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Spatial and temporal patterns in native and invasive crayfishes during a 19-year whole-lake invasive crayfish removal experiment

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Abstract

1. Understanding where, when, and how native species persist in the face of invasive species-driven ecosystem change is critical for invasive species management and native species conservation. In some cases, ecological interactions among native and invasive species are spatially structured, and spatial segregation can be a key coexistence mechanism for ecologically similar taxa.
2. We evaluated 19-years of spatially explicit crayfish community data from a long-term whole-lake experiment, which includes 8 years of invasive rusty crayfish (*Faxonius rusticus*) removal followed by 11 years of post-removal data collection. We quantified the within lake spatiotemporal patterns of virile crayfish (*F. virilis*) and rusty crayfish, and relate their dynamics to site-level habitat conditions.
3. In response to removal efforts, rusty crayfish catch rates declined by >95%, and native virile crayfish catch rates increased by more than 20-fold. Ten years after ceasing removals, rusty crayfish have stayed at this relatively low abundance, and the virile crayfish population has remained stable. During removal, rusty crayfish abundances decreased non-uniformly throughout the lake. Only after rusty crayfish populations were at their lowest levels did the native virile crayfish population begin to show signs of a recovery.
4. Virile crayfish recovery was highly localized within the lake, and likely influenced by habitat and rusty crayfish abundance. Initially, virile crayfish made the most substantial resurgence in an area of the lake with rocky habitat conditions, but through time their distribution shifted into adjacent suboptimal macrophyte and muck habitats as rusty crayfish became more abundant in nearby areas. In general, when the two species overlapped in space, virile crayfish abundance stayed low, or the population shifted to adjacent areas with fewer competitively dominant rusty crayfish.
5. Our results suggest that habitat heterogeneity allowed virile crayfish to maintain a foothold despite high rusty crayfish densities. Removal efforts led to the recovery of virile crayfish, and spatial segregation facilitated both species coexisting at comparable abundances for a decade. Our results highlight that invasive species

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control, even in the absence of complete eradication, can benefit native species and that spatially structured interactions can promote coexistence.

KEYWORDS

coexistence, competition, invasive species, spatiotemporal dynamics, time-series

1 | INTRODUCTION

Invasive species are key drivers of global environmental change and often alter the abundance and distribution of native species (Carpenter et al., 2011; Sala et al., 2001). In some cases, invasions lead to extirpations and extinctions, therefore mitigating such impacts is central to conserving biodiversity (Clavero et al., 2009; Gurevitch & Padilla, 2004). Often, we quantify the effects of invasive species by monitoring changes in the abundance of native and invasive species populations through time (Lockwood et al., 2013). Fine-scale spatial patterns embedded within temporal trends may reveal critical ecological processes that would otherwise be lost when analyzing temporal trends alone (Tilman & Kareiva, 1997). The spatial distribution of invasive species may also provide deeper insights into mechanisms for impacts on native species (Kolb et al., 2002; Stotz et al., 2016; Wilson et al., 2004). Because spatial partitioning of shared resources can reduce competition, understanding fine-scale spatial patterns of interacting native and invasive species can help us better understand how native species persist in the face of invasions (Boeye et al., 2014; Chesson, 2000; Lehman & Tilman, 1997). Fine-scale spatial patterns and habitat use is a clear knowledge gap in our understanding of freshwater invasive species and their impacts, and may provide new insights into more commonly studied temporal trends.

This study examines the spatiotemporal patterns of native virile crayfish (*Faxonius virilis*) and invasive rusty crayfish (*F. rusticus*) populations in a north-temperate lake during and after an intensive rusty crayfish removal experiment (Hein et al., 2006, 2007). Rusty crayfish are native to the Ohio River basin and have spread predominately throughout the Midwestern U.S. and parts of Canada (Lodge et al., 2000; Phillips et al., 2009; Puth & Allen, 2005), with scattered introductions in the western U.S. (Messager & Olden, 2018; Olden et al., 2009). Rusty crayfish exert strong and pervasive ecological impacts on aquatic ecosystems (Hansen, Hein, et al., 2013; Lodge et al., 1994; Twardochleb et al., 2013), adversely affecting macrophytes (Baldridge & Lodge, 2014; Olsen et al., 1991; Rosenthal et al., 2006), macroinvertebrates (Kreps et al., 2012; McCarthy et al., 2006), and fish communities (Kreps et al., 2016; Wilson et al., 2004). Rusty crayfish can displace ecologically similar congeners (Butler & Stein, 1985; Hill & Lodge, 1994, 1999; Olden et al., 2006). This displacement is likely due to a combination of exploitative and interference competition for food resources and predation refuge (Butler & Stein, 1985; DiDonato & Lodge, 1993; Hill & Lodge, 1999). Rusty crayfish are competitively dominant for shelter, while also being less vulnerable to predation and non-consumptive effects of predators (Hill & Lodge, 1999). However, not all populations of virile crayfish are extirpated following rusty crayfish invasion (Peters & Lodge, 2013). The probability that a virile crayfish population is extirpated by rusty crayfish is higher in lakes with high amounts of cobble and sand habitat, as opposed to muck and macrophyte dominated habitats (Peters & Lodge, 2013). Despite having similar habitat preferences, in lakes where both species coexist, rusty crayfish are more common in cobble habitat while virile crayfish tend to inhabit macrophytes. This suggests competitive exclusion of virile crayfish into less-preferred habitats (Garvey et al., 2003; Peters & Lodge, 2013). It is possible that specific configurations of habitat within lakes can facilitate spatial segregation, which reduces interspecific competition and promotes coexistence (Boeye et al., 2014; Chesson, 2000; Smith et al., 2019). At the ecosystem scale, coexistence between competing species may be related to the configuration and amount of different habitat types (Boeye et al., 2014). Thus, habitat availability and configuration may influence among- and within-system variability in virile crayfish persistence.

Due to the high impact of rusty crayfish invasions, preventing further spread is the top management priority for minimizing impact. However, control efforts can in some cases be a viable management option (Blackburn et al., 2011; Vander Zanden et al., 2010). A whole-lake experiment to control rusty crayfish was initiated in 2001 in a mesotrophic seepage lake in Northern Wisconsin, USA (Hein et al., 2006, 2007). Rusty crayfish were removed from 2001 to 2008, resulting in a ≥95% reduction in abundance (Hein et al., 2007). The decline in rusty crayfish allowed the native virile crayfish, macrophytes, gastropods, and *Lepomis* sunfishes to recover (Hansen, Hein, et al., 2013). The data that resulted from this removal effort was spatially explicit, such that trap locations were tracked since the onset of the experiment. While previous analyses of the experimental results focused on change in average catch and abundance of rusty crayfish over time, how these changes have manifested spatially has not been evaluated. In the case of Sparkling Lake, the rusty crayfish removal provided an opportunity to observe both the spatial and temporal dynamics of native virile crayfish recovery (Hansen, Hein, et al., 2013; Hein et al., 2006).

Here we report on this long-term whole-lake rusty crayfish removal experiment, with an emphasis on understanding spatiotemporal patterns of rusty and virile crayfish abundance. This study has three main objectives; (a) We evaluate invasive and native crayfish populations' temporal trends over 19 years, focusing on both species' post-removal response. (b) We quantify and visualize complex spatiotemporal patterns of rusty and virile crayfish. (c) We combine our modeling efforts with habitat data to infer the importance of habitat in explaining dynamic spatial patterns. By examining changes in both the abundance and distribution of competing species, we

gain insight into how competing species respond to each other and how habitat can mediate interactions.

2 | METHODS

2.1 | Study system

Sparkling Lake is a mesotrophic, seepage lake in the Northern Highlands Lake District in Vilas County, Wisconsin, USA (46.01°, −89.7°, Figure 1). It is roughly 64 ha with a maximum depth of 20 m. Sparkling Lake has a diverse fish community, with over 35 species documented (Magnuson et al., 2019). There are three crayfish species present in Sparkling Lake; native virile crayfish, invasive rusty crayfish, and invasive northern clearwater crayfish (*F. propinquus*). The northern clearwater crayfish and rusty crayfish were introduced in the early 1970s, likely through bait buckets (Capelli, 1982). In general, there is a competitive hierarchy among the three crayfish, with the northern clearwater crayfish often displacing virile crayfish and rusty crayfish displacing both the northern clearwater crayfish and virile crayfish. We focus our discussion on virile and rusty crayfish because the northern clearwater crayfish has been very rarely detected in Sparkling Lake in the last 20 years (Magnuson et al., 2019). Additionally, rusty crayfish negatively impact northern clearwater crayfish through hybridization (Arcella et al., 2014; Perry et al., 2001), which may explain why northern clearwater crayfish are so rarely observed in our system.

2.2 | The experiment and sampling

A whole-lake experiment to reduce rusty crayfish was initiated in 2001. Crayfish populations were sampled using modified Gee-style wire-mesh minnow traps; the trap's mouth was expanded to a diameter of 35 mm. Based on a comparison of diver surveys and crayfish traps, it was found that while traps tend to be male-biased, they are reliable for tracking changes in abundance (Capelli & Magnuson, 1983; Olsen et al., 1991). The traps were baited with ~120 g of beef liver and placed at the 1–2 m depth contour for 1–3 days. We express crayfish catch-per-unit effort (CPUE) as crayfish per trap-day. All rusty crayfish sampled from 2001 to 2008 were removed, while other crayfish species were returned to the lake. Forty-three sites were sampled from 2001 through 2019 between June and August (Figure 1). We conducted spatially-explicit sampling in all years, except for 2007, 2008, 2012, and 2014. Sampling intensity varied from year to year, depending on field staff's availability (Table 1). This resulted in 15 years of spatially explicit data, covering 24 to 43 sites with a total of 5,584 unique sampling date-location combinations (Table 1).

In addition to trapping, the Wisconsin Department of Natural Resources changed the fishing regulations in 2001 to protect predatory fish populations that may consume crayfish. The daily harvest limit for smallmouth bass (*Micropterus dolomieu*) decreased from 5 to 1 fish, and the minimum length increased from 357 to 457 mm (Hein et al., 2006). It is unclear what effect the regulation changes had on predator populations, but fish predation contributed to the suppression of rusty crayfish by consuming large quantities of smaller crayfish while trapping removed mostly larger, more fecund individuals that are less vulnerable to fish predation (Hein et al., 2007). These efforts resulted in decreased rusty crayfish CPUE, increases in *Lepomis* sunfishes, increases in virile crayfish populations, and a return of macrophyte beds (Hansen, Hein, et al., 2013).

2.3 | Habitat data

Littoral habitat was surveyed in 2002 and 2003 using SCUBA and was characterized as either predominately sand, cobble, or macrophytes using 23 transects perpendicular to the shore. Habitat along a transect was characterized from 0 to 8 m. Habitat deeper than 8 m was classified as muck. Habitat in the entire littoral zone was interpolated between transects using bathymetric maps to extend the habitat data from each transect to the midpoint between other transects. Macrophyte cover increased since 2003 following the decline in rusty crayfish abundance (Hansen, Hein, et al., 2013). Therefore, we simplified our habitat data to proportion cobble for each transect because we believe macrophytes predominately recovered in more sandy areas.

2.4 | Statistical analysis

We used generalized additive models (GAMs) to examine the spatial and temporal variability of rusty and virile crayfish CPUE in Sparkling Lake from 2001 to 2019. GAMs are a flexible regression method that can estimate smooth, non-linear trends (Pedersen et al., 2019; Wood, 2017). We used GAMs because our crayfish sampling is an unevenly spaced time series, making the application of traditional time series methods extremely challenging to implement due to the requirement of evenly spaced sampling (Simpson, 2018). Separate GAMs were parameterized for rusty and for virile crayfish. We used crayfish counts per trap from each unique trapping event (Table 1) as our response variable with negative binomial distributed errors and a log link function (Zuur, 2009). To account for differences in sampling effort, we included the log of trap-days (number of traps multiplied by nights soaked) as an offset variable. All covariates used to model crayfish CPUE were included as smooth functions. Year was included as a Gaussian process smoother fitted using a Matérn correlation function (Kammann & Wand, 2003). Because catches can vary seasonally, we included Julian date as a main effect with a cyclic smooth term (i.e., cyclic cubic spline basis). Cyclic cubic splines constrain the spline's endpoints to be equal to each other, allowing for continuity between the first and last day of the year (Wood, 2017). To model the spatial variability of crayfish CPUE, we assigned each of the 43 sampling locations encircling the perimeter of the lake a distance along the shoreline (km), which was included in

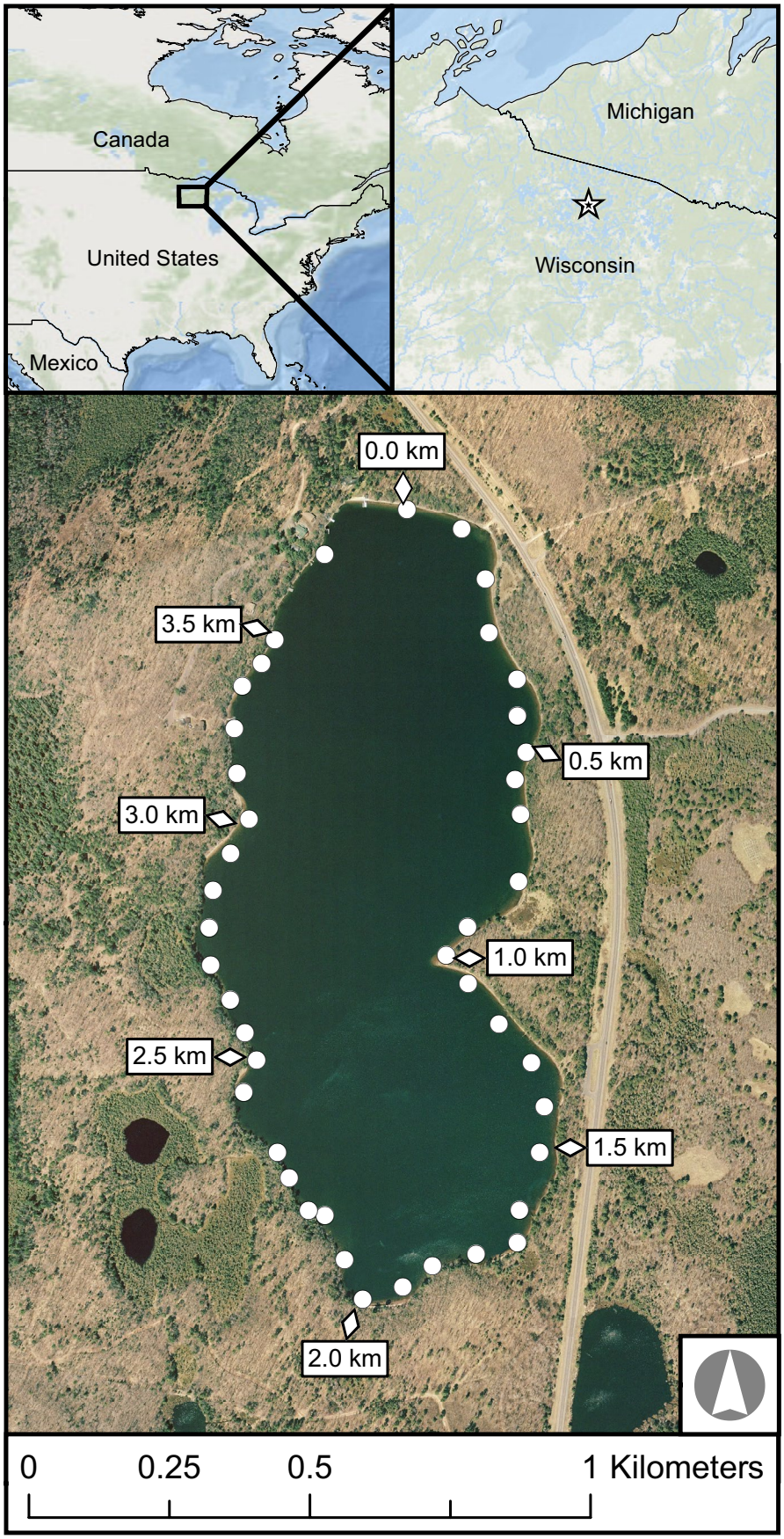

FIGURE 1 Location of Sparkling Lake in Vilas County, Wisconsin, USA. Crayfish sampling locations are indicated by a white circle and the distance along the shoreline is indicated by a white diamond (total shoreline length: 3.78 km)

TABLE 1 Distribution of crayfish sampling effort by year. Unique locations sampled is the number of unique locations that were sampled in a year and indicates the spatial coverage of sampling. Unique dates sampled represents the number of unique sample outings, which indicates the intensity of sampling in a year. The total number of trapping events is the number of unique location-date combinations, which is the sample size by year

Year	Unique locations sampled	Unique dates sampled	Total number of trapping events
2001	43	19	369
2002	43	41	563
2003	43	53	953
2004	43	49	1,592
2005	43	3	129
2006	43	4	172
2007	0	0	0
2008	0	0	0
2009	29	11	276
2010	26	20	514
2011	29	10	278
2012	0	0	0
2013	24	6	89
2014	0	0	0
2015	25	8	200
2016	25	2	50
2017	25	6	148
2018	26	5	126
2019	25	6	125

the model (Figure 1). Like modeling the seasonal effect, the effect of distance along the shoreline was modeled with a cyclic cubic spline smoother, which allowed for the beginning and end sites along the shoreline perimeter to be adjacent. Adjacent sites are assumed to be more similar to each other than sampling locations located across the lake. This assumption is reasonable for an organism that is primarily restricted to the littoral zone and with relatively small home ranges (Byron & Wilson, 2001). Sparkling Lake is relatively deep and stratified with a mud bottom in the deposition zone, which makes it unlikely that crayfish occupy this area because there is little to no predation refuge, and it contains cold hypolimnetic water.

We included an interaction term between year and distance along the shoreline (i.e., tensor product). This final term allows us to model any variation from the main temporal or spatial trend shared among years or sites, respectively. In summary, these GAMs allowed us to model the seasonal variation, the main temporal trend, the spatial variability, and the interaction between the spatial variability and temporal trend of crayfish CPUE. GAMs were fit using the "mgcv" package (version 1.8-31, Wood, 2017) in R (version 3.6.3, R Project for Statistical Computing). The optimal basis dimensions (k') for each specific smoother was found using 'gam.check' iterations from the "mgcv" package. k' was increased until the p-value was >0.05 or until the maximum number degrees of freedom was reached. To visualize the broad temporal and spatial patterns of rusty and virile crayfish while controlling for seasonal effects on catch rates, we use the species-specific GAMs to predict CPUE as a function of distance along the shoreline moving clockwise from the northernmost point on the lake and year, with Julian date fixed at a median value of 203 (range 154–242). This approach allowed us to calculate confidence intervals and make predictions for locations or years that were not sampled.

3 | RESULTS

3.1 | Temporal trends

Sparkling Lake's crayfish assemblage has undergone dramatic changes due to the experimental removal of rusty crayfish (Figure 2). Virile crayfish population rebounded, while rusty crayfish declined substantially. Rusty crayfish were very abundant in the early years, with an annual mean CPUE of 9.4 in 2001. CPUE declined due to the removal efforts, with 11 of 12 years having a mean CPUE of <1 from 2004 to 2019 (Figure 2). Rusty crayfish comprised 99.9% of the catch from 2001 to 2008 compared to 73.9% from 2009 to 2019. Rusty crayfish were more abundant than virile crayfish in all years except for 2011, where both species were equally abundant. Virile crayfish CPUE began to increase around 2006 once rusty crayfish CPUE had been reduced (Figure 2). The mean virile CPUE from 2001 to 2008 was 0.005, while the mean CPUE from 2009 to the present was 0.107. Thus, the virile crayfish population increased and has remained relatively stable since the rusty crayfish decline, although rusty crayfish CPUE remains about double that of virile crayfish.

3.2 | Spatial patterns

The distribution of virile and rusty crayfish was spatially and temporally dynamic within Sparkling Lake. Rusty crayfish were sampled throughout the perimeter of the lake, with the southwest region having relatively higher CPUE (Figure 3a). Generally, rusty crayfish were abundant in most regions of the lake, and their distribution became more heterogeneous in later years of the removal. Despite being reduced in numbers, the proportion of sites where rusty crayfish were present remained stable and ranged from 72% to 100% (Figure 4). Virile crayfish were relatively rare and absent from most locations within Sparkling Lake during the rusty crayfish removal years (Figure 3a). The few sites where they consistently occurred were in the southeast corner (Figure 3). The proportion of sites occupied ranged from 2.3% to 20.9% from 2001 to 2006 (Figure 4). Once rusty crayfish populations declined, virile crayfish began to recover (Figure 3). Virile crayfish presence at sites increased to 31% in 2009 and stabilized around 57% from 2010 to 2019 (range 50%-68%, Figure 4). Virile crayfish expanded northward along the eastern shore, with a few occurrences on the north shore in 2015–2017, but

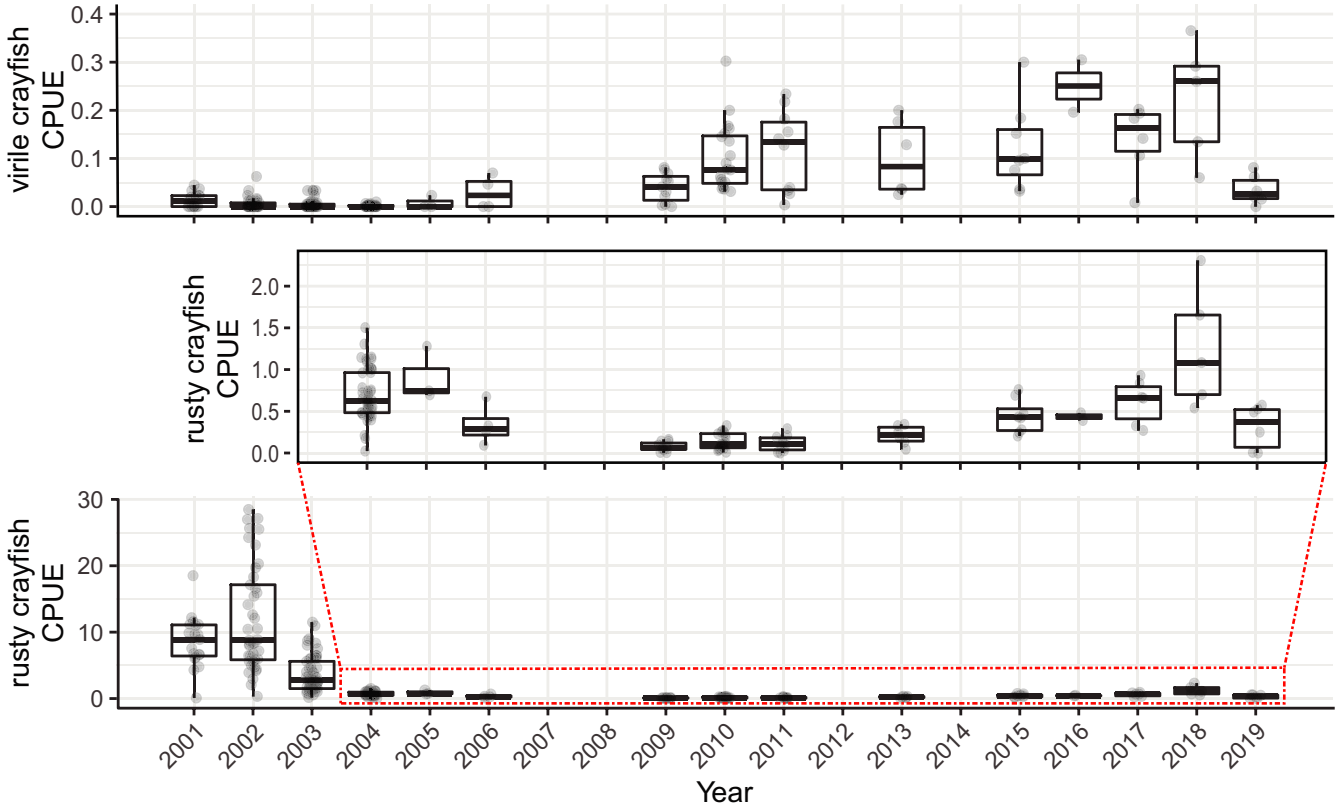

FIGURE 2 Time series of rusty and virile crayfish CPUE. Rusty crayfish were removed from 2001 to 2008. The inset shows a zoom of rusty crayfish CPUE after abundances decreased. Box plots show 1st and 3rd quartile, along with the median. The whiskers are quartiles ±1.5× interquartile range. Each point represents a lake-wide mean for a unique date of sampling. There are no spatially explicit data available for 2007, 2008, 2012, and 2014

virile crayfish were once again limited to Sparkling Lake's southern half in 2019. The species composition also changed at each site over time (Figure 3b). Rusty crayfish comprised most of the crayfish sampled at many sites, with virile crayfish beginning to make up more of the catches in the lake's southeast quarter from 2009 to 2019 (Figure 3b).

3.3 | Species-specific GAMs and predictions

The deviance explained by species-specific GAMs was 76.7% for virile crayfish and 82.8% for rusty crayfish. The non-linear smoothing terms for Julian date, year, distance along the shoreline, and the interaction term between year and distance along the shoreline were significant in both crayfish models ($p < 0.0001$). Our analysis showed that the abundance and distribution of rusty and virile crayfish shifted over time (Figure 5).

During the removal years (2001–2008), rusty crayfish abundance decreased sharply, but the decrease was non-uniform in space (Figure 5). Rusty crayfish CPUE decreased faster in some areas of the lake, most notably when comparing panel 2001 to 2004. Rusty crayfish distribution became more uniform beginning in 2007 until around 2013. Around this time, rusty crayfish hotspots developed around the 2.5 and 3.5 km markers. These locations of higher rusty crayfish CPUE were consistent from 2013 to 2019.

Virile crayfish were exceptionally rare from 2001 to 2008. A virile crayfish hotspot emerged at around the 1.8 km marker in 2009. As rusty crayfish became more abundant in nearby habitats, peak virile crayfish CPUE shifted away from the 1.8 km marker (see 2010 in Figure 6) to around the 1.2 km marker (see 2017 in Figure 6). The resurgence of virile crayfish was highly localized and began once rusty crayfish abundances were reduced through trapping. The region where rusty crayfish decreased the fastest is where a virile crayfish hotspot initially developed, but this hotspot shifts over time, away from emerging nearby rusty crayfish hotspots.

These spatial patterns appear to be associated with habitat (Figure 6). In the 2010 panel in Figure 6, the initial recovery of virile crayfish occurred in an area with a mixture of substrate sizes, including some sand and cobble (1.8 km marker). In the 2017 panel of Figure 6, the virile crayfish hotspot had shifted out of the intermediate cobble areas and into a primarily sandy area (1.2 km marker) as rusty crayfish in adjacent habitats become more abundant. We used the GAMs to predict abundance at each site through time and visually inspect trends across a proportion cobble gradient (Figure 7). In general, virile crayfish recovery trajectories varied along this littoral

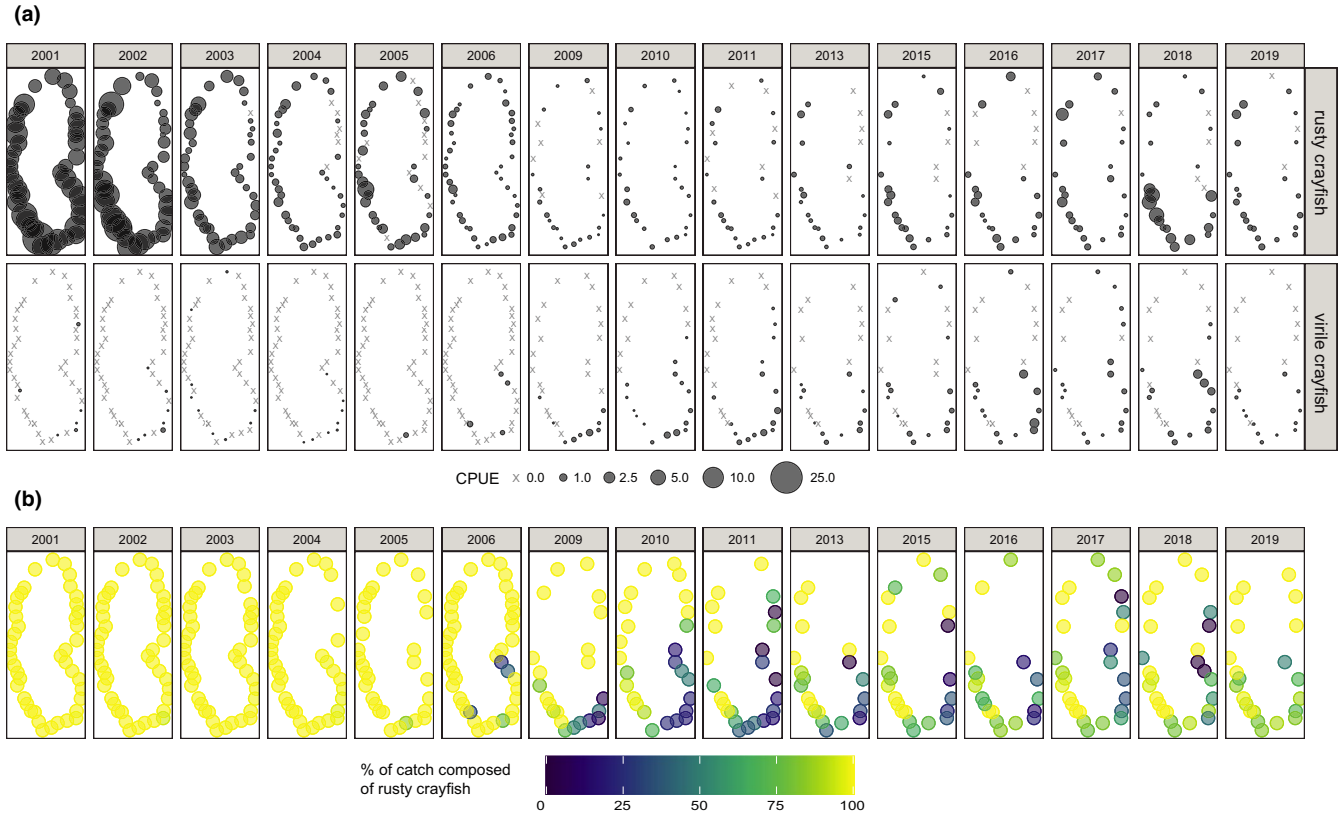

FIGURE 3 Observed spatiotemporal patterns of crayfish abundance and species composition showing concentrations of rusty and virile crayfish. Each panel represents a year and each point represents data for a location along the perimeter of Sparkling Lake. Note there are gaps for 2007, 2008, 2012, and 2014. (a) Each point is an annual mean for a sampling location along the perimeter, with size indicating CPUE. An x indicates that sampling was conducted but no individuals of that species were sampled, and no point indicates a site was not sampled in that year. Rusty crayfish CPUE is the top row and virile crayfish CPUE is the middle row. (b) Color of each point indicates the percent of the annual catch that is made up of rusty crayfish. Lighter colors indicate more rusty crayfish and darker colors indicate more virile crayfish

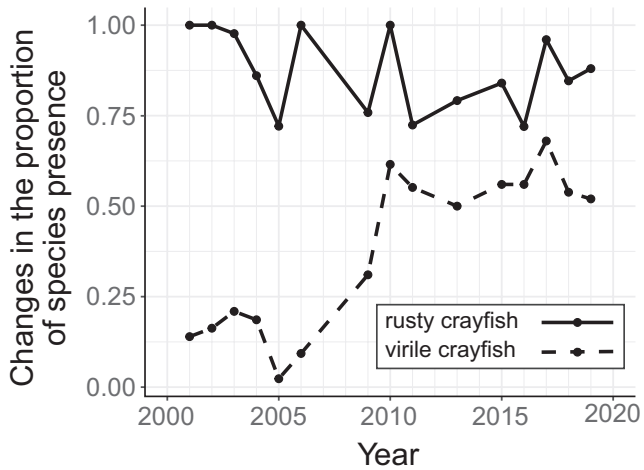

FIGURE 4 Time series showing changes in the proportion of rusty and virile crayfish presence at sampled sites (rusty crayfish = solid line, virile crayfish = dashed line)

habitat gradient. Sites with low cobble (≤50%) showed a stronger resurgence of virile crayfish compared to higher cobble areas (Figure 7). Meanwhile, rusty crayfish trajectories post-removal were highly variable and appear not to be as strongly tied to substrate characteristics as virile crayfish, although cobble habitats generally had higher rusty crayfish CPUE.

4 | DISCUSSION

This study reports on a 19-year whole-lake experiment, which includes eight years of invasive rusty crayfish removal followed by 11 years of post-removal data collection. Recognizing that many ecological dynamics occur over multi-decadal timescales, the unique combination of a long-term study, a whole-ecosystem experiment, and spatiotemporal analysis aims to improve our understanding of the spatial ecology of competing native and invasive species. First and foremost, rusty crayfish populations remained low after removal efforts ended over a decade ago. Although the removal efforts were a major undertaking, this suggests that suppression of this problematic invasive species is possible without complete eradication. Further, we documented a subsequent ~20-fold increase in the abundance of native virile crayfish, implying that the rehabilitation of displaced native crayfish populations is also possible.

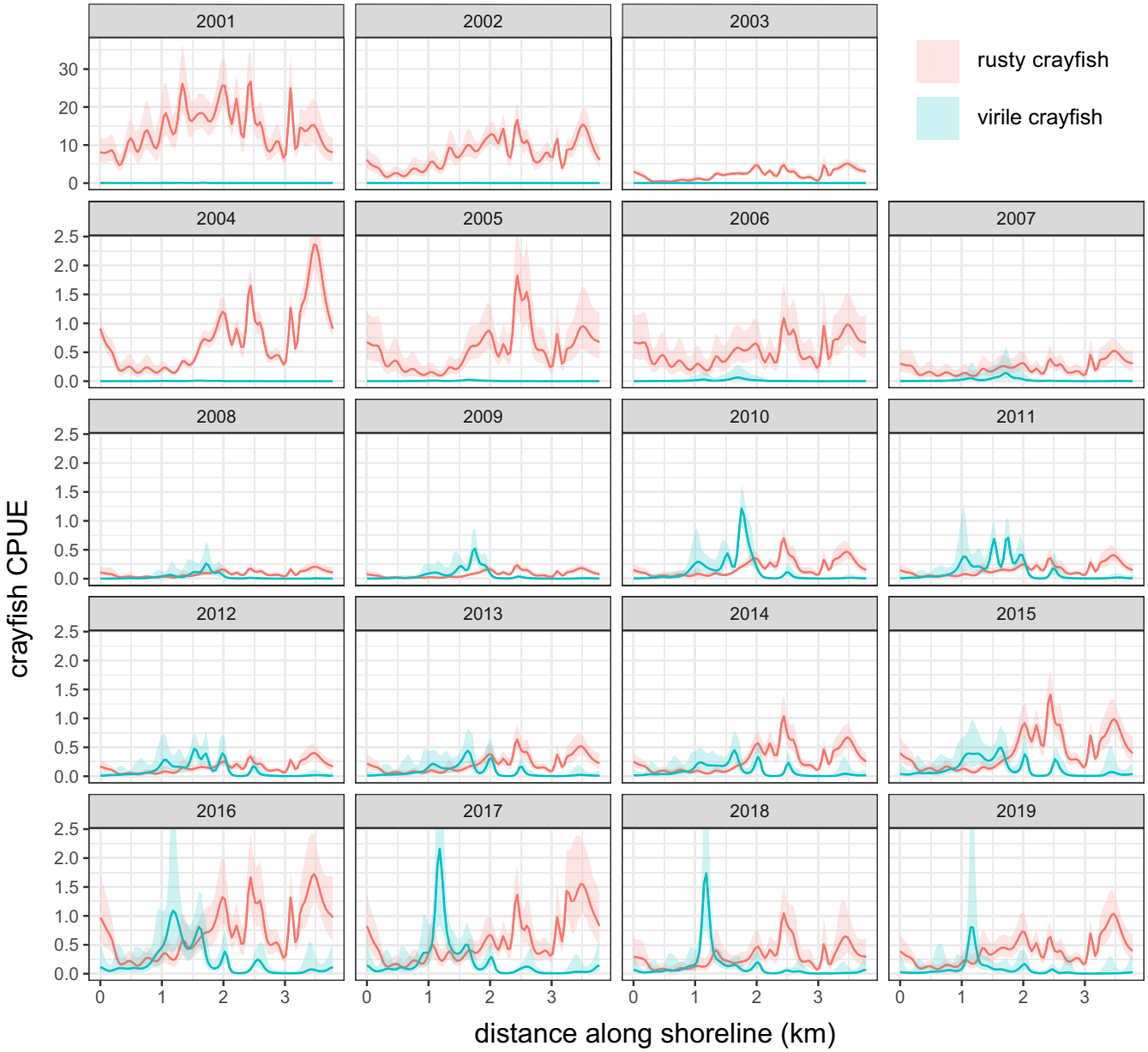

FIGURE 5 Generalized additive model predictions of rusty (red) and virile (blue) crayfish CPUE, and 95% confidence intervals showing change in spatial distribution by year. To visualize annual and spatial patterns in CPUE, we fixed Julian date at a median value of 203 (range 154–242). Note that the cyclic cubic spline regression forces the ends of the CPUE lines to match. The top three panels have a different y axis than the rest of the panels. The values in the 2007, 2008, 2012, and 2014 are entirely interpolated because no spatially explicit data exists for those years

Additionally, our analysis of 15 years of spatially explicit crayfish sampling data demonstrated that virile and rusty crayfish occurred in spatially distinct areas, and that abundance hotspots were temporally dynamic. In general, the distribution of virile crayfish and rusty crayfish hotspots minimally overlapped, and their dynamics appeared to be related to substrate characteristics. Our results suggest that the coexistence of these competing crayfish species was promoted by the intensive removal of invasive rusty crayfish, but also the habitat heterogeneity in this system. This allowed for spatial segregation of these two species, with the caveat that the spatial distribution of these species varied notably through time.

The original goal of the removal experiment that began in 2001 was to test if alternative stable states exist in this system and if removal efforts, coupled with fisheries management, could suppress a problematic population of rusty crayfish. Interestingly, the rusty crayfish population has remained at a low abundance compared to historical highs, despite ceasing removal efforts over a decade ago. While this study did not formally test whether the documented changes in Sparkling Lake represent alternative stable states, our results, in addition to modeling efforts by Hansen, Ives, et al. (2013) and empirical support of proposed positive feedbacks that keep rusty crayfish populations low or high (Roth et al., 2007), suggest

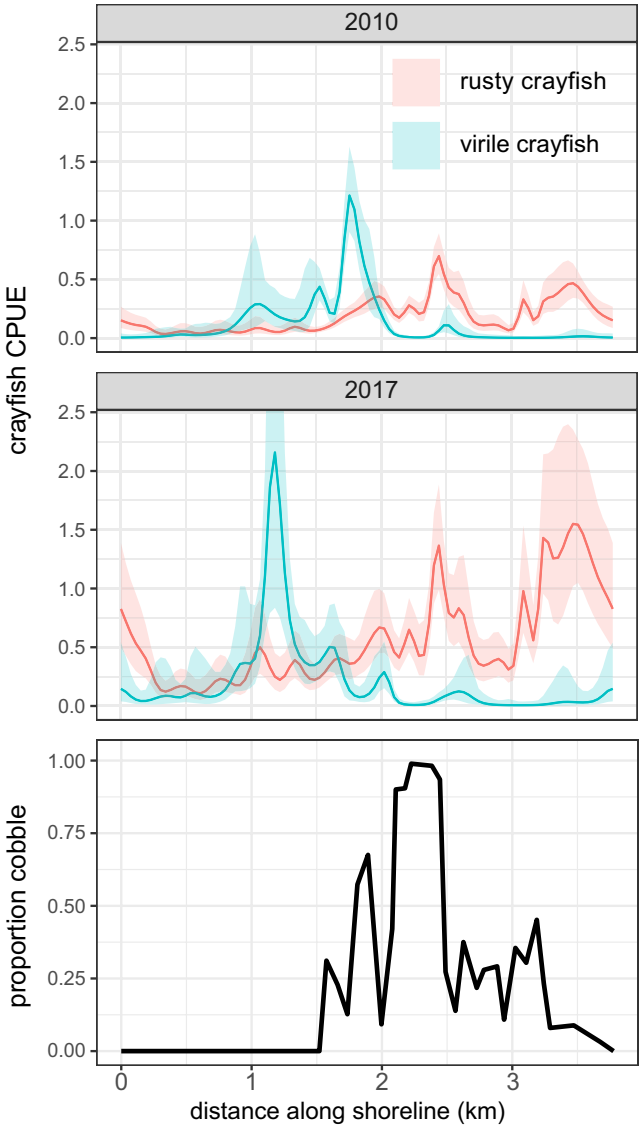

FIGURE 6 Predicted crayfish CPUE for 2010 and 2017 (reprinted from Figure 5) and littoral habitat characteristics along the shoreline. Predicted rusty (red) and virile (blue) crayfish CPUE and 95% confidence intervals showing change in spatial distribution by year. The bottom panel is the proportion of cobble habitat along Sparking Lake's shoreline

this may be the case. Rusty crayfish populations are thought to be controlled by reciprocal relationships between crayfish, macrophytes, and predatory centrarchid fishes (Roth et al., 2007). Macrophyte beds, and thus centrarchids that depend on macrophytes, can recover once rusty crayfish populations are reduced. Once centrarchids become more abundant, they exert predation pressure on juvenile rusty crayfish. The persistence of rusty crayfish populations at low levels in Sparkling Lake suggests some of these feedbacks were strong enough to suppress rusty crayfish populations for a decade without further intervention. Additionally, given that the removal of rusty crayfish with traps primarily targets larger individuals (Hein et al., 2006), and that competitive outcomes among crayfish species are size dependent (Lorenz et al., 2019; Nakata & Goshima, 2003; Rabeni, 1985), it is possible that virile crayfish may be partially controlling rusty crayfish populations once many of the larger individuals were removed.

There have been many ecological changes associated with the reduction of rusty crayfish populations in Sparkling Lake (see Hansen, Hein, et al., 2013). The resurgence of virile crayfish in response to the collapse of rusty crayfish populations has been especially encouraging. In Sparkling Lake, virile crayfish were rarely sampled from 2001 to 2005. However, virile crayfish have since become more abundant, with the lowest mean CPUE occurring in 2004 and the highest in 2016 (0.0012 vs. 0.25 CPUE). Further illustrating their recovery, virile crayfish presence at sites has more than doubled since the end of rusty crayfish removal efforts. Because rusty crayfish often displace and replace virile crayfish (Olden et al., 2006; Olsen et al., 1991; Roth & Kitchell, 2005), a reversal of this trend is an indication that the removal efforts have strongly mitigated the negative impacts of rusty crayfish (Hansen, Hein, et al., 2013). Other researchers have suggested that the recovery of a virile crayfish population displaced by rusty crayfish is unrealistic for several reasons (Hill & Lodge, 1999). In general, virile crayfish are more vulnerable to fish predation and suffer higher mortality rates due to non-consumptive effects compared to rusty crayfish (DiDonato & Lodge, 1993; Hill & Lodge, 1999). Specifically, the presence of rusty crayfish increases predation on virile crayfish by excluding them from refuge (Wilson et al., 2004). Thus, any increase in predatory fish populations would be expected to disproportionately impact virile crayfish. Further, rusty crayfish tend to be bolder and can feed longer, and therefore maintain higher growth rates than virile crayfish under similar conditions (Hill et al., 1993). Despite literature suggesting that recovery of virile crayfish populations is unlikely, our results indicate that a displaced virile crayfish population can recover and persist if rusty crayfish populations are reduced.

This study's unique contribution is the analysis of spatial patterns in abundance of two co-occurring crayfish species and how these patterns change over time. Habitat heterogeneity, habitat selection, and competitive interactions between these two crayfish species most likely underlie the documented spatial patterns. There is strong literature support for the idea that crayfish species have specific habitat associations but that these associations can change when other crayfish species are present (Garvey et al., 2003; Smith et al., 2019). In general, virile and rusty crayfish have similar preferences for cobble, and to a lesser extent, muck bottom macrophyte habitats when not sympatric (Hill & Lodge, 1994). In sympatry, virile crayfish tend to occupy soft substrates among macrophytes, likely due to competitive exclusion by rusty crayfish (Garvey et al., 2003; Peters & Lodge, 2013; Smith et al., 2019).

Virile crayfish increased notably after rusty crayfish abundance declined, but the increase was confined to specific regions of the lake. This may have been affected by rusty crayfish abundances in nearby habitats and local habitat conditions. Virile crayfish are competitively subordinate to rusty crayfish and adjust habitat associations in response to rusty crayfish. In Sparkling Lake, the initial

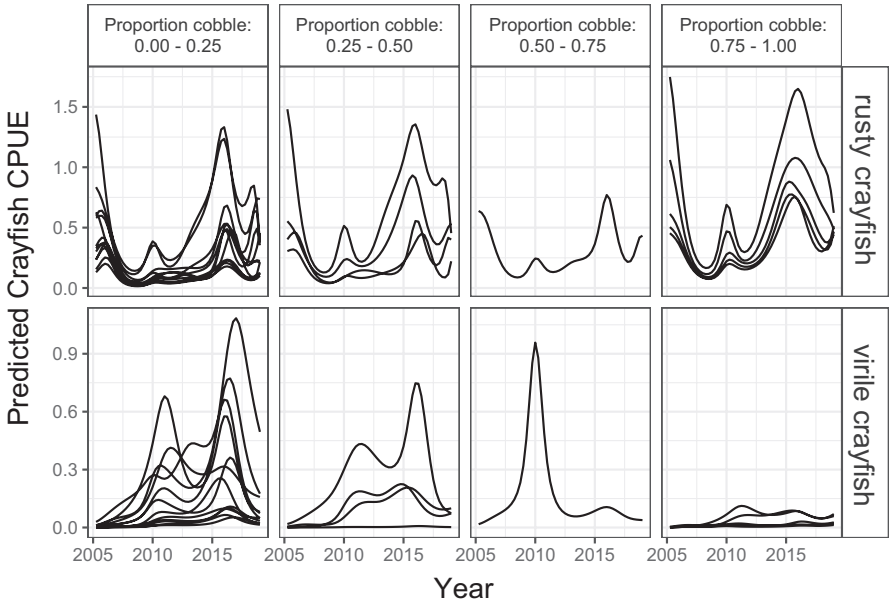

FIGURE 7 Generalized additive model predictions of rusty (top row) and virile (bottom row) crayfish CPUE time series, faceted by proportion cobble at a site, showing different recovery trajectories by habitat. Each line represents a sampling location with at least 12 of 15 years of spatially explicit data available. Low cobble sites are in the leftmost column of panels, with the highest cobble proportion sites in the right column. The time series start at 2005 to highlight the dynamics once rusty crayfish abundances were reduced

recovery area of virile crayfish was not the same as the hotspot that emerged in later years. Virile crayfish initially recovered in areas where rusty crayfish declined most rapidly, but eventually shifted away from these areas as rusty crayfish increased in adjacent areas following the cessation of trapping. This shift likely represents a habitat selection trade-off between ideal habitat conditions and the density of a competing species (i.e., ideal free distribution, Fretwell & Lucas, 1970; Křivan et al., 2008). Together, these lines of evidence suggest that intermediate cobble areas were ideal for virile crayfish when rusty crayfish populations were less abundant, but as rusty crayfish abundance increased, these areas became less suitable for virile crayfish. Regardless of how these hotspots arise, spatial habitat segregation likely facilitates coexistence, as intraspecific aggregation has been shown to be an important coexistence mechanism in other systems (Ives, 1991).

In contrast to the above scenario, other areas of the lake with similar mixed cobble and sand did not show similar patterns of initial virile crayfish recovery, further illustrating how virile crayfish respond to rusty crayfish. These other locations had higher abundances of rusty crayfish at the end of the removal period, which may have preempted recolonization by virile crayfish. These areas serve as interesting comparisons; both areas have similar substrate characteristics but had different abundances of rusty crayfish when virile crayfish were beginning to recover in the lake around 2009. The area with higher rusty crayfish never saw the same level of virile crayfish recovery that occurred in the lower rusty crayfish area, likely due to some degree of spatial preemption. By combining temporal and spatial approaches to understanding the dynamics of these two crayfishes, our results suggest that the abundance of rusty crayfish can alter the site-specific recovery trajectory of virile crayfish in otherwise favorable habitats.

Habitat likely plays a role in the recovery of both species as well. In general, the recovery trajectory for virile crayfish was related to substrate characteristics, with more sandy and mucky sites having a stronger resurgence. While the recovery trajectories among habitat type were variable, none of the cobble dominated sites (≥50% cobble) showed appreciable increases of virile crayfish, likely because these cobble dominated areas represent population strongholds for rusty crayfish. It is unclear why virile crayfish recovery was more pronounced in the more sandy, mucky, macrophyte dominated habitats. These areas often represent suboptimal crayfish habitat due to lack of predation refuge and increased mortality rates due to adverse abiotic conditions (DiDonato & Lodge, 1993; Peters & Lodge, 2013). On the other hand, rusty crayfish recovery trajectories were far more variable among habitat types. While rusty crayfish showed appreciable recovery in most of the cobble dominated areas, they also demonstrate similar patterns in less cobble dominated areas. Our data agree with previous literature that indicates cobble is preferred rusty crayfish habitat, and that virile crayfish are relegated to suboptimal habitat when rusty crayfish are present (Larson et al., 2019; Smith et al., 2019).

While we attempt to explain the spatiotemporal patterns of virile and rusty crayfish using habitat data, our analysis leaves open the possibility that other habitat or biotic characteristics can play a key role. Specifically, our habitat data does not include macrophyte coverage or coarse woody habitat density, both of which can be key littoral zone attributes (Strayer & Findlay, 2010). Macrophytes in Sparkling Lake demonstrate their own complex spatiotemporal dynamics, especially in the context of the experimental removal of rusty crayfish. Macrophytes recovered following the rusty crayfish removal (Hansen, Hein, et al., 2013; Hein et al., 2006). Unfortunately, we lack data on macrophytes at the appropriate spatial resolutions to properly inform the patterns we document. Similarly, we lack data on the spatial distribution of predatory fish, which likely affects the distribution and abundance of crayfish (Garvey et al., 2003; Wilson et al., 2004). Similar to macrophytes, the fish assemblage in Sparkling Lake dramatically changed in response to the reduction of rusty crayfish. *Lepomis* sunfishes recovered following rusty crayfish removal,

and likely play a key role in suppressing rusty crayfish population growth (Hansen, Hein, et al., 2013). However, more research must be conducted to deduce how the increase in predatory fish populations has affected within lake distributions of crayfish. Further, multi-year droughts can influence the quantity and quality of littoral habitats via water level fluctuations, and have done so in Sparkling Lake (Gaeta et al., 2014; Perales et al., 2020; Watras et al., 2014). During the rusty crayfish removal, water levels decreased, presumably decreasing the amount of coarse substrate available to crayfish, which may have contributed to their decline. However, water levels have since risen to record highs, likely increasing the amount of cobble habitat available, yet the post removal resurgence of rusty crayfish has been weak. Although unexplored in our system, it has been suggested that negative impacts from *Microphallus* trematode infections may be another mechanism maintaining low rusty crayfish populations (Sargent et al., 2014).

While the outcome of the whole-lake rusty crayfish removal is encouraging, there remains some uncertainty regarding whether rusty crayfish will continue to remain at low abundances. Some of our results could be interpreted as early indicators of a reversal of the experimental removal of rusty crayfish. For instance, over time, rusty crayfish has pushed virile crayfish into suboptimal habitat, and are more abundant in cobble habitats. Rusty crayfish catch has increased somewhat since removal efforts ceased, with a mean of 0.079 CPUE in 2009 and a peak in 2018 of 1.27. 2019 was the first year since 2005 that rusty crayfish comprised the majority of crayfish sampled at all sites. A key question is whether this system is poised to transition back to a rusty crayfish dominated state. Assessing this will require continued monitoring. Further, our study illustrates the value of spatially explicit analysis as a more comprehensive approach to tracking ecologically important changes in abundance. By examining the changes in animal distributions during either recovery or decline, we gain rich insight into how interacting populations respond to each other and how habitat can mediate those interactions.

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DATA AVAILABILITY STATEMENT

The data that support this study are publicly available at https://doi.org/10.6073/pasta/64ce4692762ae512925f5cac4d91d8d1.

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