



Submerged Aquatic Vegetation Patch Size Affects Fish Communities in a Turbid-Algal Lake

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Submerged aquatic vegetation (SAV) is declining worldwide, leading to subsequent reductions in the ecological functions associated with SAV in shallow aquatic ecosystems, including providing habitat for fishes. Extensive restoration efforts are required to reverse this trend, but studies focusing on aquatic vegetation have been uncommon in recent years relative to other primary producers. Evaluations of the most beneficial SAV species and characteristics for fishes are especially rare. Because of the potentially complex and inconsistent responses of fish to different management actions, further research is necessary to evaluate the species-specific and community-level effects of SAV to inform restoration decision-making. To examine what SAV characteristics increase fish habitat use in a turbid-algal lake undergoing restoration, we sampled 29 areas around Lake Apopka, Florida (USA) with fyke nets and trotlines. We examined the impact of eight environmental variables on fish abundance, biomass, community structure, and predation potential. For each approximated 0.6 m² increase in SAV patch size, total fish biomass catch increased 6.5 g hr⁻¹. Fish community composition based on abundance also changed with an increase in SAV patch size. The number of bait items missing from trotlines, a measure of predation potential, was most affected by water temperature, wind speed, and time of day, but not by the SAV variables tested. These results expand existing knowledge of fish habitat use of SAV and will inform future management efforts to conserve and restore fish communities by focusing on specific SAV characteristics such as patch size.

Keywords: restoration, plant-animal interactions, habitat, macrophytes, *Vallisneria*, *Potamogeton*, *Hydrilla*

INTRODUCTION

Submerged aquatic vegetation (SAV) plays a critical role in the ecological functions of shallow lake ecosystems, including reducing sediment resuspension, increasing water clarity and quality, and providing important habitat for fauna including fishes (Carpenter and Lodge, 1986; Martin and Valentine, 2012; Short et al., 2016). Intermediate coverage (10–40%) of vegetation may promote high species richness, growth, foraging, and survival of fishes, notably juveniles and smaller individuals, due to optimal spaces for predator-prey interactions and edge effects (Killgore et al., 1993; Lauridsen and Buenk, 1996; Thorp et al., 1997; Richardson et al., 1998). Furthermore, at least nineteen freshwater fish families, such as Centrarchidae and Cyprinidae, occupy or rely on

vegetation for ideal refuge, food resources, reproduction, and nursery habitat (Dibble et al., 1997). Despite its value in freshwater ecosystems, global aquatic vegetation is declining at an accelerating rate, especially for SAV and in lakes that are >50 km² (Zhang et al., 2017).

Planting SAV as part of lake restoration efforts has the potential to increase desirable fish communities in lakes. Fish communities may react differently, however, depending on a variety of factors. These factors include the architectural differences among plant species (Dibble et al., 1996; Martin and Valentine, 2011), whether a water body is in a turbid or clear-water state (Van Onsem et al., 2010), if vegetation is restored or natural (Slagle and Allen, 2018), or the amount of light diffusion through SAV (Harrel and Dibble, 2001). Effectively increasing vegetation coverage can require extensive restoration efforts (Zhang et al., 2017). Additionally, management actions may have counterintuitive results on fish communities, such as a sudden decline in recruitment after habitat improvement (Pine et al., 2009), further complicating restoration efforts. Such varying responses can result in confounding conclusions that are difficult to translate into management recommendations (Pine et al., 2009), requiring further research to ascertain what defines optimal SAV for fish habitat use.

In order to inform future SAV restoration and conservation efforts, we examined differences in fish abundance, biomass, community composition, and predation potential among SAV habitats and how other variables, such as time of day and water temperature, affect fish habitat use. To accomplish this, we sampled the fishes in bare substrate and SAV meadows of different sizes and species assemblages in Lake Apopka, Florida (USA)—a site of ongoing, extensive lake restoration efforts. We hypothesized phytophilic fishes, such as Centrarchids, would increase with SAV coverage while pelagic, schooling fishes, such as *Dorosoma* spp., would decrease.

METHODS

Study Site

Lake Apopka is located northwest of Orlando, in Lake and Orange Counties, Florida (28° 37' N, 81° 37' W). The lake is relatively large (~124 km²) and shallow (mean depth 1.7 m); (Bachmann et al., 1999). Until 1947, Lake Apopka was characterized by mostly clear water and dense macrophyte coverage of 70% (Clugston, 1963). Beginning in the 1920's, Lake Apopka experienced a number of anthropogenic and natural disturbances that subsequently caused a shift from a macrophyte-dominated state to a turbid-algal state that persists to this day (US Environmental Agency, 1978; Bachmann et al., 1999, 2001). Populations of the less desirable gizzard shad (*Dorosoma cepedianum*) began increasing in Lake Apopka (Clugston, 1963), while the largemouth bass (*Micropterus salmoides*) population, which had supported a popular fishery, began declining and remains lower than expected compared to other nearby lake systems (Bachmann et al., 1996; Murphy, 2005). The loss of largemouth bass is suspected to be related to the loss of macrophytes (Bachmann et al., 1999) as opposed to the change in trophic state (Bachmann et al., 1996). Recently, large-scale

plantings of SAV have been underway at Lake Apopka, making it an ideal location to examine how fish utilize SAV in a turbid-algal lake. The SAV planting efforts have focused on *Vallisneria americana* and *Potamogeton illinoensis*, as both were historically present in Lake Apopka before its switch to a turbid-algal state (Bachmann et al., 2001). *Hydrilla verticillata*, an invasive SAV species, has also recently expanded in the lake (Murphy, 2005).

Field Sampling

We sampled fish abundance, biomass, community composition, and predation potential in addition to environmental variables at a total of eight sites around the north and east shores of Lake Apopka (**Supplementary Figure 1**) from mid-June to mid-August 2019. Sites were selected based on their inclusion in an ongoing restoration effort in Lake Apopka to both inform the goals of the restoration as well as to more broadly study the impacts of SAV on fish communities. Only restoration sites that had at least one SAV habitat and one bare habitat were sampled; therefore only eight sites and 29 habitats were sampled. Three habitats—one bare habitat and two SAV habitats—were sampled at five of the sites. At both sites AP9 and AP20, where many SAV patches were present, two sets of three habitats were sampled. At AP21, where fewer patches were present, only one bare habitat and one SAV habitat were sampled. Each habitat within a site was sampled once. Habitats included *V. americana*, *P. illinoensis*, a mix of the two, or bare (*V. americana* and *P. illinoensis* not present). Each SAV habitat was at least 1.5 by 1.5 m. Any *P. illinoensis* was planted as part of Lake Apopka restoration projects in the past 5 years. The *V. americana* may have been naturally occurring, planted within the past 5 years, or planted over 5 years ago as part of historical restoration efforts—vegetative spread and/or unclear success from recent or historical plantings make identifying the source difficult. Sites were at least 100 m apart and each habitat sampled was at least 10 m from another sampled habitat or unsampled SAV meadow.

We also took environmental data at each site or habitat. At each site, we measured salinity (ppt), depth (m), dissolved oxygen (mg L⁻¹ and % saturation), temperature (°C), continuous wind speed (m s⁻¹) and direction, and secchi depth (m) in open water in the approximated center of the site and within 50 m of the habitats sampled. Water quality measurements were taken with a YSI ProDSS and associated probes held just below the water surface. Continuous wind speed was measured with a Proster TL017 handheld anemometer, and wind direction was measured with a handheld compass. For each habitat within a site, we estimated the patch size based on an index of 0–5 with 0 being a bare habitat and each increase of 0.5 in the index being equivalent to an approximated increase in patch size of 0.75 by 0.75 m (**Supplementary Figure 2**). We did not measure shoot counts because of poor water visibility and high numbers of plants. We estimated the distance of the center of the habitat from shore and we recorded the presence/absence of *H. verticillata* (**Supplementary Table 1**). Other SAV (e.g., *Ceratophyllum demersum*, *Najas guadalupensis*) were occasionally observed in low abundances in bare habitats, but *H. verticillata* was the only species with comparable abundance to *V. americana* and *P. illinoensis*, so it was the only

species accounted for as a separate variable. Across sampling days, the weather was relatively similar, with clear skies or partly cloudy at the beginning of sampling in the morning and afternoon storms beginning shortly after ending sampling.

We sampled fishes at each habitat on consecutive days using two techniques, fyke nets and trotlines. These methods were chosen because they are passive approaches minimally destructive to SAV; they were meant to target different fish sizes, species, and trophic levels; and they have been shown to be effective in freshwater fish sampling (Diana et al., 2006; Hubert et al., 2012; Bonvechio et al., 2014). Each fyke net was made up of two rectangular conduit 0.9×1.2 m frames, five 63.5 cm galvanized hoops, two throats, a 15.24 m long lead, and 0.6 cm mesh size with a black net coat treatment. Each trotline had 24 hooks (sizes alternating between 5/0, 3/0, 4/0, and 2/0) with each hook baited with half of a nightcrawler worm (4–7 cm), purchased from the same supplier. The bait and hook sizes were chosen based on expert advice and published diet contents to cover a broad range of target species (most notably, Centrarchids and Ictalurids); (Froese and Pauly, 2019). Both gear types were deployed perpendicular to shore for 2–3 h, since pilot tests and catch accumulation curves indicated catch-per-unit effort was maximized over this interval (**Supplementary Figure 3**). We also tested trotlines overnight for ~12 hours at two sites in all habitat types ($n = 6$), but only one fish was caught among the trotlines, thus the overnight deployment was not repeated. Both gear types were deployed starting at the shore if the habitat distance from shore was 0–3 m. Otherwise, the gear types were deployed at the shoreward edge of the habitat. In the case of the SAV habitat types, fyke nets and trotlines were deployed through the middle of the SAV patch, with SAV on both sides of the gear. Due to the small size of many of the SAV patches sampled, the entire fyke net wall or all the trotline hooks were not necessarily within the SAV patch. We considered this minimal extension (<7 m) beyond the edge of the patch to be fishing edges of the habitat and thus fish catch attributable to the patch itself. All captured fishes were identified to species, measured (mm), weighed (g), and returned to the lake. We also recorded the number of worms missing from hooks on the trotlines as a measure of predation potential similar to a tethering experiment (Puntilla et al., 2012).

We validated that our chosen sampling methods and protocols were effective at sampling fish communities with comparison testing at Lake Apopka and nearby Little Lake Conway. Little Lake Conway was chosen because of its proximity to Lake Apopka (40.2 km) and because it is a less degraded lake consisting of extensive macrophytes, visibility to the bottom (>3 m), sandy substrate, and near 100% SAV coverage throughout. In mid-September, we sampled using fyke nets and trotlines at two SAV habitats at Lake Apopka and two SAV habitats at Little Lake Conway. Sampling was successful, with Little Lake Conway having higher catch and more worms missing than Lake Apopka (**Table 1**), thus demonstrating the efficacy of our sampling methods.

Data Analysis

We conducted statistical analyses to assess which habitat and environmental variables had a statistically significant ($p <$

0.05) or marginally significant ($p = 0.05$ – 0.10) effect on fish abundance, biomass, community composition, and predation potential per unit effort (fyke net or trotline soak time expressed in hours). For the fyke net data, analyses of fish community composition using both the abundances of each species caught (hereafter, fish community abundance) and the biomasses of each species caught (hereafter, fish community biomass) were made using a multivariate approach, while analyses of total fish abundance and biomass, diversity indices, and individual species abundances used a univariate approach. The number of worms eaten at the end of trotline soak times were also analyzed with a univariate approach. We conducted all statistical analyses in R (R Core Team, 2019) version 3.5.1 (2018-07-02) with packages “vegan” (Oksanen et al., 2019), “reshape” (Wickham, 2007) and “ggplot2” (Wickham, 2016).

The environmental data (i.e., both habitat and site characteristics and measurements) used in analyses consisted of eight variables: sampling time of day, continuous wind speed (m s^{-1}), the estimated size of SAV patch sampled (index of 0–5, as described above), the estimated distance of the center of each habitat sampled to the shoreline (m), the habitat type (*P. illinoensis* $n = 8$, *V. americana* $n = 8$, mix $n = 3$, or bare $n = 10$), the presence ($n = 11$) or absence ($n = 18$) of *H. verticillata*, water temperature ($^{\circ}\text{C}$), and water depth (m). Salinity (ppt) and secchi depth (m) were consistent across all sites (0.16–0.18 ppt and 0.30–0.55 m respectively) and dissolved oxygen (mg L^{-1}) was highly dependent on time of day, so they were excluded from the analysis (**Supplementary Table 2**). The non-categorical environmental data were log-transformed, and all of the environmental data were scaled. Fyke net fish community abundance and biomass data were Hellinger-transformed (Legendre and Gallagher, 2001). Two samples had zero fish caught and so were excluded from the fish community analyses.

A detrended correspondence analysis of the fyke net fish community data demonstrated that a canonical correspondence analysis (CCA) was the appropriate constrained ordination analysis for the data. We ran the CCA on all 12 species and all eight variables. To reduce the number of environmental variables to that appropriate for a CCA, we conducted forward selection with a relaxed α of 0.1 to capture marginally statistically significant results. For the fish community abundance data, the only variable selected was patch size. The result was the same when habitat type was excluded as a variable because of the multicollinearity with patch size (>0.7 correlation value). When patch size was excluded, habitat type was selected. Because patch size was selected when both habitat type and patch size were included, the patch size variable is the focus of our results.

We calculated the Shannon and Simpson diversity indices of the fyke net catches. We used linear regression to evaluate how the Shannon diversity index, Simpson diversity index, and individual species abundances from the fyke net catches changed with SAV patch size to further describe the change in fish community abundance. We also examined the most abundant species in the fyke nets, threadfin shad (*Dorosoma petenense*), by running a Similarity Percentage (SIMPER) analysis of their contribution to Hellinger-transformed community structure in the Bray Curtis dissimilarity index. We used multiple linear

TABLE 1 | Results of method validation testing in Lake Apopka and a macrophyte-dominated lake, Little Lake Conway.

Sampling method	Lake sampled	Habitat type	SAV patch size	Sampling results	Sampling results per hour
Fyke nets	Little Lake Conway	mix	5	8 bluegill, 3 fliers	5.28 fishes
		<i>P. illinoensis</i>	5	4 bluegill, 5 fliers	5.29 fishes
	Lake Apopka	mix	4.5	3 threadfin shad, 1 coastal shiner	2.05 fishes
		<i>P. illinoensis</i>	4.5	0 catch	0 fishes
Trotlines	Little Lake Conway	mix	5	12 worms missing, 0 catch	5.53 worms
		<i>P. illinoensis</i>	5	11 worms missing, 0 catch	5.08 worms
	Lake Apopka	<i>P. illinoensis</i>	4.5	0 worms missing, 0 catch	0 worms
		<i>P. illinoensis</i>	2	2 worms missing, 0 catch	1.14 worms

SAV patch sizes were estimated based on an index of 0–5, with 0 being a bare habitat and each increase of 0.5 in the index being equivalent to an approximated increase in patch size of 0.75 by 0.75 m.

regression with forward selection ($\alpha = 0.05$) to evaluate how total biomass per soak time hour, total abundance per soak time hour, and the worms missing from trotlines per soak time hour changed with the same transformed and scaled environmental variables as the fish community data analysis. A more comprehensive description of the data analyses, including which R functions were used for each test, is included in the **Supplementary Material**.

RESULTS

Fyke net total fish biomass increased 6.5 g hr^{-1} per approximated 0.6 m^2 increase in SAV patch size (**Figure 1**; linear regression: adjusted R-squared = 0.1998, $F_{1,27} = 7.991$, $p = 0.009$, residual standard error: 24.98, from lm function). SAV patch size also contributed to marginally significant differences in the fyke net fish community abundance (CCA: adjusted R-squared = 0.02, $F_1 = 1.5593$, $p = 0.08$). No other environmental variables contributed significantly to the variation in fish community abundance or total fish biomass. None of the environmental variables included in the analysis contributed significantly to the variation in fish community biomass or total fish abundance.

Differences in abundance with SAV patch size varied by fish species (**Figures 2A,B**). A total of 12 species were caught in the fyke nets: threadfin shad, warmouth (*Lepomis gulosus*), bluegill (*Lepomis macrochirus*), brown bullhead (*Ameiurus nebulosus*), gizzard shad, Seminole killifish (*Fundulus seminolis*), golden silverside (*Labidesthes vanhyningi*), dollar sunfish (*Lepomis marginatus*), redear sunfish (*Lepomis microlophus*), spotted sunfish (*Lepomis punctatus*), coastal shiner (*Notropis petersoni*), and black crappie (*Pomoxis nigromaculatus*). The abundance of threadfin shad decreased 46% ($\pm 61\%$) from bare to large SAV patch size. Furthermore, SIMPER analysis of their contribution to community structure in the Bray-Curtis dissimilarity index indicated high contribution (97%) to the community dissimilarity between SAV patch size 0 and 1, but only 25% between size 4.5 and 5. The other fish species caught in more than one fyke net showed some increase in abundance with an increase in SAV patch size, though the rate of increase was relatively small and varied among species (**Supplementary Table 3**). Warmouth was the only species whose

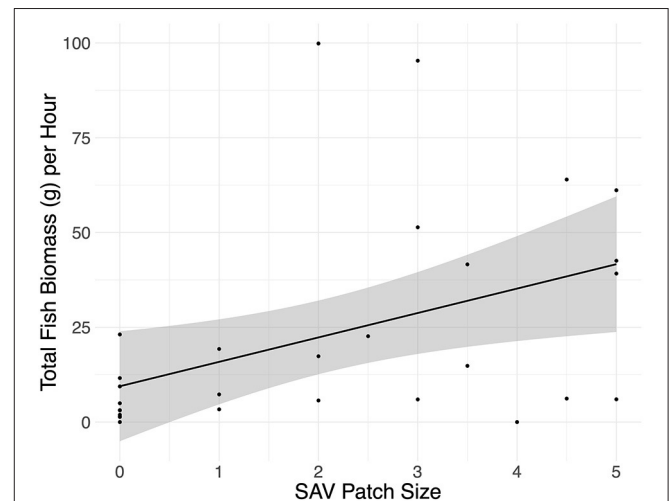
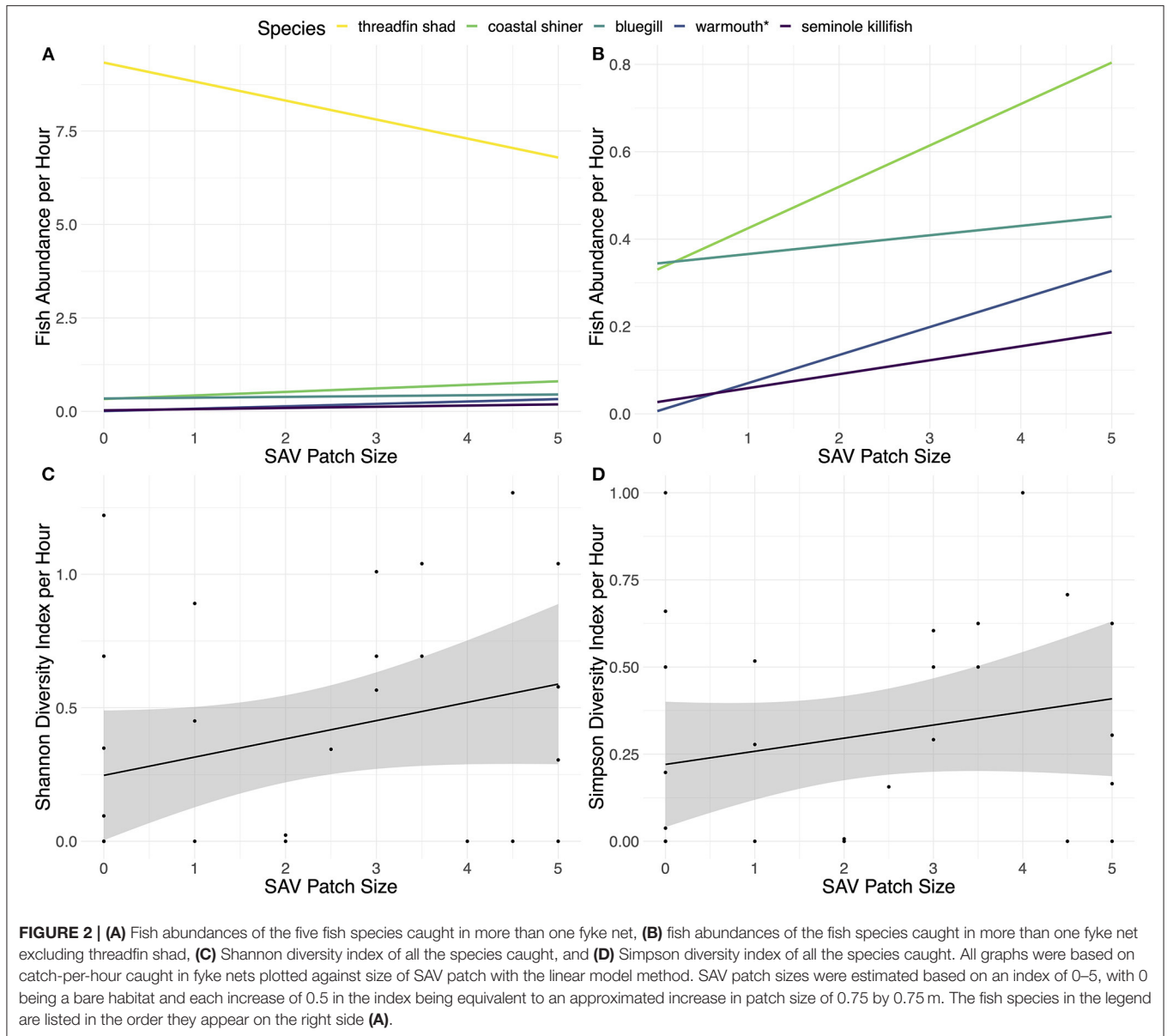


FIGURE 1 | Total fish biomass caught per hour in the fyke nets plotted against SAV patch size with the linear model method. SAV patch sizes were estimated based on an index of 0–5, with 0 being a bare habitat and each increase of 0.5 in the index being equivalent to an approximated increase in patch size of 0.75 m by 0.75 m.

abundance showed a statistically significant relationship with SAV patch size (linear regression: adjusted R-squared = 0.107, $F_{1,27} = 4.356$, $p = 0.04645$, residual standard error: 0.3123, from lm function). The Shannon diversity index of the fish communities showed some increase with SAV patch size, though not significantly (**Figure 2C**; linear regression: adjusted R-squared = 0.025, $F_{1,27} = 1.719$, $p = 0.2008$, residual standard error: 0.4008, from lm function) and the Simpson diversity index showed little to no increase (**Figure 2D**; linear regression: adjusted R-squared = -0.006013 , $F_{1,27} = 4.356$, $p = 0.3696$, residual standard error: 0.8326, from lm function). All of the species that were only caught in a single fyke net were found in SAV patch sizes 2.5 or larger (**Supplementary Table 4**). Although individual trends were almost entirely not significant, the cumulative response to SAV patch size drives the marginally significant changes detected in fish community abundance.

A total of six fish were caught on all 29 2-h trotlines that were deployed. The species caught were two brown bullhead, one yellow bullhead (*Ameiurus natalis*), one redear sunfish, and two



bowfin (*Amia calva*). A brown hoplo (*Hoplosternum littorale*) was also caught on one of the overnight trotlines. The brown hoplo is invasive and was the only fish caught in a bare habitat. All other species were caught in an SAV habitat (Table 2). Because of the low catch number, we lacked statistical power to perform any quantitative tests on the data. The number of worms eaten per hour, a measure of predation potential, was most affected by water temperature, wind speed, and time of day (multiple linear regression: adjusted R-squared = 0.3043, $F_{3,25} = 5.082$, $p = 0.007$, from anova function), but not any of the SAV-related variables.

DISCUSSION

SAV patch size was the most significant contributing environmental variable to fish community structure and

total fish biomass. The abundance of threadfin shad, a pelagic schooling planktivore, decreased while all other species, many of them small and phytophilic, showed some increase with an increase in SAV patch size, as expected from their life-history traits (Bettoli et al., 1993). Total fish biomass increased more as a result of changing community composition than increasing abundance, as the community changed from being dominated by threadfin shad (average 1.0 g per individual among those sampled) to other species with strong associations to SAV for foraging and refugia, such as warmouth (average 56.6 g per individual among those sampled) and both juvenile and adult bluegill (average 5.4 g per individual among those sampled).

Compared to bare habitat or open water substrate, SAV usually increases abundance, biomass, and diversity of underwater communities (Lauridsen and Buenk, 1996; Thorp et al., 1997; Richardson et al., 1998). Intermediate to high

TABLE 2 | All fishes caught on 2-h trotlines and overnight trotlines and the habitat type and SAV patch size in which they were captured.

Trotline deployment	Habitat type	SAV patch size	Fish caught
2-h trotlines (n = 29)	<i>V. americana</i>	1	1 brown bullhead, 1 redear sunfish
	<i>V. americana</i>	4	1 brown bullhead
	<i>P. illinoensis</i>	2.5	1 bowfin
	<i>P. illinoensis</i>	3.5	1 yellow bullhead
	mix	3	1 bowfin
Overnight trotlines (n = 6)	bare	0	1 brown hoplo

SAV patch sizes were estimated based on an index of 0–5, with 0 being a bare habitat and each increase of 0.5 in the index being equivalent to an approximated increase in patch size of 0.75 by 0.75 m.

coverage of SAV also tends to lead to favorable community changes over low coverage of SAV (Beckett et al., 1992; Hargeby et al., 1994). An increase in SAV patch size would decrease the ratio of edge habitat to interior habitat. Aquatic communities may change between the exterior to the interior of SAV meadows possibly due to differences in predation, oxygen, or nutrients (Johnson and Hatch, 1991; Lauridsen and Buenk, 1996; Strayer et al., 2003; Fisher et al., 2012; Kauffman et al., 2018), and so changes in the quantity of edge habitat could lead to the documented differences in fish communities. The SAV patches sampled in Lake Apopka were the result of SAV restoration successes in a turbid-algal lake but were still relatively small compared to the SAV patch sizes expected in macrophyte-dominated lakes. As a result, it is possible the trends associated with increasing SAV patch size may be more parabolic than linear in nature.

SAV species assemblages, as represented by the habitat type and *H. verticillata* presence/absence environmental variables, did not have as large an impact as patch size in the results of our field sampling. SAV preferences can vary widely, even amongst similar functional groups. For example, Kondo and Abe (1995) demonstrated that one species of perch (*Lates angustifrons*) preferred *Vallisneria* sp. while the closely related *L. mariae* preferred *Potamogeton schweinfurthii*. Likewise, mosquitofish (*Gambusia holbrooki*), sailfin mollies (*Poecilia latipinna*), and dollar sunfish were all shown to prefer different SAV species (Chick and McIvor, 1997). Community assemblages of organisms like macroinvertebrates or free-floating zooplankton also occasionally do not vary at all between SAV species (Theel et al., 2008; Van Onsem et al., 2010; Cunha et al., 2011; Martin and Valentine, 2011). Effects of SAV species were not detected in our field sampling but can be important in determining habitat use of faunal communities.

Despite *H. verticillata* being the second most studied invasive aquatic macrophyte after *Myriophyllum spicatum* (Evangelista et al., 2014), the exact impacts of *H. verticillata* on fish

communities remain equivocal. As an example, there have been mixed results of studies investigating *H. verticillata*'s impacts on largemouth bass. A reduction in *H. verticillata* has been reported to improve growth, survival, reproduction, and recruitment, and to change predation and movement behavior of largemouth bass (Brown and Maceina, 2002; Allen et al., 2003; Sammons et al., 2003). In other studies, however, increased *H. verticillata* increased juvenile populations and year-class strength (Allen et al., 2003; Nagid et al., 2015) and reduced *H. verticillata* decreased recruitment, fishing effort, and catch of trophy-sized fish (Johnson et al., 2014). Still others showed no impact of *H. verticillata* on largemouth bass movement or catch rates (Maceina et al., 2008) or more widely on fish community measures (Hoyer et al., 2008). In our own field sampling, the presence or absence of *H. verticillata* did not significantly explain fish abundance, biomass, community composition, or predation potential. These variety of responses may be due in part to the negative impacts on fish *H. verticillata* can have at its highest densities, making it comparably beneficial to other SAV species only at lower, managed levels (Johnson et al., 2014).

The data from our field sampling did not have high predictive power due to several possible explanations. In the fyke nets, there was large variation in the catch of each sample, with one fyke net catch having 230 threadfin shad and three coastal shiners, far exceeding all other catches. Additionally, over half of the species caught in the fyke nets were only present in a single sample and the trotlines caught too few fish to analyze the data statistically. Lake Apopka has reportedly lower than expected abundance of largemouth bass (Murphy, 2005) and our method validation testing in Little Lake Conway suggests that Lake Apopka has overall lower or more disparate fish populations, which could explain the lower catches. Both sampling methods targeted more mobile species, and so may have excluded stationary species. Large predatory fish may occur in higher numbers in other habitats, such as emergent vegetation or woody debris (Sammons et al., 2003) and would therefore have been missed in our sampling. Both sampling methods used are also passive and may therefore not catch less abundant species due to low encounter rates. Much greater replication may have overcome these difficulties, which in our study was limited by suitable sites with adequate habitat availability. Our results were also limited to a single lake, so sampling more lakes would provide context for how widely they may be generalized. Despite the low predictive power, bias in species sampled, and limited spatial scope, the data collected were supported by the literature (Beckett et al., 1992; Hargeby et al., 1994; Lauridsen and Buenk, 1996; Thorp et al., 1997; Richardson et al., 1998) and still indicate a clear trend that SAV patch size is important in determining fish habitat use.

The results of our field sampling support the hypothesis that SAV restoration can increase fish habitat. In highly degraded lakes like Lake Apopka, adding any quantity of SAV is beneficial, but larger SAV patch size was more favorable, particularly for phytophilic fishes such as warmouth, bluegill, and other Centrarchids. There were no clear thresholds in upper and lower SAV patch sizes at least up to an approximated 7.5 by 7.5 m—the largest SAV patch sampled—though the literature suggests there may be detrimental effects to fish at higher SAV coverage

and density (Beckett et al., 1992; Hargeby et al., 1994). Given the beneficial aspects of SAV patch size demonstrated in our study, when planning SAV restoration, focusing on areas that already have large patches of SAV that can be increased or replicated nearby may be more optimal than areas that have only produced small patches or less successful plantings. While SAV species assemblages can also impact fish habitat use, the species-specific preferences make it difficult to recommend one SAV species over another, and a more justified approach may be selection of SAV species based on the unique goals of each restoration.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The animal study was reviewed and approved by the Florida Fish and Wildlife Conservation Commission for sampling under permit #FNC-19-002 and by the University of Florida Institutional Animal Care and Use Committee under protocol #202009978.

AUTHOR CONTRIBUTIONS

AL, LKR, CRA, and CWM conceptualized and designed the study and contributed to the revision of the manuscript. AL conducted

the field sampling, performed the data analysis, prepared figures, and wrote the initial draft of the manuscript. All authors reviewed and agreed to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fcosc.2021.657691/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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