



## Seasonal bias and overlooked climate impacts in mangrove ichthyoplankton research: emerging threats and knowledge gaps

José Pedro Vieira Arruda Júnior<sup>a,\*</sup> , Ana Cecilia Pinho Costa<sup>a</sup> , Tatiane Martins Garcia<sup>a</sup> ,  
Tommaso Giarrizzo<sup>a</sup> , Carolin Müller<sup>b</sup> , Marcelo O. Soares<sup>a</sup> 

<sup>a</sup> Marine Ecology and Conservation Laboratory (MARES), Marine Science Institute of Marine Sciences (LABOMAR) - Universidade Federal do Ceará (UFC), Fortaleza, Brazil

<sup>b</sup> Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany

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### ABSTRACT

Mangrove ecosystems are among the most productive coastal habitats and serve as key nursery zones for fish eggs and larvae (ichthyoplankton). While seasonal variation in ichthyoplankton has been relatively well studied, the impacts of extreme climate events remain poorly understood. This perspective paper presents a narrative literature review and interpretative synthesis of 80 studies at a global scale on mangrove ichthyoplankton. We identified general ecological patterns and potential effects of climate-driven disturbances on fish eggs and larvae. Four main research themes emerged: seasonal variation (63 studies), human-induced changes in ichthyoplankton dynamics (7 studies), advances in identification through molecular versus morphological approaches (8 studies), and impacts of climate change (2 studies). Seasonal variation dominated the literature, whereas human-induced effects were mostly reported in Malaysian mangroves. Human impacts approaches provided insights into larval resilience to pollution, including microplastics. Only a few studies directly addressed climate extremes. Research on the consequences of extreme climatic extremes in mangrove-ecosystems suggest that, by altering water quality and habitat integrity, these events probably compromise the nursery function of mangroves and affect fisheries and estuarine food webs. Despite their ecological importance, the lack of long-term studies limits understanding of climate extremes on mangrove ichthyoplankton. Future research should include long-term monitoring, predictive modeling, and molecular tools to assess resilience. Strengthening research in this field is essential for designing conservation strategies that maintain mangroves as nurseries and support fisheries and coastal livelihoods under global climate change.

### 1. Introduction

Mangroves occur in estuarine systems such as rivers, lagoons, bays and islands, across tropical and subtropical regions worldwide (Alongi, 2015; Friess et al., 2019). These ecosystems provide a wide range of ecosystem goods and services, including coastal protection, carbon sequestration (i.e., blue carbon), nutrient cycling and support for fisheries, which are fundamental for the livelihoods of traditional human communities (Das et al., 2022; Bera and Maiti, 2022). Mangroves are also functionally connected to other coastal and freshwater habitats, such as rivers, coral reefs, rhodoliths, and seagrass beds, forming integrated seascapes that sustain fish populations throughout their life cycles (Nagelkerken et al., 2008; Kimirei et al., 2013; Sheaves et al., 2015;

Guerrero et al., 2021). This ecological connectivity enhances the role of mangroves as critical nursery areas for fish, linking estuarine productivity to adjacent coastal fisheries.

Mangrove ecosystems are crucial for the development of ichthyoplankton (i.e., fish eggs and larvae) and juvenile fishes due to high nutrient availability that sustains estuarine food webs, as well as the structural complexity provided by mangrove roots, which reduce predation pressure (Abrantes et al., 2015; Tarimo et al., 2022). Within mangroves, early life stages benefit from favorable feeding conditions, shelter and retention mechanisms that enhance survival during critical developmental phases (Nagelkerken et al., 2008; Vorsatz et al., 2021). After hatching, growth and initial development, fish larvae may disperse or migrate to other coastal habitats, contributing to adult populations

\* Corresponding author.

E-mail addresses: [pedarruda@alu.ufc.br](mailto:pedarruda@alu.ufc.br) (J.P. Vieira Arruda Júnior), [anaceciliapcosta@gmail.com](mailto:anaceciliapcosta@gmail.com) (A.C. Pinho Costa), [tatianegarcia@ufc.br](mailto:tatianegarcia@ufc.br) (T.M. Garcia), [tgiarrizzo@gmail.com](mailto:tgiarrizzo@gmail.com) (T. Giarrizzo), [carolin.mueller@leibniz-zmt.de](mailto:carolin.mueller@leibniz-zmt.de) (C. Müller), [marcelosoares@ufc.br](mailto:marcelosoares@ufc.br) (M.O. Soares).

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and supporting regional fisheries productivity (Ooi and Chong, 2011; Nanjo, 2022; Tarimo et al., 2022).

Ichthyoplankton drift within the water column, where their abundance and diversity are regulated by a complex interaction of biotic and abiotic factors such as temperature, salinity, food availability and hydrodynamics (Houde, 2001; Nhezdoli et al., 2002; Motos et al., 2004). From an ecological and economic perspective, understanding these early life stages is essential, as their survival directly influences recruitment success and fish stock dynamics (Koslow and Wright, 2016). Moreover, ichthyoplankton play a central role in predator-prey interactions and contribute to the structuring of aquatic food webs (Montagnes et al., 2010; Queiroz et al., 2024). Due to their high sensitivity to environmental variability, fish early life stages are widely recognized as effective indicators of environmental change in estuarine and coastal systems (Bonecker et al., 2007; Primo et al., 2011; Monteiro et al., 2021).

Extreme climate events are recognized consequences of global environmental change and include phenomena such as droughts, heatwaves, storm surges and extreme rainfall (Dube, 2024; Joyce et al., 2024; Qiu et al., 2024). These events can drastically alter environmental conditions, pushing organisms beyond their physiological and ecological thresholds (Soares et al., 2020; França et al., 2020; Mulla et al., 2023). Increasing frequency and intensity of such events have amplified their impacts on ecosystem structure and functioning worldwide (Zittis et al., 2022; González-Trujillo et al., 2023). Mangroves play a key role in climate change mitigation, particularly through carbon storage; however, they are simultaneously highly exposed to climate extremes (Rahman et al., 2021; Alongi, 2015). In arid and semiarid regions, events such as megadroughts, flash floods, cyclones and storm surges represent major disturbances, directly affecting estuarine hydrology and potentially impacting fish eggs and larvae (Alongi, 2015; Ward et al., 2016).

The ecology of ichthyoplankton in mangroves is shaped by the interaction of multiple biotic and abiotic drivers (Vorsatz et al., 2021). While the effects of environmental variables such as salinity, temperature, dissolved oxygen and hydrodynamics on fish early life stages are relatively well documented, the impacts of extreme climate events remain poorly understood (Zhang et al., 2022). Despite growing evidence of climate-driven effects on coastal and marine biodiversity, studies specifically addressing ichthyoplankton responses to extreme events in mangrove ecosystems are still scarce, largely due to the lack of long-term and integrative datasets (Reynalte-Tataje et al., 2020; Zhang et al., 2022).

Given the ecological importance of mangroves as nursery habitats and the increasing occurrence of climate extremes, assessing their potential impacts on ichthyoplankton is essential to improve ecological predictions and support science-based conservation and nature-based adaptation strategies (Zimmer and Helfer, 2022; Lovelock et al., 2024).

This perspective paper synthesizes current knowledge on mangrove ichthyoplankton, identifying key ecological drivers, existing biases in research topics and major knowledge gaps. It explores how extreme climate events (e.g., droughts, flash floods and heatwaves) may affect early life stages in mangrove ecosystems and outlines future research directions aimed at improving predictions of climate-driven impacts on fish recruitment.

## 2. Methods

This perspective paper was structured as a narrative literature review with an interpretative approach, focusing on the ecology of ichthyoplankton in mangroves. Based on the reviewed literature, we integrated ecological patterns with the findings about extreme climate events (extreme droughts, floods and heatwaves) and their known effects on mangroves to infer possible impacts on the ichthyoplankton dynamics. We discuss potential scenarios of impacts and ecological processes, drawing on how ichthyoplankton communities respond to environmental factors and on evidence from experimental, modeling and field studies in mangroves involving or not fish larvae. Additionally, we

proposed key questions to guide research on this topic, particularly considering the lack of long-term studies addressing the influence of extreme climate events of mangrove-associated ichthyoplankton.

### 2.1. Literature search

A systematic search for peer-reviewed articles published in English until October/2023 was conducted across four major databases: Google Scholar (n = 333), ScienceDirect (n = 60), Scopus (n = 226) and Web of Science (n = 424), totaling 1043 articles records. The search used combinations of terms, such as “Ichthyoplankton” OR “Fish larvae” AND “Larval Fish” AND “Mangroves”, in titles, abstracts and keywords. An additional 17 studies were identified from the reference list of the papers included. To reduce bias, studies published in other languages (e.g., Portuguese, Spanish, Indonesian) and gray literature (e.g., conference papers, theses, books) were excluded.

Following PRISMA guidelines (O’dea et al., 2021) and Rayann platform (Johnson and Phillips, 2018) for screening, 273 duplicates were removed. Of the remaining 787 records, 707 were excluded based on title and abstract, primarily due to a focus on aquaculture or non-mangrove estuarine systems. A total of 80 studies meets the eligibility criteria, which included data on community composition and/or environmental influences of fish eggs and/or larvae in mangrove-associated estuarine systems (Fig. 1).

### 2.2. Data analysis and representation

Data were compiled and organized in Microsoft Excel, including information on the country where each study was conducted, the corresponding marine realm (following the classification by Spalding et al., 2007), the number of studies per country and realm and the research topic addressed. Figures summarizing the distribution of research topics and geographic coverage were also generated in Excel, while spatial mapping of study sites was carried out in QGIS 3.34.3 to highlight mangrove areas where ichthyoplankton was sampled. It is important to note that the number of mapped locations does not necessarily match the number of studies, since some investigations were conducted in more than one estuarine mangrove system.

## 3. Results

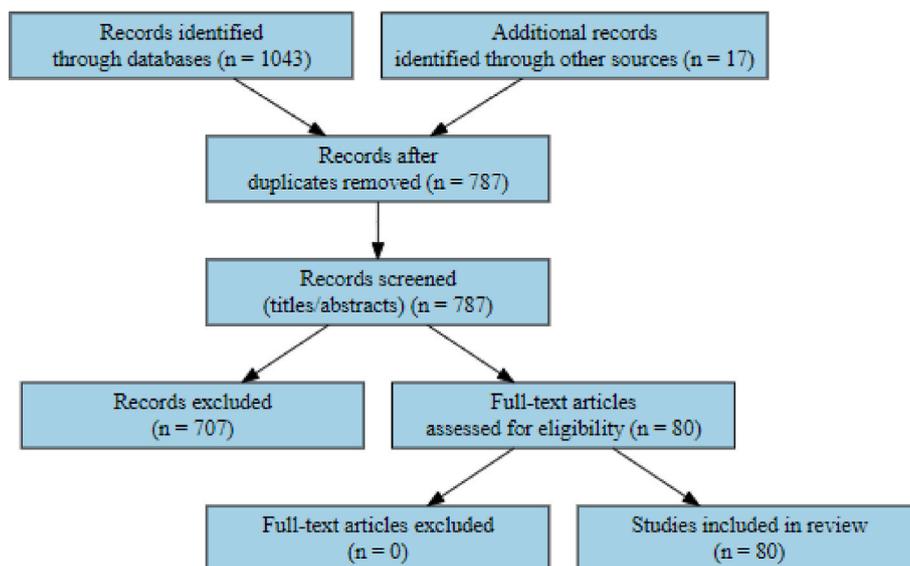
### 3.1. Ecology of ichthyoplankton in mangroves: general patterns and current knowledge

By reviewing the available literature and considering the framework presented in a previous review entitled *Fish and Fisheries in Tropical Estuaries* (Babcock et al., 2019), we developed four main research topics: 1) *Seasonal variation of ichthyoplankton*, 2) *Human-induced changes in ichthyoplankton dynamics*, 3) *Advances in Ichthyoplankton Identification: Molecular vs. Morphological approaches* and 4) *Impacts of climate change on ichthyoplankton dynamics*. The information relevant to the ecology of ichthyoplankton in mangroves is shown in Table 01, which describes the number of papers classified in each subgroup, the main regions where the studies were conducted, the factors analyzed and the main findings.

These topics depicted in Fig. 2 underscore the strong emphasis on studies related to seasonal variation. Although countries like Brazil and Malaysia exhibit a broad range of research themes, molecular and morphological studies are prominent specifically in Malaysia.

### 3.2. Seasonal variation of ichthyoplankton in mangroves

Seasonality is a key temporal structuring factor that significantly influences the composition and dynamics of ichthyoplankton in estuarine mangrove ecosystems. These seasonal variations result from fluctuations in environmental variables, such as temperature, salinity, rainfall, freshwater discharge and primary and secondary production



**Fig. 1.** PRISMA flow diagram illustrating the literature search, screening and selection adopted in this perspective paper. The diagram was generated in the R environment.

**Table 01**

Summary of relevant information on the general knowledge of the ecology of ichthyoplankton in mangroves. The table presents the number of papers, the regions where the studies were conducted, the factors analyzed and key findings on each subgroup.

Research topics	Number of papers	Main regions	Main factors analyzed	Key findings
<i>Seasonal variation of ichthyoplankton</i>	63	Brazil, Mexico, India, Malaysia, China, USA, Honduras, Costa Rica, Colombia, French Guiana (France), Kenya, Mozambique, South Africa, Tanzania, Sri Lanka, Vietnam and Taiwan.	Temperature, Salinity, Dissolved oxygen, Precipitation, pH, Transparency, Depth, Conductivity, Plankton Biomass, Organic and inorganic nutrients, currents, tidal heights, geomorphology, habitat integrity and structure.	Variations across different temporal scales directly shape the structure of the ichthyoplankton community in mangroves. These fluctuations lead to changes in both the density and diversity of the community with mangroves, potentially harboring estuarine, freshwater and marine species depending on the season and specific ecological needs, such as feeding habitats and environmental conditions optimum for development.
<i>Advances in Ichthyoplankton Identification: Molecular vs. Morphological approaches</i>	8	Malaysia and India	Accuracy of Morphological Identifications and Barcoding Efficiency; Meristic and morphological characteristics in different fish families	Molecular techniques enhance the accuracy of ichthyoplankton identification, overcoming the limitations of morphological approaches, but their application still faces challenges due to lack of comprehensive genomic databases.
<i>Human-induced changes in ichthyoplankton dynamics</i>	7	Brazil, Colombia, Malaysia, Australia.	Pollution by microplastics and other anthropogenic debris, coastal development and urbanization, metal contamination and water quality.	Dominance of a few resilient species after disturbances, potentially reducing the community diversity; impacts on the trophic web and fish stocks that rely on mangrove nursery grounds, widespread presence of microplastics, with the density occasionally surpassing that of fish larvae.
<i>Impacts of climate change on ichthyoplankton dynamics</i>	2	Brazil and Senegal	Prolonged droughts in semi-arid regions	Restriction of the nursery zone for marine species, simplifying the ichthyoplankton community, with negative impacts on fish recruitment and fisheries.

(Blaber et al., 1997; Bonecker et al., 2007; Selvam et al., 2013a,b; Rosa et al., 2016; Aceves-Medina et al., 2008). Studies on the ecology of ichthyoplankton in mangroves structure their data based on seasonality, highlighting changes in the density and diversity (Ara et al., 2013; Ara et al., 2013a,b; Wu et al., 2018; Vorsatz et al., 2021). Therefore, it is essential to understand how seasonal patterns structure the community, influence the nursery role of mangroves and implications for the trophic web and fisheries (Barletta-Bergan et al., 2002b; Ara et al., 2016, 2020).

These patterns can be based on the alternation between the dry and rainy periods (Ekau, 2001; Sarpedonti et al., 2008; Costa et al., 2011; Soares et al., 2020), focusing on just one period of maximum larval

capture or with the aim of highlighting the effects of a particular season (Rooper et al., 1996; Bonecker et al., 2007), based on the monsoons in Asia (Balakrishnan et al., 2015), or on the subtropical distribution limits of mangroves, focusing on the typical seasons of temperate environments (summer, winter, spring and fall) (Sanvicente-Añorve et al., 2002; Wasserman et al., 2010). In association with seasonal variations, other factors are also tested secondarily such as tidal dynamics (flood and ebb), time of day (night and day), depth of the water column (surface, middle or bottom) and lunar variations (Schwamborn and Bonecker, 1996; Barletta and Barletta-Bergan, 2009; Bonecker et al., 2009; Rajeshree and Shivakumar, 2023; Coutiño-Sánchez et al., 2023). Despite the

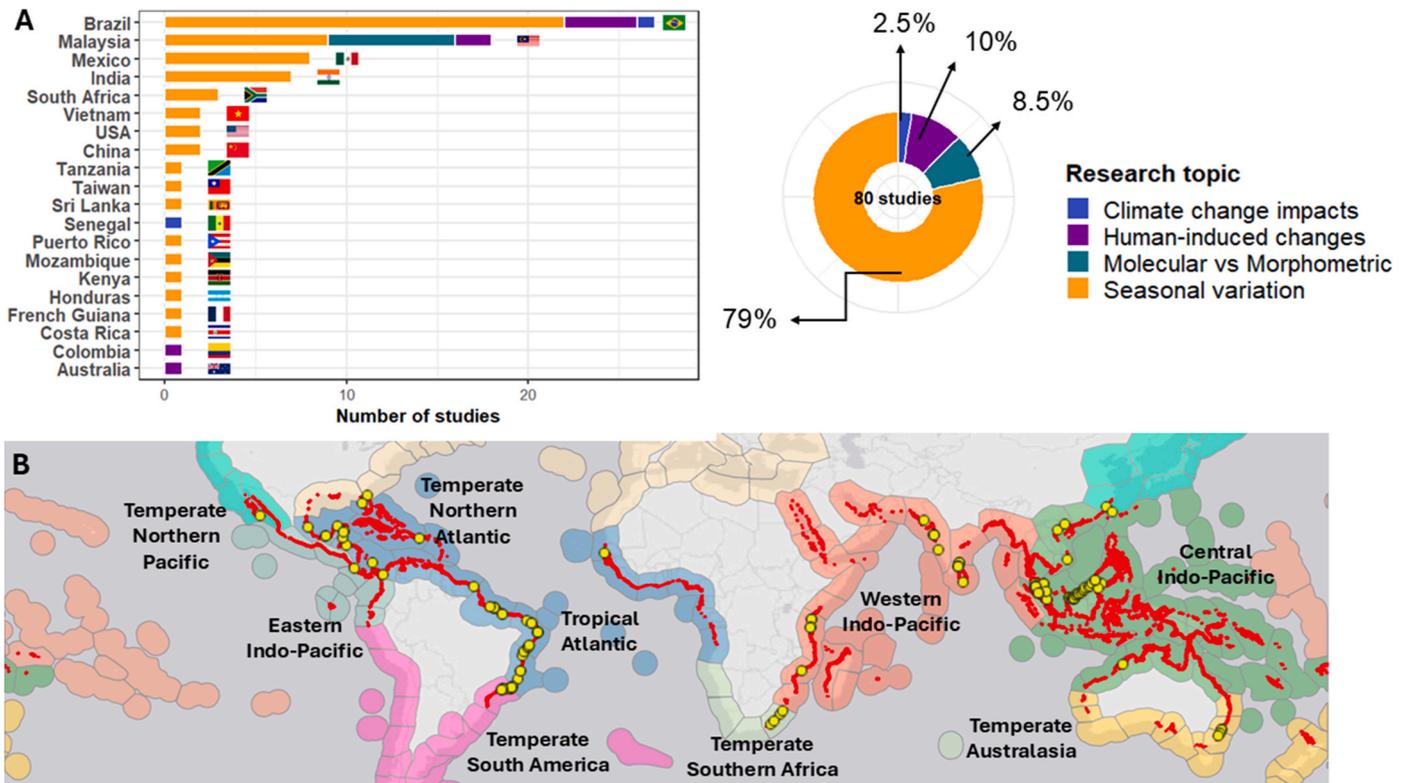


Fig. 2. (a) Number of studies per country, reflecting the greater contribution and diversification of studies in Brazil and Malaysia. The majority of these studies (79%) focus on understanding the seasonal variation on the ichthyoplankton communities, (b) spatial distribution of sampling systems (yellow dots) across marine realms defined by Spalding et al. (2007). Red lines represent mangrove distribution.

great variation in estuarine factors, seasonality is perceived mainly by the variation in freshwater discharge through precipitation, which alters salinity, a factor of great importance in the structure and dynamics of fish eggs and larvae (Whitfield et al., 2023).

The input of continental water into the system due to increased rainfall brings with it nutrients and organic matter, altering turbidity and primary and secondary production (food for the fish larvae), creating a favorable environment (lower salinity and higher food availability) for the entry of fish larvae and the reproduction of adults (Santos et al., 2017a; Mocuba et al., 2023). However, during periods of heavy concentrated rainfall, the speed of the water makes it difficult for fish eggs and larvae to enter and for these organisms to remain in the mangrove ecosystem (Barletta-Bergan et al., 2002a).

In terms of diversity, the ichthyoplankton community is composed of freshwater species, which take advantage of the reduction in salinity, estuarine residents and even marine species, the latter restricted to the river mouth (Rousseau et al., 2017). During the dry season, mangroves serve as nursery areas for estuarine and marine species and there may be freshwater species restricted upstream of the estuarine system, but as the drought intensifies, these species disappear, giving way to fish larvae of resident and marine species (Little et al., 1988; Arévalo-Frías and Mendoza-Carranza, 2015; Badú et al., 2022). Despite spatial and temporal variability observed in the studies, general patterns indicate that ichthyoplankton dynamics are directly affected by the changes caused by freshwater discharge (like the reduced influence of it in arid and semi-arid regions), salinity variation and food availability.

### 3.3. Advances in ichthyoplankton identification: molecular vs. morphological approaches

The accurate identification of fish eggs and early larval stages remains a major challenge, limiting the assessment of habitat disturbance impacts at the species level. This difficulty arises because diagnostic

morphological characters are often absent or poorly developed in fish eggs and preflexion larvae (Miranda-Chumacero et al., 2020; Costa et al., 2011). In tropical regions, the identification of ichthyoplankton still relies predominantly on taxonomic keys, encyclopedias and field guides developed for temperate systems, where knowledge of fish developmental stages is more comprehensive. This dependence often results in misidentifications or restricts taxonomic resolution to higher levels, such as family (Puncher et al., 2015; Chen et al., 2021).

Research conducted in Malaysia mangroves has compared morphological and molecular approaches, highlighting both their limitations and strengths. These studies went beyond and accessed the real diversity of fish larvae in Malaysian mangroves, providing key data for regional guides, a molecular database and a general comprehension of the nursery role of this ecosystem. (Ara et al., 2013a,b; Ara et al., 2014; Rezagholinejad et al., 2016; Azmir et al., 2017; Chu et al., 2021). Nevertheless, challenges remain, particularly the need to expand genetic databases for reference analyses, especially for species that use mangroves (Ram et al., 2020; Alshari et al., 2021).

In this context, the integration of molecular tools with traditional morphological characterization can enhance species identification and the development of comprehensive genetic databases, improving our understanding of the diversity of fish eggs and larvae in mangroves worldwide (Azmir et al., 2020; Duke and Burton, 2020; Jiang et al., 2022; Lira et al., 2023). Nonetheless, further improvements, particularly the expansion of local reference genetic libraries, are essential to enable more accurate species-level identifications.

### 3.4. Human-induced changes in ichthyoplankton dynamics

The construction of ports, deforestation for real estate development and the establishment of aquaculture ponds are examples of anthropogenic disturbances that directly affect the structure and dynamics of ichthyoplankton in mangroves (Paleologos et al., 2019; Newton et al.,

2020). These activities result in the loss of vegetation cover, where fish larvae find shelter from predators; contamination by heavy metals, which can lead to morphological abnormalities; and pollution, such as plastic debris (Lima et al., 2014; Bhagarathi and DaSilva, 2024).

The influence of changes before and 30 years after the construction of a Power Plant in the Klang Strait (Malaysia) was examined (Chu et al., 2021). Although the initial hypothesis predicted a decline in larval abundance, the results refuted this, revealing that the ichthyoplankton community exhibited resilience to changes, as dominant species persisted after 30 years. This resilience may be attributed to the dietary plasticity of fish larvae, which, despite shifts in zooplankton composition due to the Power Plant disturbances, adapted by exploring alternative sources of food (Quah et al., 2022).

However, the persistence of dominant taxa does not necessarily indicate ecological stability. In estuarine systems subjected to anthropogenic pressure, the maintenance of a few tolerant species may occur simultaneously with a reduction in overall species richness and the loss of sensitive taxa, leading to biotic homogenization. Recent studies on fish larvae assemblages in Brazilian estuaries have demonstrated that increasing anthropogenic influence promotes simplified and more homogeneous communities dominated by a small number of species (de Lima et al., 2024). Such patterns suggest that apparent resilience in larval abundance may mask underlying structural and functional degradation of the ecosystem.

The dominance of a few species of fish larvae after human-induced disturbances in mangroves demonstrate that some fish taxa can thrive even in modified estuarine conditions (McKinley et al., 2011). However, although this simplification can benefit the species that remain in the estuarine system, the structure of the trophic web is affected by reducing other links between higher and lower trophic levels (Santos et al., 2017b).

Mangroves are also negatively impacted by pollution from anthropogenic debris, particularly plastic, originating from urbanization, domestic effluents and continental water discharge (Alves et al., 2025). These pollutants can become trapped in the mangrove sediment, where they may be suspended during high tide, or accumulate in aquatic macrophytes and mangrove roots (Correa-Herrera et al., 2017). Microplastics are extensively found in mangroves and sometimes even surpass the density of fish larvae, especially during periods of freshwater discharge (Lima et al., 2014; Lima et al., 2015a,b). These particles can be ingested by fish larvae which can cause damage at different biological levels (physiological, tissue and cellular) (Wang et al., 2024). Such impacts may be exacerbated by ongoing climate change, as more frequent extreme weather events, such as heavy rainfall, can increase freshwater discharge and, consequently, plastic inputs into these ecosystems (Hitchcock, 2020; Chen et al., 2024).

### 3.5. Impacts of climate change on ichthyoplankton dynamics

Fish eggs and larvae can tolerate a certain range of environmental fluctuations, particularly in key factors such as salinity and temperature, due to their broad environmental tolerance windows rather than rapid adaptive responses (Munday et al., 2008; Pittman et al., 2013). However, when these variables shift beyond their tolerance limits, especially under more intense and frequent changes, the physiological stress can exceed survival thresholds, leading to increased mortality (Pankhurst and Munday, 2011; Pistevos et al., 2017). In this context, understanding the influence of extreme climate events on mangroves is crucial to evaluate how such drastic changes impact the structure and dynamics of ichthyoplankton assemblages.

Despite the ecological significance of these disturbances, research linking long-term effects of climate change and the ecology of ichthyoplankton in mangroves remains scarce. To date, only two papers (one in Africa and one in Latin America) (Sloterdijk et al., 2017; Arruda-Júnior et al., 2023) have specifically addressed the influence of estuarine hypersalinization on fish eggs and larvae communities in mangroves,

highlighting the need for further investigation on this issue. Both studies were carried out in semi-arid tropical regions, where prolonged droughts, multiple dams and high temperatures are key drivers of hypersalinity (Tweedley et al., 2019; Soares et al., 2021; Largier, 2023).

In the mangroves of the Sine Saloum estuary (Senegal), a system undergoing salinity inversion due to extreme temperatures and low precipitation during most of the year, 41 taxa were identified, but the diversity was lower compared to other mangrove systems. Both abundance and richness were negatively correlated with increasing salinity, leading to the disappearance of freshwater species and their replacement by marine-estuarine species. This shift altered ichthyoplankton dynamics and reduced the role of mangroves as nursery grounds (Sloterdijk et al., 2017).

In the low-inflow Piranji estuarine system (Northeast Brazil), hypersalinity ranging from 38 to 62 was observed after a prolonged drought lasting almost five years, resulting in a decline in fish eggs and larvae densities, with only nine species recorded. Similar to the findings in Senegal, the community structure was simplified to only marine and estuarine species, lacking freshwater species (Arruda-Júnior et al., 2023).

## 4. Extreme climate events and its potential impact on ichthyoplankton in mangroves

An extreme climate event is defined by a persistent pattern of weather in which a variable exceeds or falls below a specific threshold for a continuous period, such as a season, being characterized by both its intensity and duration (Seneviratne et al., 2021). These events are becoming more frequent and intense due to global climate change, profoundly impacting ecosystems and biodiversity. In ichthyoplankton communities, extreme droughts, floods and heavy precipitation and heatwaves can exceed tolerance limits, impair development and alter community structure (Cajado et al., 2022; Hasan et al., 2023). Mangroves, essential nursery habitats for fishes from freshwater, reef and oceanic environments (Whitfield, 2017), remain understudied in this context. Understanding how such disturbances affect early life stages of fish is crucial and this section integrates known patterns of ichthyoplankton dynamics with climate-driven disruptions to identify potential and observed impacts, providing a basis for proposing future research priorities in mangrove ecosystems.

### 4.1. Extreme droughts

Drought is defined as an extended period (months or years) of below average precipitation, leading to water scarcity and affecting both natural systems and economic sectors (Cunha et al., 2019; Seneviratne et al., 2021). A drought becomes extreme when it becomes prolonged and severe (megadroughts), often intensified by climate change and anthropogenic factors such as greenhouse gas emissions and increasing water consumption (Vicente-Serrano et al., 2020; Aghakouchak et al., 2021). In coastal aquatic systems, extreme droughts cause declines in water quality and dissolved oxygen concentration, hypersalinization (e.g., mangroves and other estuarine systems) and habitat fragmentation (e.g., occurrence of sandbars), all of which, individually and/or combined, can severely impact biodiversity (Bond et al., 2008). Ichthyoplankton are particularly vulnerable to these disruptions due their limited physiological tolerance, negatively affecting survival rates, dispersal patterns and recruitment success (Houde, 2001; Bucater et al., 2013).

One of the primary consequences of extreme droughts in estuarine systems is the reduction of freshwater input, leading to hypersalinity (Tweedley et al., 2019). Under extreme salinity conditions mangroves, as observed by Arruda-Júnior et al. (2023), fish eggs and larvae may exhibit lower growth rates and higher mortality due to increased energetic cost of osmoregulation, which diverts resources that would otherwise be allocated to growth and development (Vaka and Tamata,

2024). Additionally, osmotic stress associated with low concentration of dissolved oxygen can reduce hatching rates and increase larval mortality, particularly in freshwater and stenohaline species (Whitfield, 2021; Seale et al., 2024).

Extreme droughts also alter trophic interactions by modifying the availability of food resources (Ledger et al., 2013). The reduction of freshwater input and hypersaline condition can lead to shifts in planktonic community structure, reducing the diversity and density of key zooplankton species in mangrove systems (Nelson et al., 2015; Rogers et al., 2024). This decline in zooplankton availability is likely to reduce larvae feeding success, leading to lower recruitment rates in fish populations that rely on mangroves during a part of their life cycle (Breux et al., 2019; Campos et al., 2022). Additionally, these altered environmental conditions may favour opportunistic and euryhaline species, potentially leading to a decline in stenohaline and freshwater species that depend on stable and low salinity levels, respectively, for early development (Baptista et al., 2010).

Another significant consequence of extreme droughts in mangrove estuaries is habitat fragmentation (Syamjith and Ramani, 2014). The low water levels caused by prolonged droughts can reduce the size of aquatic habitats and disrupt connectivity, driving organisms to seek refugia (Leigh et al., 2015). In low-inflow estuaries, sandbars formed by wave-driven sediment import can block the connection between the estuary and the ocean, limiting the arrival of breeding adults (Houde, 2022) and dispersal of ichthyoplankton (Tweedley et al., 2019). These changes may increase competition and predation pressures in ichthyoplankton that are already confined to smaller and more fragmented habitats (Arevalo et al., 2023). Furthermore, low-inflow estuaries are particularly vulnerable to extreme climatic events because such harsh conditions are intensified by them (Carrasco et al., 2010; Largier, 2023).

#### 4.2. Floods and heavy precipitation

Extreme precipitation events, such as tropical cyclones, flash floods and heavy rainfall, become intense and frequent due to global warming, resulting in structural and hydrodynamic disturbances in aquatic systems that can persist for days or even months (Seneviratne et al., 2021). In mangroves, seasonal shifts in estuarine community structure are often associated with freshwater discharges, whether through natural rainfall or artificial water releases from dams (Joyeux et al., 2004). Extreme storm events and intense and frequent freshwater discharges into aquatic systems alter the estuarine environment and limit the survival of the early stages of the fish, particularly among marine and resident species (Barletta-Bergan et al., 2002a).

One immediate impact of freshwater discharge into mangroves is the sudden reduction in salinity, leading to osmotic stress in larvae, particularly marine species, which have direct effects on the community structure (Arévalo-Frías and Mendoza-Carranza, 2015; Medina-Contreras et al., 2014). Additionally, intense riverine discharge, particularly in high flow systems, not only prevent marine fish larvae and breeding adults from entering the systems, but also result in flushing of fish eggs and larvae beyond estuarine retention zones to less productive areas, thereby compromising recruitment success (Barletta-Bergan et al., 2002a; Teodósio and Garel, 2015; Arevalo et al., 2023).

Although the input of nutrients may boost primary production in mangrove environments, excessive nutrient loads lead to eutrophication (Manna et al., 2010; Clementson et al., 2021; Liu et al., 2024). Along with the nutrients, contaminants, such as heavy metals, xenobiotics and microplastics, find their way into the mangroves and become bioavailable for fish larvae (Bayen, 2012; Borrell et al., 2019; Mendes et al., 2023). The effects of these chemical disturbances are associated with fish eggs and larvae deformities and decline in reproductive success, leading to failure on recruitment (Sfakianakis et al., 2015).

#### 4.3. Heatwaves

Heatwaves are extreme high temperature events that cause significant physiological, behavioral and ecological impact on aquatic organisms (Smale et al., 2019; Giménez and Torres, 2025). These effects vary depending on the species, thermal tolerance, developmental stage and the intensity and duration of the event (Smith et al., 2023). In mangrove ecosystems, heatwaves can lead to high vegetation mortality due to inhibited photosynthesis, increased water loss and desiccation risk, ultimately reducing mangrove coverage and compromising their role as nurseries (Sippo et al., 2018; Babcock et al., 2019). Other consequences are extreme temperature rises, increased salinity, reduced dissolved oxygen (high metabolic rates) and proliferation of harmful phytoplankton species (Alberto et al., 2024).

For fish eggs, even slight warming can cause breeding adults to produce low-quality gametes, reducing embryonic viability (Irish et al., 2024). It can also increase embryonic mortality and accelerate development, shortening the incubation period and potentially leading to a mismatch between hatching and optimal environmental conditions for larval survival (Pankhurst and Munday, 2011; Godoy et al., 2023). In larvae, elevated temperatures raise metabolic rates and growth, shortening the pelagic larval duration and reducing exposure to predators; however, these benefits come with trade-offs, higher energy demands increase the risk of starvation and reduce growth efficiency when food is limited (Pankhurst and Munday, 2011). Additionally, the faster it grows, the closer it gets to the settlement, reducing its dispersal capacity and confining organisms to unsuitable areas (Raventós et al., 2021).

The effects of extreme temperature events on early life stages of fish are highly complex and influenced by species-trait, latitude, food availability and the magnitude of thermal stress (Pankhurst and Munday, 2011; Spinks et al., 2019). Regarding the influence of heatwaves on mangrove ichthyoplankton, current knowledge is largely based on potential effects inferred from experimental studies and research conducted in other aquatic environments, such as the open ocean (Gold et al., 2024), even though heatwaves are reported in mangroves.

### 5. Expected impacts of extreme climate events on mangrove ichthyoplankton: central and emerging questions for future research

Based on experimental studies and field assessments in other coastal environments, we describe a series of effects, alone or in combination, which have the potential to cause disturbances in the dynamics of ichthyoplankton in mangroves. The following effects are highlighted here are described in Fig. 3.

Although the listed impacts are likely to affect the ichthyoplankton community in mangroves in compromising the nursery role of this ecosystem, there is still a lack of long-term studies that provide clear evidence of these effects. To address this gap and guide future research in this topic, we propose one central question and five sub-questions based on the impacts described and the likely resilience capacity of mangrove ichthyoplankton (Fig. 4). The core question aims to understand how mangrove-estuarine ichthyoplankton will respond to the cumulative effects of extreme climate events?

### 6. Conclusions

Current knowledge on mangrove ichthyoplankton ecology is relatively robust; however, this review highlights a strong imbalance in the literature. Most studies focus on seasonal variability, while the influence of extreme climatic events remains poorly explored. Direct empirical evidence addressing the effects of climate extremes on fish eggs and larvae in mangrove systems is scarce, with only a few case studies, particularly those examining hypersalinization, explicitly documenting such impacts. These gaps limit our ability to draw firm conclusions about the magnitude and consistency of extreme-event effects in

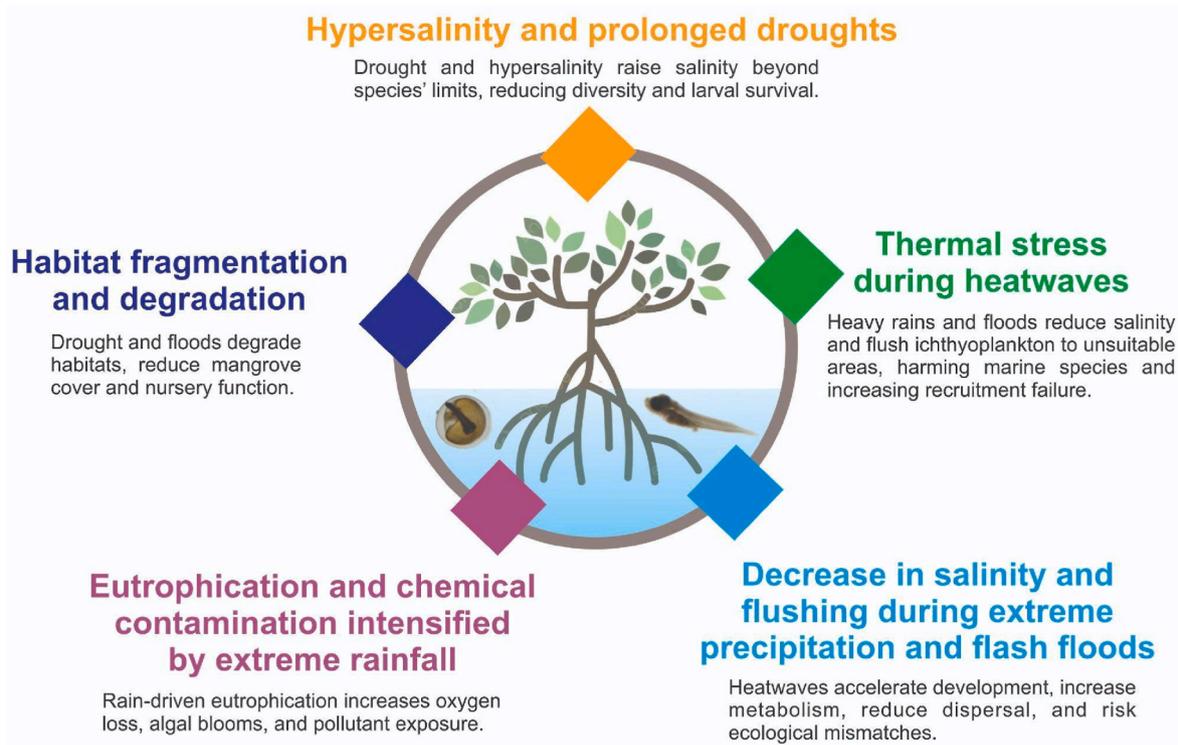


Fig. 3. Extreme climate effects, alone or in combination, which have the potential to cause disturbances in the dynamics of ichthyoplankton in mangroves based on experimental studies and field assessments in other coastal environments.

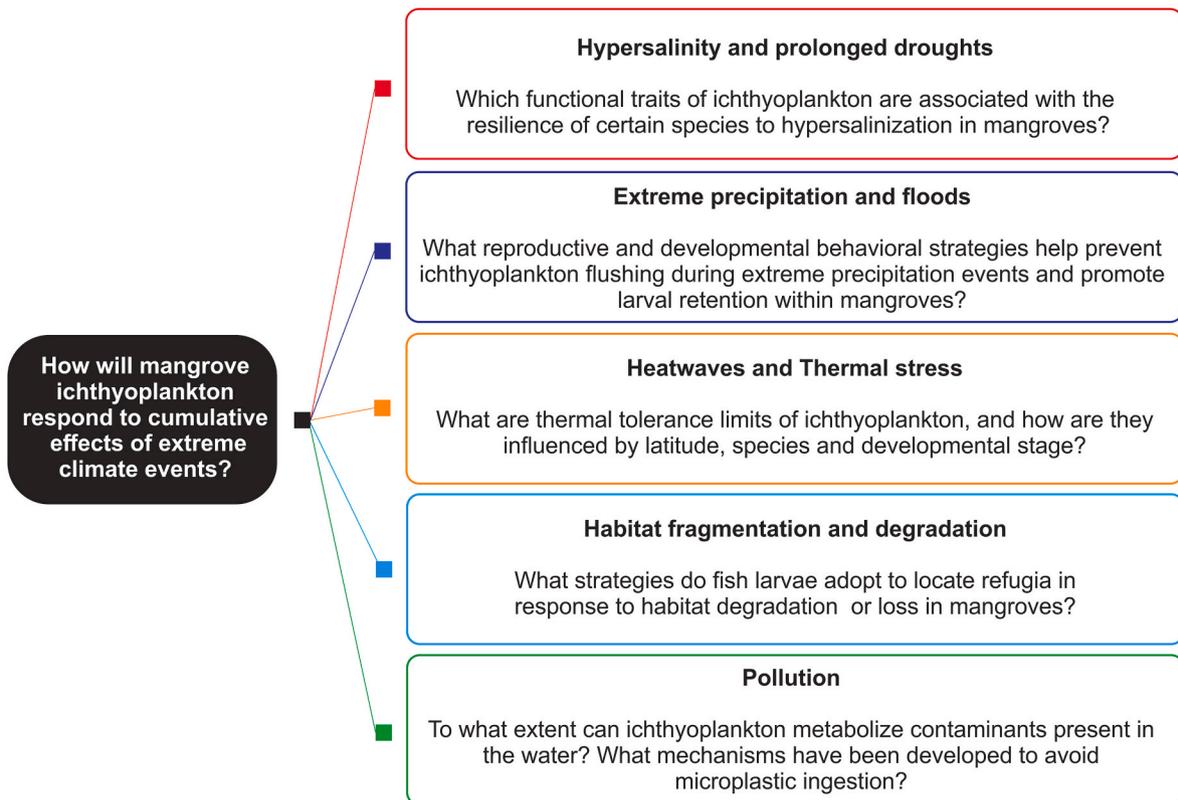


Fig. 4. Flowchart summarizing the core question and five key research questions on the impacts of extreme climate events on mangrove ichthyoplankton, highlighting knowledge gaps related to resilience, tolerance and adaptive strategies.

mangrove ichthyoplankton.

Despite this limited direct evidence, mechanistic understanding

derived from physiology, life-history theory, and studies conducted in other aquatic systems suggests that extreme climatic events may disrupt

key processes during early fish development. Altered temperature and salinity regimes can plausibly affect survival, growth, and recruitment pathways of ichthyoplankton cohorts. However, for mangrove ecosystems specifically, these impacts should be regarded as expected or potential outcomes inferred from known mechanisms rather than as effects directly demonstrated by the current body of evidence.

Given the projected increase in the frequency and intensity of extreme climatic events, such as prolonged droughts, intense rainfall, floods, tropical storms, and heatwaves, future research should prioritize approaches capable of capturing episodic responses. Long-term monitoring, predictive and modeling frameworks, and the integration of molecular tools are essential to reduce current uncertainties and improve our understanding of mangrove ichthyoplankton dynamics under climate extremes. Strengthening research capacity and methodological diversity will be critical to support effective conservation, management, and climate adaptation strategies in mangrove ecosystems.

#### CRedit authorship contribution statement

**José Pedro Vieira Arruda Júnior:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ana Cecilia Pinho Costa:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Formal analysis, Conceptualization. **Tatiane Martins Garcia:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Tommaso Giarrizzo:** Writing – review & editing, Visualization, Supervision, Methodology, Conceptualization. **Carolin Müller:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Methodology, Formal analysis, Conceptualization. **Marcelo O. Soares:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition, Formal analysis, Conceptualization.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2026.107946>.

#### Data availability

Data will be made available on request.

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