YELLOW PERCH RECRUITMENT AND ZOOPLANKTON AVAILABILITY IN NORTHERN WISCONSIN LAKES WITH DIFFERENT WALLEYE RECRUITMENT HISTORIES

By

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Executive Summary

Some northern Wisconsin lakes that previously supported natural Walleye *Sander vitreus* recruitment have exhibited recruitment declines over the last few decades. Previous research conducted on thirteen lakes in northern Wisconsin suggested that a recruitment bottleneck was occurring at or before mid-July in lakes with declining Walleye recruitment. Recent research suggested that Walleye and Yellow Perch *Perca flavescens* recruitment are influenced by similar environmental factors, but current status and historical trends of Yellow Perch recruitment in Wisconsin are unknown. To better understand factors influencing both Walleye and Yellow Perch recruitment, the objectives of my study were to determine if: 1) differential trends in age-0 Yellow Perch abundance occurred between lakes with different Walleye recruitment histories (i.e., declining, sustained); 2) catch per effort (CPE) of larval Yellow Perch in ichthyoplankton tows or electrofishing CPE of age-0 perch in June-July predicted perch year-class strength as indexed by age-0 CPE in fall electrofishing; and 3) zooplankton densities and spatial and temporal trends in these densities differed among lakes with different Walleye recruitment histories.

In 2021, I sampled three lakes with declining Walleye recruitment (D-NR) and three lakes with sustained Walleye recruitment (S-NR) to evaluate age-0 Yellow Perch CPE and zooplankton densities. In 2022, I expanded the study to include four additional lakes for a total of five D-NR and five S-NR lakes. I used ichthyoplankton nets in May to mid-June and hand-held anode electrofishing in late-June to October to collect age-0 Yellow Perch. In 2021, zooplankton samples were collected via vertical and horizontal tows concurrent with larval fish sampling. Additionally, vertical tows were continued through the last week of August on a subset of four lakes to assess temporal trends. In 2022, zooplankton sampling was limited to nighttime vertical

tows concurrent with larval fish sampling. I used *t*-tests, repeated-measures analysis of variance, and mixed effects models to compare age-0 Yellow Perch CPE between D-NR and S-NR lakes at several points throughout their first year of life. I also regressed $\log_e$ transformed age-0 Yellow Perch CPE against electrofishing sampling periods to compare mortality rates between lakes with different Walleye recruitment histories. Spearman's rank correlations were used to determine if CPE of larval Yellow Perch and CPE of age-0 Yellow Perch in June-July were correlated with CPE of age-0 perch in October. Additionally, error matrices were used to evaluate whether strong or weak larval perch CPE and CPEs of age-0 perch in June-July accurately predicted strong or weak CPE of age-0 Yellow Perch. I used *t*-tests, generalized linear models, and repeated-measures ANOVA to compare zooplankton densities and total lengths between Walleye recruitment histories.

Larval Yellow Perch CPE was similar between lakes with different Walleye recruitment histories within years, and similar between years for the six lakes sampled during both 2021 and 2022. Age-0 Yellow Perch electrofishing CPE was significantly higher in S-NR lakes than D-NR lakes in June-July 2021, but there were no significant differences in any other electrofishing sampling period. Age-0 Yellow Perch mortality rate estimates did not differ between recruitment histories in either year. Larval and age-0 June-July Yellow Perch CPEs were significantly positively correlated with age-0 October Yellow perch CPE (larval $r_s = 0.60$, $P = 0.01$; post-larval $r_s = 0.73$, $P < 0.01$). Both larval CPE and age-0 Yellow Perch CPE in June-July were 69% accurate in correctly predicting relative year-class strength of age-0 Yellow Perch in October.

Mean zooplankton densities and total lengths of *Daphnia* spp., cyclopoid copepods, and calanoid copepods collected in nighttime vertical tows during May-June were similar in D-NR and S-NR lakes during both years. There were no significant interactions between Walleye recruitment history and depth for both day and night when comparing densities and total lengths for *Daphnia* spp. and both orders of copepods, but there were significant differences in density of *Daphnia* spp. during the day among depths, $\log_e$ density of cyclopoid copepods between recruitment histories during the day, and calanoid copepod total length during the day among depths. For the four lakes where vertical zooplankton tow samples were conducted through the last week of August, there were no significant interactions between Walleye recruitment history and sampling period when explaining variation in $\log_e$ transformed densities for *Daphnia* spp. and both orders of copepods and for total lengths of both orders of copepods, but there were significant differences in $\log_e$ density of *Daphnia* spp. and cyclopoid total length between several sampling periods. There was a significant interaction between recruitment history and sampling period for *Daphnia* spp. total length, but there were no significant differences between lakes with different Walleye recruitment histories during an individual sampling period.

My results suggest that lakes with declining Walleye recruitment are capable of producing age-0 Yellow Perch year classes that are similar to year classes observed in S-NR lakes. Although age-0 Yellow Perch CPE was only significantly different between sampling periods in June-July 2021, observed catch rates were higher in S-NR lakes in subsequent periods but also more variable. This trend did not continue in 2022, as some S-NR lakes sampled in 2021 showed decreased Yellow Perch recruitment in 2022 and some D-NR lakes had relatively high age-0 Yellow Perch CPE. Similarities in age-0 Yellow Perch CPE between lake types may be due to similar environmental conditions across northern Wisconsin. More research is necessary to better describe Yellow Perch recruitment trends, as perch recruitment is highly variable.

While factors contributing to declines in Walleye recruitment remain unclear, this study provides additional evidence that a lack of zooplankton in larval Walleye diets is likely not due to low zooplankton densities, and that larval Yellow Perch may be a more preferred prey. Collectively, field-based research on Walleye recruitment declines in northern Wisconsin indicate that identifying the specific mechanisms resulting in Walleye recruitment declines in northern Wisconsin lakes may be difficult given the inherent variation in these systems. Additionally, identifying these mechanisms may not provide for direct management actions that can be implemented to increase Walleye recruitment. Consequently, efforts to identify lakes where management actions like changes to harvest regulations or stocking may be effective in maintaining Walleye fisheries within a Resist-Accept-Direct framework seems prudent.

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Contents

Introduction

Understanding recruitment is critical to making informed management decisions regarding exploited fish populations because recruitment can influence age structure, growth rates, and overall population abundance (Sissenwine et al. 1988; Madenjian et al. 1996; Allen and Hightower 2010). However, understanding the effects of recruitment on fish population dynamics and demographics can be difficult because recruitment is highly variable (Allen 1997; Isermann 2007; Houde 2009) and is influenced by a multitude of abiotic and biotic factors (Sissenwine 1984; Baccante and Colby 1996) that may include water temperatures (Bozek et al. 2011; Lynch et al. 2016), abundance of predators and prey (Sissenwine 1984; Silbernagel and Sorensen 2013), and the number or biomass of spawning adults (Myers and Barrowman 1996; Hansen et al. 1998).

Numerous mechanisms operating in the first year of life are important in determining year-class strength (DiCenzo and Duval 2002; Quist et al. 2003; Honsey et al. 2020). Although most fishes are highly fecund (Smith 1941; Colby et al. 1979; Serns 1982; Sissenwine et al. 1988), mortality rates at egg, larval, and post-larval stages are typically high (Hjort 1914; Serns 1982; Sissenwine 1984). Most of this mortality likely occurs via starvation or predation (Hunter 1982; Sissenwine 1984; Bailey and Houde 1989). Fish can experience both direct and indirect effects of starvation (Houde 1989; Jonas and Wahl 1998). Larval fish may starve if they do not spatially and temporally overlap with zooplankton prey (i.e., a match-mismatch scenario; Cushing 1990; Chick and Van Den Avyle 1999). Additionally, larval fish are more susceptible to predation due to their small size (Miller et al. 1988; Houde 1989), and recruitment in some populations may be regulated by predation in the first year of life (Hartman and Margraf 1993; Brooking et al. 1998; Santucci and Wahl 2003).

Walleye *Sander vitreus* support important fisheries across much of their range in North America. The native range of Walleye includes the Midwestern USA and extends into Canada, but Walleye can be found across most of North America as a result of stocking (Billington et al. 2011). Most Walleye fisheries are recreational in nature, but several tribes in Wisconsin, Minnesota, Michigan, and Canada participate in traditional fisheries that employ nets or spearing (Staggs et al. 1990; Kozich et al. 2020). Commercial fisheries are generally relegated to relatively large bodies of water in Canada, including the Canadian waters of Lake Erie. Walleye are one of the most sought-after fish among Wisconsin's recreational anglers and are important to tribal members who participate in spearing fisheries that occur in the Ceded Territory of northern Wisconsin (Schmalz et al. 2011). As a result, the Wisconsin Department of Natural Resources (WDNR), the Great Lakes Indian Fish and Wildlife Commission (GLIFWC), and individual tribes dedicate significant resources towards managing Walleye fisheries in northern Wisconsin each year.

Some lakes in northern Wisconsin have exhibited a downward trend in Walleye recruitment over the last decade or more, demonstrated by declining catch rates of age-0 fish in fall electrofishing (Hansen et al. 2015b; Gostiaux et al. 2022). These declines prompted research into factors that regulate recruitment success (Kelling 2014; Hansen et al. 2017; Gostiaux et al. 2022; Brandt et al. 2022). At a broad scale, Walleye recruitment success in northern Wisconsin appears to be related to conductivity (productivity), growing degree days, and lake surface area (Hansen et al. 2015b). Lake surface area has been identified as the most important predictor for Walleye recruitment success (Hansen et al. 2015b), likely because larger lakes have greater habitat availability (Jackson et al. 2001) and higher diversity of prey species (Tonn and Magnuson 1982).

Focused research on a subset of lakes (Gostiaux et al. 2022) has shown that in some Wisconsin lakes with declining recruitment trends (referred to herein as D-NR lakes), age-0 Walleye may be lost at or before the end of July. In several cases, larval Walleye were captured in D-NR lakes, but no age-0 Walleye were collected in subsequent sampling on these lakes, which included micro-mesh gill nets set in late July and standard electrofishing which occurs in September-October. While the findings of Gostiaux et al. (2022) help to eliminate many possible hypotheses for the lack of age-0 Walleye in D-NR lakes, the potential reasons for recruitment bottlenecks occurring early in life remain unknown. However, the sampling protocol employed by Gostiaux et al. (2022) for collecting age-0 Walleye did not encompass the period between the larval (ichthyoplankton tows in May) and post-larval phases, which may be a critical period for Walleye. Adult Walleye abundance was lower and mean TL of adults was higher in D-NR lakes when compared to lakes showing sustained recruitment (S-NR lakes; Gostiaux et al. 2022) but these differences could reflect both cause and effect of recruitment declines. Additionally, no other differences were detected in conductivity, Secchi depth, relative abundance of larval Yellow Perch *Perca flavescens*, and zooplankton density between lakes with different Walleye recruitment histories (Gostiaux et al. 2022). This previous work suggests that the mechanisms responsible for Walleye recruitment declines in D-NR lakes may be more complex than one or two simple factors.

Failure to transition to zooplankton prey after the yolk sac is absorbed has been identified as a potential recruitment bottleneck for many species (Hjort 1914; Li and Mathias 1982; Nunn et al. 2012). Moreover, larval Walleye and Yellow Perch growth and mortality rates may be influenced by zooplankton prey abundance (Li and Mathias 1982; Hokanson and Lien 1986; Graeb et al. 2004; Hoxmeier et al. 2004). Gostiaux et al. (2022) showed that density of edible zooplankton was similar between D-NR and S-NR lakes during the period that larval Walleye were pelagic, but piscivory was more prevalent than would be expected based on previous literature (Priegel 1970; Mathias and Li 1982; Engel et al. 2000). Only one larval Walleye from D-NR lakes consumed zooplankton, but nearly all of the larvae examined were from one D-NR lake (Sawyer Lake). Engel et al. (2000) observed that 71% of larval Walleye < 15 mm in Escanaba Lake, Wisconsin, contained larval fish in their diets (likely Yellow Perch), which is similar to results reported by Gostiaux et al. (2022). However, Engel et al. (2000) also showed that crustacean zooplankton were by far the most prevalent prey in larval Walleye diets, which was not consistent with Gostiaux et al. (2022). Previous studies (Spykerman 1974; Mathias and Li 1982; Galarowicz et al. 2006) also suggest that zooplankton were the primary food source for Walleye < 20 mm. Additional research is needed to determine if the results of Gostiaux et al. (2022) indicate a spatial match-mismatch scenario between larval Walleye and zooplankton prey where edible zooplankton may be available, but larval Walleye do not overlap with these prey. Another alternative is that spatial overlap between predator and prey is occurring, but larval Walleye are not utilizing zooplankton prey to the same degree as reported in previous studies (Spykerman 1974; Mathias and Li 1982; Engel et al. 2000).

Yellow Perch are a common component of the fish community in many northern Wisconsin lakes and may affect Walleye recruitment in a variety of ways (Chevalier 1973; Hall and Rudstam 1999; Engel et al. 2000; Brandt et al. 2022). Some Yellow Perch populations in the Midwestern USA have shown signs of decline in recent years (Bethke and Staples 2015; Holbrook et al. 2022), but specific causes of these declines are unclear. Yellow Perch recruitment is typically highly variable and influenced by biotic and abiotic factors (Newsome and Aalto 1987; Isermann et al. 2007). Abiotic factors that influence Yellow Perch recruitment success include temperature, hatch date, and wind (Newsome and Aalto 1987; Kaemingk et al. 2014; Brandt. et al 2022); influential biotic factors include predator abundance and prey availability (Hartman and Margraf 1993; Dettmers et al. 2003). Zooplankton are the primary food source for juvenile Yellow Perch; larvae primarily feed on copepod nauplii before transitioning to adult copepods and eventually cladocerans (Whiteside et al. 1985; Fisher and Willis 1997; Graeb et al. 2004).

Yellow Perch population dynamics are often closely related with Walleye population dynamics and demographics (Forney 1980; Hansen et al. 1998). Yellow Perch abundance usually has a positive effect on the growth and survival of larval Walleye (Forney 1974; Engel et al. 2000), because they serve as both forage and a prey buffer (Forney 1974; Hall and Rudstam 1999). Brandt et al. (2022) showed that the probability of Walleye recruitment success in Wisconsin lakes during 2000-2006 (i.e., prior to observed Walleye recruitment declines) was related to relative abundance of juvenile Yellow Perch and that Walleye and Yellow Perch recruitment may be affected by similar environmental factors. Possibly, observed declines in Walleye recruitment in northern Wisconsin lakes are also indicative of declines in Yellow Perch recruitment that have gone undetected. Moreover, declining Yellow Perch recruitment could result in declining Walleye recruitment, if Yellow Perch are a critical prey item for larval Walleye, as indicated by Gostiaux et al. (2022). While Gostiaux et al. (2022) showed that larval Yellow Perch abundance was not different between D-NR and S-NR lakes over a 2 year period, whether or not recruitment bottlenecks also exist for Yellow Perch in D-NR lakes remains unknown.

Although Yellow Perch and Walleye are taxonomically similar and may respond similarly to environmental conditions (Brandt et al. 2022), they have key differences that allow

Yellow Perch to have greater adaptive capacity than Walleye. Both species spawn in early spring at water temperatures of 7.2-11.1˚C for Yellow Perch (Herman et al. 1959; Johnson 1971) and 3.3-6.7˚C for Walleye (Becker 1983) in Wisconsin. Both species are broadcast spawners (Harrington 1947; Eschmeyer 1950; Priegel 1970), but typically utilize different spawning habitat. Walleye in lakes typically spawn along shorelines over cobble and gravel substrates (Eschmeyer 1950; Johnson 1961; Williamson 2008). Due to these specific requirements, abundance and distribution of naturally recruiting Walleye populations can be limited by the abundance of spawning habitat (Schneider et al. 2007). Yellow Perch deposit eggs in accordion-like skeins that are typically distributed on vegetation and woody debris (Scott and Crossman 1973; Fisher et al. 1996) but a variety of substrates can be used (Herman et al. 1959; Schneider et al. 2007).

Despite their important roles as both prey and predators, little is known about Yellow Perch early life history and recruitment in Wisconsin lakes because standardized sampling conducted by WDNR and other agencies does not specifically target Yellow Perch (Brandt et al. 2022). Hence, previous studies have relied on data describing the adult segment of Yellow Perch populations to reconstruct historical patterns in recruitment (Feiner et al. 2017; Brandt et al. 2022). Directly describing the early life history of Yellow Perch in northern Wisconsin lakes and identifying potential recruitment bottlenecks requires a sampling regime that encompasses several life history stages (Forney 1971; Sanderson et al. 1999; Boehm et al. 2020). Many different gears have been used to sample Yellow Perch in their first year of life, including ichthyoplankton nets (Isermann and Willis 2008; Dembkowski et al. 2012), beach seines (Forney 1971; Dembkowski et al. 2012), and bottom trawls (Pope et al. 1996; Marsden and Robillard 2004). While towing ichthyoplankton nets is a viable option for sampling larval Yellow Perch and recent work conducted by Brandt (2021) suggests modified boat electrofishing (similar to Jackson and Noble [1995]) during August-September offers an efficient means of capturing age-0 perch at end of summer, there is not a clear method for collecting age-0 perch between these two points. Bottom trawls and beach seines are not feasible options for sampling age-0 Yellow Perch in most northern Wisconsin lakes due to lake size (too small for reasonable bottom trawl transects), and an abundance of aquatic vegetation and woody debris prevent effective trawling and seining.

Therefore, the objectives of my research were to determine if: 1) differential trends in age-0 Yellow Perch abundance occurred between lakes with different Walleye recruitment histories; 2) catch per effort (CPE) of larval Yellow Perch in ichthyoplankton tows or electrofishing CPE of age-0 perch in June-July predicted perch year-class strength as indexed by age-0 CPE in fall electrofishing; and 3) zooplankton densities and spatial and temporal trends in these densities differed among lakes with different Walleye recruitment histories. To address these objectives, I assessed different sampling methods for capturing age-0 Yellow Perch during June-July.

Methods

Study Sites

My study occurred on six northern Wisconsin lakes in 2021 and ten lakes in 2022 (Table 1; Figure 1). Only six lakes were sampled in northeastern Wisconsin in 2021 while I focused on developing a sampling protocol to collect age-0 Yellow Perch. In the second year of this project, I expanded the study to include four lakes in northwestern Wisconsin. This is similar to the approach previously used to assess first-year Walleye recruitment trends in these lakes, where Boehm et al. (2020) used two northern Wisconsin lakes to develop a multi-stage sampling protocol for age-0 Walleye before this protocol was expanded to eleven additional lakes. The ten lakes in my study were chosen because they were part of previous studies on Walleye recruitment bottlenecks in northern Wisconsin lakes (Boehm 2016; Gostiaux 2018; Brandt 2021), with the exception of Windigo Lake. Each lake was categorized as having either sustained natural Walleye recruitment (S-NR) or declining natural recruitment (D-NR) based on age-0 CPE in standardized fall electrofishing surveys conducted by WDNR or GLIFWC from 2007-2019. Using the criteria defined by Gostiaux et al. (2022), lakes in the S-NR category had a long-term mean age-0 Walleye CPE of $\geq$ 45 fish/h, and lakes in the D-NR category had recent age-0 CPEs < 9 fish/h. Hansen et al. (2015b) suggested that a CPE of approximately 6.2 age-0 Walleye per/km, or approximately 15 age-0 Walleye/h (based on Serns [1982] conversion) is a minimum threshold for where subsequent recruitment to the fishery is expected. Windigo Lake was added as an additional S-NR lake that was logistically easier to sample than some of the other lakes sampled by Gostiaux et al. (2022) and because Windfall Lake, which had been classified as an S-NR lake appeared to be experiencing declining Walleye recruitment during the Gostiaux (2018) evaluation.

Sample Collection and Processing

<u>Larval Yellow Perch</u>

Sampling for larval Yellow Perch took place on each lake in May-June at 7–10 d intervals. Each lake was sampled six times in 2021 and three times in 2022. Similar to Gostiaux et al. (2022), larval sampling periods were defined based on sampling date and each lake was sampled once in each period (Table 2). A conical ichthyoplankton net (1,000-µm mesh; 0.75-m mouth diameter; 3:1 length-to-mouth ratio) was towed at the surface for 5 minutes at different locations on each lake (Isermann and Willis 2008; Gostiaux et al. 2022). Ichthyoplankton tows took place at night (Boehm 2016). A General Oceanics© Model 2030R flowmeter was attached on the mouth of the net to estimate volume of water sampled. Tow sites were selected by dividing each lake into three to six approximately equal zones (depending on the lake's surface area) and randomly selecting one inshore (< 100 m from shore) and one offshore ($\geq$ 100 m from shore) site conducted in each zone. Larval samples were preserved in 95% ethanol.

Larval percids were identified to species using morphometric and meristic characteristics (Auer 1982) and enumerated. A randomly selected subsample of 125 larvae visually identified as Yellow Perch and all larvae visually identified as Walleye were genetically tested in the Molecular Conservation Genetics Laboratory at the University of Wisconsin-Stevens Point to verify species identification in 2021. A subsample of up to 10 larval Yellow Perch per ichthyoplankton tow was measured to the nearest mm. Larval density in tows was measured as the number of larval Yellow Perch per 1,000 m^3.

Age-0 Yellow Perch

To develop a protocol for collecting age-0 Yellow Perch in June-July, mini-fyke nets and hand-held anode electrofishing were used on Escanaba Lake and Little John Lake in June 2021. These sampling gears were chosen because Brandt (2021) suggested that both are effective methods of sampling small (< 150-mm) Yellow Perch. Mini-fyke nets (0.92 × 0.92-m frames, 4.76-mm mesh, 0.61-m diameter hoops, a single 50.8 × 50.8-mm throat, and a 25.4-mm mesh exclusion netting) were deployed with the net frames in 1.0-1.5 m of water by fixing the lead onshore (Sullivan et al. 2019). The frames of the nets were completely submerged, and lead length varied based on shoreline slope. Between 6 and 8 mini-fyke nets were fished for two nights at Little John Lake and one night at Escanaba Lake depending on lake surface area and habitat availability. Mini-fyke nets were checked the next day (maximum soak time = 18 h).

Relative abundance in mini-fyke nets was measured as the number of Yellow Perch per net night. Mini-fyke nets were only used in June 2021.

Hand-held anode boat electrofishing (pulsed DC) was used to target age-0 Yellow Perch in June-October 2021 and July-October 2022 with a total of four sampling periods in 2021 and three in 2022. Sampling periods were defined based on sampling date and each lake was sampled once in each period, with the exception of sampling period 1 in 2021. Sampling periods were typically 1 week long in 2021 and 1.5 weeks in 2022. In sampling period 1 in 2021, lakes were sampled three times over the course of three weeks and averaged to obtain a single mean age-0 Yellow Perch CPE for each lake. I chose to keep these sampling events in a single sampling period because they occurred within a short time frame. Subsequent sampling periods took place at 3–4 week intervals until October of each year.

A hand-held circular anode attached to a 1.2-m pole was powered through a Midwest Lake Electrofishing Systems (MLES) Infinity Box (MLES, Polo, MO; Figure 2). This electrofishing method was used by Brandt (2021) and is similar to methods used by Jackson and Noble (1995) and Sammons et al. (1999). Electrofishing was conducted with a crew of three people using a 4.9-m aluminum boat with a 60-horsepower motor, and all electrofishing took place at night. One long-handled dip net (approximately 1.8 m) with 0.48-cm mesh was used to collect fish and the boat was driven at relatively slow speed, ranging from 1.2-2.4 km/h. Five 10-min shoreline transects were conducted on each lake and starting points of the transects were selected in order maximize spatial coverage during each sampling event while sampling a variety of habitat types (i.e., transect locations were not fixed). Number of Yellow Perch collected at each transect was recorded; up to 15 Yellow Perch were measured per transect, and a subsample of fish between 35 and 165 mm were frozen for age estimation using otoliths. This length range was designed to include age-0 and age-1 Yellow Perch so I could identify a length-based boundary for designating unaged fish as age-0 Yellow Perch in each sampling period.

These fish were re-measured in the laboratory before extracting otoliths. Whole otoliths were submerged under water in a black dish and viewed under a dissecting microscope to estimate age. I pooled fish with otolith ages among lakes and years within each sampling period and plotted the otolith-based age compositions for all lakes within 2-mm total length bins for perch up to 114 mm total length to identify an upper total length boundary between age-0 Yellow Perch for each sampling period. I used this approach rather than a traditional age-length key (Ricker 1975) because previous work suggested that most total length bins encountered in our samples would consist of fish that were a single age and that the "transition" from age-0 to age-1 might occur over a very small range of total lengths (Redman et al. 2011; Janetski et al. 2013). Pooling across years was not possible for sampling period 3 as no sampling occurred in September 2022; only 2021 data were used in establishing the length boundary for this sampling period.

To calculate electrofishing CPE of age-0 Yellow Perch for a specific lake in a specific sampling period, I multiplied Yellow Perch CPE observed for individual transects by the percentage of fish measured for that transect that were $\leq$ the upper TL boundary identified for age-0 perch for the specific sampling period. Individual transect CPEs were averaged to obtain lake-level CPE estimates for each sampling period.

Zooplankton

Zooplankton were collected at offshore ichthyoplankton tow sites during May-mid June when larval Walleye and Yellow Perch were expected to be pelagic (Gostiaux et al. 2022). A Wisconsin plankton net (30-cm opening, 3:1 length to diameter ratio, 80-µm mesh, 63-µm mesh collection bucket) was lowered to one meter above bottom and retrieved vertically (Dodson et al. 2008). In 2021, vertical zooplankton tows were conducted at every offshore larval tow site during each larval sampling event. In 2022, vertical zooplankton tows were only conducted at three fixed offshore larval tow sites per lake during larval sampling events.

In 2021, two D-NR lakes (Sawyer Lake and Kawaguesaga Lake) and two S-NR lakes (Little John Lake and Escanaba Lake) were intensively sampled to describe spatial distributions and temporal trends in zooplankton communities. In addition to the vertical zooplankton tows described previously, during May-mid June, zooplankton were also collected at the water's surface and at approximately 1 and 2 m below the surface at both offshore and inshore ichthyoplankton tow sites. To collect zooplankton samples at these depths, the same plankton net used for vertical tows was attached to a net head and walked around the boat at each depth at each larval tow site (Figure 3). Sampling zooplankton at these depths was conducted in daylight and at night to account for diel patterns in zooplankton distribution, as many species have been shown to migrate up in the water column at night and then descend during the day (Hutchinson 1967). Additionally, daytime vertical zooplankton tows at offshore tow sites were conducted starting the first week of July through the last week of August on these lakes at 10–14 d intervals. All zooplankton samples were preserved with 95% ethanol.

In the laboratory, a 1-mL subsample extracted with a Hensen-Stempel pipette was placed in a zooplankton counting wheel for identification and enumeration. Adult copepods were classified to order (calanoid or cyclopoid) and cladocerans were classified to genus (*Daphnia*, *Bosmina*, *Diaphanosoma*, *Leptidora*) by using a dissecting microscope from 20 to 50x magnification. Three 1-mL subsamples were enumerated for each sample and the average density (number/mL) of zooplankton taxa among the three subsamples was used to calculate zooplankton density for the entire sample (number/L). Total length (top of head to end of caudal spine) was measured to the nearest µm for up to five individuals per sample from *Daphnia*, *Bosmina*, cyclopoid, and calanoid using a Nikon™ DS-Fi2 camera mounted to a Nikon™ SMZ1500 microscope and Nikon™ Elements software.

Analyses

To address objective 1, *t*-tests were used to compare mean number of larval Yellow Perch/1,000 m^3 between lakes with different Walleye recruitment histories for each year of sampling as not all lakes were sampled each year. Homogeneity of variance was tested using a folded *F* test available in the PROC TTEST function in SAS version 9.4 (SAS Institute, Cary North Carolina), and *t*-tests for unequal variance (i.e., Satterthwaite corrected degrees of freedom) were used when appropriate. Repeated-measures analysis of variance (ANOVA) was conducted in SAS version 9.4 (SAS Institute, Cary North Carolina) with Walleye recruitment history and year as main effects and a recruitment history*year interaction was used to compare mean number of larval Yellow Perch/1,000 m^3 in the six lakes that were sampled in both years. The first two larval sampling periods in 2021 were removed from analyses due to low abundance of larval Yellow Perch (i.e., sampling began before the majority of fish hatched). All larval sampling periods in 2022 were used in the analysis for a total of four larval sampling periods in 2021 and three larval sampling periods in 2022 (Table 2).

Electrofishing sampling design in 2021 did not provide sufficient degrees of freedom for testing the interaction term of sampling period*lake type in an ANOVA format, so I compared age-0 Yellow Perch CPE between lakes with different Walleye recruitment histories within each of the four sampling periods (N = 3 for each recruitment history) using *t*-tests. Homogeneity of variance was tested using a folded *F* test available in the PROC TTEST function in SAS version

9.4 (SAS Institute, Cary North Carolina), and *t*-tests for unequal variance (i.e., Satterthwaite corrected degrees of freedom) were used when appropriate. I expected CPE to decline over subsequent sampling periods due to mortality. To compare mortality rates between Walleye recruitment histories I regressed $\log_e$ transformed CPE of age-0 Yellow Perch + 1 against sampling period (similar to a catch curve; Ricker 1975) to estimate the slope of the decline in CPE observed for each lake and then compared the average slope between recruitment histories using a *t*-test. This assumes that catchability of age-0 Yellow Perch was similar among lakes within each sampling period.

For lakes sampled in 2022, I used mixed effects models in SAS version 9.4 (SAS Institute, Cary North Carolina) with recruitment history and sampling periods as fixed effects and lake within recruitment history included as a random effect to compare age-0 Yellow Perch CPE between lakes with different Walleye recruitment histories. Lake within recruitment history was used as a random effect to account for the fact that lakes were being repeatedly sampled over time. Similar to 2021, I regressed $\log_e$ transformed age-0 Yellow Perch CPE against sampling period to estimate slopes for each lake and then compared the average slope between recruitment histories using a *t*-test. Additionally, slopes from regression analyses conducted for northeastern Wisconsin lakes in 2021 and 2022 were combined and average slopes were compared between lakes with different Walleye recruitment histories using a *t*-test.

To address objective 2, Spearman's rank correlations ($\alpha = 0.05$) were used to determine if peak CPE of larval Yellow Perch in ichthyoplankton tows and average CPE of post-larval Yellow Perch were correlated with CPE of age-0 Yellow Perch in October electrofishing. I used the term "post-larval" to differentiate between age-0 Yellow Perch captured in June-July (sampling period 1) and age-0 Yellow Perch captured in October. Similar to Boehm et al. (2020), I also used a more categorical approach to determine if relative CPE (strong or weak) at larval and post-larval stages could predict relative year class strength of age-0 Yellow Perch in October (strong or weak). To do this, peak larval CPE and average CPEs of post-larval and age-0 stages were determined for individual lakes for each year, resulting in 16 lake-year pairings for each life stage. For each life stage, values of CPE for each lake-year pairing were classified as strong (≥ median for all 16 observations) or weak (< median for all 16 observations).

Error matrices (Congalton and Mead 1983; Boehm et al. 2020; Dembkowski et al. 2022) were used to evaluate whether strong and weak larval and post-larval CPEs accurately predicted strong or weak year classes of age-0 Yellow Perch in October electrofishing. True positives occurred when larval or post-larval CPE was strong (i.e., predicted condition = positive) and fall age-0 Yellow Perch CPE was also strong (i.e., true condition = positive). True negatives occurred when larval or post-larval CPE was considered weak (i.e., predicted condition = negative) and fall age-0 Yellow Perch CPE was also considered weak (i.e., true condition = negative). False positives occurred when larval or post-larval CPE was considered strong but fall age-0 Yellow Perch was considered weak. False negatives occurred when larval or post-larval CPE was considered weak and fall age-0 Yellow Perch CPE was considered strong. Accuracy was calculated as the ratio of true positives and true negatives to the total number of observations (N = 16) for larval or post-larval stages (Congalton and Mead 1983).

To address objective 3, two-sample *t*-tests were used to determine if zooplankton density and total lengths collected in vertical zooplankton tows differed between Walleye recruitment histories during the larval fish sampling period (May-early June), which replicates the comparison previously completed by Gostiaux et al. (2022) but with some differences in study lakes. Comparisons were conducted for both density and total lengths of *Daphnia* spp., cyclopoid copepods, and calanoid copepods.

I used a generalized linear model (GLM) to determine if zooplankton density and total lengths at three depth strata (surface, approximately 1 m below surface, and approximately 2 m below surface) differed between lakes with different Walleye recruitment histories during May-June 2021. I used separate models for day and night and included the interaction term between recruitment history and depth. Cyclopoid copepod density and calanoid copepod density were $\log_e$ transformed before analysis due to unequal variances. A series of Tukey (HSD) *post hoc* tests was used for pairwise comparisons of factor- or treatment-level least-squares means.

For the four lakes where vertical zooplankton tows were conducted through the last week of August, I used a repeated-measures ANOVA in SAS version 9.4 (SAS Institute, Cary North Carolina) with Walleye recruitment history and sampling period as main effects and a Walleye recruitment history*sampling period interaction term to determine if temporal patterns in zooplankton density and average total lengths differed between recruitment histories. A Tukey (HSD) *post hoc* test was used for pairwise comparisons of factor- or treatment-level least-squares means if ANOVA indicated differences between factors. *Daphnia* spp., cyclopoid copepod, and calanoid copepod densities were $\log_e$ transformed due to unequal variances and non-normal distributions. All zooplankton analyses were conducted separately for *Daphnia* spp., calanoid copepods, and cyclopoid copepods. Alpha (α) was set at 0.05 for all analyses and were conducted in R (version 4.2.2; R Core Development Team 2022) unless otherwise noted.

Results

Objective 1: Yellow Perch Recruitment Patterns

In 2021, mean density of larval Yellow Perch in ichthyoplankton tows conducted on S-NR lakes ranged from 90 fish/1,000 m^3 to 893 fish/1,000 m^3 (mean of means = 604 fish/1,000 m^3; SE = 258). Mean density of larval Yellow Perch in D-NR lakes ranged from 197 fish/1,000 m^3 to 1,995 fish/1,000 m^3 (mean of means = 864 fish/1,000 m^3; SE = 569). In 2022, mean density of larval Yellow Perch in S-NR lakes ranged from 291 fish/1,000 m^3 to 4,092 fish/1,000 m^3 (mean = 2,051 fish/1,000 m^3; SE = 619), and mean density of larval Yellow Perch in D-NR lakes ranged from 370 fish/1,000 m^3 to 7,495 fish/1,000 m^3 (mean of means = 3,433 fish/1,000 m^3; SE = 1,287; Figure 4). Larval Yellow Perch densities in the six northeastern Wisconsin lakes that were sampled in both 2021 and 2022 were similar among years and between Walleye recruitment histories (F = 0.27, df = 1,4, P = 0.63).

Due to high variability in catch, high processing times associated with catches in some nets, and logistical and gear limitations, mini-fyke nets were only used during the trial sampling period in June 2021. I would have only been able to sample three lakes in a week due to a limited number of mini-fyke nets available for use, soaking time per sampling event (1 night), and net drying time (approx. 24 hours) to reduce the chance of spreading invasive species between lakes. Hand-held anode electrofishing allowed me to sample different lakes on consecutive nights.

The coefficient of variation ([SD/mean] x 100; CV) of age-0 and age-1 Yellow Perch CPE collected via mini-fyke nets and hand-held anode electrofishing in Escanaba was 171% and 21%, respectively; CV of age-0 and age-1 perch CPE collected via mini-fyke nets and hand-held anode electrofishing in Little John was 100% and 61%, respectively. Only age-0 Yellow Perch CPE from hand-held electrofishing were used in analyses.

A total of 411 Yellow Perch were retained for age estimation. In June-July, individuals $\leq$ 60 mm were considered age 0, in August individuals $\leq$ 72 mm were considered age 0, in September individuals < 78 mm were considered age 0, and in October individuals < 82 mm were considered age 0 **(**Figure 5). In 2021, age-0 Yellow Perch CPE ranged from 0 age-0 Yellow Perch/h to 4,240 age-0 Yellow Perch/h. Overall mean CPE declined across sampling periods; mean CPE in sampling period 1 was 1,452 age-0 Yellow Perch/h, mean CPE in sampling period 2 was 1,019 age-0 Yellow Perch/h, mean CPE in sampling period 3 was 417 age-0 Yellow Perch/h, and mean CPE in sampling period 4 was 219 age-0 Yellow Perch/h (Figure 6). Age-0 Yellow Perch CPE was significantly higher in S-NR lakes during sampling period 1 (t = -4.39, df = 1,4, P = 0.01) but not in subsequent sampling periods (Table 3). Slopes associated with declines in $\log_e$ age-0 Yellow Perch CPE over successive sampling periods ranged from -1.13 to -0.25 (mean = -0.75; SD = 0.31). Mean slopes did not differ between lakes with different Walleye recruitment histories (Figure 7). Mean slopes associated with declines in $\log_e$ age-0 Yellow Perch CPE +1 over successive sampling periods did not differ between lakes with different Walleye recruitment histories (Figure 7).

For lakes sampled in 2022, age-0 Yellow Perch CPE ranged from 1 age-0 Yellow Perch/h to 12,009 age-0 Yellow Perch/h. Overall mean CPE declined across sampling periods; mean CPE in sampling period 1 was 2,450 age-0 Yellow Perch/h, mean CPE in sampling period 2 was 711 age-0 Yellow Perch/h, and mean CPE in sampling period 3 was 298 age-0 Yellow Perch/h (Figure 8). There was no significant interaction between recruitment history and sampling period (F = 1.63, df = 2,16, P = 0.23) in explaining variation in age-0 Yellow Perch electrofishing CPE. The effect of recruitment history was not significant (F = 1.13, df = 1,8, P = 0.32), whereas the effect of sampling period was significant (F = 3.65, df = 1,16, P = 0.049). Slopes associated with declines in $\log_e$ age-0 Yellow Perch CPE over successive sampling periods ranged from -1.86 to -0.07 (mean = -0.97; SD = 0.60) and average slopes did not differ between lakes with different Walleye recruitment histories (Figure 9). For the set of six northeastern Wisconsin lakes sampled in both years of my study, age-0 Yellow Perch CPE was not different between Walleye recruitment histories within any sampling period during 2022 (Figure 10). Mean slope did not differ between lakes with different Walleye recruitment histories (t = -0.81, df = 1,4, P = 0.81; Figure 11).

Objective 2: Predicting Age-0 Yellow Perch Year-Class Strength

Median CPE observed for larval stage was 2406 fish/1,000 m^3, 1234 fish/h for post-larval stage, and 232 fish/h for age-0 stage. Ranked larval and ranked post-larval Yellow Perch CPE were significantly positively correlated (larval r_s = 0.60, P = 0.01; post-larval r_s = 0.73, P < 0.01) with October age-0 Yellow Perch CPE (Figure 12). Error matrices indicated that the relative strength (strong or weak) of larval Yellow Perch CPE was 69% accurate (11 of 16 pairings) in correctly predicting the relative year-class strength (strong or weak) of fall age-0 Yellow Perch. Relative strength of Yellow Perch CPE during June-July was also 69% accurate in correctly predicting the year-class strength of age-0 Yellow Perch sampled in October.

Objective 3: Zooplankton Densities, Spatial and Temporal Distributions

Mean densities (number/L) and mean total lengths (µm) of *Daphnia* spp. and both orders of copepods collected in nighttime vertical zooplankton tows in May-June did not differ between lakes with different Walleye recruitment histories for both years (Table 7; Figure 13; Figure 14). There was no significant interactions between Walleye recruitment history and depth for both day and night when comparing densities or $\log_e$ transformed densities and total lengths for *Daphnia* spp. and both orders of copepods (Table 5; Table 6; Figure 15; Figure 16). There was a significant difference (*F* = 6.12, df = 2, *P* = 0.04) in mean number of *Daphnia* spp./L during the day between the surface (2 *Daphnia* spp./L) and approximately 1 m below surface (8 *Daphnia* spp./L; Table 5; Figure 15; Figure 17). The mean $\log_e$ number of cyclopoid copepods/L was significantly higher (*F* = 7.27, df = 1, *P* = 0.04) in D-NR lakes (2 $\log_e$ cyclopoid copepods/L) than S-NR lakes (1 $\log_e$ cyclopoid copepods/L) during the day (Table 5; Figure 15; Figure 17). There was a significant difference (*F* = 10.30, df = 2, *P* = 0.01) in mean calanoid copepod total length during the day between the surface (637 μm) and approximately 1 m below surface (742 μm; Table 5; Figure 16; Figure 17).

For the four lakes where vertical zooplankton tow samples were conducted through the last week of August, there were no significant interactions between Walleye recruitment history and sampling period when explaining variation in $\log_e$ transformed densities for *Daphnia* spp. and both orders of copepods and for total lengths of both orders of copepods (Table 7; Figure 18; Figure 19; Figure 20). The recruitment history*sampling period interaction term was significant for explaining variation in mean *Daphnia* spp. total length (*F* = 4.21, df = 6, *P* = 0.03), but there were no significant differences between recruitment histories during an individual sampling period (Table 7; Figure 18; Figure 21). There were significant differences in mean $\log_e$ number of *Daphnia* spp./L (*F* = 9.52, df = 6, *P* < 0.01) and mean cyclopoid total length (*F* = 6.62, df = 6, *P* < 0.01) between several sampling periods (Table 7; Figure 18; Figure 19; Figure 21).

Discussion

My results indicate that lakes with declining Walleye recruitment can produce year classes of Yellow Perch with age-0 CPEs that are on average similar to age-0 CPEs observed in S-NR lakes. This suggests that conditions resulting in declining Walleye recruitment may allow for continued recruitment of Yellow Perch, which is not surprising given there are many lakes across North America where perch recruitment occurs, but Walleye recruitment does not. While annual variation in Walleye and Yellow Perch recruitment in northern Wisconsin lakes might be related to similar environmental variables (Brandt et al. 2022), the two species typically use different spawning strategies and habitats (Johnson 1961; Priegel 1970; Whiteside et al. 1985; Fisher et al. 1996) which might explain why perch support self-sustaining population in many lakes where Walleyes do not. Water clarity has, on average, increased in Wisconsin lakes over the past few decades (Peckham and Lillesand 2006), likely resulting in increased macrophyte growth which is favorable Yellow Perch spawning habitat. Additionally, Yellow Perch are generally more tolerant and adaptable to environmental conditions, like temperature, habitat, and water quality parameters (Scott and Crossman 1973; Hokanson 1977; Schneider et al. 2007). Moreover, adult Yellow Perch can thrive with a diet of either fish or invertebrates (Morrison et al. 1997; Knight et al. 1984; Koenig et al. 2022), while adult Walleye are primarily piscivorous (Knight et al. 1984; Liao et al. 2002). Whatever changes have contributed to Walleye recruitment declines in northern Wisconsin lakes over the last decade or more, Yellow Perch appear to be more resilient to these changes than Walleye. Possibly, declines in Walleye abundance have contributed to sustained Yellow Perch recruitment in D-NR lakes because Walleye prey upon age-0 perch (Nielsen 1980; Hartman and Margraf 1993). However, declines in Walleye predation may have been offset by increases in the abundance of other Yellow Perch predators like Largemouth Bass *Micropterus salmoides* (Hansen et al. 2015c; Kelling et al. 2016).

Although I did not observe significant differences in age-0 Yellow Perch CPE between Walleye recruitment histories (with the exception of sampling period 1 in 2021), two of the three D-NR lakes sampled both years (Sawyer and Kawaguesaga) had consistently low age-0 Yellow Perch CPE. Yellow Perch abundance may be low in some lakes with declining Walleye recruitment, but perch abundance in those lakes may have been low prior to declines in Walleye recruitment. Further research is necessary to better understand Yellow Perch recruitment trends, particularly in D-NR lakes.

Both hand-held anode electrofishing and mini-fyke nets were effective for sampling age-0 Yellow Perch in June-July. I experienced high catch rates in a few mini-fyke nets (one net contained over 11,000 perch), leading to extended processing times and higher likelihood of mortality. Additionally, mini-fyke net locations had to be limited to areas with the appropriate depth. Moreover, abundant macrophytes or woody debris prevented us from sampling some areas with mini-fyke nets where we could sample with hand-held anode electrofishing. We note that hand-held anode electrofishing may not be as effective in lakes with high turbidity or in areas of excessive vegetation where shocking is not possible.

My results suggest that larval sampling or hand-held anode electrofishing in June-July could provide useful methods to index age-0 Yellow Perch year class strength in Wisconsin lakes based on age-0 CPEs observed at the end of summer. However, additional research would be needed to determine whether these predictive capabilities extend beyond the first year of life. For example, larval Yellow Perch CPE was significantly related to late-summer age-0 Yellow Perch CPE in eastern South Dakota lakes (Fisher and Willis 1997; Anderson et al. 1998), but Dembkowski et al. (2022) reported that neither larval nor juvenile Yellow Perch CPE was related to age-2 Yellow Perch CPE for lakes within this region. It remains unclear how age-0 abundance relates to abundance in subsequent years. Age-0 Yellow Perch are particularly vulnerable to overwinter mortality (Nielsen 1980; Fitzgerald et al. 2006), so year-class strength in Wisconsin may not be fixed until after the first year of life. Conversely, Bogner et al. (2016) reported that fall age-0 Yellow Perch CPE was significantly related to both age-1 and age-2 Yellow Perch

CPE in a north central Nebraska lake. Validation of age-0 CPE metrics as predictors of Yellow Perch recruitment in Wisconsin lakes would require continued sampling of age-0 perch in at least some lakes and efforts to estimate corresponding year class strength at older ages, which might be accomplished using perch captured in sampling targeting adult Walleye (e.g., Brandt et al. 2022). I would suggest that larval sampling offers the least attractive option as a possible Yellow Perch recruitment index, given the significant investment in personnel time required to process and identify fish collected in ichthyoplankton tows.

Hand-held anode electrofishing may also provide a means for collecting age-0 Walleye from Wisconsin lakes prior to standard boat electrofishing that occurs in September-October. During my gear comparison trials, only three Walleye were captured from Escanaba in 8 net-nights of mini-fyke net sampling, while four were captured in 1.65 h of handheld electrofishing. No Walleye were captured in 12 net-nights of mini-fyke net sampling in Little John, while four were captured in 1.47 h of handheld electrofishing. Gostiaux et al. (2022) suggested that Walleye recruitment bottlenecks occur in D-NR lakes before mid-July because larval Walleye were captured from some D-NR lakes, but few were encountered in micro-mesh gill nets set in late July. However, I captured a total of 4 Walleye in June-July from D-NR lakes and 60 from S-NR lakes during my study. Consequently, hand-held anode electrofishing in June-July may provide an alternative to micro-mesh gill nets for sampling age-0 Walleye and predicting age-0 Walleye year-class strength (e.g., Boehm et al. 2020), but more research is needed to determine if this is the case.

Similar to Gostiaux et al. (2022), my results indicate that lack of larval Yellow Perch and zooplankton as prey do not seem to be limiting factors to age-0 Walleye survival and recruitment in D-NR lakes. Results of my study suggest that availability of *Daphnia* spp. and calanoid and cyclopoid copepods are similar between D-NR and S-NR lakes. Cyclopoid copepods are a primary diet item for larval Walleye and Yellow Perch (Johnston and Mathias 1994; Graeb et al. 2004; Gostiaux et al. 2022) and are likely not limiting in D-NR lakes. My study provides additional evidence that a lack of zooplankton in larval Walleye diets is likely not due to low zooplankton densities, and larval fish may just be a preferred diet item. Large confidence intervals for most zooplankton densities and total lengths made it difficult to detect differences between lake types. While we considered our zooplankton sampling "intensive", analyses were limited by low numbers of replicates (lakes) for each lake type. Zooplankton sampling conducted at this scale took a large amount of effort and adding more lakes to this study was not feasible as efforts were primarily directed toward Yellow Perch sampling. Despite these limitations, I suspect conclusions would be similar if we had included more lakes in the zooplankton analyses.

Future Research

Although my study suggests that Yellow Perch populations may not be experiencing low recruitment in D-NR lakes, there is limited long-term data on Yellow Perch populations available for northern Wisconsin lakes to assess recruitment trends over a meaningful scale. Declines in Walleye recruitment in northern Wisconsin were documented over a couple of decades (Hansen et al. 2015a; Hansen et al. 2015c). The two years of Yellow Perch recruitment data I collected are not enough to fully describe perch recruitment trends because Yellow Perch recruitment is highly variable (Forney 1971; Isermann et al. 2007). It is unknown whether age-0 Yellow Perch CPE is a useful metric for indexing recruitment in Wisconsin. To further develop methods to index perch recruitment trends, future research should focus on determining when perch year-class strength can be considered fixed in northern Wisconsin. After determining the age that

Yellow Perch year-class strength is fixed in Wisconsin, annual sampling should take place to monitor trends in recruitment and potential differences between Walleye recruitment histories.

Zooplankton communities are likely not a factor contributing to differences in Walleye recruitment in northern Wisconsin lakes and future research should focus on other variables that could influence Walleye recruitment. Thermal-optical habitat area (TOHA) plays a significant role in Walleye production (Lester et al. 2004) and could be declining in some northern Wisconsin lakes. Estimating TOHA in lakes with different Walleye recruitment histories may provide additional insight on potential habitat differences between D-NR and S-NR lakes that may help in identifying lakes where Walleye recruitment will continue to occur and lakes where management actions like stocking or harvest regulations may be necessary to maintain Walleye fisheries. Classifying lakes in this manner will be particularly beneficial for utilizing a Resist-Accept-Direct framework to manage Walleye fisheries in Wisconsin (Feiner et al. 2022; Schuurman et al. 2022).

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Table 1. Lake, Walleye recruitment history (S-NR = sustained natural recruitment, D-NR = declining natural recruitment), area (ha), maximum depth (m), average depth (m), and trophic status for study lakes in northern Wisconsin sampled in 2021-2022. Asterisks indicate lakes that were only sampled in 2022. Lake characteristics were obtained from Wisconsin Department of Natural Resources.

Lake	Rec. Hist.	County	Area (ha)	Max Depth (m)	Avg. Depth (m)	Trophic Status
Little John	S-NR	Vilas	61	6	3	Mesotrophic
Escanaba	S-NR	Vilas	123	8	4	Mesotrophic
Big Arbor Vitae	S-NR	Vilas	433	12	5	Mesotrophic
Sand*	S-NR	Sawyer	384	15	6	Eutrophic
Windigo*	S-NR	Sawyer	204	16	4	Mesotrophic
Sawyer	D-NR	Langlade	73	9	3	Mesotrophic
Kawaguesaga	D-NR	Oneida	283	13	5	Mesotrophic
Lac Vieux Desert	D-NR	Vilas	1626	12	3	Mesotrophic
Durphee*	D-NR	Sawyer	80	5	3	Eutrophic
Big Sissabagama*	D-NR	Sawyer	326	15	3	Eutrophic

Table 2. Dates of spring ichthyoplankton tows and hand-held anode electrofishing sampling periods in 2021 and 2022.

	2021	
Ichthyoplankton Tows	Sampling Period 1	May 17 - May 24
	Sampling Period 2	May 25 - May 31
	Sampling Period 3	June 1 - June 7
	Sampling Period 4	June 9 - June 14
Hand-Held Anode Electrofishing	Sampling Period 1	June 23 - July 22
	Sampling Period 2	August 11 - August 19
	Sampling Period 3	September 9 - September 15
	Sampling Period 4	October 8 - October 14
	2022	
Ichthyoplankton Tows	Sampling Period 1	May 22 - May 29
	Sampling Period 2	May 31 - June 7
	Sampling Period 3	June 9 - June 16
Hand-Held Anode Electrofishing	Sampling Period 1	July 5 - July 14
	Sampling Period 2	August 9 - August 29
	Sampling Period 3	September 29 - October 9

Table 3. Results from *t*-tests used to test for differences in mean age-0 Yellow Perch CPE (fish/h) between Walleye recruitment histories in 2021. Significant differences at $\alpha = 0.05$ are highlighted in bold (Figure 6). Variances in CPE were not equal between lakes with different Walleye recruitment histories for sampling period 2 and Satterthwaite adjusted degrees of freedom were used.

Year	Metric	*df*	*t*	*P*
2021	**Sampling Period 1 Age-0 Perch CPE**	**1,4**	**-4.39**	**0.012**
	Sampling Period 2 Age-0 Perch CPE	1,2	-1.62	0.246
	Sampling Period 3 Age-0 Perch CPE	1,4	-1.75	0.155
	Sampling Period 4 Age-0 Perch CPE	1,4	-1.10	0.335

Table 4. Results from *t*-tests used to test for differences in mean densities (number/L) and mean total length (TL; µm) of *Daphnia* spp., cyclopoid copepods, and calanoid copepods between Walleye recruitment histories collected from vertical zooplankton tows during May-June 2021 and 2022 (Figure 13; Figure 14).

Year	Metric	*df*	*t*	*P*
2021	Mean # *Daphnia* spp./L	4.0	0.59	0.588
	Mean # cycplopoid copepods/L	2.1	2.07	0.170
	Mean # calanoid copepods/L	4.0	0.26	0.807
	Mean *Daphnia* spp. TL (µm)	2.0	-0.82	0.495
	Mean cyclopoid copepod TL (µm)	4.0	-0.29	0.785
	Mean calanoid copepod TL (µm)	4.0	-0.05	0.965
2022	Mean # *Daphnia* spp./L	8.0	0.86	0.417
	Mean # cycplopoid copepods/L	5.4	2.04	0.092
	Mean # calanoid copepods/L	8.0	0.72	0.493
	Mean *Daphnia* spp. TL (µm)	8.0	-0.43	0.682
	Mean cyclopoid copepod TL (µm)	8.0	0.55	0.598
	Mean calanoid copepod TL (µm)	8.0	1.72	0.124

Table 5. Results from generalized linear models evaluating Walleye recruitment history, depth (surface, approximately 1 m below surface, and approximately 2 m below surface), and their interaction for comparisons of mean # *Daphnia* spp./L, $\log_e$ mean # cyclopoid copepods/L, $\log_e$ mean # calanoid copepods/L, mean *Daphnia* spp. total length (μm), mean cyclopoid copepod total length (μm), and mean calanoid copepod total length (μm) from daytime samples collected in May-June 2021. Significant differences at α = 0.05 are highlighted in bold (Figure 15; Figure 16).

Metric	*df*	*F*	*P*	Metric	*df*	*F*	*P*
Mean # *Daphnia* spp./L				Mean *Daphnia* spp. TL (μm)			
Recruitment History	1	1.42	0.279	Recruitment History	1	1.24	0.308
Depth	**2**	**6.12**	**0.036**	Depth	2	0.73	0.518
Recruitment History*Depth	2	0.04	0.957	Recruitment History*Depth	2	0.75	0.514
$\log_e$ mean # cyclopoid copepods/L				Mean cyclopoid copepod TL (μm)			
Recruitment History	**1**	**7.27**	**0.036**	Recruitment History	1	0.4	0.552
Depth	2	0.67	0.547	Depth	2	2.81	0.137
Recruitment History*Depth	2	0.004	0.995	Recruitment History*Depth	2	0.74	0.515
$\log_e$ mean # calanoid copepods/L				Mean calanoid copepod TL (μm)			
Recruitment History	1	4.06	0.091	Recruitment History	1	3.71	0.102
Depth	2	0.24	0.796	**Depth**	**2**	**10.3**	**0.012**
Recruitment History*Depth	2	0.003	0.997	Recruitment History*Depth	2	1.38	0.32

Table 6. Results from generalized linear models evaluating Walleye recruitment history, depth (surface, approximately 1 m below surface, and approximately 2 m below surface), and their interaction for comparisons of mean # *Daphnia* spp./L, $\log_e$ mean # cyclopoid copepods/L, $\log_e$ mean # calanoid copepods/L, mean *Daphnia* spp. total length (µm), mean cyclopoid copepod total length (µm), and mean calanoid copepod total length (µm) from nighttime samples collected in May-June 2021 (Figure 15; Figure 16).

Metric	*df*	*F*	*P*	Metric	*df*	*F*	*P*
Mean # *Daphnia* spp./L				Mean *Daphnia* spp. TL (µm)			
Recruitment History	1	2.18	0.19	Recruitment History	1	0.95	0.367
Depth	2	0.89	0.46	Depth	2	0.47	0.644
Recruitment History*Depth	2	0.11	0.900	Recruitment History*Depth	2	0.28	0.762
$\log_e$ mean # cyclopoid copepods/L				Mean cyclopoid copepod TL (µm)			
Recruitment History	1	4.18	0.087	Recruitment History	1	2.53	0.163
Depth	2	0.15	0.868	Depth	2	0.02	0.980
Recruitment History*Depth	2	0.06	0.940	Recruitment History*Depth	2	0.007	0.993
$\log_e$ mean # calanoid copepods/L				Mean calanoid copepod TL (µm)			
Recruitment History	1	3.9	0.096	Recruitment History	1	0.14	0.726
Depth	2	0.1	0.903	Depth	2	0.06	0.941
Recruitment History*Depth	2	0.06	0.938	Recruitment History*Depth	2	0.55	0.602

Table 7. Results from repeated-measures ANOVA models evaluating recruitment history, sampling period, and their interaction for comparisons of mean $\log_e$ number of *Daphnia* spp./L, mean $\log_e$ number of cyclopoid copepods/L, mean $\log_e$ number of calanoid copepods/L, mean *Daphnia* spp. total length (µm), mean cyclopoid copepod total length (µm), and mean calanoid copepod total length (µm). Significant differences at α = 0.05 are highlighted in bold (Figure 18; Figure 19; Figure 20; Figure 21).

Metric	*df*	*F*	*P*	Metric	*df*	*F*	*P*
$\log_e$ mean # *Daphnia* spp./L				Mean *Daphnia* spp. TL (µm)			
Recruitment History	1	1.34	0.375	Recruitment History	1	1.04	0.415
Sampling Period	**6**	**9.52**	**<0.001**	**Sampling Period**	**6**	**7.10**	**0.005**
Recruitment History*Sampling Period	6	0.57	0.746	**Recruitment History*Sampling Period**	**6**	**4.21**	**0.027**
$\log_e$ mean # cyclopoid copepods/L				Mean cyclopoid copepod TL (µm)			
Recruitment History	1	0.036	0.868	Recruitment History	1	4.67	0.163
Sampling Period	6	1.19	0.374	**Sampling Period**	**6**	**6.62**	**0.003**
Recruitment History*Sampling Period	6	1.99	0.147	Recruitment History*Sampling Period	6	1.02	0.460
$\log_e$ mean # calanoid copepods/L				Mean calanoid copepod TL (µm)			
Recruitment History	1	0.43	0.581	Recruitment History	1	5.24	0.149
Sampling Period	6	0.27	0.941	Sampling Period	6	0.62	0.713
Recruitment History*Sampling Period	6	0.45	0.831	Recruitment History*Sampling Period	6	0.61	0.718

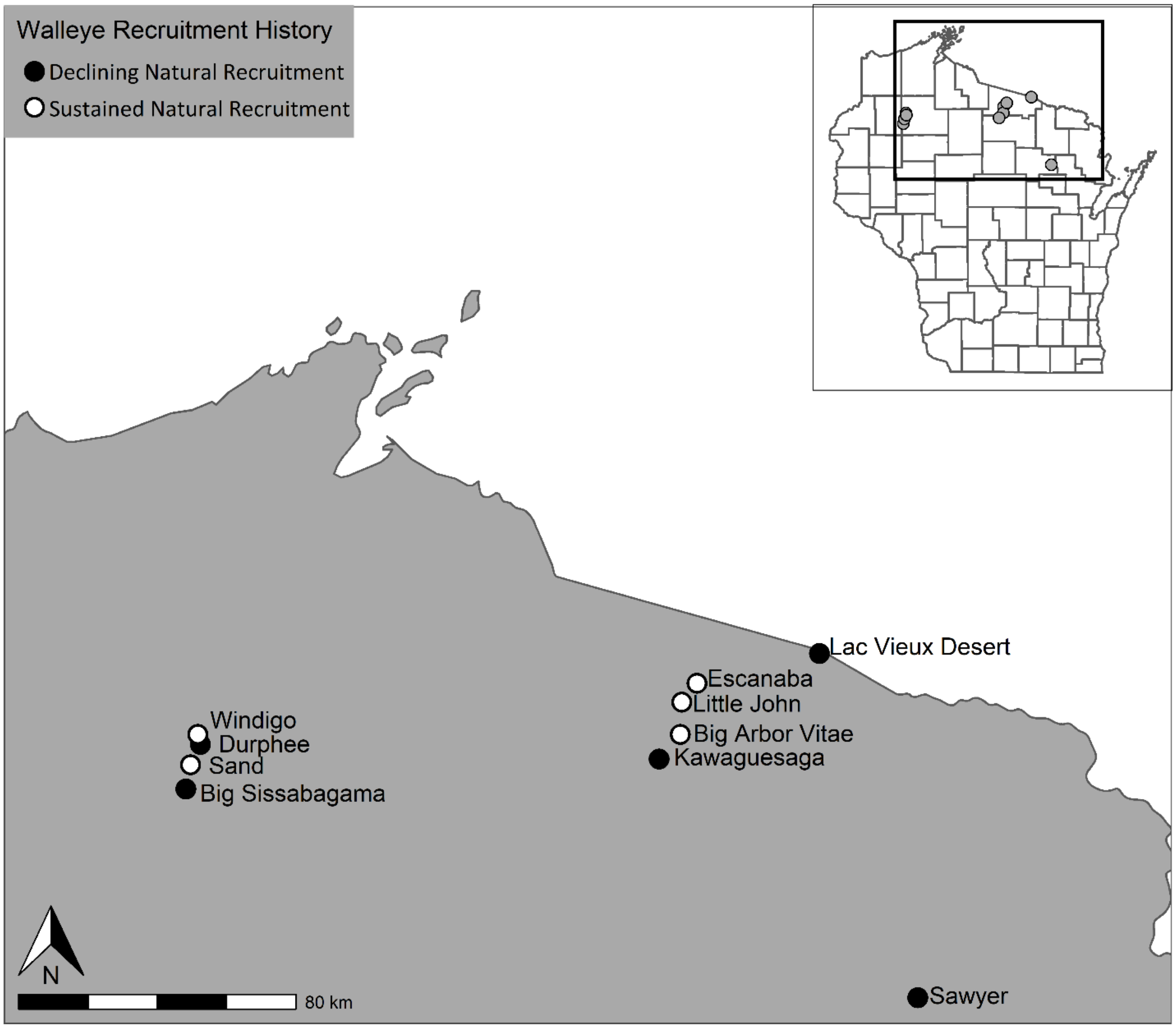

Figure 1. Map of 10 study lakes in northern Wisconsin. Lakes with declining Walleye recruitment are represented by black circles and lakes with sustained Walleye recruitment are represented by white circles.

Figure 2. A hand-held circular anode that was used to target Yellow Perch from a 4.9-m boat with a 60-horsepower motor.

Figure 3. Zooplankton net attached to a net head and walked around the boat to collect zooplankton samples at three different depths (surface and approximately 1 m and 2 m below surface).

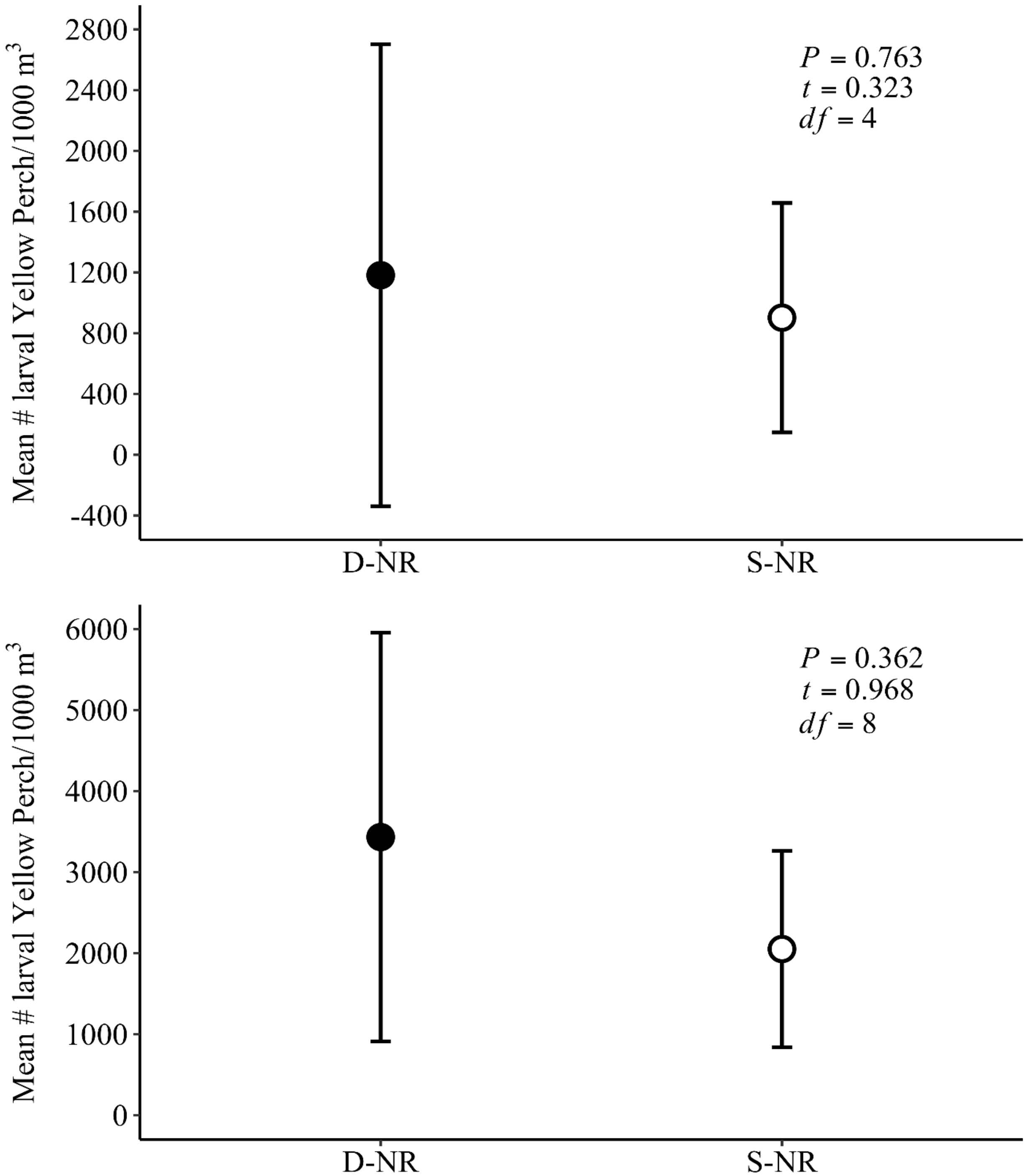

Figure 4. Mean number of larval Yellow Perch/1,000 m^3 collected from nighttime May-June surface ichthyoplankton tows in 2021 (top) and 2022 (bottom) in lakes with declining Walleye recruitment (D-NR; black circles) and lakes with sustained Walleye recruitment (S-NR; white circles). A *t*-test for each year determined that there were no significant differences in mean number of larval Yellow Perch/1,000 m^3 between recruitment histories, and repeated measures ANOVA determined that there was no significant difference in mean number of larval Yellow Perch/1,000 m^3 between years and recruitment histories for the six lakes sampled during both years. Error bars represent 95% confidence intervals.

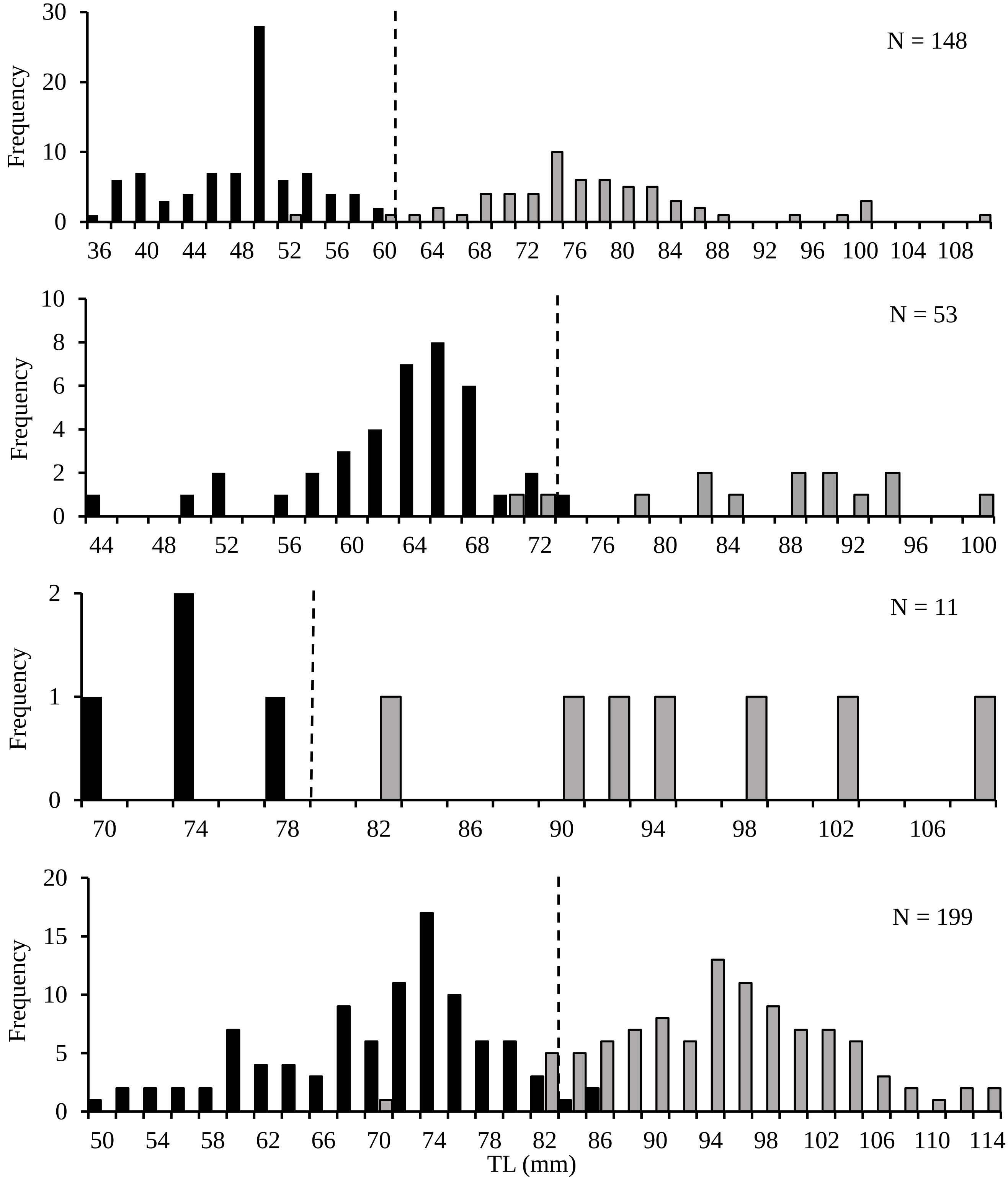

Figure 5. Length-frequency distributions of age-0 (black) and age-1 Yellow Perch (gray) collected in June-July (top), August (second from top), September (third from top), and October (bottom) 2021 and 2022. Dashed lines represent designated length boundary between age-0 and age-1 fish.

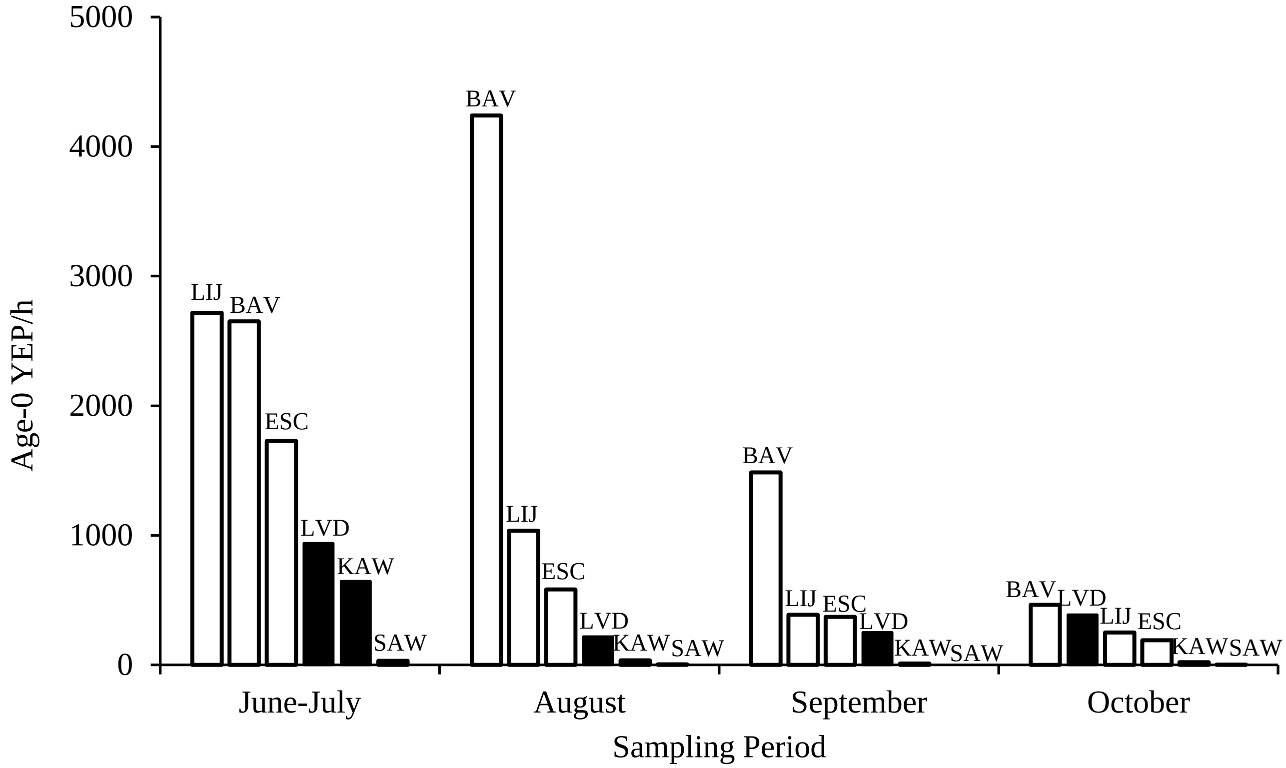

Figure 6. Relative lake rankings of age-0 Yellow Perch CPE (number of age-0 Yellow Perch/h) by sampling period in 2021 in lakes with declining Walleye recruitment (black) and sustained Walleye recruitment (white). Bars within each sampling period represent age-0 Yellow Perch CPE of an individual lake. A series of *t*-tests determined that Yellow Perch CPE was significantly higher in S-NR lakes in June-July but was similar between lake types in subsequent sampling periods.

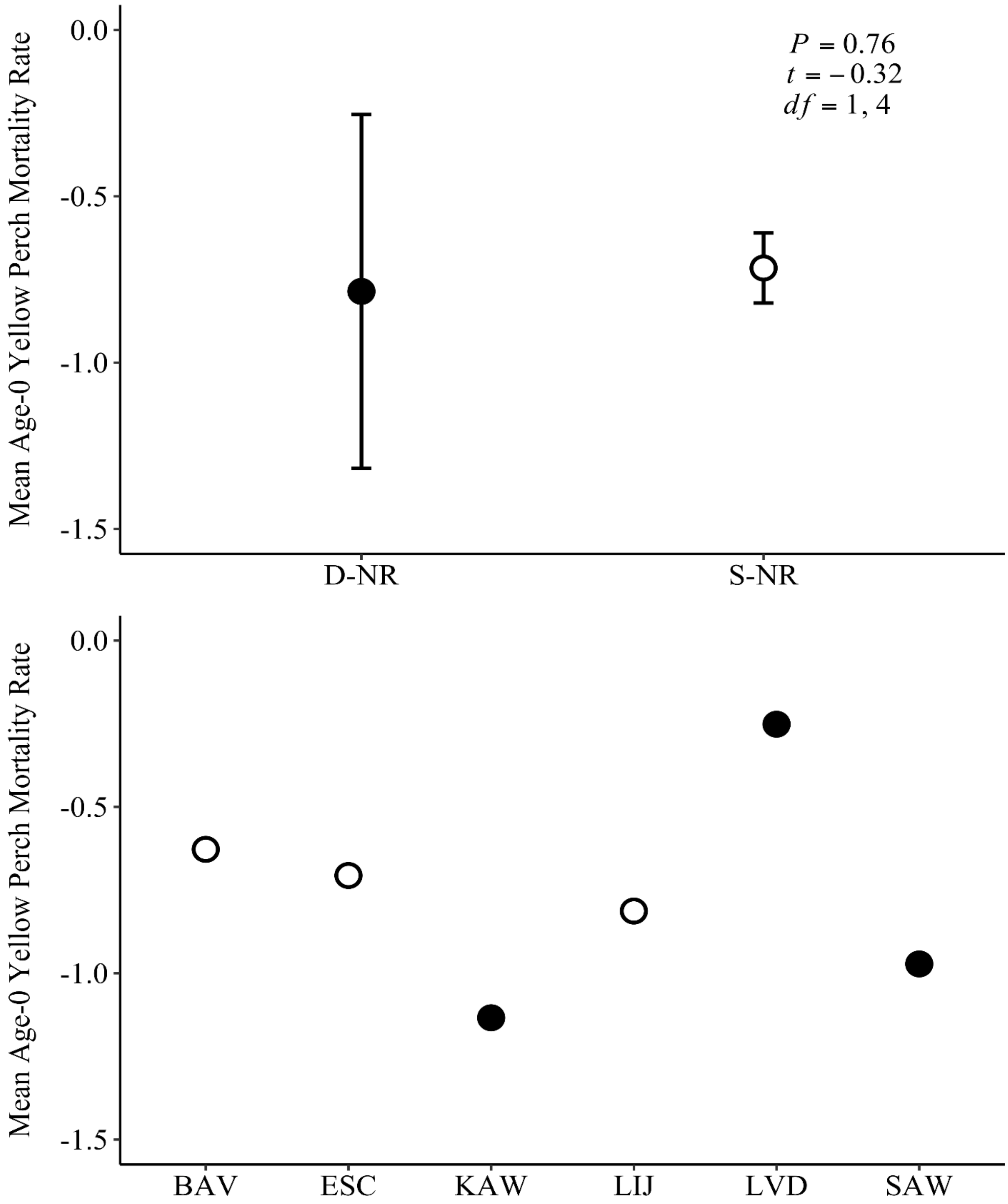

Figure 7. Mean age-0 Yellow Perch slopes associated with declines in $\log_e$ transformed age-0 Yellow Perch CPE across four successive sampling periods in June-October 2021 for D-NR (black) and S-NR (white) lakes. The top figure represents mean age-0 Yellow Perch mortality rates of each lake type; error bars represent 95% confidence intervals. The bottom figure represents slopes observed for individual lakes. A *t*-test determined there was no significant difference in slopes between lake types.

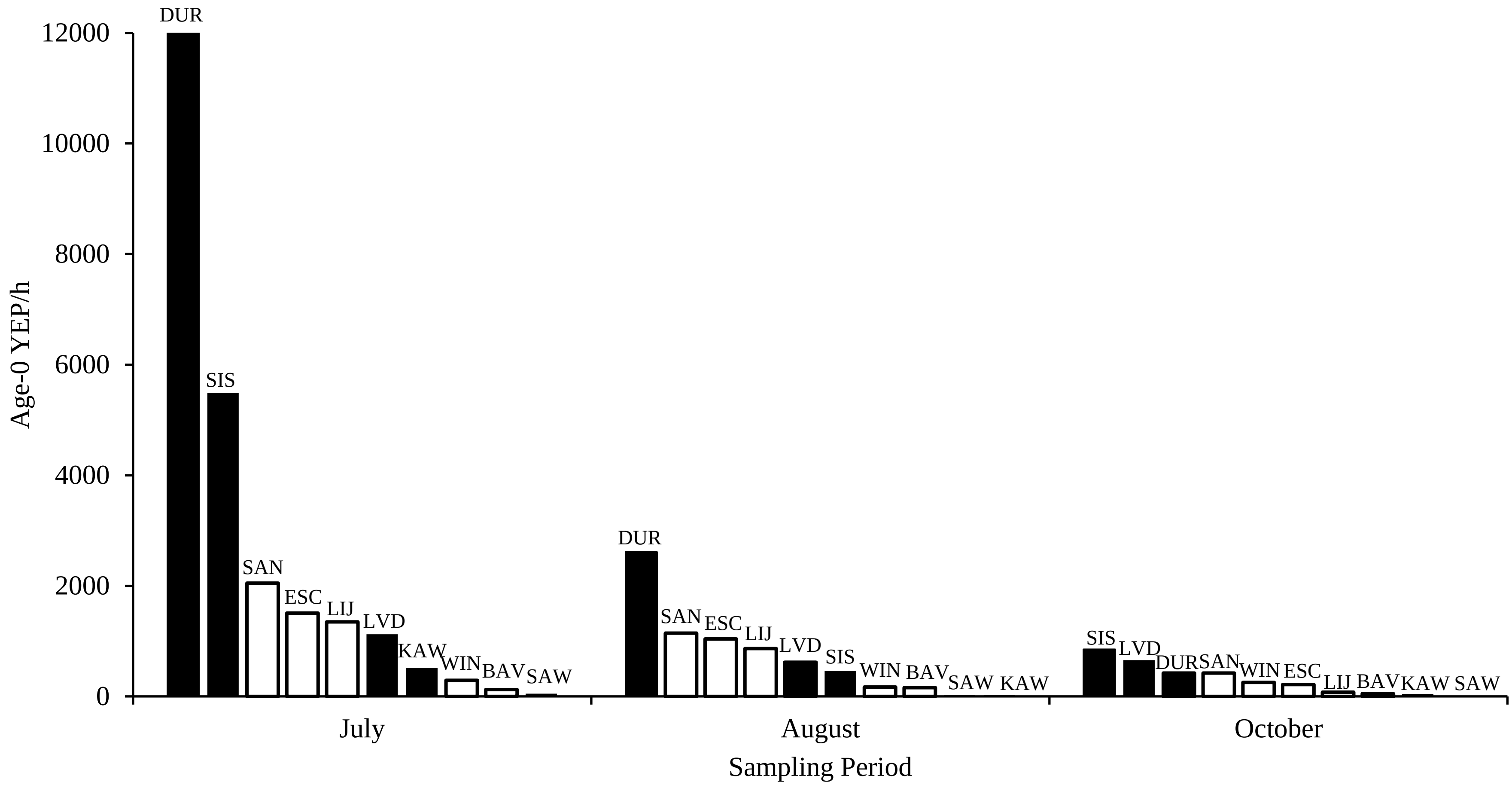

Figure 8. Relative lake rankings of age-0 Yellow Perch CPE by sampling period in 2022 in lakes with declining Walleye recruitment (black) and sustained Walleye recruitment (white). Bars within each sampling period represent age-0 Yellow Perch CPE of an individual lake. Mixed effects models determined there was no significant interaction between recruitment history and sampling period.

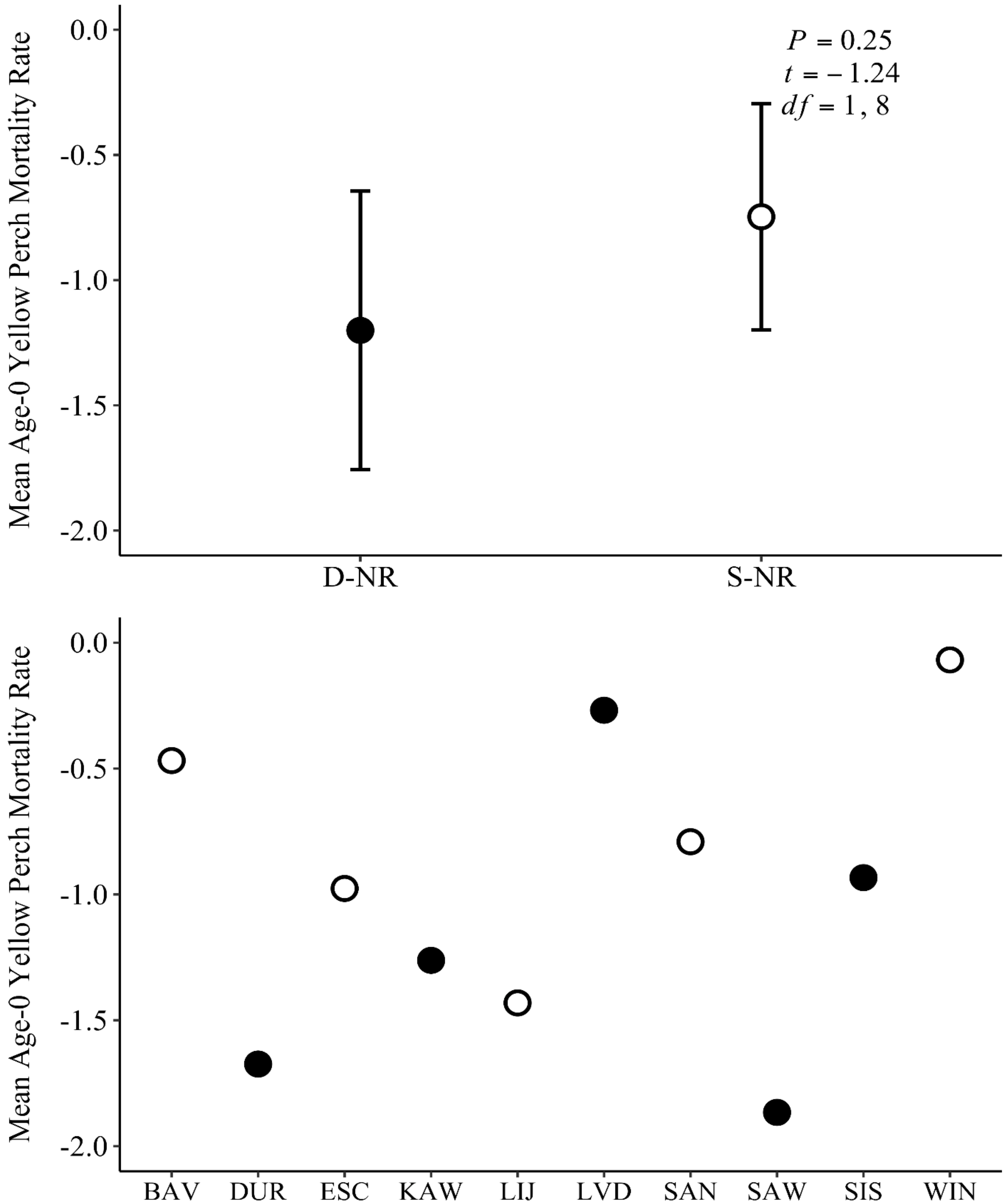

Figure 9. Mean age-0 Yellow Perch slopes associated with declines in $\log_e$ transformed age-0 Yellow Perch CPE across three successive sampling periods in July-October 2022 for all D-NR (black) and S-NR (white) lakes. The top figure represents mean age-0 Yellow Perch mortality rates of each lake type; error bars represent 95% confidence intervals. The bottom figure represents slopes observed for individual lakes. A *t*-test determined there was no significant difference in slopes between lake types.

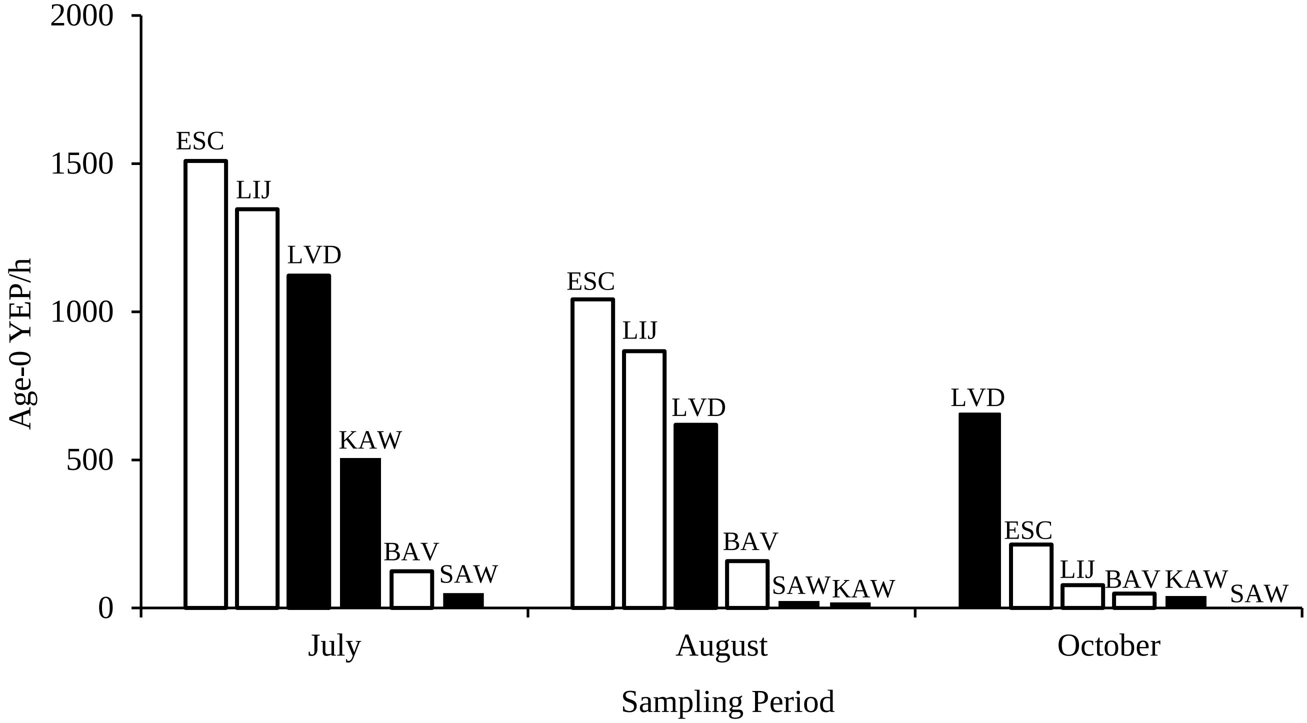

Figure 10. Relative lake rankings of age-0 Yellow Perch CPE by sampling period in 2022 for Minocqua area lakes with declining Walleye recruitment (black) and sustained Walleye recruitment (white). Bars within each sampling period represent age-0 Yellow Perch CPE of an individual lake.

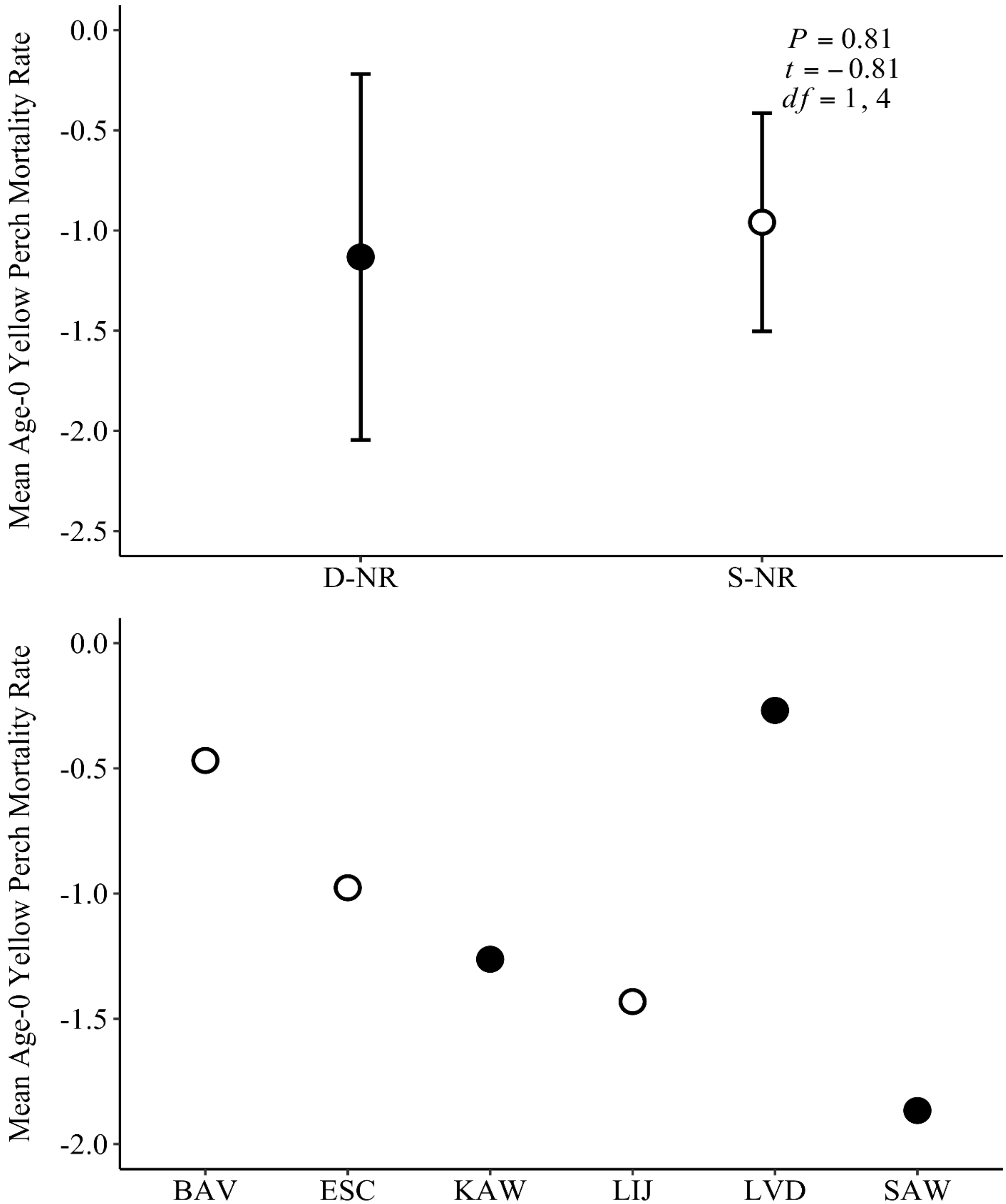

Figure 11. Mean age-0 Yellow Perch slopes associated with declines in $\log_e$ transformed age-0 Yellow Perch CPE across three successive sampling periods in July-October 2022 for Minocqua area D-NR (black) and S-NR (white) lakes. The top figure represents mean age-0 Yellow Perch mortality rates of each lake type; error bars represent 95% confidence intervals. The bottom figure represents slopes observed for individual lakes. A *t*-test determined there was no significant difference in slopes between lake types.

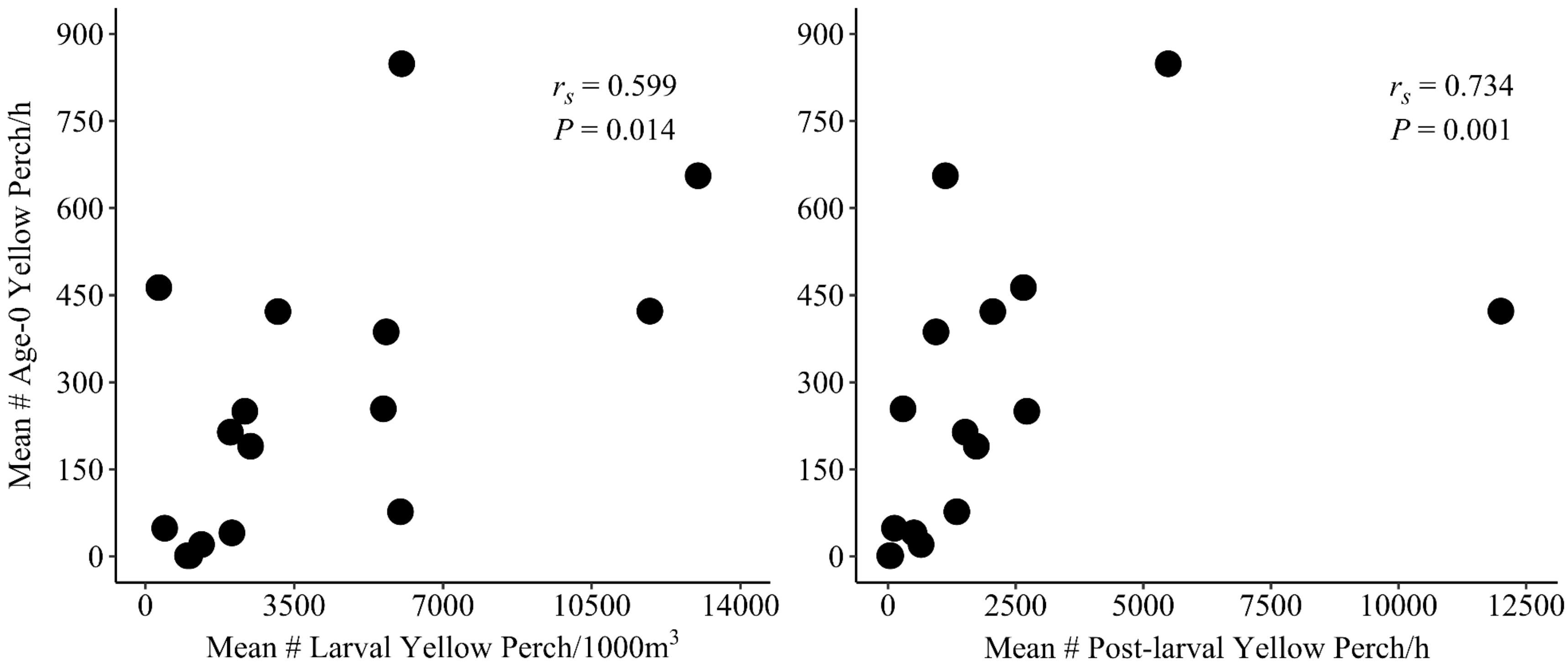

Figure 12. Scatter plots of mean number of age-0 Yellow Perch/h from fall electrofishing in relation to mean number of larval Yellow Perch/1,000m^3 estimated from ichthyoplankton tows (left) and mean number of post-larval Yellow Perch/h from June-July electrofishing (right) for 6 lakes sampled in 2021 and 10 lakes sampled in 2022. Spearman's rank correlation coefficients (r_s) and associated probability values (P) are reported.

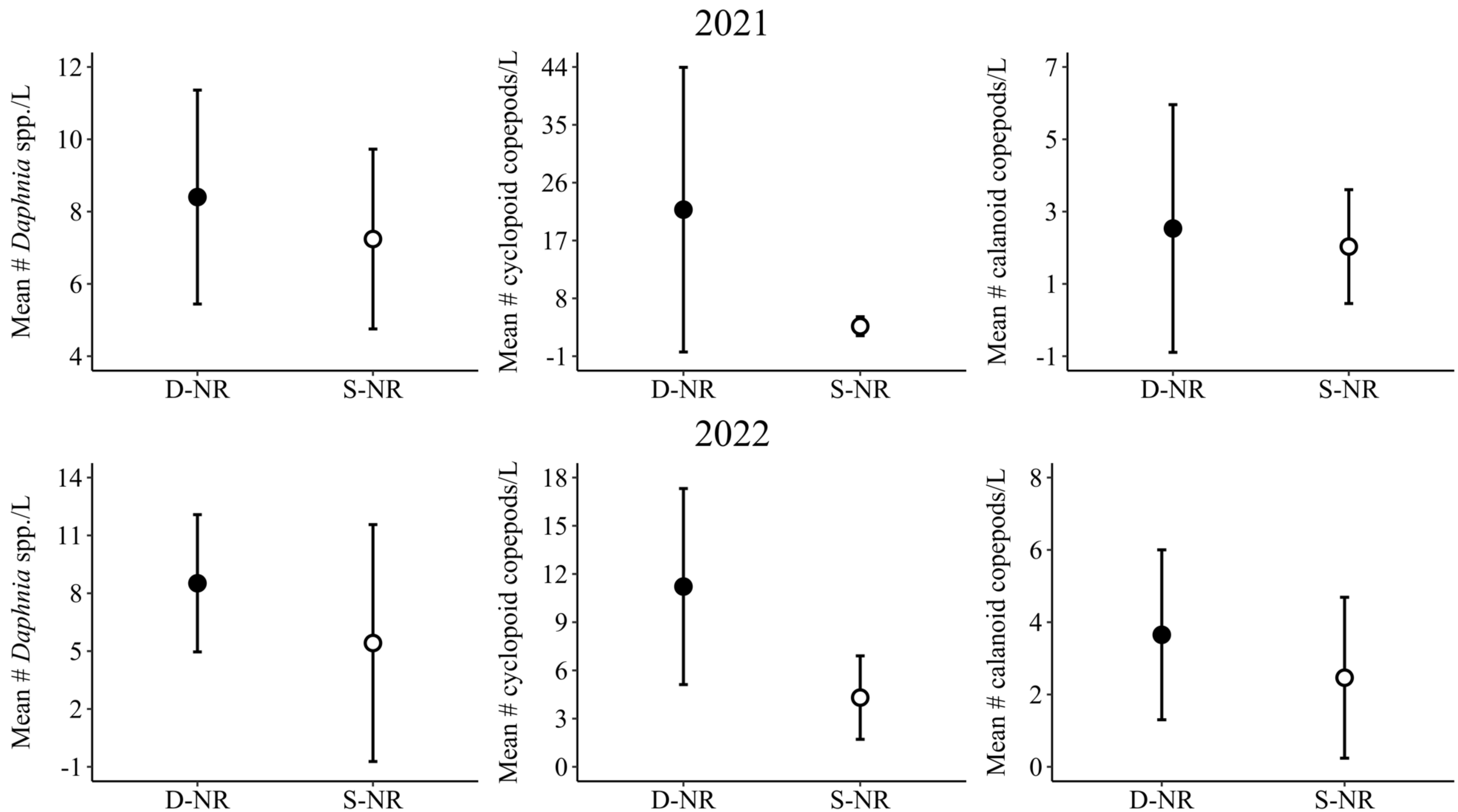

Figure 13. Mean densities (#/L) of *Daphnia* spp., cyclopoid copepods, and calanoid copepods collected from nighttime vertical tows in May-June 2021 (top row) and May-June 2022 (bottom row) for lakes with declining Walleye recruitment (D-NR; black circles) and sustained Walleye recruitment (S-NR; white circles). There were no significant differences in zooplankton densities between recruitment histories (Table 4). Error bars represent 95% confidence intervals.

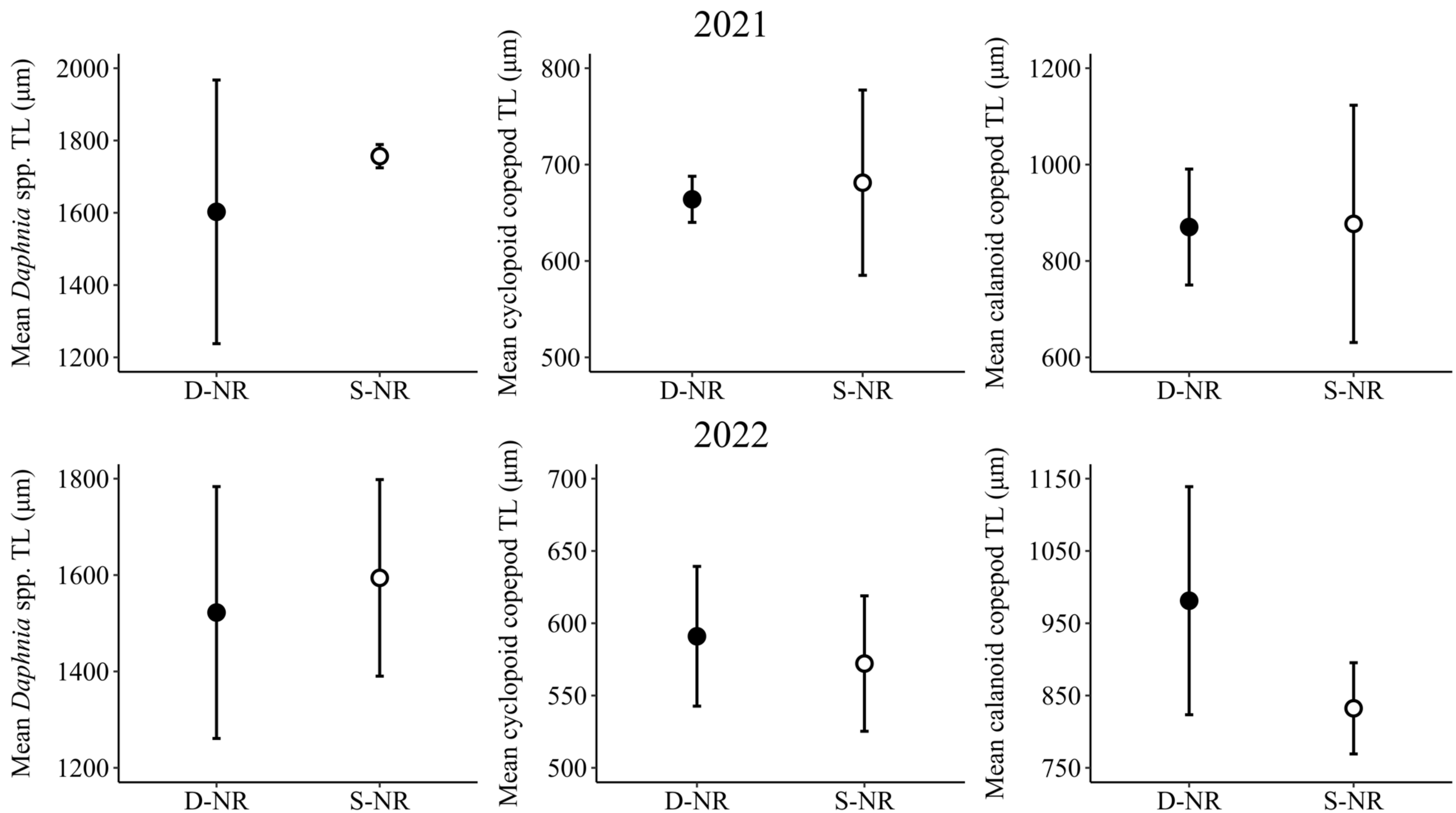

Figure 14. Mean total length (TL; µm) of *Daphnia* spp., cyclopoid copepods, and calanoid copepods collected from nighttime vertical tows in May-June 2021 (top row) and May-June 2022 (bottom row) for lakes with declining Walleye recruitment (D-NR; black circles) and sustained Walleye recruitment (S-NR; white circles). There were no significant differences in zooplankton total length between recruitment histories (Table 4). Error bars represent 95% confidence intervals.

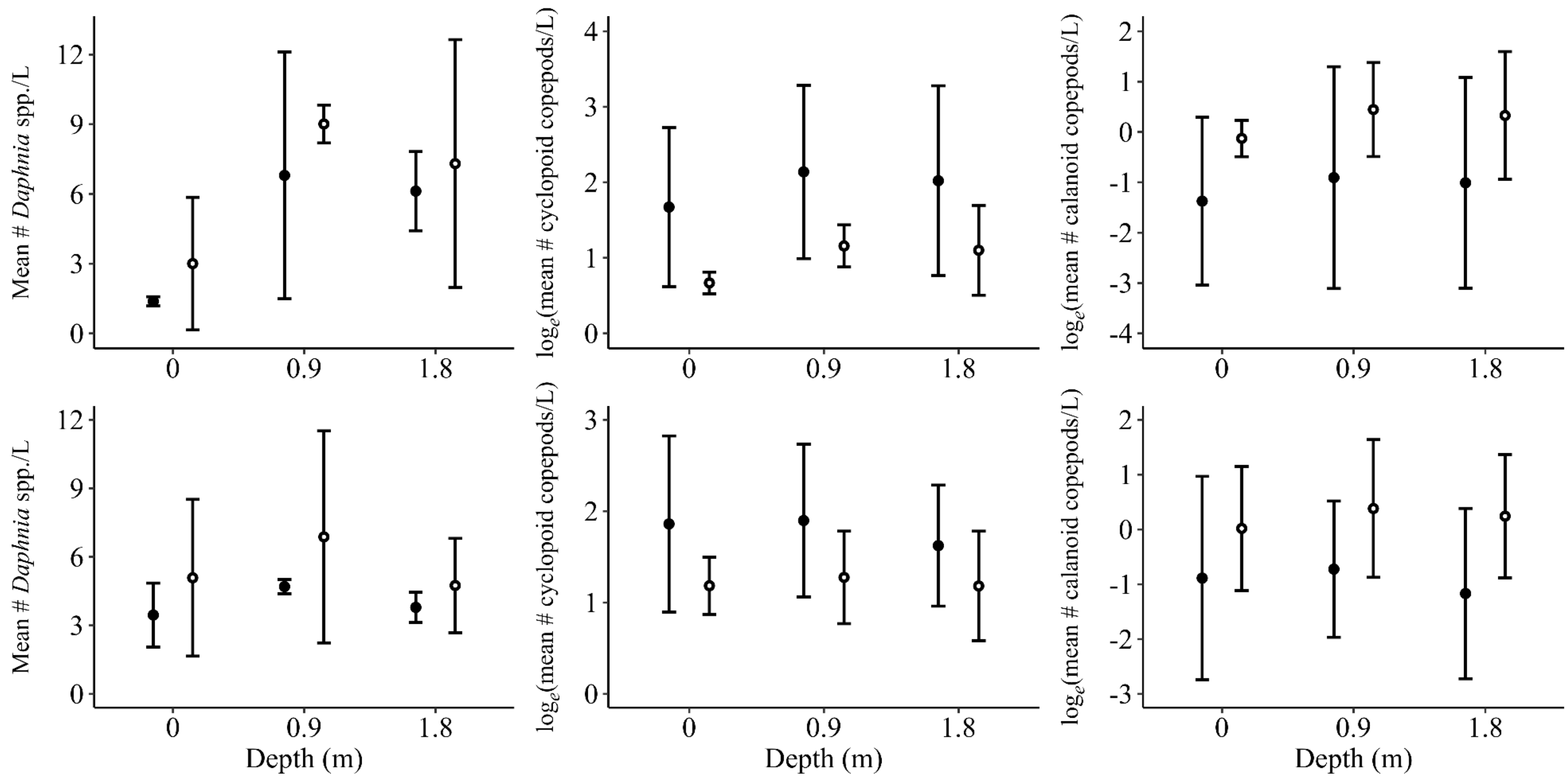

Figure 15. Mean density (#/L) of *Daphnia* spp., cyclopoid copepods, and calanoid copepods from horizontal tows at three depths (surface, approximately 1 m below surface, and approximately 2 m below surface) in May-June 2021 during the day (top row) and night (bottom row) from lakes with declining Walleye recruitment (D-NR; black circles) and sustained Walleye recruitment (S-NR; white circles). Mean cyclopoid copepod and calanoid copepod densities were log$_e$ transformed prior to statistical analysis. A generalized linear model indicated no significant interactions between Walleye recruitment history and depth. There were significant differences in *Daphnia* spp. density (day) among depths, and a significant difference in cyclopoid copepod density (day) between recruitment histories (Figure 16; Tables 5-6). Error bars represent 95% confidence intervals.

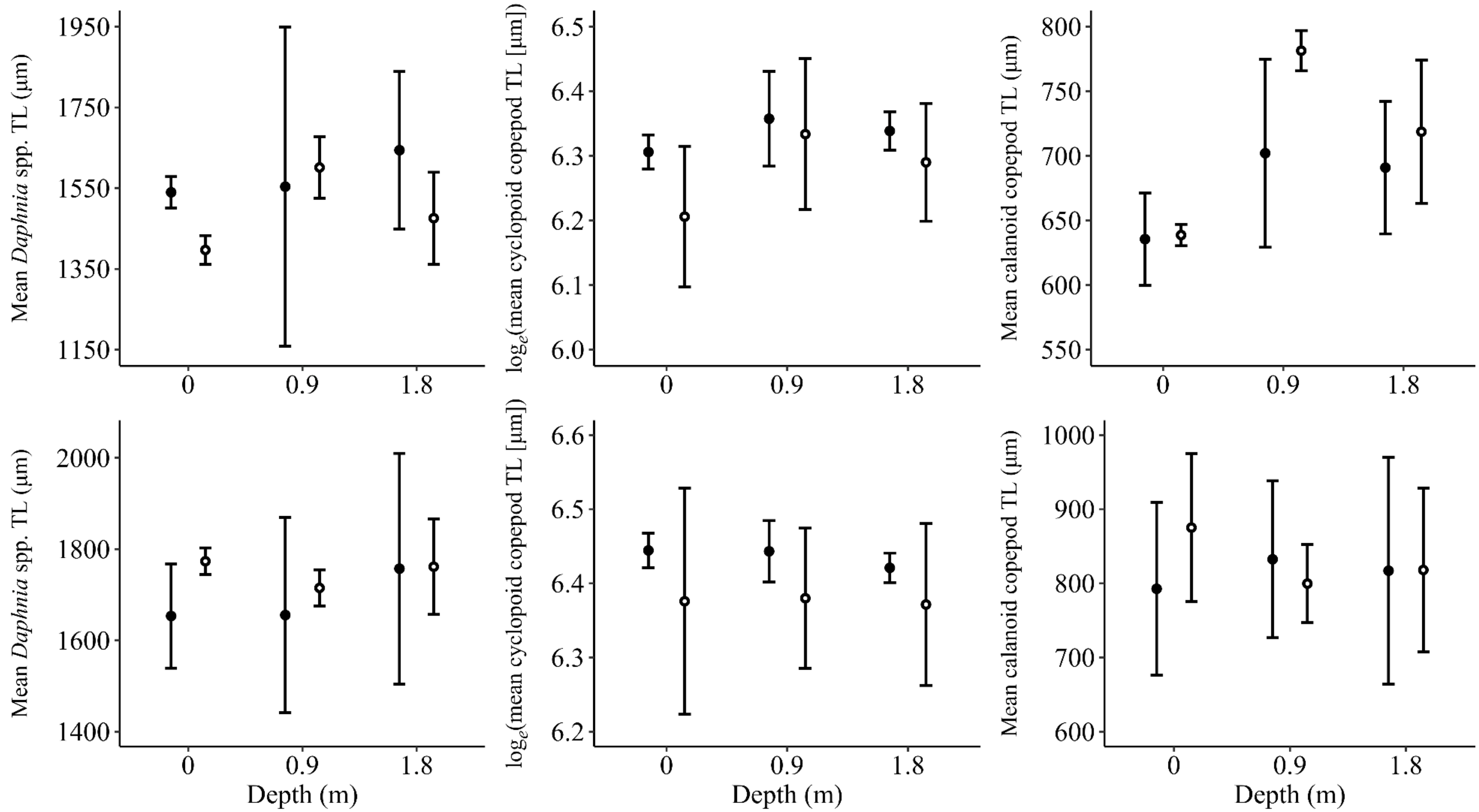

Figure 16. Mean total length (TL; µm) of *Daphnia* spp., cyclopoid copepods, and calanoid copepods from horizontal tows at three depths (surface, approximately 1 m below surface, and approximately 2 m below surface) in May-June 2021 during the day (top row) and night (bottom row) from lakes with declining Walleye recruitment (D-NR; black circles) and sustained Walleye recruitment (S-NR; white circles). Mean cyclopoid copepod total length was log$_e$ transformed prior to statistical analysis. A generalized linear model indicated no significant interactions between Walleye recruitment history and depth. There were significant differences in calanoid copepod total length (day) among depths (Figure 15; Tables 5-6). Error bars represent 95% confidence intervals.

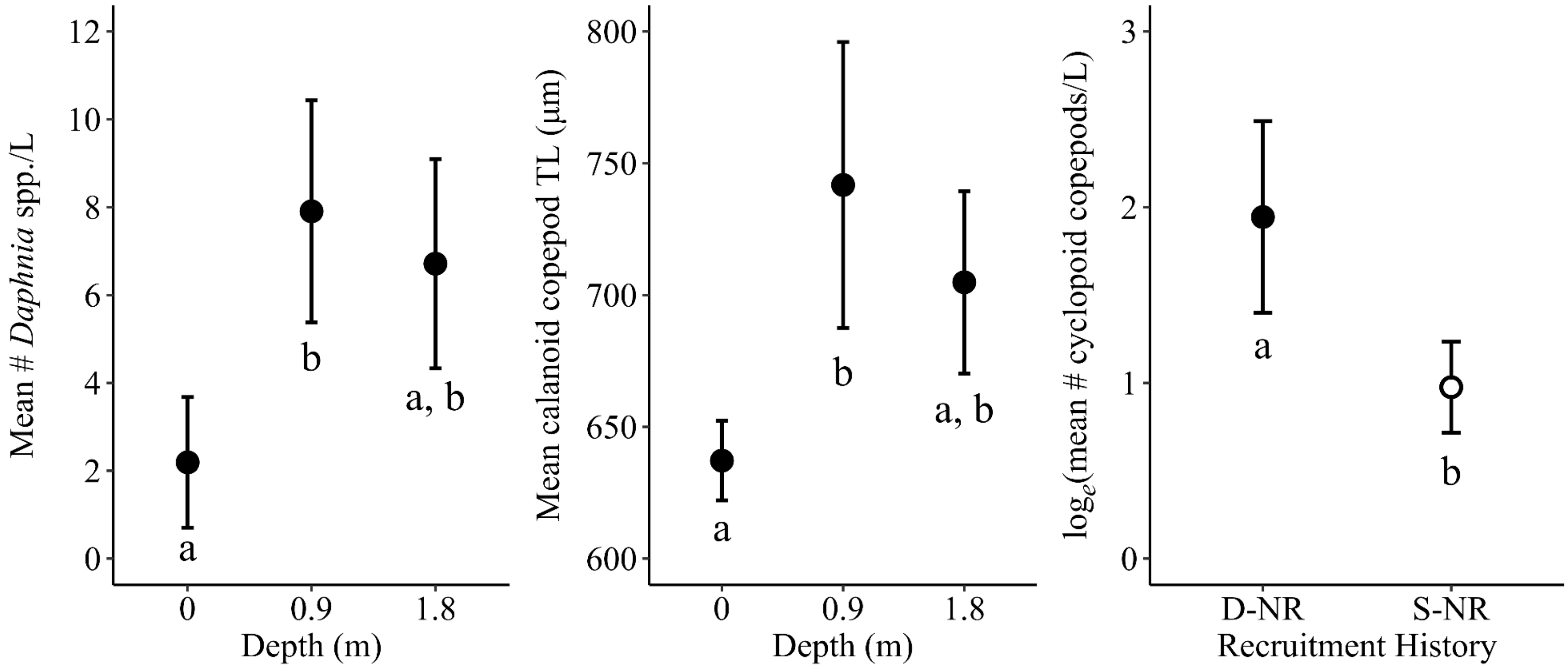

Figure 17. Mean *Daphnia* spp. density (left), mean calanoid copepod total length (middle), and mean log$_e$ cyclopoid copepod density (right) during the day at three depths (surface, approximately 1 m below surface, and approximately 2 m below surface) in May-June 2021. Mean cyclopoid copepod density was log$_e$ transformed prior to statistical analysis. ANOVA determined significant differences in mean *Daphnia* spp. density and mean calanoid copepod total length between depths, and a significant difference in mean cyclopoid density between recruitment histories. Tukey (HSD) *post hoc* tests determined mean *Daphnia* spp. density was significantly lower at the surface than at approximately 1 m below surface, calanoid copepod total length was significantly lower at the surface than at approximately 1 m below surface, and cyclopoid copepod relative abundance was significantly lower in S-NR lakes than D-NR lakes when averaged for all depths. Different letters indicate significant differences between groups. Error bars represent 95% confidence intervals.

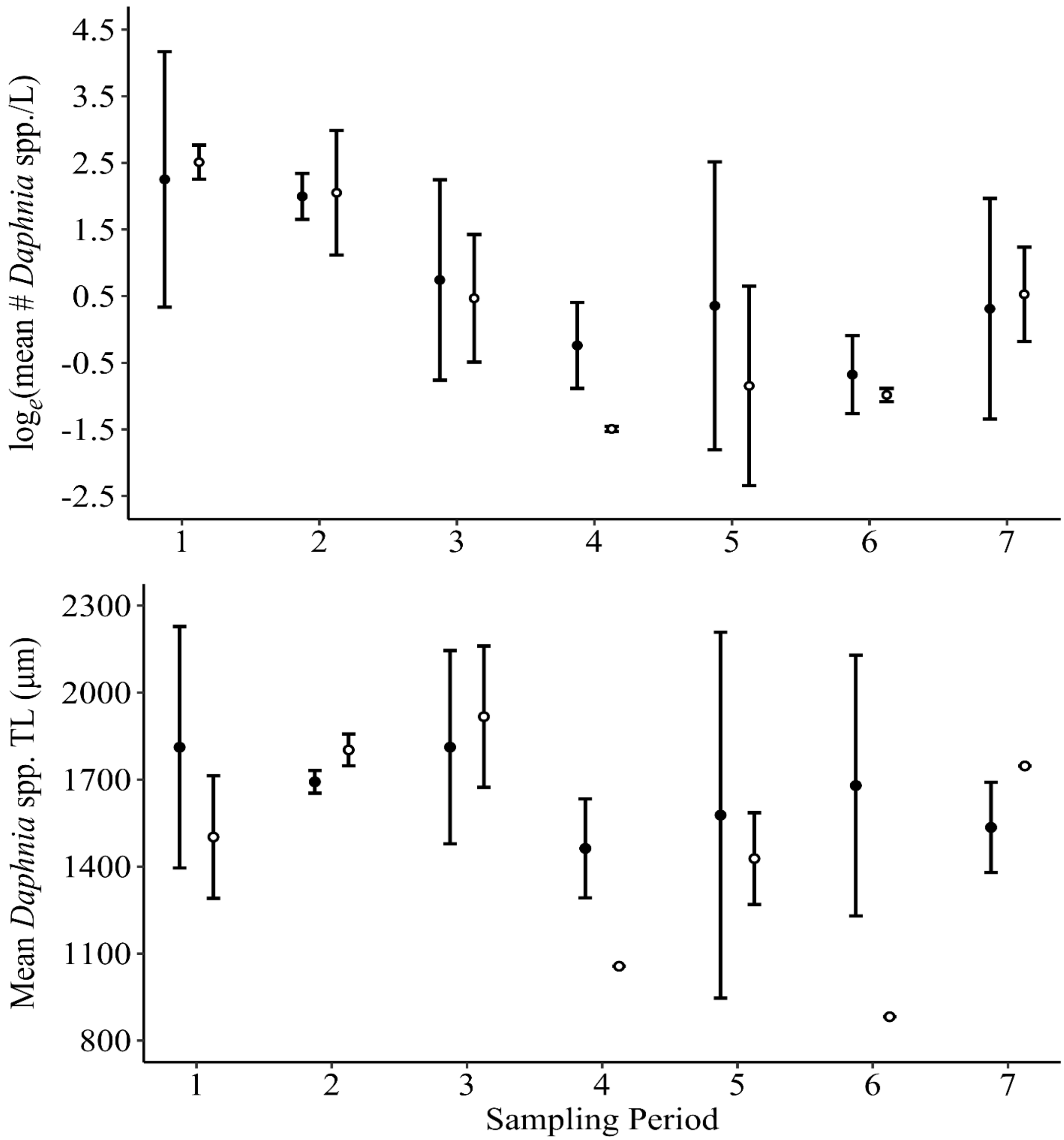

Figure 18. Mean density (#/L; top) and total length (µm; bottom) of *Daphnia* spp. from vertical tows collected in May-August 2021 at 10–14 d intervals from lakes with declining Walleye recruitment (D-NR; black circles) and sustained Walleye recruitment (S-NR; white circles). Density values were log$_e$ transformed prior to statistical analysis. Repeated-measures ANOVA indicated significant differences in mean log$_e$ number of *Daphnia* spp./L among sampling periods and a significant interaction between recruitment history and sampling period for *Daphnia* spp. total length (Table 7). A Tukey (HSD) *post hoc* test determined mean *Daphnia* spp. total length differed between sampling periods and lake types, but there were not significant differences between lake types in the same sampling period. Error bars represent 95% confidence intervals. Mean *Daphnia* spp. total length of S-NR samples in sampling periods 4, 6, and 7 are only one value and therefore do not have confidence intervals.

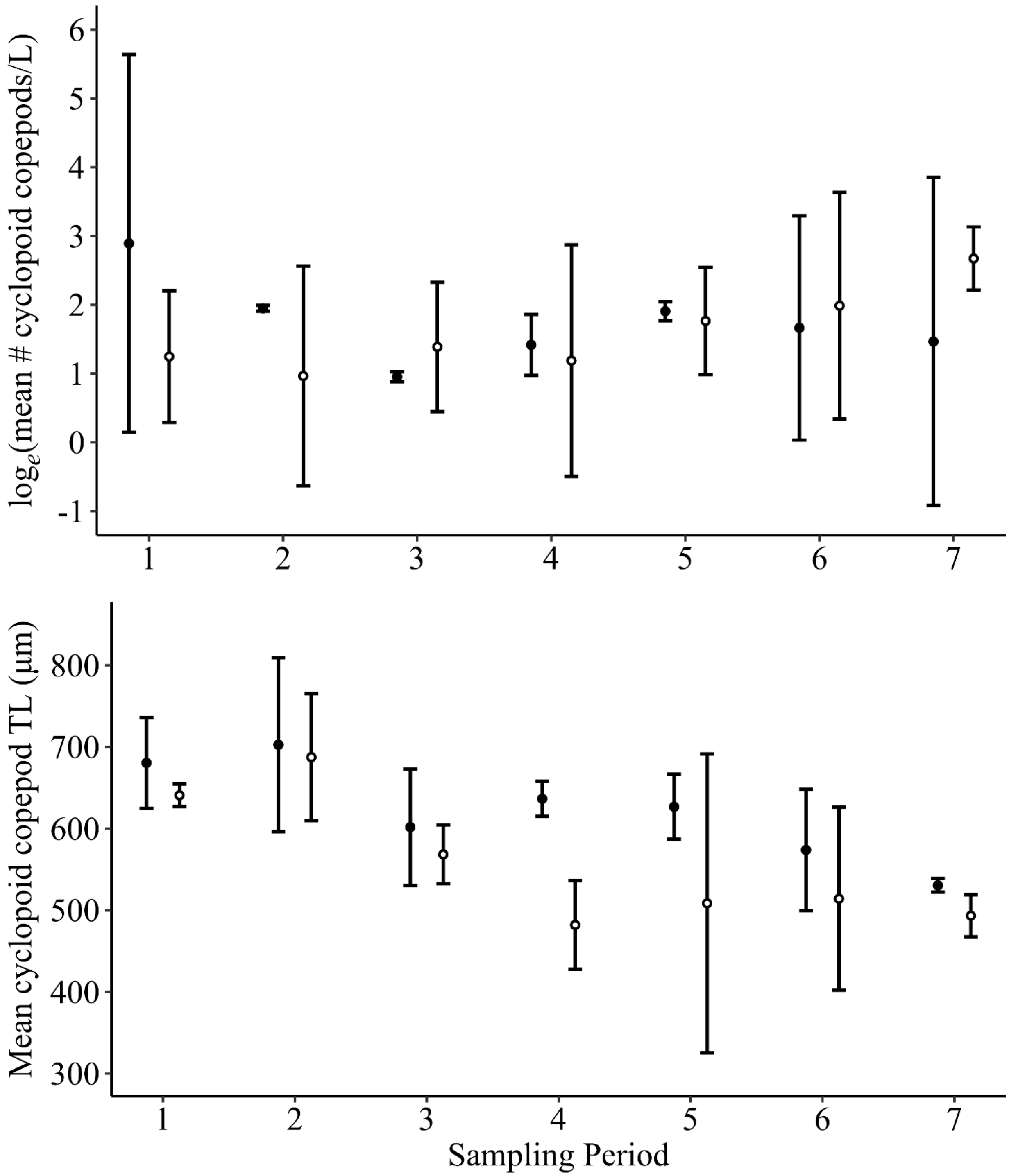

Figure 19. Mean density (#/L; top) and total length (µm; bottom) of cyclopoid copepods from vertical tows collected in May-August 2021 at 10–14 d intervals from lakes with declining Walleye recruitment (D-NR; black circles) and sustained Walleye recruitment (S-NR; white circles). Density values were log$_e$ transformed prior to statistical analysis. Repeated-measures ANOVA indicated significant differences in mean cyclopoid copepod total length between sampling periods. Error bars represent 95% confidence intervals.

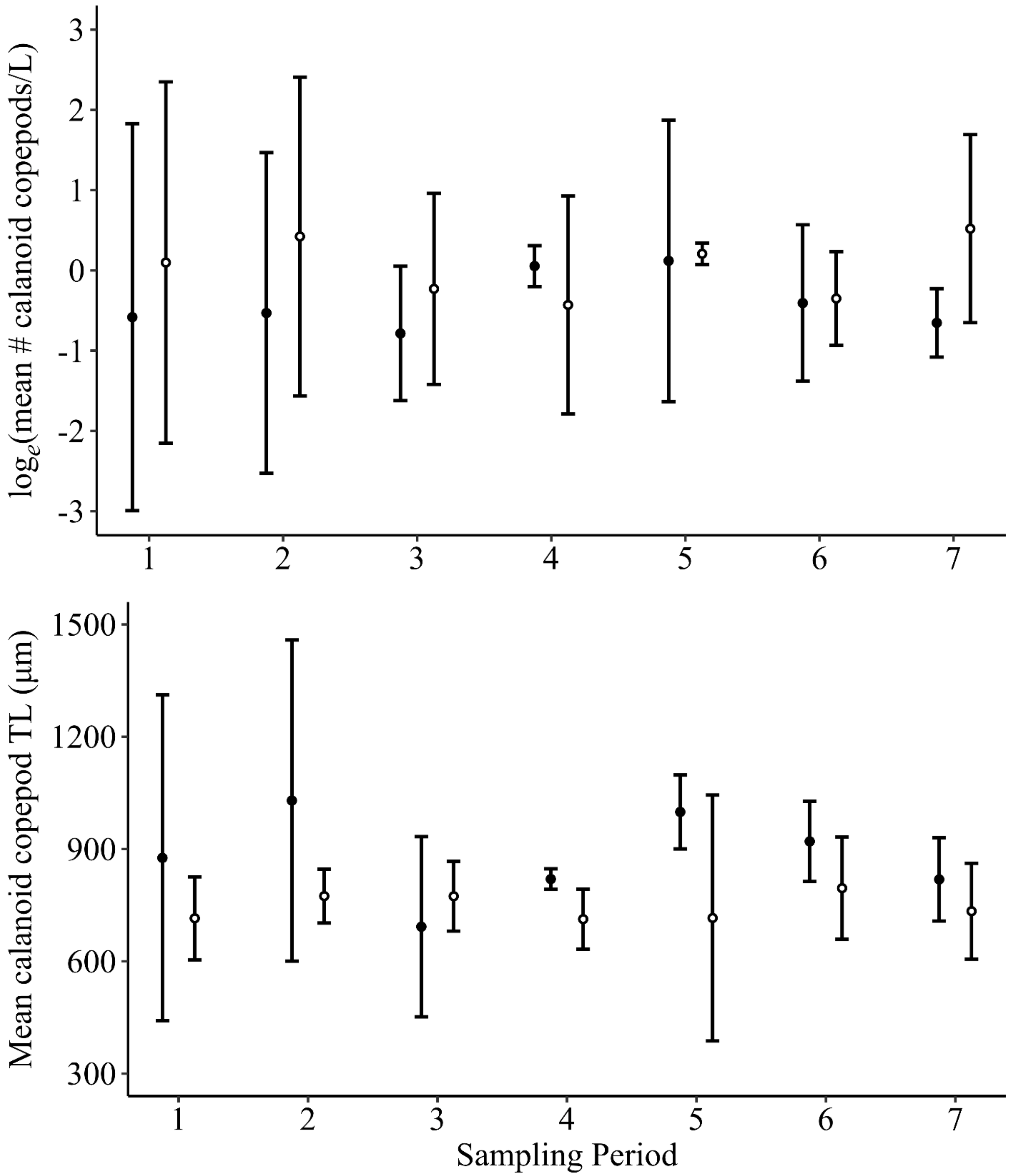

Figure 20. Mean density (#/L; top) and total length (μm; bottom) of calanoid copepods from vertical tows collected in May-August 2021 at 10–14 d intervals from lakes with declining Walleye recruitment (D-NR; black circles) and sustained Walleye recruitment (S-NR; white circles). Density values were log$_e$ transformed prior to statistical analysis. Repeated-measures ANOVA indicated no significant interactions between Walleye recruitment history and sampling period. Error bars represent 95% confidence intervals.

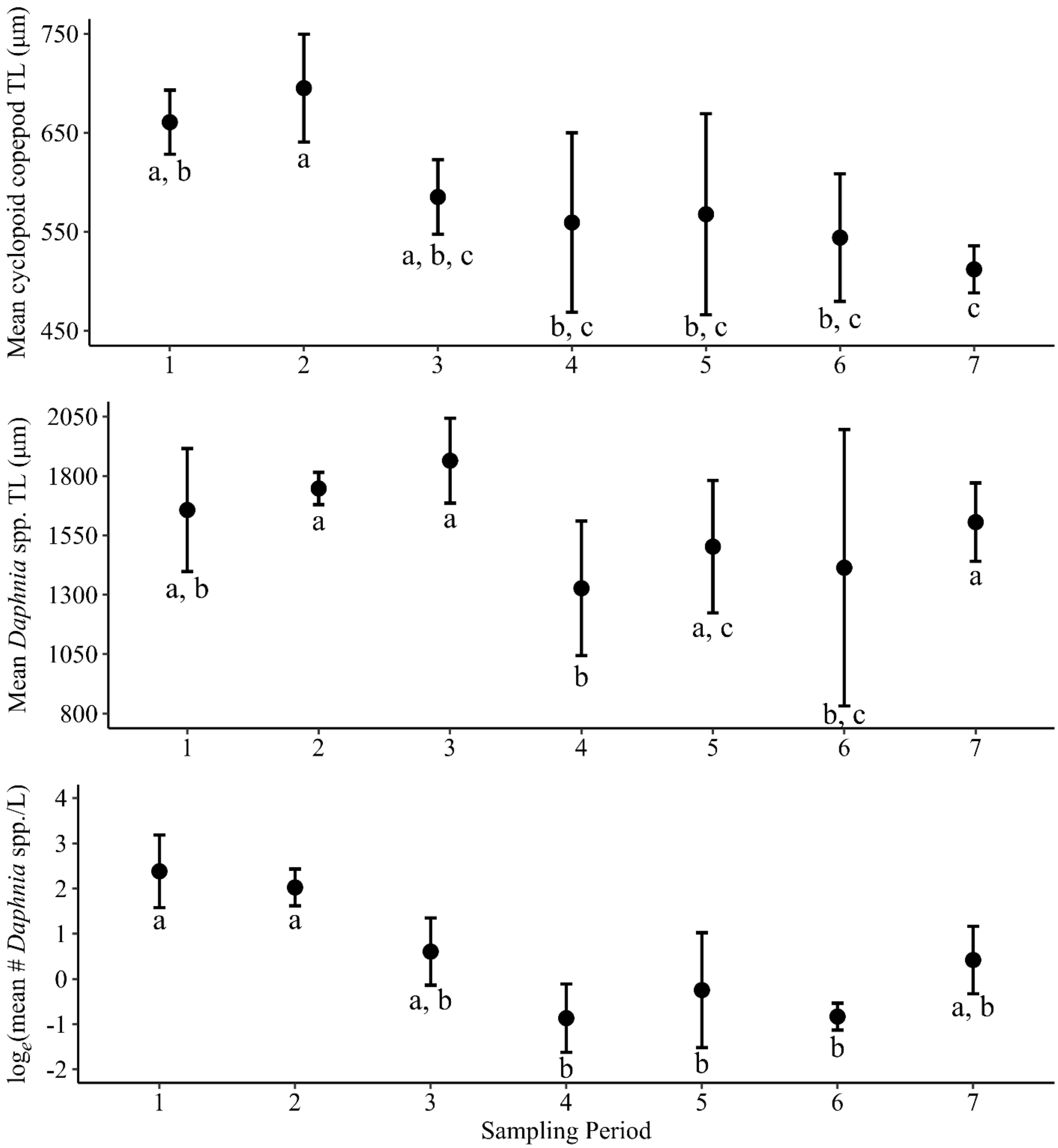

Figure 21. Mean cyclopoid copepod total length (top), mean *Daphnia* spp. total length (middle), and mean $\log_e$ number of *Daphnia* spp./L (bottom) from vertical tows collected in May-August 2021 at 10–14 d intervals. Mean number *Daphnia* spp./L was $\log_e$ transformed prior to statistical analysis. Repeated-measures ANOVA determined significant differences in mean cyclopoid copepod total length, mean *Daphnia* spp. total length, and mean *Daphnia* spp. relative abundance among sampling periods (Table 7). Tukey (HSD) *post hoc* tests were used to identify significant relationships. Different letters indicate significant differences between groups. Error bars represent 95% confidence intervals.