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REVIEW PAPER

A review of the ecological role of aquatic macrophytes on freshwater fish

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Abstract Macrophytes play a central role in the structure and functioning of aquatic ecosystems. In this paper, we review the role of macrophytes in shaping fish attributes. By acting as physical barriers, macrophytes modify the abiotic environment, creating conditions preferred by fish, such as higher oxygen concentrations and lower CO_2 concentrations, particularly in the case of submerged macrophytes. The habitat complexity provided by macrophytes of different life forms favors fish, providing protection from predation and serving as sites for reproduction, acting as spawning substrates and nursery habitats for larvae and juveniles. Moreover, macrophytes contribute to fish foraging dynamics by providing food resources (e.g., periphyton and attached invertebrates) within structurally complex habitats. Consequently, macrophytes foster increased fish diversity compared to open water. Beyond these indirect influences, macrophytes serve as direct feeding resources for some species of fish, both herbivorous and detritivorous. Additionally, macrophytes function as fish dispersal vectors, assisting migration and enhancing gene flow in diverse ecosystems. Despite positively affecting fish, at extremely high biomasses, macrophytes can impair fish by degrading water quality and hindering fish movement and feeding. Understanding these intricate relationships provides insights for future research and management strategies, supporting the conservation and sustainable management of aquatic ecosystems.

Keywords Biodiversity · Macrophyte–fish interactions · Habitat complexity · Food webs · Ecosystem services

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Introduction

The ecological relationship between macrophytes and fish has been a focal point for biologists and limnologists since the beginning of Ecology and Limnology.

In the seminal paper "The Lake as a Microcosm" (published in 1887), recognized as one of the earliest and most influential works in ecological history, Stephan Forbes underscored the significance of macrophytes in relation to fish. After observing that the carnivorous macrophyte *Utricularia* utilizes "…myriads of small insects and Crustacea…" and that "…these are of the kinds most useful as food for young fishes of nearly all descriptions…," Forbes deduced that "…these plants compete with fishes for food and tend to keep down their number by diminishing the food resources of the young." Forbes extended his analysis by noting that "The plants even have a certain advantage in this competition, since they are not strictly dependent on Entomostraca, as the fishes are, but sometimes take root, developing then but very few leaves and bladders." Thus, according to Forbes, carnivorous macrophytes negatively influenced young fish through competitive interactions.

The rather unique competitive relationship between animals (fish) and plants (macrophytes) has received limited attention in ecological studies since Forbes' work, except for a recent paper that revisited this relationship experimentally (Davenport & Riley, 2017). Instead, various other types of ecological relationships, such as the provision of habitat, use of macrophytes for spawning, and the availability of feeding resources, have taken precedence in several ecological studies over the past few decades. By querying "macrophyte* and fish*" in the Web of Science all databases (as of November 28, 2024), we identified a total of 5768 papers, with the earliest one in the dataset dating back to 1966. The number of papers has seen a steady rise, increasing from one in 1966 to 238 in 2020. This trend underscores the growing interest among limnologists in issues related to fish–macrophyte interactions.

One approach to investigating macrophyte–fish relationships involves examining how fish impact macrophytes. An example of direct influence is herbivory, a factor that has led to a significant reduction in macrophyte biomass (Dibble & Kovalenko, 2009; Bakker et al., 2016; Wood et al., 2017). Indirect effects of fish on macrophytes encompass bioturbation caused by fish, resulting in adverse effects on submerged macrophytes (Mormul et al., 2012; Adamek & Marsalek, 2013) and nutrient inputs through fish excretion that can either stimulate (Pinnegar et al., 2007; Yu et al., 2021a) or inhibit (Yu et al., 2021b) macrophyte growth. Furthermore, fish can exert a negative influence on macrophyte growth through top-down mechanisms, involving the predation of invertebrates that feed on periphyton, for example (Brönmark & Vermaat, 1997).

An alternative perspective, contrasting the previous one, investigates the influence of macrophytes on fish populations and communities (e.g., Dibble et al., 1996; Petr, 2000; Schultz & Dibble, 2012). Macrophytes dominate shallow water bodies, serving as habitats for micro- and macro-organisms. Additionally, along with attached microbiota, they alter the water medium through their presence and metabolism (Wetzel, 2001; Caraco et al., 2006). Macrophytes play an important role by providing feeding resources directly through living (Bakker et al., 2016) and dead (detritus) tissues (Ye et al., 2006) and indirectly through attached microalgae, micro- and macroinvertebrates, which serve as feeding resources for fish (Quirino et al., 2015; Cardozo et al., 2020). Due to these factors, macrophytes have both direct and indirect influence on the aquatic ecosystem and its biota, including fish. Indeed, the presence, abundance, diversity and morphology of macrophytes are acknowledged as key determinants of fish population and community attributes in various ecosystems in temperate and tropical regions (Dibble et al., 1996; Petr, 2000; Rozas & Odum, 1987; 1988; Agostinho et al., 2003; 2007; Wang et al., 2003; Dibble & Pelicice, 2010; Kovalenko et al., 2010a; Bhagat & Ruetz III, 2011; Schultz & Dibble, 2012; Chaparro et al., 2015; Jin et al., 2019; Quirino et al., 2021a; Marsh et al., 2022, Quirino et al., 2023). In floodplains, for instance, where macrophytes communities change seasonally in response to the flood pulse (Camargo & Esteves, 1996; Padial et al., 2009a, b), stands of macrophytes may be so important that they can function as "sources of fish", restarting the succession process after flood disturbances (Gomes et al., 2012).

Despite the central roles that macrophytes and fish play in ecosystem functioning and the services they provide (Pelicice et al., 2023; Thomaz, 2023), relatively few studies have attempted to synthesize the interactions between these two communities. An extensive review by Dibble et al. (1996) summarized how aquatic macrophytes influence fish richness, abundance, growth, and survival, while also discussing the methods used to study fish–plant interactions.

Petr (2000) provided a comprehensive review of the use of macrophyte habitats by fish for feeding and spawning, the role of macrophytes in food webs and fish interactions (e.g., predation), and other applied topics, such as aquatic plant management and control using fish. Notably, Petr acknowledged the complexity of summarizing macrophyte–fish interactions, stating: "The more research results become available, the more complicated the aquatic macrophyte–fish interrelationships appear to be." More recently, Schultz and Dibble (2012) reviewed the influence of macrophytes on freshwater fish and macroinvertebrate communities, focusing on how the traits of invasive plants affect these animals.

In the present work, we build on those previous studies and provide a review on the influence of aquatic macrophytes on fish populations and communities, particularly from freshwater ecosystems (summarized in Fig. 1). Specifically, we explore the following issues: (i) the effects of macrophytes on fish through alterations in the abiotic medium; (ii) the role of the physical structure provided by macrophytes, serving as refuges, reproductive sites, and feeding grounds for fish; (iii) the intricate relationships between macrophytes and fish diversity; (iv) the direct utilization of macrophytes' living and dead tissues as feeding resources, encompassing herbivory and detritivory, respectively; (v) the transfer of carbon from macrophytes to fish through intermediary organisms in the food chain; and (vi) the utilization of macrophytes as vectors for dispersion. We updated the previous reviews, a timely effort given the substantial body of literature published since their release. In doing so, we addressed less-explored topics (e.g., the role of macrophytes in fish reproduction) and previously overlooked issues (e.g., the use of stable isotope analysis to clarify the role of macrophytes in fish carbon acquisition and the role of macrophytes on fish dispersal). Additionally, we incorporated numerous examples from tropical ecosystems, which have recently gained increased attention in this field.

Effects of macrophytes on fish through changes in the abiotic medium

Macrophytes exert influence on the physical and chemical properties of water in various ways. Serving as a physical barrier, they diminish underwater light, water circulation, and flow (Madsen et al., 2001; Villamagna & Murphy, 2010). Concurrently, in association with reduced water movement, the photosynthesis and respiration of macrophytes, particularly the submerged ones along with attached algae and microbes, induce pronounced spatial (both vertical and horizontal) and temporal (both diel and

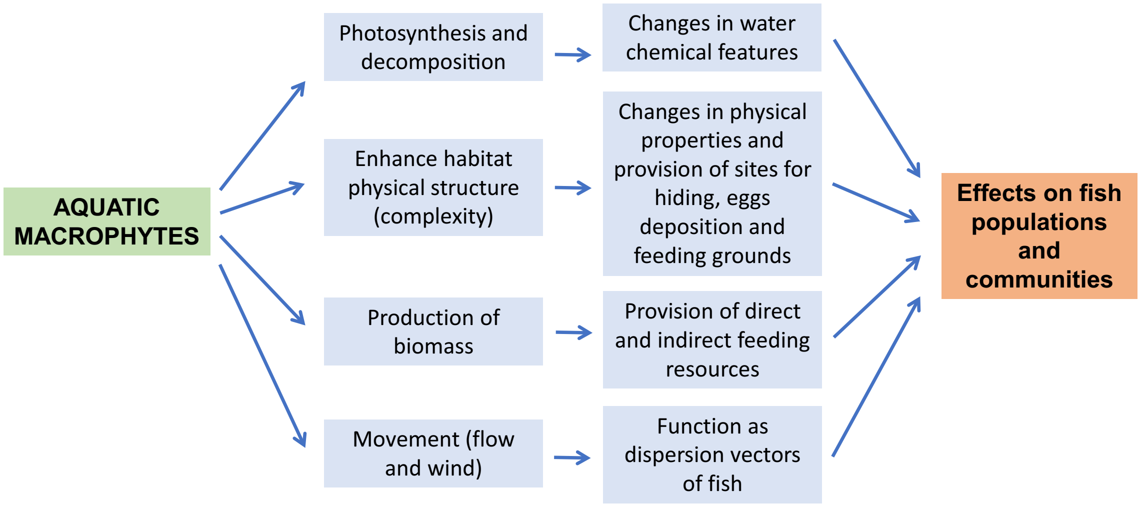

Fig. 1 Rationale of the present paper. Through various processes (second column), macrophytes modify water characteristics, enhance habitat complexity, provide food, and aid in dispersion (third column), subsequently influencing attributes of fish populations and communities

seasonal) variations in dissolved oxygen (DO), CO_2, and pH. For instance, the photosynthesis of submerged macrophytes generates an increase in DO and pH. An outcome of the alkaline pH in microhabitats surrounding leaves is the conversion of NH_4^+ into the unionized gas NH_3 (Wetzel, 2001), which is toxic to fish. In contrast, plant respiration and associated microbes consume DO, which is also utilized in the decomposition of the macrophyte detritus themselves (Fontenot et al., 2001; Bianchini Jr. et al., 2008, 2011; Rabaey et al., 2021). The decomposition of organic matter attached to macrophyte roots and other tissues also contribute to decrease DO concentrations (Poi de Neiff et al., 1994; Caraco et al., 2006; Chimney et al., 2006). Hence, the presence and activity of macrophytes significantly impact fish survival, growth, and colonization capacity by interfering with water features, primarily those related to pH, DO, CO_2, and NH_3 (see Fig. 2).

The reduction in underwater light caused by macrophytes, particularly free-floating species, can affect fish in several ways. For example, shading by macrophytes reduces photosynthesis in algae (Schultz & Dibble, 2012) and exacerbates hypoxia (Killgore & Hoover, 2001). Additionally, in dense macrophyte patches, decreased underwater light can impact fish populations (Nurminen et al., 2007; Chaparro et al., 2015), leading to alterations in food web structures (Villamagna & Murphy, 2010; Schultz & Dibble, 2012).

The waterscape within macrophyte stands is far from homogeneous. Due to the limited water movement, physical and chemical properties are unevenly distributed, prompting fish to actively seek more suitable sites at a micro-scale, akin to physiological "micro-refuges" (Miranda et al., 2000; Caraco et al., 2006; Wilson et al., 2015; Bradshaw et al., 2015). In general, fish tend to concentrate in areas where temperature and pH are lower and DO is higher (Reid et al., 2013). Within submerged macrophyte stands, fish aggregate near the surface or in oxygenated pockets in the upper layers of the plant canopy during periods when DO is low in deep water (Fig. 2). Conversely, they avoid the surface when it becomes hyperoxic or hyperthermic (Miranda et al., 2000). However, some fish species, such as largemouth bass, exhibit a preference for warmer waters associated with macrophyte stands (Christensen & Moore, 2008).

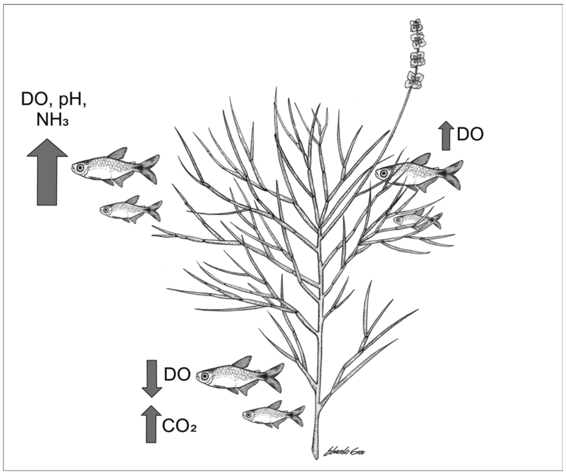

Fig. 2 Selected key abiotic factors influenced by macrophytes that play a significant role in shaping fish distribution. An increase in dissolved oxygen (DO) at microscales within submerged macrophyte patches serves as an attractant for fish (upper right). Conversely, excessive amounts of DO during periods of high photosynthesis rates contribute to an elevation in pH and the accumulation of toxic ammonia (NH_3), resulting in the repulsion of fish (upper left). In addition, fish tend to avoid areas where detritus decomposition depletes DO and increases CO_2 (lower left). The size of the arrows corresponds to the concentrations of gases or pH values

Concerning pH, laboratory investigations have demonstrated that fish tend to avoid elevated pH levels (9.5–10.0), which may occur within submerged macrophyte stands during well-lit periods of intense photosynthesis (Serafy & Harrell, 2006). At these alkaline values, there is an accumulation of unionized NH_3, a gas that can be harmful to fish (e.g., Souza-Bastos et al., 2017), and whose toxicity increases at higher pH levels (Ardeniswan et al., 2017). However, available evidence on the effects of NH_3 on fish survival is primarily limited to experiments and aquaculture settings (e.g., Kracko & Noble, 1993; Parvathy et al., 2023), and we did not find studies on macrophyte-mediated increases in NH_3 affecting fish in natural ecosystems. This dearth of research could be attributed to the fact that NH_3 concentrations may not reach levels capable of adversely affecting fish survival in nature or it could be due to the limited number of investigations measuring this gas in field studies.

CO_2 is another gas that undergoes noticeable changes within macrophyte stands in response to macrophyte and attached organisms' respiration, as well as detritus decomposition, leading to adverse effects on fish. In the Pantanal, the largest South American wetland, instances of fish kills during inundations have been attributed to extremely high concentrations of CO_2 (alongside DO depletion) released by macrophyte roots and their decomposition (Calheiros & Hamilton, 1998).

Among the chemical factors, DO has attained the most attention because it stands as the primary limiting factor for fish (as well as other organisms) in aquatic ecosystems. The limitation of DO arises from its substantial consumption by both micro- and macro-organisms and by the fact that its diffusion in water is several orders of magnitude lower than in the atmosphere (Sculthorpe, 1967; Wetzel, 2001). Macrophytes play a dual role in relation to DO, as extremely high or low values can be found in macrophyte stands (Caraco et al., 2006). For instance, saturation values of up to 300% have been measured within submerged macrophyte patches at dusk (Miranda et al., 2000). In a seasonal point of view, macrophyte decomposition during winter may lead to fish kills through anoxia, especially in clear-water lakes dominated by submerged vegetation (Lindeman, 1941; Rabaey et al., 2021). In contrast, during events of extreme hypoxia resulting from detritus decomposition, patches of submerged macrophytes that remain active and maintain high DO concentrations may serve as physiological refuges for juvenile fish (Fontenot et al., 2001).

The DO concentration may vary within the same macrophyte stand, with areas of suitable oxygen adjacent to areas of hypoxia, stressful for fish (Miranda et al., 2000). Generally, there is a gradient of increasing DO concentrations from the innermost part (near the shore) to the stand edge (near the limnetic region), and this gradient also influences fish distribution (Miranda & Hodges, 2000; Yamanaka et al., 2007; Agostinho et al., 2007; Lopes et al., 2015). Additionally, there is a trend of decreasing DO (increasing hypoxia events) with increasing macrophyte abundance (Yamaki & Yamamuro, 2013; Hagerthey et al., 2014; Bradshaw et al., 2015; Bunch et al., 2015; Lopes et al., 2015; Cunha et al., 2019; Rabaey et al., 2021). For this reason, higher fish abundance (Miranda & Hodges, 2000; Bunch et al., 2015; Chaparro et al., 2015; Ceschin et al., 2019) and richness (Killgore & Hoover, 2001; Petry et al., 2003; Agostinho et al., 2007; Lopes et al., 2015; Cunha et al., 2019) are sometimes recorded in less dense macrophyte stands where DO concentrations are more suitable.

The impact of macrophytes on DO and, consequently, on fish depends on the plant life form (Miranda & Hodges, 2000; Caraco et al., 2006; Chimney et al., 2006; Troutman et al., 2007), depth (Miranda et al., 2000), time of day, and seasons (Caraco et al., 2006; Bradshaw et al., 2015; Kauffman et al., 2018). For instance, submerged macrophytes contribute to enhancing DO (along with pH) in surface waters (Carter et al., 1991; Miranda et al., 2000; Caraco et al., 2006; Chimney et al., 2006; Hagerthey et al., 2010). However, submerged macrophytes may cause hypoxia when present in high biomass, which is generally observed for invasive species, such as *Hydrilla verticillata* (LF) Royle and *Myriophyllum spicatum* L. (Bradshaw et al., 2015). The decrease in DO levels is particularly noticeable at night (Kauffman et al., 2018). Floating-leaved macrophytes and free-floating macrophytes, in general, deplete DO (Petr, 2000; Killgore & Hoover, 2001; Caraco & Cole, 2002; Caraco et al., 2006; Villamagna & Murphy, 2010; Schultz & Dibble, 2012; Chaparro et al., 2015; Ceschin et al., 2019). Most of the cited investigations provide evidence that, in general, fish tend to avoid areas with low DO concentrations created by macrophytes.

Fish species exhibit individual responses to changes in DO associated with the metabolism of macrophytes and their decomposition (Killgore & Hoover, 2001; Soares et al., 2006; Bunch et al., 2015). An investigation involving 20 fish species that colonize macrophytes and floating grasses subjected to hypoxia in the Amazon floodplain revealed diverse strategies to cope with hypoxia, including physiological, biochemical, and behavioral mechanisms (Soares et al., 2006). For instance, despite the general reduction of DO beneath free-floating macrophytes, certain fish species can utilize the DO exuded by the roots of these macrophytes in extreme hypoxic conditions (Saint-Paul & Soares, 1987; Soares et al., 2006). Due to these and other adaptive strategies, numerous fish species that inhabit macrophyte stands can tolerate DO concentrations below 0.5 mg/l (Crampton, 1998; Killgore & Hoover, 2001).

It is essential to note that abiotic factors interact with other ecological factors to determine the occurrence of fish inside macrophyte stands. For instance, both juveniles and adults may benefit by the shelter provided by macrophytes (refer to "Use of physical structure provided by macrophytes") even when the environment within plant stands is hypoxic, illustrating that safety can, in some circumstances, take precedence over physiological compromise (Miranda et al., 2000; Sloman et al., 2006; Yamanaka et al., 2007; Chaparro et al., 2015; Kauffman et al., 2018). A more intricate situation was revealed by Wilson et al. (2015), who found that the utilization of habitat by *Lepomis* depends on the interaction among DO, habitat complexity, and fish densities. These fish tend to use low-quality habitats (in terms of DO and habitat complexity) at high fish densities, likely to reduce intra-specific competition. Considering these interactive factors, fish densities and DO concentrations within macrophyte stands do not always exhibit a positive correlation.

The relationship between macrophytes, DO, and fish holds practical implications for conservation. For instance, the control of excessive macrophyte growth serves as a strategy to enhance DO conditions, thereby positively influencing fish diversity (Mitsuo et al., 2014; Bunch et al., 2015). Under different circumstances, habitat restoration efforts can establish a physiological refuge for native fish that rely on macrophyte stands as their habitat (Yamanaka et al., 2007; Yamanaka, 2013). Another aspect of practical interest is that changes such as global warming and eutrophication may alter the relationships between macrophytes and fish through their effects on the abiotic environment. The consequences of these two global changes are complex, but at least two potential outcomes can be anticipated. For instance, global warming may accelerate macrophyte decomposition rates (e.g., Carvalho et al., 2005), which, combined with reduced DO solubility at higher temperatures, could worsen conditions for fish survival due to lower oxygen availability. Eutrophication, on the other hand, favors the dominance of free-floating macrophytes over submerged species, which can significantly alter the abiotic environment by reducing underwater light and DO levels, with negative consequences for fish assemblages (e.g., Petr, 2000; Villamagna & Murphy, 2010).

Finally, it is worth noting that the abiotic variables influenced by macrophytes that affect fish are usually highly correlated, making it difficult to identify which factor is responsible for a particular response. For instance, DO concentrations are negatively correlated with CO_2 concentrations and positively correlated with pH and NH_3 concentrations. Moreover, field data also confound abiotic limitations with biotic interactions, such as predation or competition. Therefore, unless experimental manipulations isolate at least some of these factors (e.g., Saint-Paul & Soares, 1987; Soares et al., 2006), it is challenging to reach firm conclusions on which abiotic factor contributes to the observed responses of fish to the presence of macrophytes.

Use of physical structure provided by macrophytes

In this section, we explore the mechanisms that elucidate the relationships between habitat complexity, provided by macrophytes, and various fish attributes. The mere presence of macrophytes enhances the physical structure of the environment, yielding positive effects on organisms in littoral zones, including fish. The enhancement of physical structure, or habitat complexity, is linked to at least two benefits (Thomaz & Cunha, 2010). Firstly, the augmentation of physical structure provides refuge against predation. This positive interaction extends to fish reproduction, as numerous fish species find suitable structures for egg deposition. Moreover, eggs, larvae, juveniles, and adults find greater protection within macrophyte stands. Secondly, more structured habitats enhance food availability, such as attached microalgae, invertebrates, and detritus, consequently exerting positive influence on fish. In fact, the physical habitat structure offered by macrophytes has been deemed more influential than water chemistry in elucidating fish community attributes in diverse freshwater ecosystems (Pelicice et al., 2005; Cvetkovic et al., 2010; Dibble & Pelicice, 2010). Because of these benefits, there are many species of fish that use the habitat provided by macrophytes belonging to different life forms (Fig. 3). However, under extremely structured habitats found at high plant densities, the negative effects may outweigh the benefits (as discussed below).

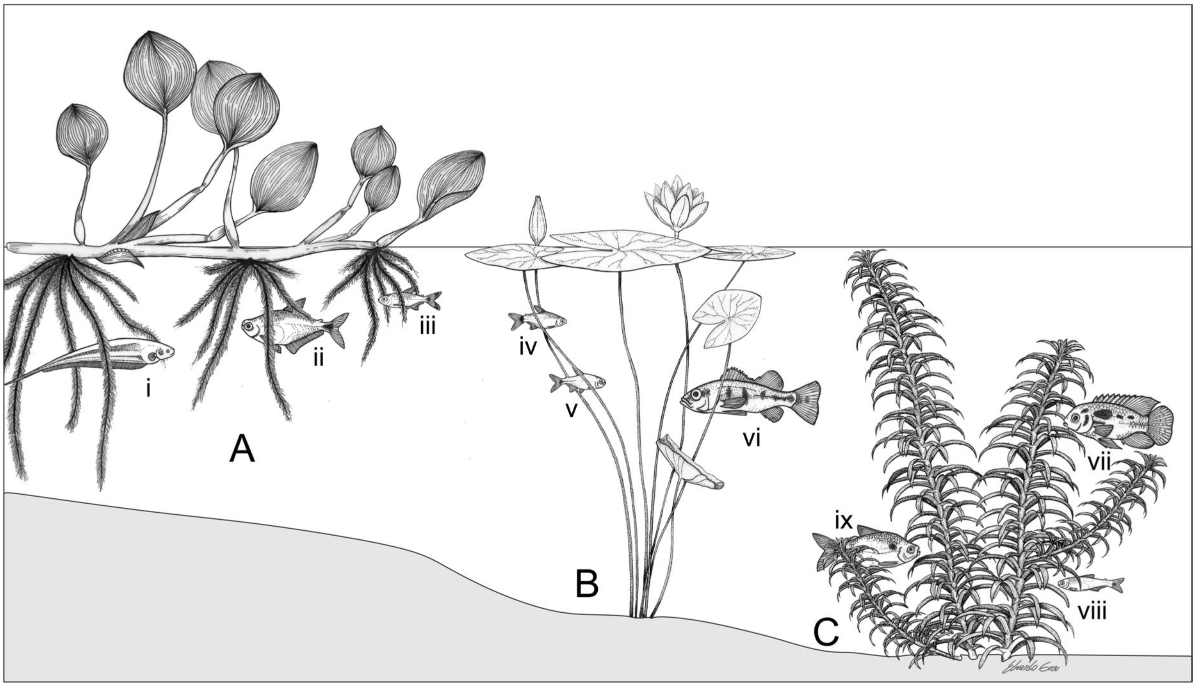

Fig. 3 Examples of small fish that use macrophytes as habitats in a Neotropical ecosystem. **A**—The floating stem macrophyte *Eichhornia azurea* (Sw.) Kunt (i. *Eigenmannia trilineata* López, Castello, 1996; ii. *Roeboides paranensis* Pignalberi, 1975, iii. *Moenkhausia intermedia* Eigenmann, 1908). **B**—The floating leaved macrophyte *Nymphaea amazonica* Mart. & Zucc. (iv. *Serrapinnus notomelas* (Eigenmann, 1915); v. *Hemigrammus marginatus* Ellis, 1911; vi. juvenile *Cichla kelberi* Kullander & Ferreira, 2006). **C**—The submerged macrophyte *Egeria najas* Planch. (vii. *Laetacara araguaiae* Ottoni & Costa, 2009; viii. *Astyanax altiparanae* Garutti & Britski, 2000; ix. *Bryconamericus exodon* Eigenmann, 1907). Examples taken from Agostinho et al. (2007), Dibble & Pelicice (2010), and Cunha et al. (2011), respectively. The sizes of fish and macrophytes do not adhere to a consistent scale

Macrophytes impact habitat complexity across various spatial scales. A literature survey revealed the influences of these plants on organisms at scales ranging from 10^{-12} to 10^5 km^2 (Thomaz & Cunha, 2010). Drawing inspiration from the theory formulated by Hutchinson (1959), these authors proposed that the habitat created by macrophytes exhibits a fractal-like configuration, elucidating why fish (and other organisms) with diverse body sizes and shapes utilize interstitial spaces with varying volumes (Fig. 4). Consequently, the mosaic of interstitial spaces clarifies why organisms and species with distinct body sizes and shapes seek refuge within macrophytes.

The patterns of macrophyte use by fish are species specific, and they are linked to macrophyte architecture and associated physical and chemical attributes. These factors mediate spatial segregation among fish (Troutman et al., 2007; Dibble & Pelicice, 2010; Bhagat & Ruetz III, 2011; Reid et al., 2013; Yamaki & Yamamuro, 2013; Lopes et al., 2015; Cunha et al., 2019). For instance, small fish show a preference for habitats with small interstitial spaces (Cunha et al., 2019) and juveniles from different species select macrophytes at different densities (Grenouillet et al., 2000). Thus, the presence of macrophyte stands with varying degrees of complexity may facilitate the coexistence of several fish species (e.g., Dibble & Pelicice, 2010), partially explaining the positive or unimodal relationships between macrophyte complexity and fish diversity (see "Relationship between macrophyte complexity and fish diversity").

Macrophyte complexity and refugia against predation

The significance of habitat complexity provided by macrophytes as refuges against predation has been underscored by experiments and observational

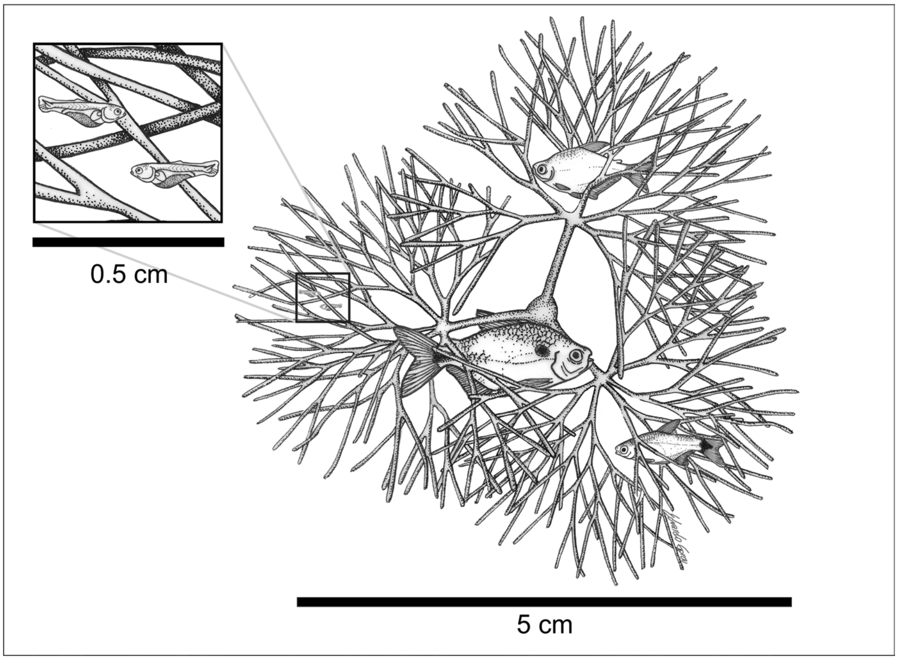

Fig. 4 The 'fractal-like' structure is created within the interstices of macrophytes, demonstrating how fish of different sizes (ranging from c. 0.2 cm in the smaller figure to c. 1–3 cm in the larger figure) make use of these spaces. Figure inspired in Thomaz & Cunha (2010)

studies conducted in areas where open water and macrophytes coexist. Prey fish are able to recognize and select between habitats differing in refuge value (Chick & McIvor, 1997). Generally, these studies reveal that small-sized fish and juveniles of large fish exhibit a preference for macrophyte zones (Chick & McIvor, 1997; Meerhoff et al., 2003; Agostinho et al., 2007; Iglesias et al., 2007; Teixeira de Mello et al., 2016), particularly during the day and in the presence of predators (Jacobsen & Berg, 1998; Figueiredo et al., 2015; Henseler et al., 2020). One of the primary explanations for this behavior relies on the refuges provided by macrophytes against predation. For small-sized fishes, some studies suggest that physical structure is a more important factor than macrophytes species, since species with similar morphology and architecture (like natives and non-natives ones) may act in the same way for refuge (Cunha et al., 2011; Figueiredo et al., 2015). Thus, the search for refuges does not depend on whether the macrophyte is native or a recent invader, indicating that the refuges themselves are more critical than the evolutionary history shared between the fish and the macrophyte (Figueiredo et al., 2015).

In the field, the role of macrophytes as refuges explains, for example, diel horizontal migrations of certain fish species that inhabit macrophyte stands during the day to conceal themselves from predators (Christensen & Moore, 2008). Even amphibious macrophytes (those predominantly growing in saturated soils in the littoral regions above the water line) may function as temporary refuges for small-sized fish in floodplain lakes during high-water periods when these plants remain submerged (Quirino et al., 2019a).

The refugia hypothesis suggested by field data is supported by experiments demonstrating the effectiveness of macrophytes in reducing the predation risk of fish within macrophyte patches compared to unvegetated controls (Savino & Stein, 1982; Rozas & Odum, 1988; Werner & Hall, 1988; Jacobsen & Berg, 1998; Stuart-Smith et al., 2007; Santos et al., 2011; Camp et al., 2012; Hanisch et al., 2012). However, the efficiency of refugia depends on the fish prey species (Eklöv & Hamrin, 1989) and on interacting factors, such as macrophyte density and turbidity (Snickars et al., 2004; Teixeira de Mello et al., 2016).

Despite the significant role of macrophytes as refuges highlighted by previous investigations, the effectiveness of macrophytes as hiding sites varies. There are instances showing that macrophytes offer limited protection for native fish against predation by invasive fish (Kovalenko et al., 2010b), especially when macrophytes have an open structure with large interstitial spaces (e.g., *Vallisneria americana*; Camp et al., 2012). However, predatory activity in these sites may sometimes decrease when dissolved oxygen levels are reduced (Yamanaka et al., 2007). Additionally, there are predator fish with ambush behavior that benefit from macrophytes to feed on small fish (Savino & Stein, 1989; Petry et al., 2010). Lastly, although not common, there are predators (e.g., *Salminus brasiliensis* (Cuvier, 1816)) with a greater ability to capture prey in macrophyte stands, which does not diminish predation risk (Santos et al., 2013).

Macrophyte complexity and fish reproduction

In addition to providing refuge for small-bodied fish, the structured and more complex habitat provided by macrophytes influence fish reproduction. Macrophytes serve as a spawning substrate (Farrell et al., 1996; Farrell, 2001), act as nursery habitats (Bryan & Scarnecchia, 1992; Brent & Farrell, 2006; Bulla et al., 2011; Iquematsu et al., 2023; Kimura et al., 2024), and offer suitable sites for the survival of larvae and juveniles by providing food availability and refuge against predation (Bryan & Scarnecchia, 1992). Larvae and juveniles of both small-sized resident fish and large migratory species can be found within macrophyte stands (Delariva et al., 1994; Nakatani et al., 1997; Daga et al., 2009; Iquematsu et al., 2023; Kimura et al., 2024). Certain fish species, typically small and sedentary, such as those belonging to the Characidae, Cichlidae, Gymnotidae, Sternopygidae, and Percidae families, utilize patches of dense macrophytes as habitats throughout their life cycles (Winemiller & Jepsen, 1998; Bulla et al., 2011). These fish rely on these plants to fulfill the majority of their requirements, including reproduction (Daga et al., 2009; Iquematsu et al., 2023). However, the utilization of macrophytes as reproduction sites is not exclusive to these particular species. Many medium- and large-sized species employing various reproductive strategies also utilize macrophyte stands during the reproduction period, and these habitats are important in the early stages of fish development (Kimura et al., 2021, 2024; Iquematsu et al., 2023), serving as critical habitats during nursery periods (Bryan & Scarnecchia, 1992; Baumgartner et al., 2004; Daga et al., 2009). Consequently, macrophytes exert a significant influence on the success of fish recruitment (Copp, 1997; Brent & Farrell, 2007).

Numerous fish species directly utilize macrophytes as a spawning substrate (Dibble et al., 1996; Petr, 2000; Crampton & Hopkins, 2005). This reproductive strategy has been observed in piranha species of the genus *Serrasalmus*, which construct nests in the roots of macrophytes for egg deposition. The larvae and early developmental stages of these species are closely associated with these plants (Honorato-Sampaio et al., 2009; Bulla et al., 2011). In the Itaipu Reservoir (Brazil), for example, it was observed that *Serrasalmus marginatus* Valenciennes, 1837 not only utilizes macrophytes for egg laying but also shelters with its young in stands of submerged macrophytes, displaying high aggressiveness during this period (Agostinho, 2003). Males of *Gymnotus mamiraua* Albert & Crampton, 2001, a medium-sized electric neotropical fish (Gymnotiformes), exclusively construct nests in the roots of floating meadows, where females lay disks of eggs and males diligently guard the eggs and hatchling juveniles (Crampton & Hopkins, 2005). According to these authors, meadows provide a dense nesting substrate near the water surface, facilitating easy air breathing for adults and juveniles. Additionally, these microhabitats are rich in plankton and small invertebrates, serving as abundant food resources. A different strategy is employed by females of *Trachelyopterus galeatus* (Linnaeus, 1766), a medium-sized species with internal fertilization, which lay fertilized eggs in macrophyte roots (Bulla et al., 2011). Their early developmental stages also remain in these roots until later stages (Bulla et al., 2011).

In addition to small- and medium-sized species, many large and long-distance migratory species also incorporate macrophytes into their reproductive process, either as a substrate for egg deposition or as a refuge and food habitat during the initial stages of development. The Australian lungfish *Neoceratodus forsteri* (Krefft, 1870), an endangered species, exhibits a discerning choice of spawning habitat, favoring structurally complex macrophyte species, with *Vallisneria gigantea* Graebn., being the most used species (Kemp, 1995; Arthington, 2009; Espinoza et al., 2013; Marshall et al., 2015). In this habitat, the eggs, protected by a jelly coat, are attached to stems or leaves. Furthermore, for lungfish embryos and newly hatched lungfish, these dense macrophyte stands serve as suitable feeding habitats, where they feed on small invertebrates, such as microcrustaceans, mollusks, and worms (Arthington, 2009). Any reduction in macrophyte habitat at this stage may impact recruitment success (Arthington, 2009). Similarly, the northern pike *Esox lucius* Linnaeus, 1758 opts for habitats with denser vegetation cover (dominated by *Potamogeton*, *Lemna*, and *Chara*) for egg laying (Farrell et al., 1996). This choice is likely an adaptation to enhance egg survival, as dense vegetation can prevent non-adhesive eggs from coming into contact with sediments, thereby preventing transport by the current (Farrell et al., 1996).

Large neotropical long-distance migratory species, such as the dourado (*Salminus brasiliensis*), the curimba (*Prochilodus lineatus* Valenciennes, 1836), and the pintado (*Pseudoplatystoma corruscans* Spix & Agassiz, 1829), spawn in open areas of rivers. However, their larvae are passively transported by the current to floodplain lakes characterized by a significant presence of macrophytes, where they complete their development (Nakatani et al., 1997; Daga et al., 2009). The utilization of these lakes, highly colonized by macrophytes, as habitats for fish larvae suggests that these plants offer favorable conditions, including shelter from predators and a source of food, enabling the survival of larvae, and ensuring success in larval recruitment (Sousa et al., 2023).

Macrophyte complexity, fish foraging, and trophic relationships

Aquatic macrophytes are important for fish as mediators of food resources. The increase in food resources associated with macrophytes is primarily driven by the expanded surface area, allowing for the attachment of a greater number of organisms, including bacteria, microalgae, and micro- and macroinvertebrates. Additionally, the proliferation of structured habitats within macrophyte stands increases refugia, providing favorable sites for these organisms (Meerhoff et al., 2007a; Dibble & Thomaz, 2009; Dibble & Pelicice, 2010; Higuti et al., 2010; Higuti & Martens, 2016; Osório et al., 2019) that serve as food for fish. In this section, we emphasize the role of macrophytes as habitats for organisms utilized by fish as feeding resources. The findings presented in this section are primarily based on the analysis of fish stomach contents.

Fish and macrophytes are interconnected through trophic interactions involving associated algae and invertebrates (Schultz & Dibble, 2012). Macrophytes offer a diverse array of microhabitats, including leaves, stems, or submerged roots (Kovalenko et al., 2012; Tokeshi & Arakaki, 2012; Masclaux et al., 2014; Strzałek & Koperski, 2019; Kurbatova & Yershov, 2020), where organisms live, feed, or seek refuge. Various organisms attached to macrophytes serve as food resources for fish (Priyadarshana et al., 2001; Hargeby et al., 2005; Thomaz & Cunha, 2010; Quirino et al., 2021b). These organisms may rely on macrophytes as their source of carbon or not. Consequently, most fish inhabiting macrophyte stands explore the interstices of submerged roots, leaves, and stems in search of feeding resources (Priyadarshana et al., 2001; Casatti et al., 2003; Yofukuji et al., 2021).

Small algivorous fish benefit from filamentous periphytic algae associated with macrophytes, which thereby mediate algae consumption by certain fish species, such as *Serrapinnus notomelas*, *Roeboides dayi* (Steindachner, 1878), and *Hyphessobrycon eques* (Steindachner, 1882) (Prejs & Prejs, 1987; Pelicice & Agostinho, 2006; Quirino et al., 2019b). The importance of periphytic algae for some fish species has been confirmed with studies using stable isotopes (Mao et al., 2016). This is due to the high abundance of periphytic algae in macrophyte stands, as they adhere to the interstices of macrophytes, utilizing the structural complexity provided by these plants (Osório et al., 2019). In addition, the efficient use of epiphytic algae by fish is associated with the fact that they have a lower C:N ratio making them more palatable than macrophytes (Sheppard et al., 2012).

Aquatic macrophytes also influence the feeding behavior of planktivorous fish or those relying on microcrustaceans in their diet. This is because numerous microcrustaceans utilize macrophytes for several purposes (Higuti et al., 2010; Strzałek & Koperski, 2019), including refuge and feeding, either through the periphyton adhered to their structures (Masclaux et al., 2012, 2014) or through bacteria and protozoa that are triggered by the release of organic substances (Kurbatova & Yershov, 2020; Matsuda et al., 2015). Thus, macrophyte stands are recognized to mediate predator–prey relationships for planktivorous fish, as the physical structure provided by them and the prey characteristics (such as escape ability and energy value) are decisive for the foraging success of these fish (Quirino et al., 2021b).

Macrophytes also provide habitat for various groups of macroinvertebrates that are consumed by fish, including spiders, decapods, annelids, ostracods, and insects in different life stages, all of which utilize these plants for various purposes (Warfe & Barmuta, 2006; Kovalenko et al., 2012; Matsuda et al., 2015). Among these invertebrates are herbivores and detritivores that feed on organisms attached to macrophytes, such as periphytic algae (Hargeby et al., 2005; Warfe & Barmuta, 2006; Osório et al., 2019), bacteria, protozoa (Kurbatova & Yershov, 2020), and detritus (Warfe et al., 2008; Kurbatova & Yershov, 2020). Consequently, macrophytes serve as mediators of food resources for invertivorous fish that forage within their interstices to feed on associated invertebrates (e.g., Priyadarshana et al., 2001; Santos et al., 2020; Yofukuji et al., 2021).

Several studies have demonstrated that fish trophic interactions, including competition and predation, can be influenced by aquatic macrophytes (Crowder & Cooper, 1982; Meerhoff et al., 2007b; Vejříková et al., 2017; Dias et al., 2022). In addition to the mere presence of macrophytes, which enhances food availability compared to open waters, fish feeding behavior can be influenced by other factors, including patch configuration (e.g., plant identity/architecture, patch diversity, and abundance), prey's ability to escape predation, and predator foraging ability. In a study by Aleixo et al. (2022) on competition among congeneric neotropical fish in different macrophyte stands, it was observed that *Moenkhausia forestii* Benine, Mariguela & Oliveira, 2009 shifted its feeding behavior from predominantly invertivorous to mostly herbivorous, depending on the resources available in the macrophyte stands. These changes, mediated by macrophytes, were interpreted as a means to avoid competitive exclusion of *M. forestii* in the presence of its congeneric *Moenkhausia bonita* Benine, Castro & Sabino, 2004. Dorenbosch & Bakker (2012) investigated the role of macrophytes as a supplementary source of animal-derived resources, even for fish in temperate regions traditionally considered strictly herbivorous, such as the rudd (*Scardinius erythrophthalmus* (Linnaeus, 1758)). The authors observed that despite its predominantly plant-based diet, the rudd supplemented its diet with animal-derived resources, indicating that macrophytes may alter fish feeding behavior.

Differences in architecture among macrophyte species, stemming from variations in leaf and stem morphologies and configurations, determine resource availability for fish (e.g., macroinvertebrates; Bogut et al., 2007; Matsuda et al., 2015). Dibble & Harrel (1997) observed that largemouth bass varied their diet between two macrophyte species with different architectures, consuming predominantly macroinvertebrates in common pondweed (*Potamogeton nodosus* Poiret) and fish prey in Eurasian watermilfoil (*Myriophyllum spicatum* L). In a tropical floodplain, *Serrapinnus notomelas* primarily consumed algae when associated with *Eichhornia azurea* and Cladocera in *Polygonum punctatum* Elliott (Quirino et al., 2019b). In fact, each macrophyte species may host a unique prey assemblage, leading to significant differences in fish diet (Carniatto et al., 2020). In this context, low macrophyte diversity implies a poor habitat for invertebrates, consequently reducing the availability of these prey (Wilcox & Meeker, 1992). For example, Yofukuji et al. (2021) found that the consumption of invertebrates increases with increasing macrophyte diversity, because it supports a variety of architectures, growth forms, and physiologies, thereby enhancing the availability of resources.

The structural complexity of the macrophyte patch, including plant architecture, size, shape, and density, influences the feeding behavior of fish by affecting prey vulnerabilities as well (Diehl, 1988; Jeppesen et al., 1998; Sagrario et al., 2009; Figueiredo et al., 2013). Despite the positive contribution of macrophytes to prey density, laboratory experiments simulating different macrophyte densities have shown that fish exhibit low foraging success in highly vegetated areas (Manatunge et al., 2000; Priyadarshana et al., 2001; Padial et al., 2009a, b). Similarly, lower feeding efficiency has been observed in heavily vegetated areas compared to less vegetated ones in nature (Xie et al., 2005; Sammons & Maceina, 2006; Kovalenko

& Dibble, 2014; Liversage et al., 2017). In terms of diet composition, increasing macrophyte density can lead fish to consume more plants and less invertebrates (Aleixo et al., 2022). These results are expected because highly dense vegetation reduces the predator–prey encounter rate, as submerged stems, foliage, and roots act as physical barriers that restrict the swimming activity of both fish and prey (Priyadarshana et al., 2001). Moreover, increasing vegetation density decreases visual contact between predator and prey, prolonging the search time (Savino & Stein, 1982; Sammons & Maceina, 2006).

In contrast, areas with low structural complexity do not impede fish movements, but prey is scarce in these habitats lacking in structure (e.g., Dibble & Thomaz, 2009). Hence, some authors suggest that moderate levels of macrophyte density can provide an appropriate habitat for prey, thereby enhancing prey production while still enabling fish predation, without hindering fish swimming and visibility (Crowder & Cooper, 1982; Miranda & Pugh, 1997). In support of this notion, Crowder & Cooper (1982) demonstrated in experimental ponds that bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819) consumed more prey at intermediate macrophyte densities compared to those at either low or high densities. In the same sense, intermediate levels of plant density may foster greater trophic niche overlap among fish species compared to low and high plant densities, which does not imply intense competition, as the prey are supposed to be abundant and easily accessible at intermediate plant densities (Quirino et al., 2022). However, certain studies have indicated no significant influence of macrophyte density on fish diet composition (Pelicice & Agostinho, 2006) or overlap (Aleixo et al., 2022).

It is important to highlight that fish often exhibit prey preferences based on prey vulnerabilities or detectability (Massa & Farrell, 2019). Macrophyte patches of greater complexity, such as those with finely dissected leaves, may offer better protection for small organisms compared to larger ones (Meerhoff et al., 2007b; Iglesias et al., 2007; Strzałek & Koperski, 2019). In line with this, an observational study revealed that a planktivorous fish primarily consumed small microcrustacean species in areas with low macrophyte biomass, while replacing them with larger species in areas with intermediate and high plant biomass (Quirino et al., 2021b). Hence, the interaction between fish and their prey mediated by macrophytes also relies on prey characteristics, such as size and escape ability.

Of particular significance is the capacity of fish to forage effectively in structured habitats (Jacobsen & Perrow, 1998; Priyadarshana et al., 2001). Each fish species possesses a unique set of traits, including body morphology, sensory capabilities, maneuvering skills, and behavior, all of which influence their utilization of dense vegetation and feeding efficacy (Winfield, 1986; Manatunge et al., 2000; Lopes et al., 2015; Quirino et al., 2021a). For instance, juvenile perch, known for being proficient visual predators of benthic invertebrates, can successfully feed even in densely vegetated areas, whereas roach demonstrates superior foraging efficiency in sparsely vegetated environments (Diehl, 1988; Persson & Eklov, 1995). Hence, the trophic interactions among fish mediated by macrophytes are not solely determined by the presence of macrophytes but rather depend on a combination of prey and predator characteristics.

The significance of macrophytes as foraging sites extends beyond individual adult fish. To ensure survival, fish larvae must locate food resources during the critical transition period from endogenous to exogenous feeding (Shepherd & Cushing, 1980), and several studies indicate that vegetated areas offer superior feeding grounds for juvenile fish compared to non-vegetated areas (e.g., Okun & Mehner, 2005; Zingel et al., 2019). Indeed, macrophyte stands can be vital for the survival of various life stages of fish; certain fish species forage among macrophytes throughout their lives, indicating that even with ontogenetic changes in their diet, they rely on resources provided by macrophytes (Abilhoa et al., 2009; Nicolle et al., 2010; Fragoso-Moura et al., 2017). However, there are instances where macrophytes play a key role primarily or exclusively in the diet of fish larvae (Santin et al., 2015; Pyrzanowski et al., 2021).

There are numerous instances demonstrating that changes in fish feeding behavior during ontogeny can be influenced by macrophytes throughout their lives. For example, in a study involving the characin *Hollandichthys multifasciatus* (Eigenmann & Norris, 1900), a species that forages among macrophytes throughout its life, Abilhoa et al. (2009) observed that the fish primarily consume oligochaetes, aquatic insects (both immature and adults), and decapods during the early stages, while shifting to terrestrial insects, spiders, and plants during later phases.

Another example of fish thriving on macrophyte stands is the roach (*Rutilus rutilus* (Linnaeus, 1758)), which demonstrates a tendency to adjust its primary dietary components across different life stages. Nicolle et al. (2010) noted that roach, living in stands of *Chara* (a macroalgae), feed on smaller microcrustaceans during the larval stage and on larger microcrustaceans as adults, utilizing macrophyte stands throughout all life stages. Additionally, Fragoso-Moura et al. (2017) investigated ontogenetic variations in the diet of *Hemigrammus marginatus*, in a floodplain and observed that the diet of young individuals mainly consists of zooplankton, while the importance of insects in their diet increases as they mature. The authors concluded that the diverse food resources provided by aquatic macrophytes throughout the lifetime of *H. marginatus* help explain the species high abundance in this habitat.

Macrophytes may also play a central role in fish diet only during the initial development stages. In a study conducted in a Polish canal, Pyrzanowski et al. (2021) observed that larvae of the weatherfish, *Misgurnus fossilis* (Linnaeus, 1758), predominantly consumed food resources associated with macrophyte stands, such as Copepoda and Cladocera. However, while adults continued to ingest these resources, albeit in smaller quantities, they predominantly relied on detritus as their primary source of nutrition (Pyrzanowski et al., 2021). Another example is the peacock bass (*Cichla kelberi* Kullander & Ferreira, 2006), which heavily relies on macrophyte stands as a primary feeding site during its juvenile phase (Quirino et al., 2019b). However, upon reaching the adult phase, the peacock bass can grow to sizes exceeding 40 cm and undergoes a dietary shift toward piscivory, foraging primarily outside macrophyte stands (Pereira et al., 2017; Mendonça et al., 2018). In the case of *Trachelyopterus galeatus* (Linnaeus, 1766), the larvae feed primarily on microcrustaceans and aquatic insects, indicating their reliance on resources within aquatic vegetation (Santin et al., 2015). In contrast, adults exhibit a more diverse diet, including invertebrates, fruits, seeds, fish, and detritus (Bianchi-Costa, 2023), which are not directly associated with macrophyte stands.

Relationship between macrophyte complexity and fish diversity

Habitat complexity is currently recognized as a universal driver of animal diversity, as proposed by the biodiversity-habitat complexity hypothesis (Stein et al., 2014; Ortega et al., 2018). The importance of habitat complexity in explaining fish diversity is linked to previously discussed factors, including reduced fish predation, the facilitation of coexistence among different fish species, and increased opportunities for feeding and reproduction in the more structured habitats created by macrophytes (Fig. 5). In line with this hypothesis, macrophytes have been considered a key determinant of fish diversity. There is ample evidence demonstrating that fish diversity or richness (referred to as ‘diversity’) is higher in littoral regions compared to limnetic regions (Dibble et al.,

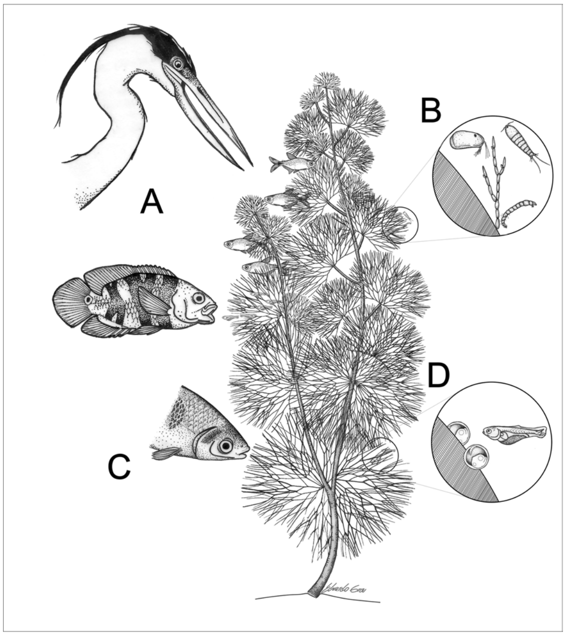

Fig. 5 Key factors enhancing fish diversity in macrophyte patches compared to open water. **A** – Refuge for larvae and small fish: Macrophyte patches provide a safe habitat for vulnerable larvae and small fish, shielding them from predators like birds and predatory fish. **B** – Feeding resources: Macrophytes offer abundant feeding resources, including periphyton, attached and free-living invertebrates, which support fish nutrition. **C** – Direct food for herbivorous fish: Herbivorous fish benefit directly from macrophytes tissues. **D** – Spawning sites: Macrophyte patches create favorable environments for fish spawning, ensuring successful reproduction

1996; Petr, 2000; Weaver et al., 1997; Petry et al., 2003; Agostinho et al., 2007; Meerhoff et al., 2003, 2007b; Gomes et al., 2012; Chaparro et al., 2015; Leela et al., 2022). In this context, fish diversity tends to decrease after the removal of macrophytes (Agostinho et al., 2003). This pattern also holds for fish larvae and juveniles, with their diversity being higher in the littoral compared to the limnetic region (Iquematsu et al., 2023).

The aforementioned comparisons are drawn from extreme conditions, contrasting the presence and absence of macrophytes (i.e., littoral *versus* pelagic regions). However, fish diversity may be greater in stands of more complex species of macrophytes compared to less complex ones (Troutman et al., 2007; Dibble & Pelicice 2010). Thus, another approach to explore the diversity-habitat complexity hypothesis is to examine fish diversity responses along the gradient of habitat complexity provided by macrophytes. This method involves measuring fish diversity in response to varying degrees of complexity, which can be assessed through parameters, such as plant biomass, plant abundance, the percentage of lake volume infested with macrophytes (PVI), or plant diversity. Using this approach, the literature documents four types of curves depicting the relationship between macrophyte complexity and fish diversity: positive, negative, neutral, or unimodal relationships.

Numerous studies have identified positive correlations between macrophyte complexity and fish diversity. This correlation pattern has been observed in both tropical and temperate regions, spanning various ecosystems, including temperate lakes (Randal et al., 1996; Tugend & Allen, 2004; Xingwei et al., 2019), floodplain lakes (Petry et al., 2003; Ye et al., 2006; Giacomazzo et al., 2023), beaver ponds (Ray et al., 2004), streams (Johnson & Hering, 2010; Dala-Corte et al., 2016), and reservoirs (Pelicice et al., 2008, 2015; do Nascimento et al., 2022). These instances strongly indicate that the mechanisms facilitated by macrophyte complexity, which positively influence fish (such as providing refuges for fish of different body sizes, feeding, and reproduction sites) and the attraction of fish from different guilds, are generally more influential than those exerting negative effects on fish (e.g., low DO and high CO_2 concentrations, challenges for swimming, and reduced feeding activity).

Among the four responses of fish diversity to macrophyte complexity (positive, negative, neutral, or unimodal relationships), the unimodal relationship is considered the most intriguing from a theoretical standpoint. The theoretical expectation of this relationship hinges on the balance between mechanisms that facilitate fish colonization and persistence within macrophyte patches (e.g., connectivity, refugia, and feeding resources) and mechanisms that difficult them (e.g., isolation, space limitations, poor environmental conditions, competition, and predation) (Cunha et al., 2019; see also the previous sections). Therefore, intermediate levels of macrophyte complexity could offer suitable habitat conditions while avoiding limiting abiotic and biotic factors. Although less common than positive relationships, some studies indeed confirm the existence of a unimodal curve between macrophyte complexity and fish diversity in nature (Dibble et al., 1996; Grenouillet et al., 2002; Cunha et al., 2019; Pander et al., 2021; Quirino et al., 2021a).

In addition to positive and unimodal correlations, a few studies have also identified negative relationships (Súarez et al., 2004; Reid et al., 2013; Brysiewicz et al., 2020) and neutral correlations (Slade et al., 2005; Tolonen et al., 2005; Sánchez-Botero et al., 2008; Kruk et al., 2009; Hilling et al., 2021) between habitat complexity provided by macrophytes and fish diversity. The negative impact of macrophytes on fish diversity is sometimes observed in instances of extremely high plant biomass, especially when alien/invasive macrophytes thrive (e.g., Perna et al., 2012; Carniatto et al., 2013). In these examples, the adverse effects associated with habitat complexity outweigh the positive ones (see the previous sections and Cunha et al., 2019).

It is important to note that negative or neutral correlations do not imply that macrophytes are insignificant determinants of fish assemblage attributes. For instance, Weaver et al. (1997) examined vegetated sites and discovered that six out of eight fish species had no significant correlations with macrophyte complexity. However, when they compared vegetated sites with unvegetated ones, they found fewer fishes in the latter. Therefore, despite neutral correlations with complexity, fish were concentrated within the littoral zones, underscoring the significance of macrophytes for fish communities in this lake.

Despite the numerous studies demonstrating positive correlations between macrophyte complexity and fish diversity, we acknowledge the potential underestimation of unimodal and negative correlations in this relationship. This potential bias may arise due to the challenges associated with sampling fish in extremely complex habitats, characterized by high plant abundance and biomass (Dibble et al., 1996; Hagerthey et al., 2014), where habitat characteristics can adversely affect fish survival. In such cases, it is possible that only the positive side of the complexity–diversity gradient is captured, leading to an increased number of observed positive relationships.

To illustrate this potential bias, we present two studies conducted in the Rosana Reservoir (Brazil). A positive relationship between macrophyte biomass and fish diversity was found in submerged macrophyte stands dominated by *Egeria najas*, where plant biomass varied from 2 to 569 g DW m^{-2} (Pelicice et al., 2008; biomass values estimated by dividing plant biomass by mean depth). Conversely, in the same reservoir, a negative relationship was observed within emergent macrophyte stands dominated by *Urochloa arrecta*, where biomass varied from 492 to 6866 g DW m^{-2} (Carniatto et al., 2013). At the extremely high values of biomass in the latter macrophyte, fish and native macrophytes were absent. The community of small-bodied fish in both studies was similar, given that the same reservoir was investigated. Thus, the contrasting responses of fish diversity to complexity can be explained by the fact that the gradient of complexity found in *E. najas* does not reach the extreme values observed in *U. arrecta*.

In addition to difficulties of sampling associated with high plant biomasses, selection biases (i.e., results that arise when the sample is not representative of the population being studied) may also interfere in the findings about the relationships between macrophyte complexity and fish diversity. For example, some investigations use fish traps that are designed to catch only small-sized fish (e.g., Dibble & Pelicice, 2010; Carniatto et al., 2013; Cunha et al., 2019), neglecting larger individuals. Studies on larvae associated with macrophytes are also rare (e.g., Iquematsu et al., 2023), making the diversity of fish belonging to this life stage much less investigated. In view of these biases, some studies reviewed might have been influenced by the way sampling strategies were selected, causing the results to not accurately reflect the true situation.

While most investigations on the relationship between macrophyte complexity and fish diversity have focused on alpha taxonomic diversity, a few studies have explored other components of diversity. For instance, Cunha et al. (2019) found that a combination of macrophyte complexity and DO influences fish beta diversity in macrophyte stands, indicating species turnover along the complexity gradient. Examining functional fish richness, Quirino et al. (2021a) demonstrated that this diversity component peaked at intermediate macrophyte density and high macrophyte diversity, while functional beta diversity responded primarily to variations in macrophyte density. In contrast, a study conducted in a neotropical reservoir revealed that fish functional richness increased with macrophyte complexity, but the opposite trend was observed for functional evenness and divergence (do Nascimento et al., 2022). These findings underscore that the complexity provided by macrophytes acts as environmental filters that select fish traits, and the responses are contingent on the type of complexity measurement (macrophyte density versus macrophyte diversity).

Finally, based on the examples above, one can predict that changes simplifying macrophyte assemblages by promoting the dominance of a few species may compromise fish diversity. This occurs because the dominance of one or a few species negatively affects at least three aspects of habitat complexity: the diversity of complexity-generating elements, the spatial arrangement of elements, and element sizes (Tokeshi & Arakaki, 2012). Such changes may arise, for instance, in response to eutrophication, global warming, and invasive species. Eutrophication and global warming, for example, encourage the growth of free-floating species like *Eichhornia crassipes* (Coetzee & Hill, 2012; Kariyawasam et al., 2021). Negative effects of this and other free-floating species are enhanced by reduced DO in water, causing fish kills where they form dense mats (Petr, 2000 and references therein). Invasive macrophytes also tend to form dense, monotypic stands (Petr, 2000; Schultz & Dibble, 2012), with potential negative consequences on fish diversity. However, the influence of invasive macrophytes on fish diversity remains unclear. A meta-analysis showed no significant effect of invasive macrophytes on fish diversity (Gallardo et al., 2016). However, at extremely high levels of invasive macrophyte biomass or cover—an area less studied due to the challenges of fish sampling—fish diversity decreases (Perna et al., 2012; Basaula et al., 2023) or fish communities are virtually absent (Carniatto et al., 2013). Regardless of their impact on fish diversity, dense stands of invasive macrophytes alter fish community composition (Schultz & Dibble, 2012) and reduce fish abundance (Gallardo et al., 2016).

In summary, the abundance of studies indicating that fish diversity is higher in littoral than in limnetic regions, coupled with the prevalent positive and unimodal relationships between macrophyte complexity and fish diversity (when macrophyte complexity gradient is investigated), underscores the critical role of these plants in sustaining fish diversity. Consequently, the protection and promotion of littoral zones, or their recovery in ecosystems where they are degraded, are acknowledged as important strategies for improving and preserving fish biodiversity across diverse freshwater ecosystems (e.g., Kovalenko et al., 2010a).

Macrophytes as a direct and indirect source of carbon for fish

Macrophyte as a direct carbon source: herbivory

Understanding plant–herbivore interactions has long been a central focus of terrestrial ecologists, with herbivory on vascular aquatic macrophytes historically considered of minimal importance until the 1990s (Wook et al., 2017). However, this perspective has since undergone a paradigm shift, as more recent investigations indicate that levels of herbivory in freshwater ecosystems either match or surpass those observed in terrestrial and marine ecosystems (Wood et al., 2017; Vejříková et al., 2018) (see Fig. 6A). Among the organisms that rely on macrophytes as a primary food source, large aquatic animals such as fish can significantly impact macrophyte biomass through direct consumption (Nurminem et al., 2003; Kapuscinski et al., 2014; Wolters et al., 2018). Moreover, direct consumption by herbivores can shape macrophyte communities by altering their biodiversity

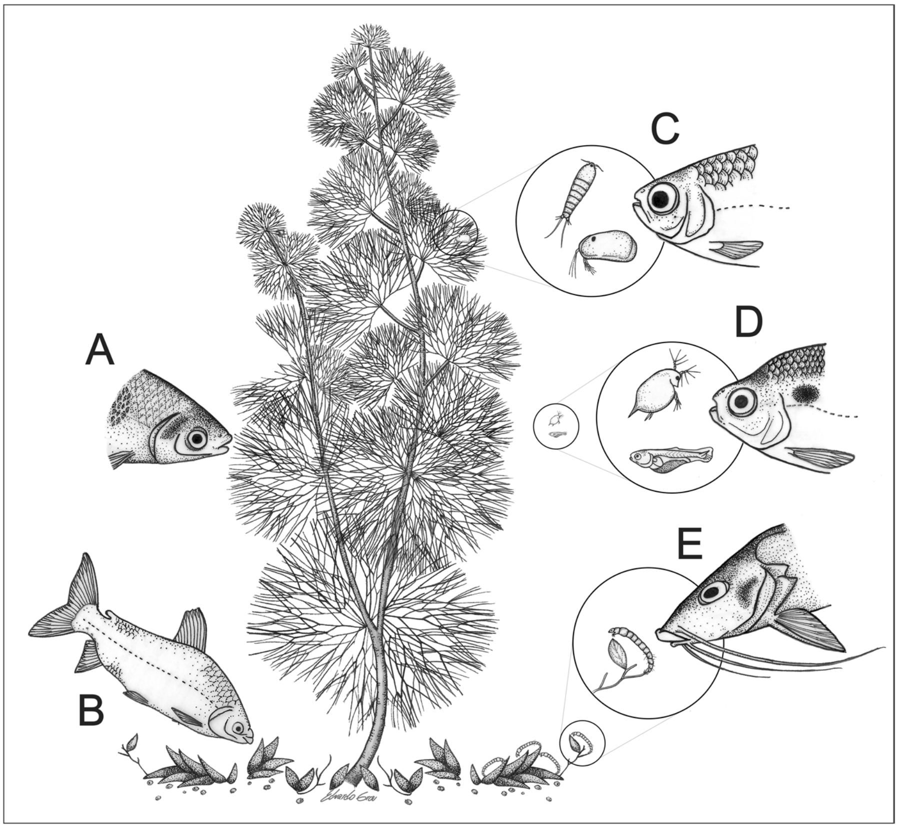

Fig. 6 Main direct (left) and indirect (right) carbon pathways from macrophytes to fish. **A** – Direct utilization of plant tissues through herbivory. **B** – Direct utilization of macrophyte detritus. **C** – Utilization of attached invertebrates that use directly or indirectly macrophytes as their food source. **D** – Utilization of free-living organisms in the pelagic region that feed directly or indirectly on macrophytes. **E** – Utilization of detritivorous organisms (invertebrates and fish) that feed directly on detritus and bacteria attached to detritus

through changes in species composition and can even trigger ecosystem shifts from clear-water to turbid-water phytoplankton-dominant states (Schallenberg & Sorrell, 2009; Kapuscinski et al., 2015). Recognizing herbivory as a potent ecological force in freshwater ecosystems underscores the importance of gaining a deeper understanding of plant–herbivore dynamics.

Despite the abundance of macrophytes and microalgae in many freshwater bodies, only a limited number of fish species are strictly herbivorous, with most aquatic plant-consuming animals being omnivores (Petr, 2000; Yu et al., 2016; Bakker et al., 2016; Wootton et al., 2017). While herbivory is often considered nutritionally inferior compared to diets containing animal prey, some hypotheses suggest potential advantages to consuming plants over animal prey (Sanchez & Trexler, 2016). For instance, the intake-efficient hypothesis proposes that aquatic herbivores can utilize macrophytes not only as a food source but also as habitat or refuge (Sih & Christensen, 2001; Horppila & Nurminen, 2009). Consequently, in environments with ample macrophyte availability, fish may engage in continuous grazing, reducing the need to expend energy on handling mobile prey or competing for resources (Horppila & Nurminen, 2009; Quirino et al., 2022).

The dietary preferences of herbivores have been associated to various characteristics of macrophytes, including nutritional quality, morphology, physical structures, and chemical defenses. Generally, aquatic herbivores are believed to preferentially select plants with the highest nutritional quality, based on the stoichiometry of their food source (i.e., carbon:nitrogen ratios – C:N) and their own body composition. Typically, the diet of herbivorous fish exhibits C:N that are 5–75 times higher than their requirements for growth (McIntyre & Flecker, 2010). To address this stoichiometry mismatch, fish appear to favor macrophytes with low C:N ratios, as demonstrated by Dorenbosch et al. (2011) through feeding trials involving both rudd and grass carp. Fish that are strictly herbivorous or primarily rely on plant material may face challenges with poor diet quality, prompting them to increase their consumption of macrophytes to meet energetic demands and acquire sufficient nutrients (Zhang et al., 2018).

Another factor influencing the feeding preferences of herbivorous fish is the presence of defenses in plants. Despite their high nutritional value, some plants can possess significant defensive mechanisms. Plant defenses against herbivores typically manifest as physical structures (e.g., spines, trichomes, tough leaves, rigidity) or chemical compounds (e.g., secondary metabolites, hormonal responses, phenolic compounds) (Miller & Provenza, 2007; Kapuscinski et al., 2014; Fares et al., 2022). Observations and experiments have shown that chemical defenses can indeed affect herbivory rates on macrophytes (Nurminem et al., 2003; Kapuscinski et al., 2014). Feeding trials involving rudd and grass carp have revealed that these species tend to avoid consuming macrophytes that produce toxic chemical compounds, as these compounds can cause histological lesions in the digestive tract (Murphy et al., 2002). Conversely, more palatable macrophytes are readily consumed (Sun et al., 2017). Furthermore, variations in chemical defenses appear to be associated with the life forms of macrophytes, with submerged species exhibiting lower levels of phenolic compounds compared to emergent or floating species (Smolders et al., 2000). Submerged macrophytes may experience lower exposure to a diverse range of herbivores (both terrestrial and aquatic) and pathogens, as well as different light availabilities, which could result in reduced chemical defenses and consequently affect herbivory rates (Smolders et al., 2000; Bakker et al., 2016). Emergent species typically possess tougher characteristics, such as thicker cell walls and cuticles, which serve to limit evapotranspiration and may reduce their palatability to herbivores (Gross & Bakker, 2012; Vermeij, 2016).

The consumption of macrophytes is also influenced by the origin of the fish. For instance, generalist and invasive herbivore species often exhibit a higher consumption rate of native macrophytes compared to non-native ones, with the selection mechanisms possibly tied to factors, such as plant structure, nutritional composition, and the presence of defenses (Miller & Provenza, 2007; Kapuscinski et al., 2015). Even when invasive herbivores possess a broad diet range, they frequently avoid consuming unpalatable macrophytes, particularly those containing allelopathic chemicals (Kapuscinski et al., 2012; Larkin et al., 2020), which may represent a functional trait commonly found in invasive macrophyte species (Schultz & Dibble, 2012; Bora & Padial, 2023). In such cases, native macrophytes may lack suitable defenses against new herbivores, as plant defenses are often tailored to specific herbivores and their effectiveness may rely on the fish's ability to handle food and resist allelopathic substances (Miller & Provenza, 2007). The replacement of native herbivorous fish species with non-native ones can have significant repercussions on macrophyte assemblages, potentially promoting the establishment and dominance of non-native macrophytes (Kapuscinski et al., 2015). Introduced fish species, such as common carp and rudd, for instance, may pose a threat to habitat restoration projects by disproportionately preying on native species (Kapuscinski et al., 2012).

Stable isotope techniques have confirmed that herbivorous fish effectively assimilate carbon from macrophytes. For instance, studies have demonstrated significant contributions of macrophyte carbon to the diet of herbivorous species, such as African tilapiine cichlids (Zengeya et al., 2011; Peel et al., 2019) and the South American *Schizodon fasciatus* Spix & Agassiz, 1829, which assimilated 47.8–65.9% of their carbon from C_4 macrophyte grasses (Forsberg et al., 1993; Oliveira et al., 2006). Similarly, in Venezuelan rivers, carbon from C_4 macrophytes played an important role for four herbivorous species, with assimilation rates ranging between 38.7% and 100% of their carbon demands (Jepsen & Winemiller, 2007). In a lake in China, herbivorous fish obtained 60.4% of their carbon from *Potamogeton maackianus* A. Benn. and *Hydrilla verticillata*. Additionally, carbon isotope analyses have confirmed the assimilation of carbon from both C_4 grasses and C_3 macrophytes by the frugivorous and seed-eating species *Colossoma macropomum* (Cuvier, 1816) in the Amazon (Benedito-Cecilio et al., 2000).

Macrophyte as a direct carbon source: detritivory

The stomach content analyses indicate that there are numerous species of detritivorous fish in freshwater ecosystems. In floodplains, for example, they represent the predominant portion of the overall abundance and biomass within fish communities (Agostinho et al., 2001; Rabuffetti et al., 2017). However, it is difficult to characterize the origin of detritus, which is composed of amorphous materials that include macrophyte debris, algae, bacteria, and other materials (Araújo Lima et al., 1986, Fugi et al., 1996). Therefore, the components of detritus found in the stomach of fish remain mostly unidentifiable (Forsberg et al., 1993; Fugi et al., 1996). In addition, it is challenging to know which of these different materials in detritus are assimilated by fish.

Previous investigations have indicated that macrophytes play an important role as a carbon source for detritivorous organisms (Fig. 6B). Some studies of the early 1960s suggested the prevalence of the detritus food chain over the grazing food chain in saltmarshes dominated by the aquatic grass *Spartina alterniflora* (Trin.) Kunth. In this context, the detritus produced by this macrophyte was identified as the primary link connecting primary production to consumers (Teal, 1962; Darnell, 1961, 1964; Odum & de la Cruz, 1967). Coupled with attached bacteria, detritus was considered a superior food source for animals, and the utilization of detritus by consumers was linked to its increasing nutritive value during decomposition (Teal, 1962; Odum & de la Cruz, 1967). Studies conducted in floodplains, characterized by high macrophyte productivity, similarly suggested that plant detritus supported diverse consumers, including fish (e.g., Junk & Howard-Willians, 1984; Soares et al., 1986). However, emerging evidence suggests that while macrophyte carbon is vital for detritivorous fish in certain ecosystems, its role may be smaller than initially presumed in others.

One of the first investigations that challenged the importance of macrophyte detritus as a source of carbon to detritivorous fish was conducted in the Amazon (Araújo-Lima et al., 1986). The authors showed that C_4 macrophytes, despite their dominance in primary production (Junk, 1985; Junk et al., 1989), contribute less than 5% of the carbon source for five species of detritivorous fish. Investigations conducted in a variety of ecosystems where macrophytes are important primary producers also found similar results, evidencing the superiority of algae-derived carbon over macrophytes to detritivorous fish (e.g., Forsberg et al., 1993; Hamilton et al., 1992; Lewis et al., 2000; 2001; Jepsen & Winemiller, 2007).

One of the reasons for algae superiority relies on the fact that algal cells have much smaller proportions of structural carbohydrates (cell wall components) than vascular plants (Lewis et al., 2000). Vascular plant material has low N and P concentrations and consists mainly of structural polysaccharides or other structural polymers (e.g., lignin) which are rarely hydrolyzed by animals (Fenchel & Jørgensen, 1977). Algae also is easier to assimilate, has more energy per unit mass (Thorp & Delong, 2002), have higher protein concentrations, and lower C:N ratios than macrophytes (Forsberg et al., 1993; Sheppard et al., 2012). Despite the unclear mechanisms explaining how the relatively high biomass of detritivorous fish relies on the small primary productivity of phytoplankton, selective ingestion, or selective digestion and assimilation of microalgae present in detritus might be involved (Forsberg et al., 1993). For example, some detritivores have morphology adapted to separate and ingest the most nutritious components from detritus (Bowen, 1983; Fugi et al., 2001).

Other investigations, however, show that the contribution of macrophyte detritus carbon to fish can be variable and in some instances can reach high percentages. For instance, two out of 11 species of detritivorous fish from an Amazonian floodplain showed considerable assimilation of carbon from C_4 macrophytes: *Pterygoplichthys radiatus* (Hancock, 1828) (10.4–41.5%) and *Hypostomus plecostomus* (Linnaeus, 1758) (12.7–42.9) (Forsberg et al., 1993). At least one species of detritivorous fish (*Oreochromis andersonii* (Catelnau, 1861)) in an African floodplain also relied on detritus derived from aquatic macrophytes for its growth (Peel et al., 2019). Other examples include *Prochilodus lineatus*, which used up to 41% of its carbon from C_4 macrophytes in the Paraná River (Lopes et al., 2007), young *Semaprochilodus insignis* (Jardine, 841), which used up to 50% of its carbon from C_3 macrophyte detritus in a floodplain in Amazon (Soares et al., 2021), and *Parabotia fasciata* Dabry & Thiersant, 1872, whose contribution from macrophytes detritus reached 43% during the wet season in a Chinese lake (Wang et al., 2011). Thus, in contrast to the previous examples, others show that macrophyte detritus may be an important source of carbon to detritivorous fish.

Taken together, the findings discussed above indicate that the extent to which fish use carbon directly from macrophyte detritus seems to be context dependent. C_4 grasses, which dominate in various aquatic ecosystems, are apparently poorly used by fish in some ecosystems but can be important in others. In addition, carbon from C_3 macrophytes detritus is also used with different efficiencies, depending on the macrophyte species, and these plants can contribute significant carbon to fish in many ecosystems. Differences in the assimilation of detritus-derived carbon by fish across ecosystems may be influenced by the dominance of macrophytes with varying chemical compositions, which affect the nutritional quality of detritus and its subsequent assimilation by fish. The presence of macrophytes from different functional groups (e.g., C3 vs. C4 plants) also contributes to these inter-ecosystem differences. Furthermore, seasonal variations in detritus derived from diverse sources (e.g., Wang et al., 2011) may further exacerbate the variability in carbon assimilation by fish among ecosystems.

Finally, it is tempting to speculate the fate of detritus carbon in those ecosystems where detritivorous fish (and other organisms) use detritus poorly as a carbon source. For floodplain ecosystems, it has been shown that detritus from higher plants is recalcitrant and largely decomposed by bacteria in the microbial loop, instead of being transferred for higher trophic levels (Bunn & Boon, 1993; Lewis et al., 2001; Thorp & Delong, 2002), which explains the apparent discrepancy between the high detritus production and the poor transference of detritus carbon to higher trophic levels.

Macrophyte as an indirect carbon source: transference of carbon to fish via other organisms

As demonstrated previously ("Macrophyte complexity, fish foraging, and trophic relationships"), stomach content analyses of numerous fish species have shown that invertebrates constitute the primary dietary components for several fish species. However, just as we explored the role of macrophytes as a direct carbon source for fish in the preceding sections, an equally important question arises: do invertebrates, whether associated with macrophytes or not, act as carbon links between macrophytes and fish (Fig. 6C, D, and E)? To address this inquiry, a pertinent strategy has been employed, combining gut content analysis with isotopic analysis (e.g., Kelly & Jellyman, 2007).

Numerous investigations have demonstrated the assimilation of C_3 and C_4 macrophyte carbon by fish across different guilds. This transference is mediated by various organisms, including zooplankton, macroinvertebrates, and small fish themselves. The percentage of carbon indirectly assimilated from macrophytes varies, with some studies reporting values exceeding 50% (Wainright et al., 2000; Jepsen & Winemiller, 2007; Jackson et al., 2013; Kovalenko & Dibble 2014; Fetahi et al., 2018; Bokhutlo et al., 2021). For instance, the dominance of macrophytes as basal resources was identified in seven species of omnivorous, invertivores, and carnivorous fish (36.8–81.0% of carbon demand) during the wet season in a lake in China (Wang et al., 2011). Another study, encompassing 58 fish species from various guilds in a Mexican river, revealed a significant contribution from C_3 macrophytes to fish during the wet season and in the lower section of the river (with values ranging from 60 to 90%) (Soria-Barreto et al., 2021). Macrophytes also emerge as important carbon sources for juvenile fish in the Rio Grande (US), where the transfer from emergent macrophytes to juvenile fish, possibly by micro-invertebrates, reached 60% during low water (Pease et al., 2006). Collectively, these findings underscore that, in numerous instances, macrophyte carbon is transferred to fish through intermediary organisms within food webs.

However, there are instances demonstrating an extremely restricted transfer of macrophyte carbon to fish and other organisms in ecosystems where these plants are abundant (Bunn & Boon, 1993; Toetz, 1997; Xu & Xie, 2004; Kelly & Hawes, 2005; Rodriguez-Graña et al., 2008). These findings, coupled with observations of the poor assimilation of detritus carbon by fish (as discussed earlier), affirm that a high macrophyte biomass, whether alive or dead, does not necessarily equate to high productivity in higher trophic levels. It is noteworthy that this perspective was preconceived much earlier by Lindeman in his study conducted at Cedar Bog Lake (Lindeman, 1941). In his conclusion, he stated that “an abundance of green plants as producers does not necessarily indicate an abundance of animals and consumers.”

Finally, it is noteworthy to point out that the importance of C_3 macrophytes as a source of carbon for fish may be underestimated in several investigations, mostly the pioneer studies, and this can be attributed to at least four reasons. First, the signature of C_3 macrophytes often overlaps with that of other terrestrial C_3 plants, phytoplankton, periphyton, and benthic macroalgae (Forsberg et al., 1993; Herwig et al., 2004; Weis, 2005; Syväranta et al., 2006; Jepsen & Winemiller, 2007; Blanchette et al., 2014; Cazzanelli et al., 2021). Second, detritus undergoes chemical and isotopic fractionation during microbial decomposition, making it challenging to identify its direct contribution to consumers (Keough et al., 1996; Herwig et al., 2004). Third, there are significant spatial and temporal variations in carbon signatures (Syväranta et al., 2006). Fourth, as discussed by Soares et al. (2021), some investigations use simple mass balance mixing models with only carbon isotope signature instead of combining carbon and nitrogen isotopes. For these reasons, many investigations utilizing carbon isotopes may conclude that while phytoplankton supports a substantial portion of higher trophic levels, periphyton and macrophytes are also likely to make significant contributions (e.g., Peel et al., 2019). Some of these limitations can be addressed by simultaneously using isotopes, such as carbon, nitrogen, and sulfur, combined with Bayesian isotopic mixing models (Moore & Semmens, 2008; Parnell et al., 2010; Hopkins III & Ferguson, 2012; Phillips, 2012). These approaches have been widely applied over the past two decades and are featured in several of the studies included in our review (e.g., Jackson et al., 2013; Kovalenko & Dibble, 2014; Peel et al., 2019; Soares et al., 2021), enhancing the reliability of findings and overcoming the limitations inherent to earlier studies.

Macrophytes as fish dispersal vectors

Macrophytes are easily dispersed by hydrochory, particularly in flowing waters, and by wave action in lentic ecosystems where wind dislodges vegetation mats primarily formed by free-floating vegetation and other macrophyte life forms that create floating islands (Pott & Pott, 2003; Bulla et al., 2011). These vegetation mats typically transport and facilitate the dispersion of fish in rivers (Schiesari et al., 2003; Bulla et al., 2011; Guerrero et al., 2017) and lakes (Oliver & Mckaye, 1982).

Fish that use macrophytes as their biotope may passively migrate downstream within the mats, while others enter the mats during transit flow (Nezdoly & Pavlov, 2019). For specific fish groups, drifting in macrophyte mats may aid seasonal migration to main river channels; however, juvenile fish sometimes avoid drifting islands in floodplain lakes, likely to prevent being flushed away from these lakes, which are preferred habitats for growth (Henderson & Hamilton, 1995).

Floating islands can transport a diverse array of fish, especially in hot spots of fish diversity, such as tropical rivers. For instance, 39 fish species were found in eight macrophyte mats (with a mean area of

9.1 m^2) in the Solimões River in the Amazon (Schiesari et al., 2003), and 28 fish species were caught in only four floating mats (with a mean area of 3.9 m^2) in the Upper Paraná river-floodplain in Brazil (Bulla et al., 2011). These researchers caught larvae, juveniles, and adult insectivores, omnivores, invertivores, and detritivores, highlighting that drift occurs for different life stages and trophic guilds.

Although fish dispersal facilitated by macrophyte mats can be beneficial for metacommunity dynamics when involving native species, it may have negative consequences when it aids the spread of invasive species to new areas. For instance, in the Upper Paraná River floodplain, the most frequently captured fish species in floating macrophyte mats was *Trachelyopterus galeatus* (Linnaeus, 1766) (Bulla et al., 2011), which is considered invasive in this region (Ota et al., 2018).

These findings underscore the importance of floating mats in facilitating fish dispersion across various ecosystems, providing protection against predation and offering feeding habitats through macrophyte roots and other submerged structures. This dispersion mechanism plays a crucial role in establishing founder populations and enhancing gene flow between populations, especially those characteristic of littoral zones (Oliver & Mckaye, 1982). This perspective aligns with recent research indicating that "floating matter" is a vital component for maintaining river integrity (Shumilova et al., 2019). Therefore, in ecosystems where floating islands are prevalent (e.g., river-floodplain ecosystems), their significance should be incorporated into models seeking to comprehend fish metacommunities, particularly during high-water seasons when mats are spread (Thomaz, 2022).

Future research

Based on this review, we outline some promising avenues for experimental and field research that could advance our understanding of macrophyte–fish interactions. This list is not exhaustive but offers general suggestions for further studies.

A first possibility involves experimental work that controls abiotic and biotic factors. Conducting experiments that simultaneously control abiotic factors (e.g., DO, CO_2, and pH) and biotic interactions (e.g., competition and predation) would greatly enhance our understanding of each factor's role in structuring fish assemblages associated with macrophytes. This approach is critical because many relevant abiotic and biotic factors are interrelated, making it difficult to isolate the specific factor responsible for observed patterns in field data.

A second perspective deals with methods for sampling in highly complex habitats (e.g., areas with high plant biomass), incorporating sampling methods suited for these habitats and for capturing fish across different size classes (see Dibble et al., 1996 and Petr, 2000 for a discussion on different sampling methods). Moreover, samplings inside macrophyte stands should include fish larvae (e.g., Iquematsu et al., 2023). Both strategies are essential for investigating the relationships between macrophyte complexity and fish density and diversity. Ideally, sampling should cover both adult and juvenile fish simultaneously to reduce sampling biases; otherwise, findings might skew the macrophyte–complexity relationship by underrepresenting large fish or very small individuals (e.g., fish larvae).

Third, systematic reviews of specific macrophyte–fish relationships would be valuable, given the rapid accumulation of publications in this area. Systematic reviews focused on particular aspects of macrophyte-fish interactions could offer quantitative insights into areas that non-systematic reviews, like ours, may not fully address. For instance, systematic studies could provide a clearer understanding of the role of macrophytes in fish reproduction success by comparing data on fish eggs and larvae in littoral versus pelagic zones. Another approach could involve calculating effect sizes for different components of fish diversity within and outside littoral zones or evaluating diversity responses to gradients in macrophyte structural complexity.

Finally, experiments examining fish behavior in relation to macrophytes would further enhance our understanding of the interactions between predators and prey. These studies can complement traditional observational studies on how macrophytes shape predator–prey interactions, either by providing shelter for prey or enhancing hunting opportunities for predators. Furthermore, they can shed light on the strategies employed by both organisms, such as prey adjusting their microhabitat use and mobility to evade fish detection or predators adapting their hunting tactics in response to the structural complexity of aquatic plants. Such insights are essential for better understanding the role of macrophytes in maintaining fish diversity.

Conclusion

In conclusion, this review sheds light on the multifaceted ecological relationship between macrophytes and fish in freshwater ecosystems. From the historical perspective, outlined in Forbes' seminal study in 1887, until the contemporary surge in research interest, the understanding of this interaction has evolved significantly. Our exploration focused on various dimensions of this relationship, highlighting the intricate effects of macrophytes on fish populations and communities. The complexities of macrophyte–fish relationships extend to their influence on fish diversity, acting as both direct and indirect sources of carbon and serving as dispersal vectors, refuge, and reproduction sites.

Despite the recognized importance of macrophytes and fish in ecosystem functioning, the scarcity of synthesis papers addressing their interactions highlights a gap in the current literature. This review aims to bridge this gap by consolidating knowledge on the effects of macrophytes on fish in freshwater ecosystems, providing a foundation for future research and management strategies. As we continue to unravel the complexities of this relationship, a comprehensive understanding will contribute to the conservation and sustainable management of aquatic ecosystems.

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Declarations

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