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Seasonal Shifts in Aquatic Macrophyte Assemblages and Their Influence on Invertebrate Habitat Complexity

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Abstract: Macrophytes are the primary structural elements shaping the physical environment in shallow freshwater lakes, but the seasonal pattern of habitat structuring in monsoonal tropical ecosystems is still underexplored. In the current study, it investigate how seasonally varying macrophyte species composition, biomass and growth form dominance influence the level of habitat complexity, resulting in variation in the abundance, richness and diversity of plant-associated invertebrates in a shallow tropical lake. Littoral zones at eight sampling stations were surveyed through four hydrological seasons: summer, southwest monsoon, northeast monsoon and winter. The cover of macrophytes, their biomass, and species richness were estimated, and habitat complexity was calculated as the fractal dimension (D) of macrophyte plant architecture. Invertebrates associated with macrophytes were sampled from 384 macrophyte individuals and identified to the family or genus level. The biomass of macrophytes varied from 94.2 g m^{-2} in the southwest monsoon to 312.8 g m^{-2} in winter, while the share of finely dissected submerged plants increased from 21.7% to 57.9%. Likewise, the fractal dimension changed seasonally (1.31 to 1.56). There was an increase of more than three times in invertebrate density between monsoon's lowest point (967 ind. 100 g^{-1}) and winter highest (3,374 ind. 100 g^{-1}) and taxa richness changed from 12.4 to 27.5. From the linear mixed models, the fractal dimension accounted for more variability in invertebrate richness than the biomass of macrophytes alone. The PERMANOVA analysis revealed that there was significant seasonal turnover in invertebrate community composition. The conclusion was drawn that seasonal changes in macrophyte growth form, and not only biomass, control the habitat complexity of invertebrates. Effective lake management by ensuring the survival of dissected submersed vegetation during the post-monsoon recovery period would ensure invertebrate diversity and food webs.

Keywords: Aquatic Macrophytes; Habitat Complexity; Fractal Dimension; Epiphytic Invertebrates; Monsoon Seasonality; Shallow Lakes; Ecosystem Health.

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I. Introduction

Shallow lakes and reservoirs rank among the most productive and the most threatened aquatic ecosystems of the world. In such ecosystems, the role of aquatic macrophytes is that of ecosystem engineers, where they stabilize sediment, sequester nutrients, provide shading to phytoplankton, and create three-dimensional habitat for periphyton, invertebrates, fish, and waterbirds. Macrophytes have been found to be highly important to the alternative clear-water and turbid ecosystem states characteristic of shallow lakes, and thus the health of the macrophyte stand becomes an essential indicator of the ecosystem condition (Scheffer et al., 1993). Thus, knowledge of how the macrophyte stand changes throughout the year, and what the implications of these changes are for the inhabitants of the macrophyte stand, is highly relevant for lake integrity assessments. The notion of habitat complexity serves as the connection between plant structure and animal response. The complexity means the sheer volume of the structural components and the way they are arranged in space, and in vegetated aquatic environments it depends on the form, size, and branching of leaves and stems (Kovalenko et al., 2012). Plants with compound leaves, like *Ceratophyllum demersum* L. and *Hydrilla verticillata (L.f.)* Royle, possess greater surface area, a higher number of interstices, and diverse sizes of refuges than plants with broad and simple leaves. There is an extensive literature on the positive correlation of structural complexity of plants with abundance and diversity of invertebrates both in natural plants and in artificial models of different architectural designs (Jeffries, 1993) (Taniguchi et al., 2003). Fractals have proven themselves especially useful in the description of this trait, since the fractal dimension (D) gives information about the space-filling pattern of the plant outlines and

allows comparisons among species with extremely different forms (McAbendroth et al., 2005; Dibble & Thomaz, 2009).

Habitat complexity further determines the outcome of biotic interactions. The presence of complex vegetation lowers the foraging efficiency of the fish and invertebrate predators, shelters the prey species, and affects the availability of food sources, such as periphyton and detritus (Warfe & Barmuta, 2004). It should be noted that the nature of the plant community itself does not play a passive role in the development of the invertebrate community; for example, exotic or invasive plants having dissected foliage can harbor different communities compared to those inhabiting the native plant species having a simpler form, even if the overall plant biomass remains unchanged (Cheruvelil et al., 2002). Heterogeneous habitats in streams and lakes where plants occur in patches and food sources depend on their type determine invertebrate abundance and richness (Ferreiro et al., 2011).

The majority of existing research on interactions between macrophytes and invertebrates is focused on a comparison of plant species or habitats at one moment in time. However, macrophyte stands are seasonal structures. Factors such as water level, illumination, water temperature, turbidity, nutrient availability, and flood disturbance differ significantly throughout the year and serve as selective filters for macrophyte vegetation and different growth forms (Bornette & Puijalon, 2011). In addition, seasonal or fluctuating conditions can influence the effect of habitat complexity on benthic communities, as disturbance might reset the community structure before it has had enough time to exploit the complexity (Taniguchi & Tokeshi, 2004). In tropical and subtropical regions with monsoon rainfall, these seasonal changes are especially pronounced: high rainfall levels increase water level and turbidity and can disturb and remove submerged vegetation during the rainy season; however, calm conditions during post-monsoon and winter periods are favorable for regrowth. It was proven by research in subtropical reservoirs that macrophyte beds harbor significant portions of the invertebrate biodiversity of an entire system (Ali et al., 2007).

Nevertheless, there has been little research on the changes that take place within these littoral stations during the monsoon period while studying both architectural structure and invertebrate response. It is unknown whether the seasonal variation of the invertebrates' community is due to either the amount of vegetation (coverage and biomass) or the quality of the vegetation (growth forms and structure). The distinction between these two factors is important from a management perspective, as any measure increasing the biomass of plants does not necessarily improve their value as habitat.

This is what the current study attempted to do for a shallow tropical lake, which is influenced by two monsoon seasons. Specifically, wanted to (i) investigate the seasonal variation in macrophyte species composition, biomass, and dominance of growth form; (ii) measure the subsequent variation in habitat complexity through fractal dimension; (iii) assess the response of invertebrate density, richness, diversity, and composition to these variations; and (iv) recommend management options to maintain the habitat complexity and its associated food-web connections. To expect that the invertebrate richness would follow the variation in fractal dimension more strongly than the variation in macrophyte biomass and that the dominance of dissected submerged vegetation following the monsoon season would indicate the highest habitat value.

II. Materials and Methods

2.1. Study Area

The experiment was conducted in a shallow, perennial, rain-fed lake in a tropical zone having a water spread of around 1.2 km² at full storage level, with an average depth of 1.4 m and maximum depth of 3.2 m. The region has a tropical monsoonal climate with a hot summer season from March to May, SW monsoon season from June to September, NE monsoon season from October to December, and a cold and dry winter season from January to February. The mean annual rainfall in the catchment is around 650 mm during the two monsoon seasons, and the lake has inflow from a seasonal stream and surface runoff from a

mixed agriculture and peri-urban catchment. The littoral area harbors submerged, floating leaf, free-floating, and emergent vegetation, and the lake is used for irrigation, fishing, and recreational purposes.

2.2. Sampling Design

Eight permanent littoral stations were selected along the lake shoreline in order to capture the variation in exposure, slope, and types of vegetation in the lake. The stations were spaced at least 150 meters apart, and they were mapped using a hand-held global positioning system (GPS). All the stations were visited once in each month of a complete annual cycle, and the monthly samples were categorized according to the four seasons mentioned above. During each visit, water depth, water temperature, and water turbidity were determined using a graduated rod, digital thermometer, and turbidimeter, respectively. The water transparency was determined using a Secchi disk, while water dissolved oxygen and conductivity were determined using a multi-parameter probe at 0.3 m below the water surface.

2.3. Macrophyte Assemblages

The macrophyte cover at each station was estimated visually in a 10 m × 10 m square plot as the percentage of the plot covered by plants in plan view. After that, the plants were harvested from three randomly chosen 0.25 m² quadrants per station using a long rake and quadrat frames. It is important to note that all shoots were collected. Then plants were sorted according to their species, washed, dried in an oven at 70 °C to a constant weight, and weighed to obtain dry biomass (g m^{-2}). Four growth forms of species have been defined: submersed dissected species (*Hydrilla verticillata*, *Ceratophyllum demersum, Najas* minor All.), submersed entire-leaved species (*Vallisneria spiralis L., Potamogeton nodosus Poir*.), floating-leaved and free-floating species (*Nymphaea pubescens* Willd*., Eichhornia crassipes* (Mart.) Solms, *Ipomoea aquatica* Forssk.), and emergent species (*Typha angustifolia L*.). The share of biomass of each of the four forms of plants was calculated for each station and season.

2.4. Habitat Complexity

The degree of habitat complexity was assessed for the most abundant species within each station through fractal dimension calculations. Ten intact shoots from each of those species that contribute over 10% of station biomass were floated in a white tray containing a scale bar and photographed from above at constant height for every season. The resulting photographs were turned into black-and-white outlines, and D was estimated through the box-counting algorithm, whereby boxes of different sizes ranging from 1 to 64 mm were used similarly to how it had been done in the case of macrophytes in previous research (McAbendroth et al., 2005; Dibble & Thomaz, 2009). The fractal dimension of the vegetation habitat was assessed through a biomass-weighted mean fractal dimension estimate per station and season.

2.5. Invertebrate Sampling and Identification

Invertebrates epiphytic on the plants were collected using a 250 µm mesh bag for encasing individual plants before clipping them at the sediment-water interface in order to prevent the loss of motile animals. Four plant samples from each sampling station during each sampling event were collected, yielding a total of 384 samples in the whole study period. In the laboratory, the plants were washed through a 250 µm sieve, and invertebrates were preserved in 70% ethanol solution. The animals were sorted and identified under a stereomicroscope to family level or genus when identification keys were available. Chironomidae were identified to subfamily level. Dried plant samples were weighed, and the density of invertebrates was calculated in number per 100 g of dry weight of plant (ind. 100 g^{-1} DW). S and H′ as well as functional feeding groups were determined.

2.6. Statistical Analysis

Differences in environmental parameters, plant metrics, and invertebrate metrics between seasons were assessed using linear mixed-effects models where season was a fixed effect, and station was a random effect. Invertebrate density data were log-transformed to $\log_{10}(x + 1)$, and model residuals were checked for normality and homogeneity of variance. Pairwise comparisons between seasons were made with Tukey

correction. To assess the importance of either plant quantity or plant quality as predictors, linear mixed models with invertebrate richness as the response variable and either biomass or fractal dimension as predictors were estimated separately. Marginal R^2 values and AIC criteria were used to compare models. PERMANOVA (9,999 permutations) on Bray- Curtis distance matrices based on square root-transformed abundances was conducted to test seasonal variation in invertebrate community composition, and NMDS was applied for visualization of data structure. Analyses were performed in R version 4.1.2, $p < 0.05$ was considered statistically significant.

III. Results

3.1. Environmental Conditions

There was evidence of distinct hydrological seasonality in the lake (Table 1). The mean depth of the lake water was the shallowest in summer months (0.82 m) while the deepest in the NE monsoon (1.91 m). There was a reduction in water temperature from 31.4 °C in the summer months to 24.3 °C in the winter months. There was maximum turbidity in the SW monsoon (38.7 NTU), where inflows introduced suspended sediments to the lake water, and the minimum turbidity in winter months (9.8 NTU). There was similarity in the levels of Secchi depth, which reached minimum levels of 0.38 ± 0.09 m in the SW monsoon and maximum levels of 1.12 ± 0.17 m in winter months. Dissolved oxygen exceeded 5.2 mg L^{-1} in vegetated sites during all seasons.

3.2. Seasonal Shifts in Macrophyte Assemblages

A total of 15 macrophytes were recorded throughout the year. Both macrophyte cover and biomass showed significant differences among seasons (mixed models; $p<0.001$ for both). The biomass decreased drastically during SW monsoon to 94.2 g m^{-2}, which was nearly half of the summer biomass, due to high water levels, turbidity and flooding effect, causing removal or damage of submerged macrophytes. The recovery process started from the NE monsoon and peaked in winter, where biomass was 312.8 g m^{-2} and cover was higher than 60% (Table 1). Species richness also showed similar trends, with values of 3.4 and 7.3 during the SW monsoon and winter, respectively.

Growth forms were showing stronger variability compared to the total biomass. Free-floating and floating-leaved plants such as *Eichhornia crassipes* and *Nymphaea pubescens* dominated during SW monsoon, contributing more than 50% of the biomass at most stations. Submerged dissected plants made up only 21.7% of biomass during the SW monsoon. After the monsoon, rapid growth was observed in *Hydrilla verticillata* and *Ceratophyllum demersum*, and during winter, the submerged dissected plant group comprised 57.9% of the total biomass. During summer, *Vallisneria spiralis* and *Potamogeton nodosus* were dominant due to the presence of shallow water and bright light conditions.

3.3. Habitat Complexity

The biomass-weighted fractal dimension varied significantly across seasons ($p < 0.001$) and was strongly related to the proportion of dissected submerged vegetation (Figure 1). The mean value of D was lowest in the SW monsoon season (1.31), highest in winter (1.56), and intermediate in summer (1.42) and NE monsoon season (1.49). Among species, the highest mean fractal dimensions were obtained for *Ceratophyllum demersum* (1.63), *Hydrilla verticillata* (1.58), and *Najas minor* (1.55) while the lowest mean values were for *Vallisneria spiralis* (1.18) and *Nymphaea pubescens* (1.12). The mean interstitial space showed the highest (6.8 ± 1.9 mm) and lowest (2.4 ± 0.7 mm) values in SW and winter months, respectively.

3.4. Invertebrate Responses

A total of 41 invertebrate taxa have been reported, which include the following orders: Insecta (Chironomidae, Baetidae, Caenidae, Coenagrionidae, Libellulidae, Corixidae, Notonectidae, Hydrophilidae, Dytiscidae and Hydroptilidae, among others); Gastropoda (Planorbidae, Lymnaeidae, Thiaridae and Viviparidae); Oligochaeta; Hirudinea; Ostracoda; Cladocera and Hydracarina. The

Chironomidae have the largest number of individuals in all seasons, although their percentage decreased from 46% during the South-Western monsoon season to 29% during winter because of the increase in mayflies, damselflies, snails, and water mites.

Density of invertebrates, taxa richness, and Shannon's diversity index showed significant differences in all four seasons ($P < 0.001$ for all). Season with the lowest density was the SW monsoon season with a mean value of 967 individuals/100 g, while in winter, density was more than three times greater (3,374 ind./100g). From summer to winter, taxa richness changed from 12.4 to 27.5 and H' from 1.52 to 2.46 (Table 1, figure 1). Pairwise comparisons revealed significant differences between winter and other seasons concerning richness and diversity, but not for density.

The fractal dimension showed a greater predictive power for invertebrates compared to the biomass of macrophytes. The mixed model using D as the independent variable accounted for 62% of the variation in richness (marginal $R^2 = 0.62$; AIC = 412.6), while the model that included biomass as the independent variable only accounted for 41% (marginal $R^2 = 0.41$; AIC = 438.9). Invertebrate richness was positively correlated with D with 5.8 taxa being added per each 0.1 unit increase in D. PERMANOVA analysis revealed significant differences in the invertebrate assemblage composition between the seasons (pseudo-$F = 9.84$, $R^2 = 0.41$, $p = 0.001$), and the non-metric multidimensional scaling (NMDS) (stress = 0.14) discriminated the samples collected during the SW monsoon season dominated by Chironomidae and Oligochaeta from the winter samples that were dominated by Baetidae, Caenidae, Coenagrionidae, Planorbidae and Hydracarina.

Table 1: Seasonal Variations in Environmental Conditions, Macrophyte Characteristics, Habitat Complexity, and Epiphytic Invertebrate Diversity

Variable	**Summer (Mar–May)**	**SW Monsoon (Jun–Sep)**	**NE Monsoon (Oct–Dec)**	**Winter (Jan–Feb)**
Water Depth (m)	0.82 ± 0.21	1.64 ± 0.33	1.91 ± 0.29	1.38 ± 0.24
Water Temperature (°C)	31.4 ± 1.2	27.6 ± 0.9	26.1 ± 1.1	24.3 ± 0.8
Turbidity (NTU)	14.2 ± 3.6	38.7 ± 8.4	22.5 ± 5.1	9.8 ± 2.7
Macrophyte Cover (%)	41.3 ± 9.8	22.6 ± 7.4	48.9 ± 10.2	63.7 ± 8.6
Macrophyte Biomass (g DW m^{-2})	186.4 ± 42.7	94.2 ± 31.5	241.6 ± 55.3	312.8 ± 61.2
Macrophyte Species per Station	5.1 ± 1.3	3.4 ± 1.1	6.2 ± 1.5	7.3 ± 1.2
Submerged Dissected Share of Biomass (%)	38.5	21.7	46.2	57.9
Fractal Dimension (D)	1.42 ± 0.06	1.31 ± 0.07	1.49 ± 0.05	1.56 ± 0.04
Invertebrate Density (ind. 100 g^{-1} DW)	1,842 ± 412	967 ± 286	2,615 ± 538	3,374 ± 601
Invertebrate Taxa Richness (S)	18.6 ± 3.2	12.4 ± 2.8	23.1 ± 3.6	27.5 ± 3.1
Shannon Diversity (H′)	1.94 ± 0.21	1.52 ± 0.24	2.21 ± 0.19	2.46 ± 0.17

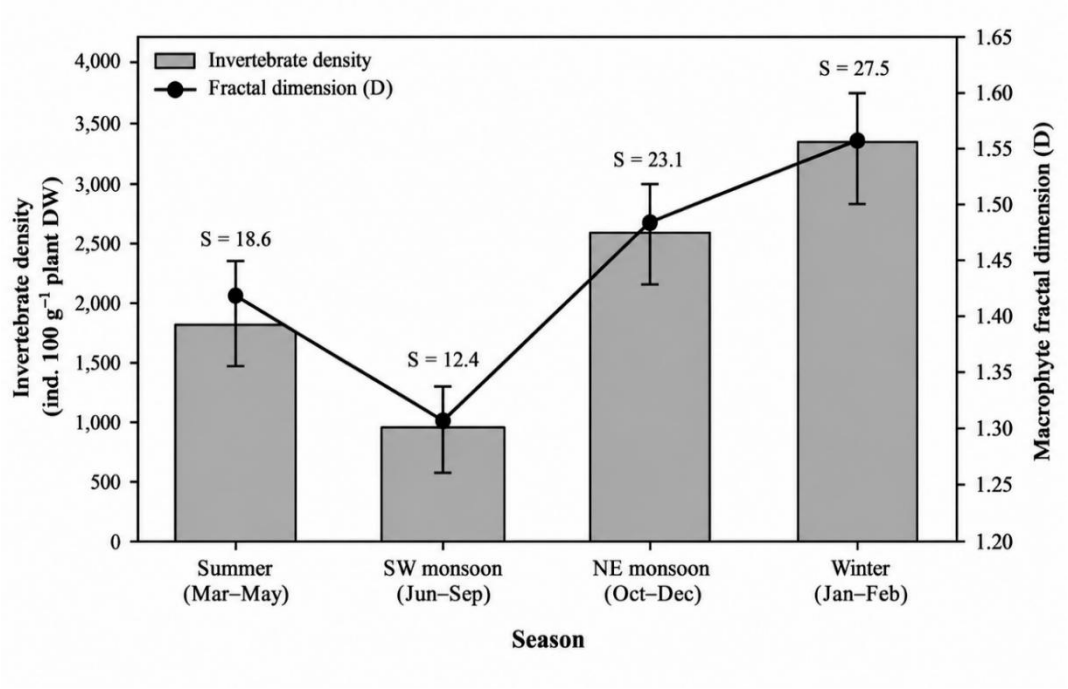


Figure 1: Seasonal Variation in Epiphytic Invertebrate Density, Macrophyte Fractal Dimension, and Taxa Richness

IV. Discussion

These results indicate that seasonal changes in the habitats of invertebrates associated with plants in the monsoonal shallow lakes involve considerable reorganization, as a result of shifts in the structure of macrophytes. Invertebrate diversity was more related to structural complexity of macrophytes, estimated using fractal dimension, than plant biomass. Replacing the floating and large-leafed plants with small-leafed submerged plants after the monsoon period increased habitat complexity and contributed to a higher diversity of invertebrates. Such a connection suggests that plant structure is an important factor influencing littoral community structure, as shown by other studies (Jeffries, 1993; Taniguchi et al., 2003; McAbendroth et al., 2005).

The direct relationship between fractal dimension and invertebrate richness is due to the presence of surfaces for attachment, sources of food, and predator hiding places in complex vegetation. Dissected macrophytes create many microhabitats, which make it easier for organisms with varied needs to colonize them (Dibble & Thomaz, 2009). It was also proven through experiments that structural complexity alone affects invertebrates, despite the absence of significant changes in plant biomass (Jeffries, 1993). In summer, the average macrophyte biomass corresponded with an intermediate number of invertebrates since there were predominantly Vallisneria and Potamogeton macrophytes that had a simple structure (Kovalenko et al., 2012; Cheruvelil et al., 2002).

The seasonal disturbances of the monsoons significantly impacted macrophyte communities and the associated invertebrates. The increase in depth of water, turbidity and hydrological disturbance led to reduction in submerged macrophytes while free floating macrophytes such as *Eichhornia crassipes* were favored. These factors led to limited availability of light and potentially reduced levels of dissolved oxygen under dense layers of free-floating plants (Bornette & Puijalon, 2011). As a result, disturbance-tolerant organisms, such as Chironomidae and Oligochaeta, were common during the southwest monsoons. Such a pattern has been noted elsewhere where unstable environmental conditions limit the advantages of complex vegetation (Taniguchi & Tokeshi, 2004).

The modification of functional groups also illustrated the importance of macrophyte morphology in the ecosystem. The presence of many scrapers in post-monsoonal seasons indicated the availability of surfaces covered by periphyton, whereas the presence of predators indicated trophic interactions in the system. Complex vegetation provides both a substrate for feeding and a shelter, which influences predator-prey relations and organization of the community (Warfe & Barmuta, 2004; Ferreiro et al., 2011).

The recovery of submerged vegetation during seasons also has consequences on the resilience of shallow-lake ecosystems. The structurally complex macrophyte beds are biodiversity hotspots and also help in the maintenance of clear water, while vegetation loss can increase the vulnerability to persistent turbidity (Scheffer et al., 1993). Their role as habitats for aquatic invertebrates goes beyond just the aquatic level and includes fish and waterbirds too (Ali et al., 2007). However, limitations are posed in the form of annual sampling, taxonomic identification up to the family level, and 2-D measures of plant complexity. These limit the extent of generalization and assessment of habitat architecture. Further studies should include multiple monsoon cycles, species identification, and 3-D measurements of vegetation. In conclusion, the results highlight the significance of seasonal variation in structural complexity of macrophytes with respect to invertebrate biodiversity and ecosystem recovery in monsoonal shallow lakes.

V. Implications for Ecosystem Management

There are a number of practical considerations arising from the findings of this study. Firstly, programs that monitor macrophytes should consider assessing growth-form composition and measures of structural complexity, in addition to coverage or biomass, since these factors better represent habitat value for invertebrates. Secondly, physical removal of submerged plants, which is performed in order to improve circulation or recreate a more open lake, should take place outside the NE monsoon and winter seasons, as at this time the dissected plants are regenerating the most important habitats. Thirdly, the control of free-floating invasive plants like *Eichhornia crassipes* prior to and during the monsoon period will ensure that shading is reduced and submerged plants can regenerate after the monsoon period. Lastly, catchment management that limits the input of sediments into the lake during monsoons will prevent turbidity, which inhibits the growth of submerged plants.

VI. Conclusion

This research has shown that seasonal changes in the composition of the macrophyte community have a key effect on habitat complexity and the structure of the invertebrate community in a tropical lake subject to monsoon conditions. In the course of a single year, the southwest monsoon led to a decrease in the biomass of macrophytes, the disappearance of finely divided submerged vegetation, the dominance of free-floating and floating-leaved plants, and the smallest fractal dimension for the year. In addition, the invertebrate density, richness, and diversity were at their lowest, being characterized by the prevalence of tolerant groups – Chironomidae and Oligochaeta. The development of *Hydrilla verticillata* and *Ceratophyllum demersum* under the influence of the northeast monsoon, especially in winter, increased the fractal dimension to its annual maximum level, decreased interstitial spaces, and promoted more than triple invertebrate density and more than double taxa richness in comparison with the wet season. Fractal dimension showed significantly greater variation in invertebrate richness than the macrophyte biomass. Seasonal replacement in the invertebrate community, particularly the increase in scrapers and predators in the post-monsoon period, suggests that such dynamics also occur in the functional structure of the littoral food web. The key take-home message from these results for lake managers is the post-monsoon period as the important time frame for the protection of dissected submerged vegetation, management of invasive floating plants, and minimisation of sediment inflow from catchments. Routine recording of growth forms and structural complexity would give a better indicator of the condition of littoral habitats and ecosystems.

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Conflict of Interest

The authors state that there are no known competing financial interests or personal relationships that may have appeared to influence the work described in this paper.

Data Availability Statement

The dataset for the above findings can be obtained from the corresponding author on request.

References

[1] Scheffer, M., Hosper, S. H., Meijer, M. L., Moss, B., & Jeppesen, E. (1993). Alternative equilibria in shallow lakes. *Trends in ecology & evolution*, *8*(8), 275-279. https://doi.org/10.1016/0169-5347(93)90254-M

[2] Kovalenko, K. E., Thomaz, S. M., & Warfe, D. M. (2012). Habitat complexity: approaches and future directions. *Hydrobiologia*, *685*(1), 1-17. https://doi.org/10.1007/s10750-011-0974-z

[3] Jeffries, M. (1993). Invertebrate colonization of artificial pondweeds of differing fractal dimension. *Oikos*, 142-148. https://doi.org/10.2307/3545104

[4] Taniguchi, H., Nakano, S., & Tokeshi, M. (2003). Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. *Freshwater biology*, *48*(4), 718-728. https://doi.org/10.1046/j.1365-2427.2003.01047.x

[5] McAbendroth, L., Ramsay, P. M., Foggo, A., Rundle, S. D., & Bilton, D. T. (2005). Does macrophyte fractal complexity drive invertebrate diversity, biomass and body size distributions?. *Oikos*, *111*(2), 279-290. https://doi.org/10.1111/j.0030-1299.2005.13804.x

[6] Dibble, E. D., & Thomaz, S. M. (2009). Use of fractal dimension to assess habitat complexity and its influence on dominant invertebrates inhabiting tropical and temperate macrophytes. *Journal of Freshwater Ecology*, *24*(1), 93-102. https://doi.org/10.1080/02705060.2009.9664269

[7] Warfe, D. M., & Barmuta, L. A. (2004). Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia*, *141*(1), 171-178. https://doi.org/10.1007/s00442-004-1644-x

[8] Cheruvelil, K. S., Soranno, P. A., Madsen, J. D., & Roberson, M. J. (2002). Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte. *Journal of the North American Benthological Society*, *21*(2), 261-277. https://doi.org/10.2307/1468414

[9] Ferreiro, N., Feijoó, C., Giorgi, A., & Leggieri, L. (2011). Effects of macrophyte heterogeneity and food availability on structural parameters of the macroinvertebrate community in a Pampean stream. *Hydrobiologia*, *664*(1), 199-211. https://doi.org/10.1007/s10750-010-0599-7

[10] Bornette, G., & Puijalon, S. (2011). Response of aquatic plants to abiotic factors: a review. *Aquatic sciences*, *73*(1), 1-14. https://doi.org/10.1007/s00027-010-0162-7

[11] Taniguchi, H., & Tokeshi, M. (2004). Effects of habitat complexity on benthic assemblages in a variable environment. *Freshwater biology*, *49*(9), 1164-1178. https://doi.org/10.1111/j.1365-2427.2004.01257.x

[12] Ali, M. M., Mageed, A. A., & Heikal, M. (2007). Importance of aquatic macrophyte for invertebrate diversity in large subtropical reservoir. *Limnologica*, *37*(2), 155-169. https://doi.org/10.1016/j.limno.2006.12.001