Brook Trout and Brown Trout age-class densities for rivers in northern portion of Michigan's Lower Peninsula (Figs. 2 and 3). We also observed numerous significant correlations in Brook Trout densities between pairs of sites in Michigan's Lower and Upper peninsulas, with fewer pairs for Brown Trout since they are less widely distributed in the Upper Peninsula (Figs. 2 and 5; Table 1). Likewise, significant correlations in Brook Trout and Brown Trout density occurred between sites in northern and southern portions of the Lower Peninsula. Such correlations align with spatial correlations in spring discharge on trout streams throughout Michigan (Zorn and Nuhfer 2007a), suggesting similarity in spring flow conditions within regions help to synchronize trout year-class strength and abundance trends (Zorn and Nuhfer 2007b) over time across the region.

In contrast to the positive mean correlations we typically observed, the mean correlations for age-0 and age-2 brown trout densities between sites in the NLP and SLP were negative, having absolute values greater than 0.1 (Table 2). Opposing

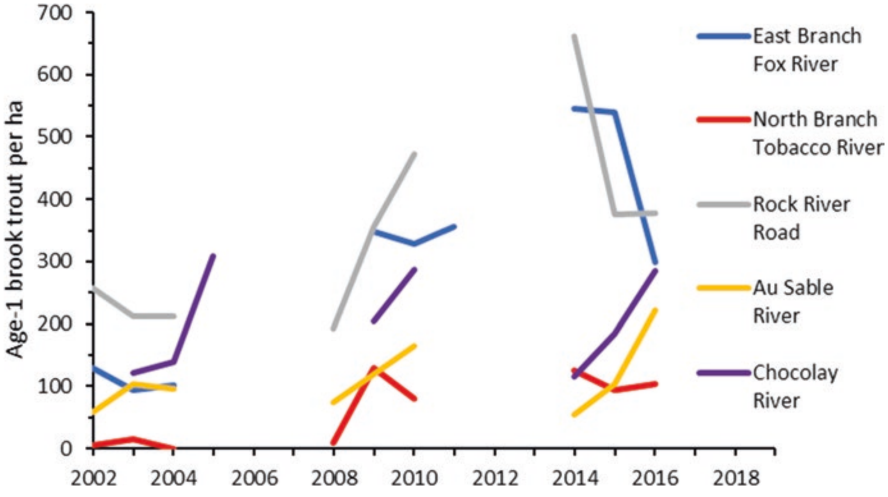

Fig. 5 Densities of age-1 Brook Trout at two fixed sites in Michigan's Upper Peninsula lacking Brown Trout (East Branch Fox River and Rock River) and three sites having both Brown Trout and Brook Trout, one in the Upper Peninsula (Chocolay River) and two in the Northern Lower Peninsula (North Branch Tobacco and Au Sable rivers)

long-term trends in spring discharge between these regions of the state (Hodgkins et al. 2007) may contribute to contrasting trends in trout recruitment, but other factors may be responsible as well.

Given the many correlations examined, one might expect a portion of them to be statistically significant due to chance. We estimated that 31 positive correlations might be statistically significant due to chance (using a two-tailed significance level of 0.05) if the 1252 correlations we examined were normally distributed. Despite our use of additional criteria to restrict selection of significantly correlated pairs of sites for mapping (Figs. 2–4), the 66 pairs we mapped represented over twice the number of significant positive correlations than would be expected by chance. In addition, correlation analyses of longer-term age-class abundance data for brook trout and brown trout at several of these sites provide further evidence of synchronous recruitment (Zorn and Nuhfer (2007a). While some correlations may be significant by chance, we conclude that most indicate populations showing synchronous patterns of recruitment.

Our study provides scarce documentation of recruitment synchrony in wild steelhead because adfluvial populations occurred at all fixed sites with Rainbow Trout, except the land-locked Au Sable and Pine river sites. Most naturally reproducing steelhead spawn in Michigan rivers between late February and early May, with peak spawning usually in April (M. Tonello, Michigan Department of Natural Resources, personal communication). Fry typically emerge in late spring or early summer and are likely similarly vulnerable to high flows as fry of Brook Trout and Brown Trout (Zorn and Nuhfer 2007a). Gowan and Fausch (1996) observed concordance in adult trout abundance in a Colorado study that included Rainbow Trout and three other trout species, but none of their study populations were adfluvial. In his study of wild steelhead population dynamics in British Columbia rivers, Smith (2000) identified flow-induced mechanisms capable of increasing juvenile mortality, loss of low-velocity refuge habitat for parr (Fausch 1993) during years of high flows and the premature flushing of juveniles out of suitable habitat or the river by high flows (Nehring and Anderson 1993; Latterell et al. 1998).

We observed significant correlations in age-1 steelhead density between distant streams in Michigan's Upper and Lower Peninsulas (Figs. 4 and 6). The relatively high level of synchrony we observed among age-1 steelhead (Table 2) may relate to the short-term nature of their interactions with resident trout (Copeland and Meyer 2011). There may also be fewer stock-recruitment influences on juvenile steelhead abundance, compared to those for stream-dwelling Brown Trout or Brook Trout (Zorn and Nuhfer 2007b), since spawning habitats in study reaches may regularly be saturated with eggs from highly-fecund female Rainbow Trout that grew to maturity in Great Lakes habitats (Chapman 1966; Nuhfer et al. 2014).

The occurrence of synchronous steelhead recruitment in Michigan streams (e.g., Fig. 4) is notable given earlier studies suggesting the considerable contribution of stocked fish to spawning runs. For example, Bartron and Scribner (2004) estimated an average of 40% of spawners in Lake Michigan tributaries in Michigan during 1998–1999 being from stocking. While our study streams were not stocked, other streams and the Great Lakes are, so the ability to detect synchrony in age-0 or age-1

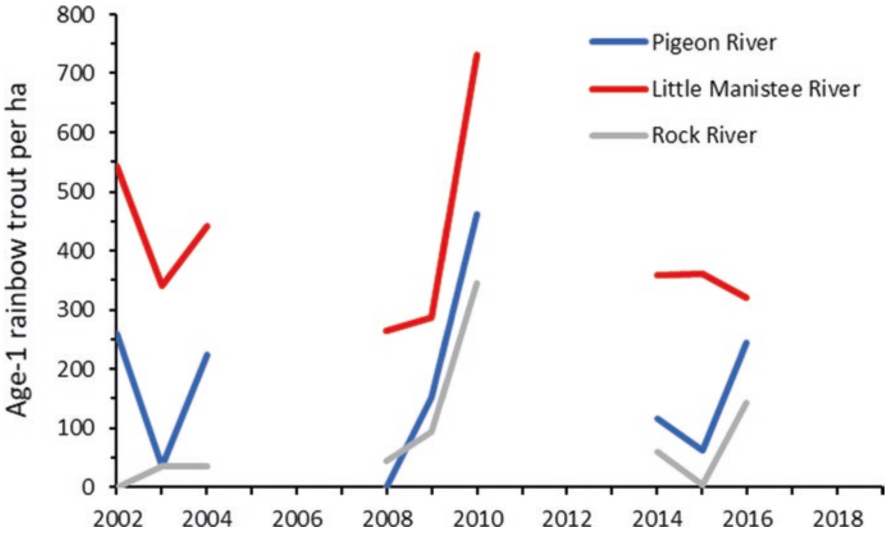

Fig. 6 Densities of age-1 migratory Rainbow Trout at one fixed site in Michigan's Upper Peninsula (Rock River) and two Northern Lower Peninsula fixed sites (Little Manistee and Pigeon rivers)

Rainbow Trout densities between some study streams could potentially be affected by spatial or temporal changes in steelhead stocking elsewhere that affect adult run size and egg deposition in study reaches.

We saw little synchrony for age-0 Rainbow Trout, but the size of age-0 fish may likely differ among rivers and years, which could influence their vulnerability to electrofishing sampling in late summer. This could limit comparability of age-0 Rainbow Trout densities among sites and years, and ultimately assessment of synchrony for age-0 fish.

We noticed that pairs of sites significantly correlated for one age-class of a species were often not correlated for other age-classes of that species. This does not necessarily indicate that synchrony does not persist between pairs of sites and may instead be indicative of immigration or emigration of fish resulting from differences between reaches in amounts of suitable habitat for each age-class of fish. Fish may stay within a reach if provides adequate habitat as they grow older and larger, but oftentimes they move elsewhere seeking food resources and habitats better suited to their changing needs. Such source-sink dynamics and differences between reaches in habitat and food resources available for a species and age-class can mask occurrence of synchrony. Thus, an apparent lack of reproductive synchrony between some nearby streams may more often relate to occurrence of habitat conditions that fish repeatedly migrate to or from than a lack of shared temporal patterns in the timing of trout spawning, incubation temperatures, or spring flow conditions (Zorn and Nuhfer 2007a).

4.1 Limitations

Some aspects of the data used in this study limit our findings, with a primary limitation being relatively small number of observations at sites. While our study covers a nearly 20-year period, streams were only sampled in half of the period due to the sampling rotation. Rotational sampling was chosen to enable greater spatial coverage of fixed sites for the limited sampling effort that was available for this work, with the understanding that it would result in fewer samples at each site over time. While this leads to greater uncertainty regarding the extent of synchrony between sites, previous documentation of synchrony among populations in some of these rivers from longer-term analysis (Zorn and Nuhfer 2007a) suggests that significant patterns of synchrony we observed in this analysis may often persist and increase in statistical significance over time as sampling continues.

While the rotational sampling enabled field crews to sample more fixed sites within their management unit, this approach sometimes hindered evaluation of synchrony between nearby fixed sites because crews often alternated annual surveys between them (i.e., their rotations differed). This issue could be addressed by periodically sampling nearby sites that were on different rotations during the same year, though this would be extra work for field crews unless scheduled sampling at other fixed sites was cancelled.

In some situations, low densities of a species at a location complicate our ability to document synchrony with certainty. Low densities of a species age-class at a site could relate to unsuitable habitat (e.g., Raleigh et al. 1986; Zorn et al. 2011), interspecific interactions that reduce the amplitude of temporal variation in abundance (Waters 1983; Nuhfer et al. 2014; Zorn et al. 2020), or other factors. To overcome this issue, we limited the selection of significant correlations to pairs of sites having densities greater than zero in most years for the species and age-class of interest. However, more years of paired observations are needed to further clarify synchrony between some pairs of sites for specific species and age-class combinations.

Deterministic processes, particularly interspecific and intraspecific interactions, are known to influence abundance of trout age-classes and can obscure effects of factors favoring synchrony in recruitment (Strange et al. 1993). In general, one might expect density-dependent survival to reduce the relative abundance of strong year-classes over time and increase the abundance of weak year-classes. Interspecific competition and predation will also alter the abundance of year-classes from levels initially “set” by flow conditions during critical periods. For example, in the relatively benign environments provided by Michigan’s groundwater-fed streams, intraspecific effects have been documented for Brown Trout and Brook Trout (Zorn and Nuhfer 2007b; Grossman et al. 2012), and interspecific effects observed for Brown Trout on Brook Trout (Zorn and Nuhfer 2007b; Zorn et al. 2020), Rainbow Trout on Brown Trout (Kocik and Taylor 1995; Nuhfer et al. 2014) and Pacific salmonids on Brown Trout and Brook Trout (Zorn et al. 2020).

4.2 Management Implications

The persistence of synchronous patterns in year-class strength to older ages highlights the importance of flow-related effects on trout recruitment and population abundance trends. The positive correlations we observed for older age-classes are consistent with previous studies with Brook Trout, Brown Trout, and migratory Rainbow Trout suggesting year-class strength effects carry through from early ages to adulthood in these species (e.g., Smith 2000; Lobón-Cerviá 2007; Zorn and Nuhfer 2007a, b). That the previous year's abundance of an age-class was often the best predictor of its abundance the following year was especially notable given significant influences of other habitat factors and inter- and intraspecific effects on age-specific densities of these species in Michigan (Zorn and Nuhfer 2007b; Nuhfer et al. 2014; Zorn et al. 2020). We suspect the propagation of recruitment and synchrony effects to older age-classes likely occurs elsewhere, given the results of trout population dynamics studies in other regions of the world (e.g., Strange et al. 1993; Elliott 1994; Gowan and Fausch 1996; Lobón-Cerviá 2007; Copeland and Meyer 2011).

By controlling for site-scale variation, our index site sampling approach enables a coherent picture of synchronous patterns in temporal variation in fish populations to emerge at the regional scale. Such temporal patterns can readily be overwhelmed by variation due to site- or stream-scale conditions when sampling locations change from year to year. For example, analysis of long-term data from four Michigan streams (i.e., mainstem Au Sable River, North and South branches Au Sable River, and South Branch Paint River) showed 50% changes in Brown Trout biomass density could be detected with 3, 3, 4, and 9 years, respectively, of pre- and post-data from the index site, while more than 15 years of pre- and post-data would be needed to detect the same change if one of these index sites was randomly chosen for sampling each year (Wills et al. 2006). Such findings highlight the need for index sites in trend monitoring programs for streams.

In addition to being of ecological interest, understanding spatial extent of synchrony has management utility. Since the waters sampled provide representative coverage of trout streams around the state, understanding the spatial extent of regional trends in trout recruitment and population synchrony better positions fishery managers to evaluate relative influences of local-scale factors and larger-scale climatic and hydrologically driven processes on trout abundance levels (Zorn et al. 2023). For example, the identification of asynchronous patterns among typically synchronous sites (e.g., low recruitment at a site during a period of high recruitment in the region) suggests local-scale factors may be affecting trout reproductive success at the site. Understanding current trout population levels is of considerable interest to anglers, fishery managers, interest groups, and individuals, so making such data publicly available is desirable. To satisfy these interests in a user-friendly manner, trout population data from fixed sites in Michigan are available online via MDNR's Stream Fish Population Trend Viewer (Zorn et al. 2023).

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