



Do rusty crayfish (*Faxonius rusticus*) invasions affect water clarity in north temperate lakes?

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Abstract

Invasive crayfish can cause shifts in lakes from clear, macrophyte-dominated states to eutrophic, phytoplankton-dominated states because of their burrowing and foraging behavior. While invasive crayfish populations have been linked to declines in water clarity of shallow lakes and wetlands in Asia and Europe, little research has been done on the potential for similar effects of invasive rusty crayfish (*Faxonius rusticus*) in large temperate lakes of the Midwestern USA. We related *F. rusticus* abundance in 17 lakes of northern Wisconsin, USA over time (1984–2018) to measures of lake clarity (chlorophyll *a* concentration and Secchi disc depth) estimated from remote sensing (Landsat imagery). Contrary to the effects of invasive crayfish in other study systems, we found a weak, positive association between *F. rusticus* abundance and water clarity. We propose that lake clarity may increase if declines in small fishes caused by *F. rusticus* lead to population growth of zooplankton and consequent decreases in phytoplankton through a trophic cascade. Alternatively, *F. rusticus* could be passengers to, rather than drivers of, lake clarity trends, responding positively to increased littoral benthic productivity when lakes are clearer. Future research should aim to determine if *F. rusticus* causes or responds to changes in water clarity, but should also investigate the impacts of crayfish invasions on water clarity across a greater variety of lentic ecosystems.

Keywords Remote sensing · Invasive species · Landsat · Secchi disc · Chlorophyll *a*

Introduction

Invasive species can be major drivers of ecological change, with negative effects on native biodiversity, human well-being, and ecosystem services (Pejchar and Mooney 2009). Aquatic invasive species are particularly harmful, with many of their impacts mediated through ecosystem engineering (Matsuzaki et al. 2009; Gallardo et al. 2016). In freshwater lakes, invasive species occasionally cause transitions in lake clarity from clear to turbid conditions, often due to bioturbation and the destruction of nearshore aquatic macrophytes (Parkos et al. 2003; Matsuzaki et al. 2009). Destroying macrophytes is particularly impactful on lake clarity because macrophytes trap nutrients in nearshore environments and

prevent their use by offshore phytoplankton (Takamura et al. 2003). Invasive common carp (*Cyprinus carpio*) are well known for causing declines in the water clarity of shallow lakes and wetlands (e.g., Williams et al. 2002; Parkos et al. 2003), but similar impacts have also been observed for other invasive species, such as the red swamp crayfish (*Procambarus clarkii*). Changes in water clarity from clear to turbid states because of macrophyte destruction and burrowing by *P. clarkii* have been documented in shallow lakes and wetlands in Asia and Europe (Angeler et al. 2001; Rodríguez et al. 2003; Geiger et al. 2005; Matsuzaki et al. 2009). Other crayfish invaders also destroy macrophytes (Usio et al. 2009; Twardochleb et al. 2013), but shifts in lake clarity like those caused by *P. clarkii* have not been documented for other invasive crayfish.

The invasive rusty crayfish (*Faxonius rusticus*), native to the Ohio River watershed of the eastern USA, was introduced to lakes in the northern USA and Canada through pathways such as the bait trade (Capelli and Magnuson 1983; Olden et al. 2006). In invaded lakes, *F. rusticus* reaches hyper-abundance relative to native crayfishes, causing declines in fishes, macrophytes, and macroinvertebrates

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such as freshwater snails (Wilson et al. 2004; Roth et al. 2007), and impacts of *F. rusticus* on these community members are consistent with other, globally invasive crayfishes like *P. clarkii* (McCarthy et al. 2006; Twardochleb et al. 2013). The loss of benthic organisms and macrophytes at the base of food webs following *F. rusticus* invasions can alter energetic pathways in lakes, further exacerbating the impacts of this species (Kreps et al. 2016; Nilsson et al. 2012). In just one county, economic costs of *F. rusticus* invasion were estimated at \$1.5 million annually due to lost fishing opportunities for yellow perch (*Perca flavescens*) and sunfish (*Lepomis* spp.; i.e., Keller et al. 2008).

The total cost of *F. rusticus* invasions (including loss of fisheries, decreased recreation, decreased home values, etc.) may be even higher than previous estimates if *F. rusticus* decreases water clarity through either its destruction of macrophytes or bioturbation while foraging (Dodds et al. 2009). Like *P. clarkii*, *F. rusticus* reduces the abundance and species richness of macrophytes by consumptive and non-consumptive effects (Lodge and Lorman 1987; Twardochleb et al. 2013). The negative relationship between *F. rusticus* and macrophytes is strong, with severe declines of macrophytes at typical abundances for this species (Wilson et al. 2004; Roth et al. 2007; Vander Zanden et al. 2017). However, changes in water clarity due to macrophyte loss or bioturbation in the temperate lakes invaded by *F. rusticus* have not been documented. The vulnerability of ecosystems to water clarity alterations is affected by characteristics such as lake size and depth (Scheffer et al. 1993; Jeppesen et al. 1997; Scheffer and van Nes 2007). Therefore, the larger, deeper lakes invaded by *F. rusticus* could be more resistant to crayfish-induced changes in water clarity than the shallow lakes and wetlands where *P. clarkii* has been studied (e.g., Rodríguez et al. 2003). Alternatively, it could be that shifts in water clarity due to *F. rusticus* invasions have just been undocumented or overlooked relative to other impacts of this invader.

We combined a long-term dataset of *F. rusticus* populations (Larson et al. 2019) with remote sensing data from Landsat satellites (e.g., Brezonik et al. 2005; Rose et al. 2017) to evaluate linkages between crayfish invasions and lake clarity in 17 north temperate lakes between 1984 and 2018. Long-term datasets are rare but important for understanding the impacts of invasive species, which vary over time and with invasion stage (Strayer et al. 2006, 2017; Sokol et al. 2017). For example, studies of the impacts of *P. clarkii* on water clarity were conducted over less than a decade, usually in single water bodies or mesocosms (Angeler et al. 2001; Rodríguez et al. 2003; Matsuzaki et al. 2009). In contrast, our use of Landsat data permitted the inclusion of lakes and time periods for which in situ measurements of water clarity were not available (e.g., Olmanson et al. 2008; Rose et al. 2017), expanding the spatial and temporal

replication of the study. We expected that *F. rusticus* might decrease water clarity in north temperate lakes due to its well-documented destruction of aquatic macrophytes, similar to the effects of *P. clarkii* in shallow lakes and wetlands in Asia and Europe. Conversely, our study lakes could be resistant to modifications in lake clarity because of their relatively large size and depth, revealing context dependency of invasive crayfish impacts to lentic ecosystems (Thomsen et al. 2011; Sokol et al. 2017).

Methods

Study region

We used a long-term dataset on *F. rusticus* relative abundance for 17 lakes in Vilas County, Wisconsin, USA (Fig. 1 and Table 1; Larson et al. 2019). Lakes of this region were formed during the last glaciation and are generally oligotrophic to mesotrophic, although some have naturally low clarity due to high concentrations of dissolved organic matter from wetlands in their watersheds (Hanson et al. 2007). Land cover in this sparsely populated study region consists of deciduous and coniferous forest (62%), wetlands (25%), and lakes (13%), but human development along lake shorelines has increased in recent decades, primarily due to the construction of summer homes (Carpenter et al. 2007; Hanson et al. 2007). Additionally, northern Wisconsin experiences severe winters, and during winter months lake surfaces are covered with ice, though climate change is causing average ice duration to decrease over time (Hewitt et al. 2018). There are also occasional periods of drought, and the consequent changes in lake water level can negatively impact aquatic organisms like crayfish (Hansen et al. 2013). *Faxonius rusticus* was introduced to Vilas County in the 1960s through invasion pathways including live fishing bait and has widely established in lakes with firm or rocky substrates and sufficient (> 2.5 mg/l) calcium levels (Capelli and Magnuson 1983; Olden et al. 2006).

Population monitoring of *F. rusticus*

Population monitoring for *F. rusticus* across 67 lakes in Vilas County, Wisconsin began in 1972 (Capelli and Magnuson 1983). Various researchers continued monitoring *F. rusticus* populations in this region following the same methods as Capelli and Magnuson (1983), creating a standardized dataset of *F. rusticus* abundance (Olsen et al. 1991; Larson et al. 2019). We chose to use *F. rusticus* abundance data from a subset of 17 lakes that were sampled most often (10–17 times; Fig. 2) between the original sampling and 2018. *Faxonius rusticus* was already the dominant crayfish in some of the study lakes when sampling began, but other

Fig. 1 The 17 study lakes in Vilas County, Wisconsin, with study lakes in blue and all other surface waters in grey. The lakes used to train remote sensing models are cross-hatched (including Trout Bog and Crystal Bog). Sparkling Lake served as a proxy lake for data on climate covariates (ice duration, water level, water temperature) that might affect water clarity



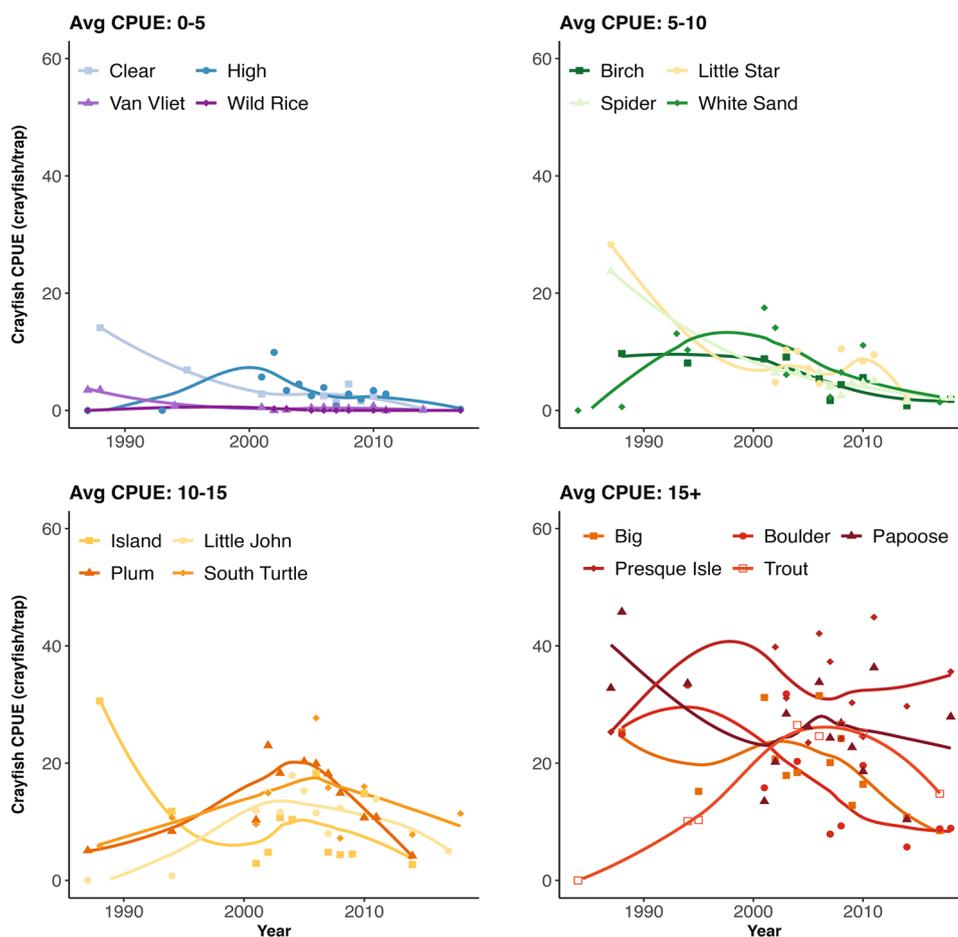
Table 1 Summary of study lake characteristics in Vilas County, Wisconsin, including GPS coordinates (latitude, longitude as decimal degrees), surface area (km²), maximum depth (m), average crayfish

catch-per-unit effort (CPUE, crayfish trap⁻¹; Larson et al. 2019), and CPUE range (crayfish trap⁻¹)

Lake	Lat, long	Surface area	Max depth	Avg. CPUE	CPUE range	Avg. Chl- <i>a</i>	Chl- <i>a</i> range	Avg. SDD	SDD range
Big	46.154, -89.769	3.35	18.6	19.5	8.5–31.5	5.71	1.37–9.72	2.71	1.66–6.45
Boulder	46.124, -89.661	2.09	7.0	16.9	5.7–33.3	10.30	1.39–21.74	2.54	1.03–7.66
Birch	46.217, -89.838	2.05	13.7	5.6	0.8–9.7	7.14	1.09–11.94	2.45	1.21–6.97
Clear	46.147, -89.811	2.08	13.7	4.0	0.1–14.1	4.76	2.48–8.45	3.28	1.83–4.91
High	46.155, -89.548	3.00	11.0	3.0	0–9.9	5.18	1.26–8.18	3.21	1.86–7.24
Island	46.116, -89.792	3.50	10.7	10.1	2.7–30.6	8.30	2.4–13.34	2.07	1.42–4.40
Little John	46.014, -89.645	0.61	5.8	10.2	0–17.9	10.44	2–33.64	2.44	1.17–5.27
Little Star	46.115, -89.861	1.05	20.4	9.1	1.7–28.3	2.77	1.08–4.50	4.31	2.82–7.28
Papoose	46.184, -89.802	1.71	19.8	26.8	10.4–45.8	4.14	1.07–6.54	3.35	2.05–7.43
Presque Isle	46.222, -89.780	4.71	31.4	32.4	23.5–44.9	2.50	0.8–3.74	4.84	3.10–9.41
Plum	46.003, -89.519	4.28	17.4	13.7	4.2–23	4.88	1.4–7.18	3.06	1.82–5.98
Spider	46.121, -89.823	1.13	13.1	6.2	1.5–23.8	5.47	2.05–10.32	2.76	1.62–4.64
South Turtle	46.211, -89.894	1.89	12.2	11.0	5.9–16	8.38	2.24–14.46	2.42	1.40–6.61
Trout	46.041, -89.671	15.64	35.7	17.2	0–26.5	2.31	0.70–3.51	5.29	3.29–10.32
Van Vliet	46.193, -89.757	0.93	6.1	0.8	0–3.5	6.95	1.26–9.98	2.43	1.63–6.98
Wild Rice	46.065, -89.797	1.55	7.9	0.1	0–0.3	6.39	2.02–12.05	2.56	1.23–4.75
White Sand	46.088, -89.594	3.02	21.6	7.0	0–17.5	3.64	1.12–5.71	3.66	2.40–7.33

Lake location, surface area, and maximum depth are from Wisconsin Department of Natural Resources (<https://dnr.wi.gov/lakes/lakepages/>). We used our remote-sensed estimates of water clarity to calculate average Chl-*a* (µg.L⁻¹), Chl-*a* range (µg.L⁻¹), average Secchi disc depth (SDD, in m), and the range of Secchi disc depth values (m)

Fig. 2 *Faxonius rusticus* CPUE by lake during the study period (1984–2018), sorted by average CPUE. For ease of interpretation, trends in *F. rusticus* CPUE are shown using locally estimated scatterplot smoothing



lakes have monitoring data which predate invasion. Many of the study lakes have maintained high *F. rusticus* abundances over time, although some have experienced recent population declines that may be due to habitat modification by the crayfish (i.e., macrophyte destruction; Larson et al. 2019) or factors such as disease (Sargent et al. 2014). Regardless, our study captures a range of *F. rusticus* abundances both between and within lakes over time (Table 1; Fig. 2).

Consistent with Capelli and Magnuson (1983), subsequent population monitoring of *F. rusticus* was conducted using cylindrical, wire-mesh Gee minnow traps with openings enlarged to 3.5 cm diameter on either end. Between 12 and 74 traps were set per lake depending on lake size and habitat heterogeneity (see Larson et al. 2019 for details), and each trap was baited with 120 g of beef liver. The same trap locations (spaced at least 100 m apart) were used each year, first identified on a bathymetric map and then later by a handheld Global Positioning System (GPS). Trapping occurred over one night at depths of 1–3 m. Because baited traps select for male crayfish, *F. rusticus* abundance was estimated by calculating catch-per-unit effort (CPUE) as male *F. rusticus* per trap, which closely matches density estimates from other methods such as SCUBA surveys (Olsen et al.

1991). Trapping almost always occurred between mid-July and late August, after *F. rusticus* had molted from its reproductively inactive Form II to its reproductively active or mature Form I.

Measures of lake clarity

We chose two measures of water clarity, chlorophyll *a* concentration (Chl-*a*) and Secchi disc depth, which represent the possible effects of *F. rusticus* on lake clarity through either bioturbation or macrophyte destruction. Chl-*a* is an index of phytoplankton production and was selected to capture any changes in lake clarity because of increased pelagic nutrient availability due to macrophyte destruction by *F. rusticus*. We chose Secchi disc depth because it functions as an estimate of overall lake clarity and thus also accounts for any possible effects of *F. rusticus* on clarity other than Chl-*a*, such as increased turbidity from bioturbation (e.g., Angeler et al. 2001). Secchi disc depth in our study lakes includes turbidity, but is strongly influenced by dissolved organic carbon or colored dissolved organic matter (Hanson et al. 2007).

Chl-*a* and Secchi disc depth have generally not been measured in our study lakes at the same time as our crayfish

population monitoring. Accordingly, we chose to estimate these measures across lakes and years using remote sensing imagery from Landsat satellites (e.g., Brezonik et al. 2005; Olmanson et al. 2008). We chose Landsat over other sources of remote-sensed data because Landsat data are available for the greatest number of years when *F. rusticus* sampling occurred. Further, we used Landsat Level-2 data (available for 1984–present) from the United States Geological Survey (USGS) because these data have been radiometrically and atmospherically corrected (USGS 2019; <https://earthexplorer.usgs.gov/>). Consequently, even though *F. rusticus* abundance has been monitored since 1972, our choice of Landsat Level-2 data limited our use of *F. rusticus* abundance data to 1984–2018.

For training water clarity models, we chose between Thematic Mapper (TM) data from Landsat 5 (e.g., Kloiber et al. 2002; Olmanson et al. 2008), Enhanced Thematic Mapper Plus (ETM+) data from Landsat 7 (e.g., Torbick et al. 2008; Olmanson et al. 2008), and Operational Land Imager (OLI) data from Landsat 8 (e.g., Yang and Anderson 2016) based on the availability of cloud-free images from each satellite both between and within years. For sampling years prior to 1999, only TM data were available. From 1999 through 2012, both TM data and ETM+ data were available, and from 2013 through 2018 both ETM+ and OLI data were available. In each year, we selected the Landsat image that was the most cloud free and taken closest to August 15th, the approximate midpoint of crayfish trapping over time, to ensure the images accurately represented water clarity when *F. rusticus* sampling occurred. In cases where data from different satellites were taken equally close to August 15th, we selected TM or OLI data over ETM+ data due to the 2003 Scan Line Corrector (SLC) failure on Landsat 7.

We trained remote sensing models of Secchi disc depth and Chl-*a* using empirical field data collected by the North Temperate Lakes Long-Term Ecological Research Network (NTL-LTER; funded by the National Science Foundation and operated by the University of Wisconsin—Madison: <https://lter.limnology.wisc.edu/>). Since 1981, Secchi disc depth and Chl-*a* have been routinely monitored for seven lakes (including Trout Lake; Fig. 1) in the study region by the NTL-LTER. The NTL-LTER measures Secchi disc depth every 2 weeks during the ice-free season at the deepest

point of each lake. The NTL-LTER uses spectrophotometry to measure Chl-*a* every 2 weeks from water samples taken at the deepest point of each lake at anywhere from two to ten different depths, depending on the lake. We only used Chl-*a* values taken at the surface of each lake. For training remote sensing models, we used water clarity measurements from the NTL-LTER lakes on the nearest available date to when each of the selected Landsat images were captured.

We sampled Landsat images using random points in each NTL-LTER water body, rather than a whole-lake average, to avoid sampling land or shallow bars during low-water years. We established 20 sampling points in large lakes (all > 30 hectares) and 10 sampling points in extremely small lakes (< 2 hectares). This was necessary in part because two of the training lakes are small bogs (Fig. 1). Because the resolution of Landsat imagery is 30 m, we required random points to be a minimum of 30 m apart to avoid sampling more than once in any Landsat raster cell. We randomly generated replacement points if any initial points were cloud covered or under SLC-off lines. At each of the sampling points, we extracted the values for red, green, and blue wavelengths. For each lake, we took an average of each of the bands (red, green, and blue) and three band ratios: blue:green, blue:red, and green:red. We trained linear regression models on the band ratios and in situ data, matching the Chl-*a* and Secchi disc measurements from the NTL-LTER with the corresponding Landsat-derived band ratio from that lake and year (Kloiber et al. 2002; Brezonik et al. 2005; Torbick et al. 2008; Olmanson et al. 2008).

We developed separate models for each sensor (TM, ETM+, OLI) with every possible combination of band and band ratio adding to a natural-log-transformed response (either Secchi disc depth or Chl-*a*). We created different models for each sensor because the sensors have slight variations in the wavelength bins that define each color. For each of the six sensor by water clarity measures, we selected the most-supported model based on Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson 2002). The variability explained by the models differed by sensor, and in all but one case, R^2 exceeded 0.5 ($R^2 = 0.48–0.89$; Table 2).

In most cases, we were able to extrapolate to the complete set of 17 study lakes using the same images used for model

Table 2 The most-supported model (by lowest AICc value) for each Landsat sensor (TM, ETM+, and OLI) estimating either Chl-*a* or Secchi disc depth, with model R^2

Chl- <i>a</i>			Secchi disc depth				
Sensor	Colors	Bands	R^2	Sensor	Colors	Bands	R^2
TM	b+b:r	1+1:3	0.56	TM	b+b:g+b:r	1+1:2+1:3	0.65
ETM+	b+g+g:r	1+2+2:3	0.56	ETM+	b+g+g:r	1+2+2:3	0.48
OLI	g+r+b:r+g:r	3+4+2:4+3:4	0.80	OLI	b+g+r+b:g+b:r	2+3+4+2:3+2:4	0.89

Colors indicate the color wavelength bins and color ratios included in each model (where b is blue, g is green, and r is red), while bands indicate the band number of each of those colors for each sensor

training. It was only when images were not sufficiently cloud free over the study lakes that we had to select a new image, and we followed the same image selection process used for model training. We selected cloud-free Landsat data taken closest in time to August 15th, and if two images were taken equally close to August 15th, we chose either TM or OLI data over ETM+ data. For 1 year (2008), a lack of cloud-free data forced us to use TM data for 6 lakes and ETM+ data for the remaining 11. Otherwise, all lakes in any given year were sampled using the same image. We sampled each image using 20 points per lake, as we did for the larger lakes in our training dataset, and then matched the data source of each image (TM, ETM+, or OLI) with the corresponding most-supported model for that sensor (Table 2). Overall, we were able to estimate Secchi disc depth and Chl-*a* (Table 1) from 1984 until 2018 ($n = 7\text{--}14$ years per lake).

Statistical analysis

We sought to relate remote-sensed estimates of lake clarity to *F. rusticus* abundance over time and across lakes. We assumed that higher *F. rusticus* abundance corresponds with decreased abundance and richness of aquatic macrophytes due to past work on this relationship in these lakes (Roth et al. 2007; Baldridge and Lodge 2014) and because our study lakes lack intensive macrophyte data over time (Larson et al. 2019). *Faxonius rusticus* may also impact water clarity in the study lakes through bioturbation caused by foraging or burrowing, although such an effect may be weaker relative to crayfish species like *P. clarkii* which are stronger burrowers (Berrill and Chenoweth 1982; Harvey et al. 2019).

We also wanted to account for other covariates besides *F. rusticus* abundance that could affect lake clarity, such as precipitation, water temperature, and winter severity. In years with higher precipitation, more dissolved organic carbon, nitrogen, and phosphorus is delivered to lakes, reducing water clarity (Williamson et al. 2014; Sinha et al. 2017). Warmer summer temperatures can improve growing conditions for phytoplankton and increase summer algae blooms (Elliott et al. 2006). Finally, mild winter conditions decrease ice duration and nitrate accumulation under ice, leading to a decline in annual nutrient availability and summer phytoplankton production (Powers et al. 2017). Though the relationships between these covariates and water clarity are not a central focus of our study, we chose to account for them to explain variation in water clarity which is not related to *F. rusticus* abundance, thus further isolating the relationship between *F. rusticus* abundance and the two measures of water clarity.

Data on precipitation, water temperature, and winter severity were not available for most of the study lakes in years with *F. rusticus* abundance data. Instead, for our three covariates we chose to use data from a proxy lake which was

not included in our dataset, but located close enough to serve as an indicator for regional climate conditions. We used water level, surface water temperature, and ice duration data from the NTL-LTER for Sparkling Lake (46.009, -89.701 ; Fig. 1) as measures of precipitation, water temperature, and winter severity, respectively. We chose Sparkling Lake as a proxy because of its proximity to the study lakes, data availability through NTL-LTER, and because it is a seepage lake with no inlets or outlets, rather than a stream-fed drainage lake, making its water level especially sensitive to precipitation and drought (Perales et al. 2020). Every 2 weeks during the ice-free season, the NTL-LTER records water level using a staff gage and water temperature using a YSI meter at 1 m intervals from the surface of Sparkling Lake. For water temperature data, we only used surface measurements because of seasonal stratification of Sparkling Lake. If two measurements of water level or temperature were taken equally close to August 15th, we used the average of the two values. Finally, we calculated ice duration as the number of days each year open water in Sparkling Lake was closed by ice, as the NTL-LTER records the last day of open water before ice in the fall and the first day of open water in the spring of each year.

We also included lake as a random effect in our statistical models because water clarity could be affected by any number of between-lake differences for which we do not necessarily have data. For example, lake clarity can be affected by factors such as density of wetlands in the watershed (Xenopoulos et al. 2003) or by lake depth and surface area (Jeppesen et al. 1997; Nöges 2009). We used linear mixed-effects models in R 4.0.0 from the *nlme* package to account for lake as a random effect (R Core Team 2019; Pinheiro et al. 2019). In the linear mixed-effects models, we included each covariate (water level, ice duration, and water temperature) and *F. rusticus* CPUE as fixed effects, and lake as a random effect. We detrended each of our covariates by time to remove temporal trends in climatic variables and instead emphasize year-to-year variability, and similarly detrended *F. rusticus* CPUE (e.g., Pathak et al. 2016; Hewitt et al. 2018). We conducted all detrending by taking the difference between the untransformed data and long-term means for each variable. We only log-transformed Chl-*a* values prior to analysis.

We evaluated the mixed-effects models using information theoretic model competition (Burnham and Anderson 2002) and ranked them based on AICc (Symonds and Moussalli 2011). We considered every possible model combination, including those with interaction terms between the three covariates. We allowed interaction terms between the covariates to account for a greater portion of the variation in water clarity and further isolate the effects of *F. rusticus* abundance. To maintain interpretability of the predictor of primary interest, we did not consider any covariate interactions

with *F. rusticus* abundance. We calculated model-averaged coefficients for each parameter using the *MuMIn* package in R (Bartoń 2020) using the full set of most-supported models ($\Delta\text{AICc} \leq 2$; Burnham and Anderson 2002). However, we did not interpret covariate effects, because they are not a central focus of our study and the presence of interaction terms complicates the interpretation of main effects (Engqvist 2005; Schielzeth 2010). All data used in models of relationships between crayfish relative abundance and lake clarity can be found at https://doi.org/10.13012/B2IDB-4293962_V1.

To assess possible multicollinearity of model parameters, we calculated the variance inflation factor (VIF) for each parameter in R using the *car* package (Fox and Weisberg 2019). No VIFs were above 10, so we retained all covariates and their interactions in our models (Montgomery and Peck 1992). Because the impacts of invasive species can vary over time (Strayer et al. 2006), we also conducted a sensitivity test in which we ran the same analyses using only years and lakes which captured the initial growth phase of *F. rusticus* populations. The sensitivity test omits post-growth population plateaus or subsequent declines where water clarity might decouple from *F. rusticus* abundance due to stable state shifts in which phytoplankton might inhibit macrophyte recovery even as crayfish populations decline (supplementary file; Hansen et al. 2013; Larson et al. 2019).

Results

We found eight most-supported ($\Delta\text{AICc} \leq 2$) models relating combinations of *F. rusticus* CPUE and our covariates to Chl-*a* and six most-supported models relating these predictors to Secchi disc depth (Table 3). For our models of Chl-*a*, R^2 ranged from 0.42 to 0.44, while for our models of Secchi disc depth, R^2 ranged from 0.28 to 0.33. Of the most-supported models, *F. rusticus* CPUE was included in four Chl-*a* models and four Secchi disc models. *Faxonius rusticus* CPUE was negatively associated with Chl-*a* (model-averaged slope = -0.001 , 95% CI = -0.004 , 0.003) and positively associated with Secchi disc depth (model-averaged slope = 0.020 , 95% CI = -0.012 , 0.051 ; Fig. 3). Model-averaged 95% confidence intervals for slopes of the relationship between *F. rusticus* CPUE, our covariates, and both water clarity responses included zero (Table 4), although some individual model slopes did not include zero in 95% confidence intervals. We interpreted *F. rusticus* CPUE despite the inclusion of zero in model-averaged coefficients because *F. rusticus* CPUE was included in several most-supported models. A sensitivity test limiting analyses to lakes and years during the growth phase of *F. rusticus* populations found no effect of crayfish abundance on either lake clarity metric (see supplementary file).

Table 3 Most-supported models relating *F. rusticus* CPUE, water level, water temperature, and ice duration to Chl-*a* or Secchi disc depth ($\Delta\text{AICc} \leq 2$)

Model combination	ΔAICc	AICc W_i	Cond. R^2
<i>Chl-a models</i>			
Water temperature + water level: ice duration	0.00	0.19	0.44
Water level * ice duration	0.33	0.16	0.44
Water level: ice duration	0.58	0.14	0.43
Water temperature + water level * ice duration	0.60	0.14	0.45
<i>F. rusticus</i> CPUE + water temperature + water level: ice duration	1.08	0.11	0.42
<i>F. rusticus</i> CPUE + water level: ice duration	1.33	0.11	0.42
<i>F. rusticus</i> CPUE + water level * ice duration	1.50	0.09	0.43
<i>F. rusticus</i> CPUE + water temperature + water level * ice duration	1.96	0.07	0.44
<i>Secchi disc models</i>			
<i>F. rusticus</i> CPUE + water temperature + water level: ice duration	0.00	0.23	0.30
<i>F. rusticus</i> CPUE + water temperature + water level * ice duration	0.87	0.15	0.31
<i>F. rusticus</i> CPUE + water level * ice duration	0.97	0.14	0.30
<i>F. rusticus</i> CPUE + water level: ice duration	1.17	0.13	0.28
Water temperature + water level: ice duration	1.46	0.11	0.31
Water temperature + water level * ice duration	1.83	0.09	0.33

Includes difference in AICc from the top model (ΔAICc), AICc weight (AICc W_i), and conditional R^2 . The symbol ':' between predictors indicates an interaction between those predictors was included in the model, while the symbol '*' between predictors indicates both the interaction term between those predictors and the individual effect of each predictor was included in the model

Fig. 3 Effects of detrended crayfish catch-per-unit effort (CPUE, crayfish trap⁻¹) on a.) log-transformed Chl-*a* ($\mu\text{g}\cdot\text{L}^{-1}$) and b.) Secchi disc depth (m) from the most-supported models (Table 3) that include crayfish. Rug plots on the axes represent the distribution of data points. Scatterplots of the raw data are not shown because the figures account for covariates and represent model-predicted relationships

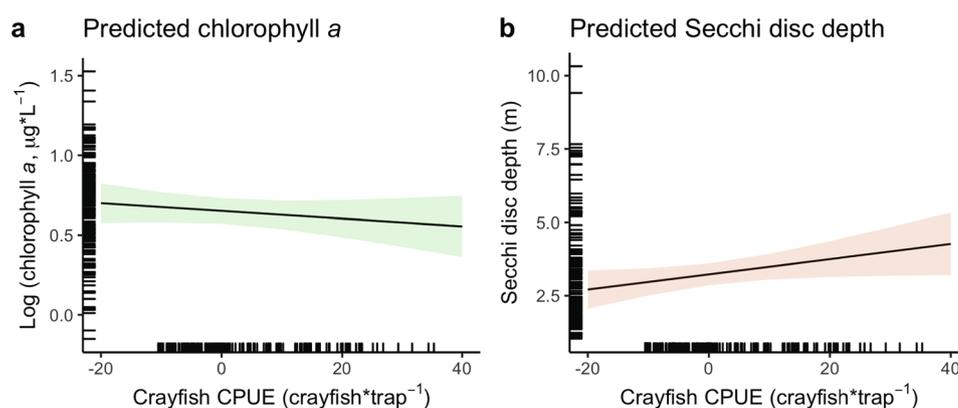


Table 4 Model-averaged slopes and 95% confidence intervals (CI) for each predictor of the most-supported models ($\Delta\text{AICc} < 2$) relating *F. rusticus* CPUE, water level, water temperature, and ice duration to Chl-*a* or Secchi disc depth (Table 3)

Predictor	Slope	CI Lower	CI Higher
<i>Chl-a models</i>			
Crayfish	-0.001	-0.004	0.003
Ice duration	< 0.001	-0.002	0.002
Ice duration: water level	+ 0.015	0.010	0.020
Water level	+ 0.041	-0.067	0.149
Water temperature	-0.009	-0.035	0.016
<i>Secchi disc models</i>			
Crayfish	+ 0.02	-0.01	0.05
Ice duration	-0.002	-0.01	0.01
Ice duration: water level	-0.08	-0.11	-0.05
Water level	-0.23	-0.88	0.41
Water temperature	+ 0.09	-0.09	0.27

Discussion

We found a weak, negative effect of *F. rusticus* abundance on Chl-*a*, and a weak, positive effect of *F. rusticus* on Secchi disc depth. We interpret the weak effect of *F. rusticus* abundance on lake clarity because it was included in several most-supported models (Burnham and Anderson 2002). This finding is the opposite of what we predicted, and diverges from the strong, negative effects of *P. clarkii* on water clarity in shallow lakes and wetlands of Asia and Europe (Angeler et al. 2001; Rodríguez et al. 2003; Matsuzaki et al. 2009). The deviation of our weak or non-existent effects from the impacts of *P. clarkii* could be explained by differences in study systems or natural history (e.g., burrowing ability) between the two crayfishes. Further, a possible positive association between *F. rusticus* and water clarity could either be a consequence of a trophic cascade caused by the crayfish in which zooplankton are freed from predation pressure from fish, or could

indicate that *F. rusticus* abundance responds to, rather than causes, changes in lake water clarity.

The divergence of our result from the water clarity impacts of *P. clarkii* was unexpected, especially because the effects of *P. clarkii* on water clarity (even more pronounced than those of *C. carpio*) are mediated mainly through declines of macrophytes (Matsuzaki et al. 2009), which *F. rusticus* similarly destroys (Lodge and Lorman 1987; Baldrige and Lodge 2014). One possible explanation for the contrast between our results and the effects of *P. clarkii* is that the two crayfishes have been studied in different types of ecosystems. For example, the lakes in our study are generally deep temperate lakes, with an average maximum depth of 16 m (Table 1). Conversely, studies which examined the impacts of *P. clarkii* in Europe were conducted in shallow lakes and wetlands such as Lake Chozas, which has a maximum depth of 1.8 m (Rodríguez et al. 2003), and the wetlands of Las Tablas de Daimiel National Park, which have an average depth of 0.91 m (Angeler et al. 2001). In Asia, Matsuzaki et al. (2009) investigated the impacts of *P. clarkii* on water clarity in experimental ponds with depths of 0.7–0.8 m. Because shallow lakes are more susceptible to changes in water clarity than deep lakes (Jeppesen et al. 1997), our relatively deep study lakes may have been more resistant to any impacts of *F. rusticus* on pelagic nutrient levels than the relatively shallow waterbodies used to study the impacts of *P. clarkii*. Consistent with this explanation, visual comparison of *F. rusticus* abundance to Chl-*a* and Secchi disc depth in our largest study lake (Trout Lake, max depth = 35.7 m, surface area = 15.64 km²) reveals no evident relationship (Fig. 4). Even in Little John Lake, which served as partial inspiration for this study because of its pronounced summer algal blooms and smaller size (max depth = 5.8 m, surface area = 0.61 km²), there is seemingly no relationship between crayfish abundance and clarity (Fig. 4). Indeed, Little John Lake had strong phytoplankton blooms in the 1930s, long before the introduction of *F. rusticus* (Wilson 1935).

Differences in water clarity impacts between *F. rusticus* and *P. clarkii* might also be partially explained by

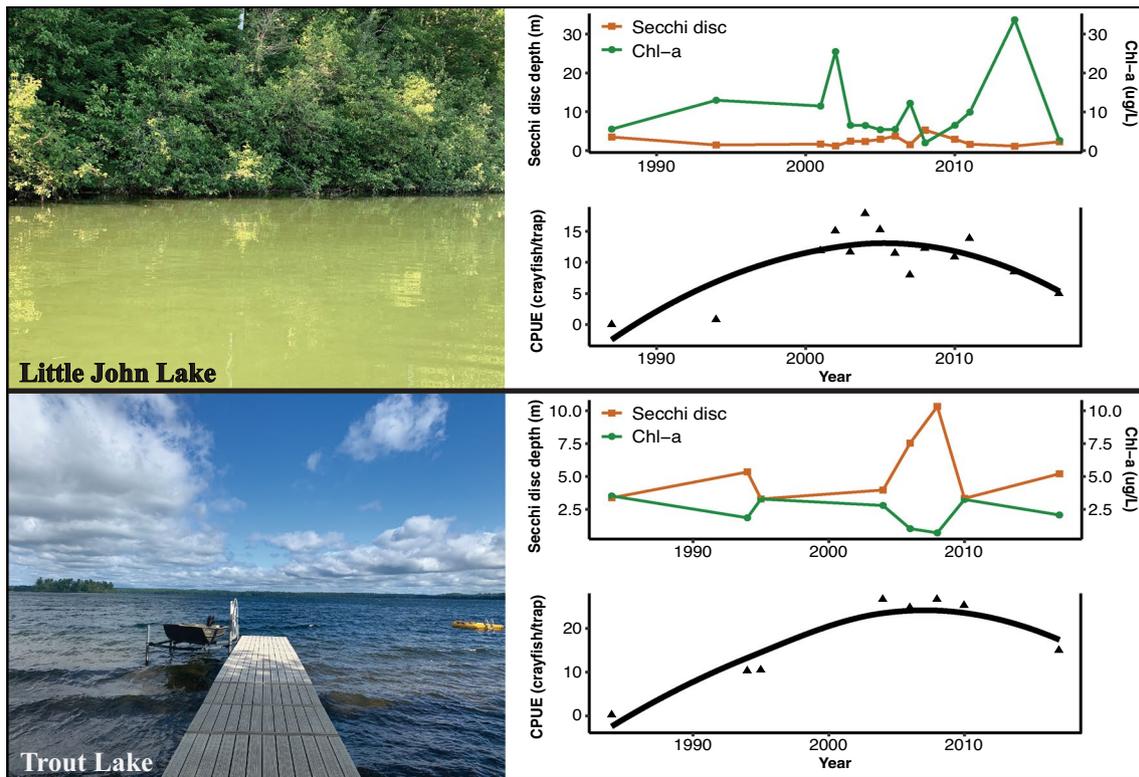


Fig. 4 Photographs, water clarity data, and *F. rusticus* CPUE for our smallest study lake (Little John Lake, top panel) and largest study lake (Trout Lake, bottom panel; Table 1). Chl-*a* (green triangles), Secchi disc depth (brown squares), and *F. rusticus* CPUE (black triangles) are shown for each lake over the duration of the study period

(1984–2018). For ease of interpretation, trends in *F. rusticus* CPUE are shown using locally estimated scatterplot smoothing. These two case studies are presented to provide transparency of our results using our two most dissimilar study lakes; i.e., the absence of strong, negative relationships between *F. rusticus* abundance and lake clarity

differences in burrowing activity and ability between these species. *Faxonius rusticus* is considered a tertiary burrower (Berrill and Chenoweth 1982), indicating a species that will burrow rarely or under duress, whereas *P. clarkii* is a secondary burrower that burrows routinely and to great effect in invaded systems (Harvey et al. 2019). Because of this natural history difference between species, we suspect that *P. clarkii* suspends a greater amount of sediment than *F. rusticus*, negatively impacting water clarity (e.g., Angeler et al. 2001). However, given the dominant role that macrophyte destruction plays in mediating the impacts of *P. clarkii* on lake clarity (Matsuzaki et al. 2009), it is more likely that our results are the consequence of differences in study system rather than differences between study species. Invasive species impacts can be highly context-dependent (Thomsen et al. 2011; Sokol et al. 2017), and future studies should investigate how invasive crayfish impacts can vary between different ecosystems.

Based on the observed negative association between *F. rusticus* abundance and Chl-*a*, and the observed positive association between *F. rusticus* abundance and Secchi disc depth, we propose that *F. rusticus* abundance may act as a

positive driver of water clarity through a trophic cascade. Some small and planktivorous fish populations are reduced by *F. rusticus* through direct consumption, loss of macrophyte habitat, and predation on fish eggs (Wilson et al. 2004; Roth et al. 2007). Because of this decreased abundance of small fishes and increased availability of *F. rusticus* for prey, the foraging of larger piscivores is increased in the littoral zone and reduced in the pelagic zone (Nilsson et al. 2012; Kreps et al. 2016). We hypothesize that the decline in small planktivores and altered feeding habits of larger piscivores due to *F. rusticus* could be releasing zooplankton grazers feeding on phytoplankton from fish predation, thereby decreasing phytoplankton and increasing lake clarity (Brooks and Dodson 1965; Vanni et al. 1997). Future studies could investigate our hypothesized trophic cascade by comparing the abundance of small fishes, zooplankton, and phytoplankton to *F. rusticus* abundance over time or across lakes, perhaps using NTL-LTER or similar long-term ecosystem data.

Alternatively, *F. rusticus* may not impact water clarity but respond to it, acting as a passenger, rather than a driver, to this particular ecosystem change in temperate

lakes (Didham et al. 2005; Light and Marchetti 2007). In lakes with lower water clarity, less light penetrates to the lakebed, and benthic primary and secondary production declines (Vadeboncoeur et al. 2008; Karlsson et al. 2009). Though omnivorous, *F. rusticus* prefers to consume zoobenthos (Roth et al. 2006), and consequently could decline in abundance in years with lower lake clarity caused by climate or other factors (i.e., eutrophication from lake-shore development; Moore et al. 2003). Future studies could investigate the effects of lake clarity on abundance, growth, or production of *F. rusticus* as mediated through primary or secondary benthic production (Abrahamsson and Goldman 1970; Nyström et al. 2006). We did not invert the order of our model to relate abundance of *F. rusticus* to lake clarity because our a priori prediction from past work on *P. clarkii* (Angeler et al. 2001; Rodríguez et al. 2003) was that *F. rusticus* might causally affect lake clarity, but future studies might consider a different model structure. Those studies could also control for factors known to affect crayfish population dynamics like habitat quality, predation pressure, or disease (Roth et al. 2007; Sargent et al. 2014; Larson et al. 2019) to reveal whether abundance of *F. rusticus* in temperate lakes is causally affected by water clarity.

While our use of Landsat imagery enabled us to include lakes and time periods for which we lacked in situ water clarity data, our remote-sensed estimates of lake clarity do have several limitations. For example, we have a relatively low number of training lakes (seven) for models of lake clarity relative to some other studies that use hundreds or thousands of training lakes (e.g., Chipman et al. 2004; Olmanson et al. 2008). Our approach could be improved by increasing replication of training lakes through emerging databases such as AquaSat, which provides 600,000 water clarity to Landsat matchups across the contiguous USA (Ross et al. 2019). The study by Ross et al. (2019) was published after we completed our data analysis, but a larger number of training lakes might improve our estimates of water clarity ($R^2 = 0.48\text{--}0.89$ in model training). We also might have considered water clarity at other times of the year than our mid-August period for crayfish population monitoring. Mid- to late summer is often the period of lowest lake clarity and lowest variability in lake clarity (Stadelman et al. 2001; Chipman et al. 2004; Olmanson et al. 2008). However, lake clarity can also be affected by spring algal blooms (Peeters et al. 2007), and subsequent work could relate *F. rusticus* abundance to water clarity throughout most of the year. Lastly, there are errors inherent in both the processing of raw Landsat data and modeling water clarity from these Landsat data, and these errors are propagated forward to our final models relating *F. rusticus* abundance and other covariates to lake clarity (e.g., Crosetto et al. 2001). Accordingly, we might have isolated stronger effects of *F. rusticus* on Chl-*a* and Secchi disk depth

if we were able to use in situ measures of water clarity rather than estimates of these responses from remote sensing.

Stronger evidence for a positive association between *F. rusticus* and water clarity would have interesting implications for lake ecosystems and their management. For example, if *F. rusticus* changes water clarity through a trophic cascade, the consequent increases in benthic production may benefit *F. rusticus* populations in a positive feedback loop. Other studies have proposed feedback loops in which *F. rusticus* populations may either benefit (Roth et al. 2007; Hansen et al. 2013) or harm themselves (Larson et al. 2019) through interactions with predatory fishes and habitat like macrophytes. However, the positive feedback loop we suggest between *F. rusticus* and water clarity would be a novel mechanism through which invasive crayfish populations could benefit themselves by a form of ecosystem engineering (Matsuzaki et al. 2009; Gallardo et al. 2016). Alternatively, if *F. rusticus* abundance instead responds to extrinsic variability or drivers of water clarity, then populations of this invasive crayfish may be more susceptible to control or eradication in years or lakes with lower water clarity. This idea is similar to findings by Hansen et al. (2013) that showed *F. rusticus* was easier to control when drought conditions stranded its preferred rocky or cobble habitat out of water in Sparkling Lake. Overall, future studies should aim to address whether *F. rusticus* is a passenger or driver of water clarity across a variety of lentic ecosystems. Changes in water clarity are a common effect of many aquatic invasive species (e.g., Matsuzaki et al. 2009; Higgins and Vander Zanden 2010; Gallardo et al. 2016) and improving our understanding of the context dependency of these impacts might enable researchers and managers to better allocate resources while protecting aquatic ecosystems.

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