Reviews in Fisheries Science & Aquaculture

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/brfs21

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To cite this article: Ian G. Cowx, An V. Vu, Zeb Hogan, Martin Mallen-Cooper, Lee J. Baumgartner, T. Quan Lai, Gunther Grill & Catherine A. Sayer (16 Sep 2024): Understanding the Threats to Fish Migration: Applying the Global Swimways Concept to the Lower Mekong, Reviews in Fisheries Science & Aquaculture, DOI: 10.1080/23308249.2024.2401018

To link to this article: https://doi.org/10.1080/23308249.2024.2401018

REVIEWS IN FISHERIES SCIENCE & AQUACULTURE
https://doi.org/10.1080/23308249.2024.2401018

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Understanding the Threats to Fish Migration: Applying the Global Swimways Concept to the Lower Mekong

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ABSTRACT
The Mekong River basin is a biodiversity hotspot and supports the largest inland capture fishery globally. The fish and fisheries, especially migratory species that underpin the capture fisheries, are, however, under threat from multiple pressures, not least hydropower development, expansion of irrigated agriculture and aggregate mining. In this paper the Global Swimways concept was used to understand migratory patterns in different Mekong fish species and provide insights for management and conservation of migratory species in the basin. Information was collated from existing databases, FishBase, and literature searches to determine the significance of migration routes of the river system. A total of 1393 fish species was recorded. About 21% of these are truly migratory species, mostly potamodromous and amphidromous species, and contribute ≈70% of catch. Distribution of fish in the Mekong River exhibits a well-defined zonation pattern, with species diversity highest in the lower floodplains and delta reaches. Three main migration zones occur in the Lower Mekong Basin (LMB) but with considerable migration of some species between zones. Some species adopt multiple migration strategies as opposed to simple longitudinal or lateral migrations, with sub-populations occurring in different reaches of the LMB exhibiting different migratory strategies. Approximately 11% of native fish species are threatened; among migratory species 35% are threatened. There are multiple challenges to maintaining swimways in the Mekong, including improved understanding of migratory pathways, managing intensification of environmental pressures and managing heavy fishing pressure. Measures to conserve and protect the migratory fish species in the Mekong are suggested.

KEYWORDS
Aquatic biodiversity; fish conservation; life history strategies; migratory guilds

Introduction

It is widely recognized that animals migrate, often considerable distances, to meet life history requirements and maximize somatic or reproductive benefits (Northcote 1978). Species tend to use specific routes between habitats for different ecological needs, and especially move between reproductive, feeding and refuge habitats. For birds, these pathways are known as flyways (Boere and Stroud 2006) and connectivity corridors are also widely recognized as important for mammals, insects such as butterflies, and marine fishes, but the concept has not yet been fully explored in freshwater environments. To better recognize the importance of these pathways for freshwater fishes, the concept of 'Global Swimways' was developed to identify river reaches that support the migration routes of biologically and/or socio-economically important freshwater fishes (Worthington et al. 2022). Understanding where these routes are located is critical because rivers globally are being impacted by water resource development, especially dams, weirs and channelization, fragmenting rivers and modifying flows, resulting in loss of their ecological integrity (Barbarossa et al. 2020; Grill et al. 2019; Nilsson et al. 2005). Such fragmentation impedes migration of fish in rivers, both up and downstream, but also laterally onto floodplains, and can result in local population decline and ultimately extinction (Liermann et al. 2012).

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Supplemental data for this article can be accessed online at https://doi.org/10.1080/23308249.2024.2401018.

Riede (2000, 2004) identified at least 1873 migratory (marine and freshwater) fish species and The Living Planet Index for Migratory Freshwater Fish (Deinet et al. 2020, 2024) suggested there are some 1100 migratory freshwater fish species. These numbers are likely underestimated given the high prevalence of migratory species in large tropical rivers (e.g. Winemiller et al. 2016). Numerous publications have highlighted the paucity of information on the timing, distance and routes of migratory freshwater fish species in many parts of the world (e.g. Loury et al. 2021; Riede 2000; Vu et al. 2022b, 2023). These data gaps have high relevance for infrastructure planning and habitat restoration, given many rivers are either heavily modified or proposed for development (Barbarossa et al. 2020; Grill et al. 2019). Planned developments may threaten migratory freshwater fish, particularly in large tropical rivers that support high endemicity (Duponchelle et al. 2021; Hermann et al. 2021). There is an urgent need to fill this crucial knowledge gap to improve management and conservation of these vital resources, which are essential sources of protein and micronutrients for many people (Ainsworth et al. 2023; Lynch et al. 2016).

To support this need, this paper applies the Global Swimways framework to the Lower Mekong River system, which is known for its rich biodiversity and reliance of local communities on fisheries (So et al. 2015; Vu et al. 2021), but are threatened by river developments that disrupt fish migrations (Dugan et al. 2010; Mekong River Commission (MRC) 2017a; Ngor et al. 2018b; Ziv et al. 2012; Hughes 2024). The criteria and metrics proposed by Worthington et al. (2022) to assess global swimways, which include socio-economic, cultural and biological values (e.g. number of threatened migratory fish species), and the scale of migrations (see http://www.explorer.globalswimways.org/), were adopted for this study. These factors were used to determine the significance of specific parts of the river system as migration routes for freshwater fishes and highlight the importance of conserving and managing these resources. By applying this framework, the intention is to gain insights into the migration patterns of fish species within the Lower Mekong Basin and evaluate the potential applicability of the concept in this specific context, and its relevance in contributing to the management and conservation of these critical resources in large tropical rivers globally (Friend et al. 2023; Orr et al. 2012; Pittock et al. 2017). Several case studies of fish migration patterns are provided to underpin the complexity and diversity of fish migration patterns in the Lower Mekong River Basin.

The Mekong River

The Mekong River is a major waterway in Southeast Asia, originating 4,200 m above sea level in Eastern Tibet and flowing through China, Myanmar, Lao PDR, Thailand, Cambodia, and Vietnam (Figure 1). Within a drainage area of approximately 795,000 km^2, it flows ≈4,900 km before reaching its mouth in the Mekong Delta, where it discharges around 457 km^3 of water annually into the ocean (Liu et al. 2009; Mekong River Commission (MRC) 2005).

To assist understanding of the migration patterns in the Mekong, the basin is broken down into nine ecological zones based on hydrogeomorphological and biotic characteristics (Figure 1). The upper Lancang portion of the river (Zone 0), which stretches for ≈2,200 km in China, constitutes 24% of the entire catchment and contributes 15–20% of the total annual flow (Kondolf et al. 2018). Additionally, it supplies approximately half of the sediment carried by the river (Kondolf et al. 2018, 2022).

The Lower Mekong Basin (LMB: zones 1–8), comprising 76% of the catchment, features a mostly flat and wide landscape (Mekong River Commission (MRC) 2005), but there are two relatively steep sections between Chiang Sean to Pak Chom (Zone 1) and Khone Falls to Kratie (Zone 4) (Figure 2). Upstream of Vientiane and extending to the Chinese border (Zones 1 and 2), the river typically flows within a well-defined channel, except during extreme flood periods when extensive localized over-bank storage occurs. Downstream of Vientiane to the Khone Falls (Zone 3), the river is characterized by large areas of floodplain habitat that are inundated during the flood season (Figure 3). The region is marked by several major tributaries, such as the Mun River draining floodplain areas of Thailand to the west. Downstream of the Khone Falls the river flows in a narrow channel to below Kratie (Zone 4) and includes the 3S tributary system (Sesan, Sre Pok, and Sekong rivers) originating from the Vietnamese highlands to the east, which is a key tributary within the lower basin.

Downstream of Kratie, river hydrology is influenced by the Tonle Sap System and the Mekong Delta in southern Vietnam (Lamberts and Koponen 2008). The Tonle Sap Great Lake (TSGL) (Zones 6 and 7), situated in western Cambodia, connects to the Mekong River through the 130-km long Tonle Sap River. The TSGL is the largest wetland in Southeast Asia (Kummu and Sarkkula 2008a; Kummu et al. 2008) covering an area of ≈67,000 km^2 (Ahmed et al. 1998). During the dry season (October – May) water drains from the

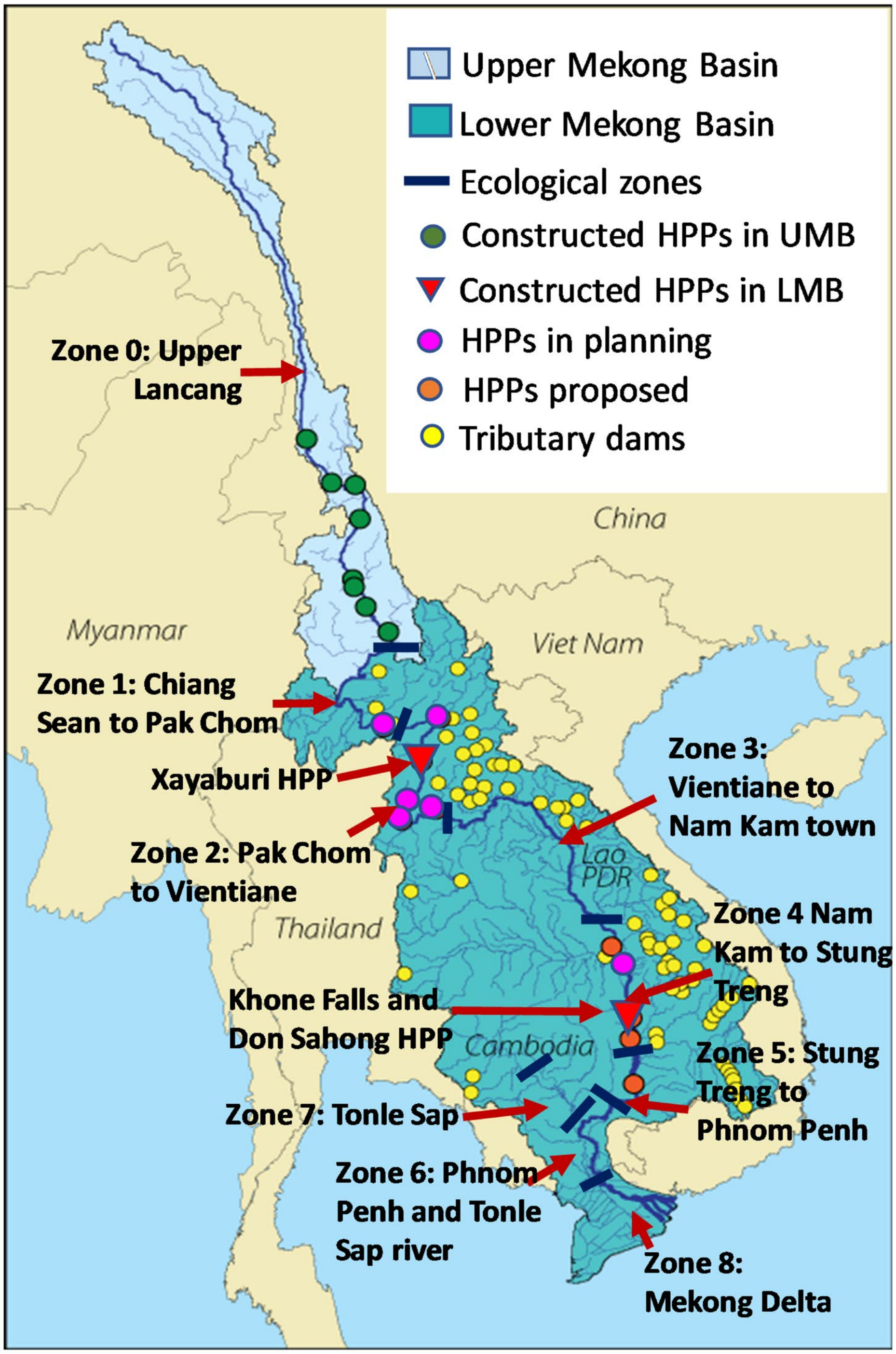

Figure 1. Mekong river basin showing main mainstem and tributary dams, and ecological zones.

TSGL into the Mekong River via the Tonle Sap River. As the wet season advances from June/July onwards, flooding in the delta downstream of Phnom Penh causes water levels in the Mekong River to rise higher than those in the TSGL. This causes flow in the Tonle Sap River to reverse and, instead of draining into the Mekong River, the waters are pushed back upstream toward the TSGL, inundating its floodplains. At the flood peak, the aerial extent of the lake increases by between three and six times from ≈3,500 km^2 during the dry season to ≈14,500 km^2 at the height of the wet season (Kummu and Sarkkula 2008a). Over this same period the lake volume increases from ≈1.5 to 60–70 km^3. Toward the end of the flood, backed-up waters in the TSGL and concurrently subsiding water levels in the Mekong River, cause flow in the Tonle Sap River to reverse once more. The waters are then carried out of the lake into the Mekong River and toward the delta. This natural mechanism provides a vital function, ensuring a flow of fresh water into the

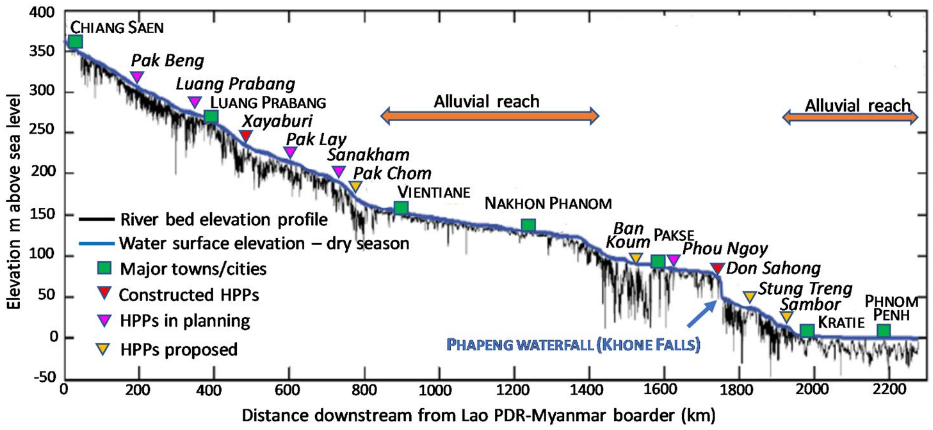

Figure 2. Thalwag longitudinal profile of the LMB showing occurrences of deep pools in relation to location of proposed hydropower dams (modified from Mekong River Commission (MRC) 2011).

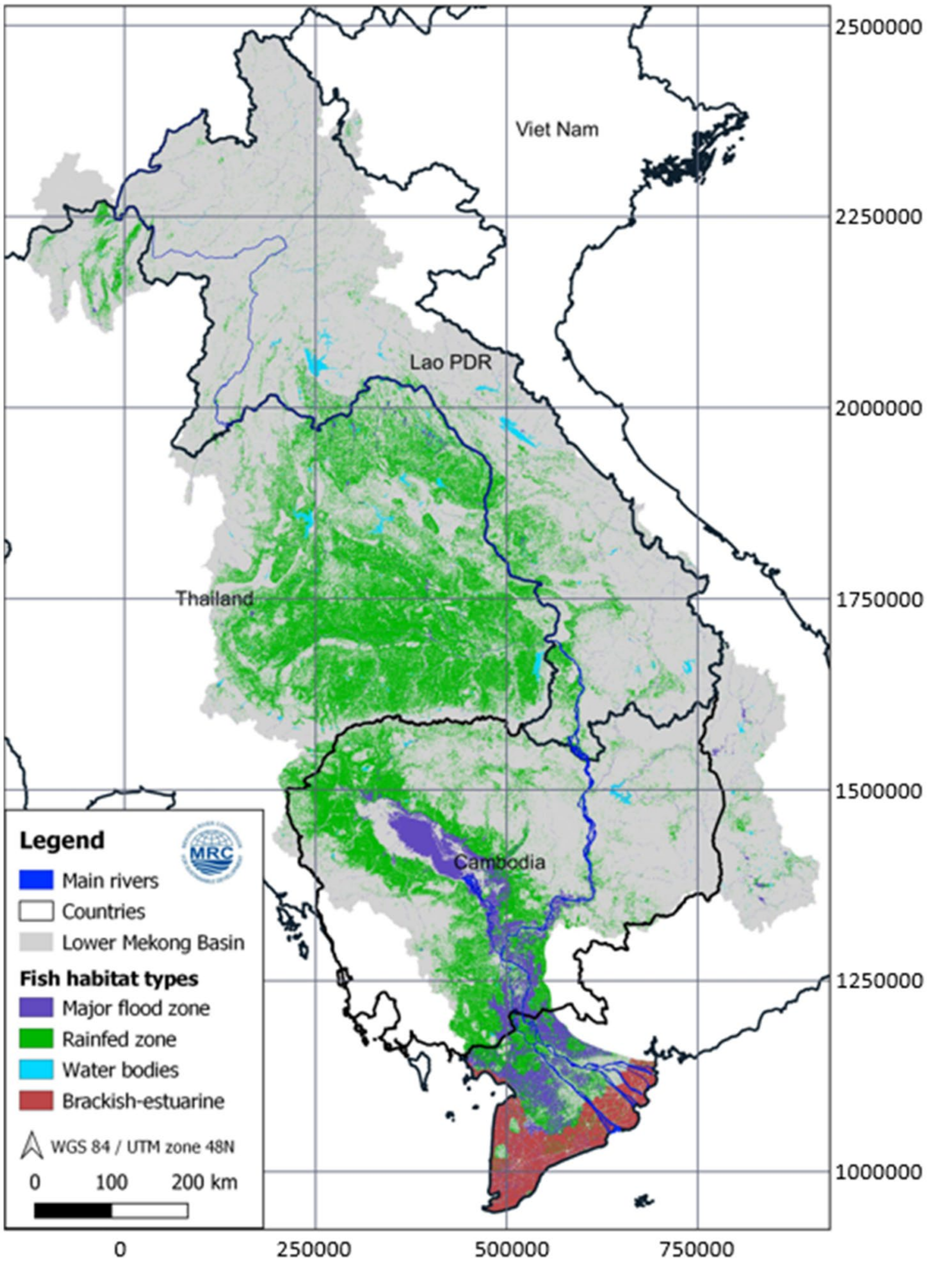

Figure 3. GIS map showing the distribution of major wetlands in the Lower Mekong Basin (*source*: Mekong River Commission (MRC) 2023a).

delta during the dry season, along with nutrients and sediments vital for productivity. This freshwater flow helps prevent saltwater intrusion into the fertile agricultural lands of the delta (Mekong River Commission (MRC) 2010).

Two key features of the LMB are the considerable alluvial floodplains in the Thai-southern Lao PDR zone upstream of the Khone Falls (Zone 3) and through Cambodia (Zones 5, 6 and 7) and the Vietnamese Delta (Zone 8) (Figure 3), and the propensity of deep pools along the thalweg, particularly in the steep sections between Chiang Sean and Kratie (Figure 2) (Halls et al. 2013). These are critical for the ecological well-being of the fisheries resources of the river, and act as refuge, nursery, feeding and reproductive habitats for different fish species depending on their life history strategies.

Recent changes in climate patterns, flow regulation, and sediment extraction have, however, disrupted the natural flow regime and geomorphology of the Mekong River. The delta region is sinking, leading to increased saline intrusion (Schmitt et al. 2017). These factors pose significant challenges to the river ecosystem and the communities dependent on it (Loc et al. 2021; Renaud et al. 2015). These factors are also particularly damaging to migratory fish communities.

Species diversity in the Mekong River Basin

Mekong fish communities are characterized by high species diversity, and the Mekong River is the third most speciose river system after the Amazon and Congo (Winemiller et al. 2016). Various studies have estimated between 1,200 and 2,000 fish species in the Mekong River (Campbell et al. 2006; Coates et al. 2003; Mekong River Commission (MRC) 2009; Kano et al. 2013; Rainboth 1996), but much depends on whether marine species are included in the inventory. The MRC Council Study (Mekong River Commission (MRC) 2017a) listed 1,133 species, but after inclusion of new species based on recent literature (Jerde et al. 2021; Kano et al. 2013; NAGAO 2021; Praxaysombath et al. 2021; So et al. 2018; Tedesco et al. 2017; Tran et al. 2013) and searching FishBase (Froese and Pauly 2022) and species from the upper Lancang (Chinese) reach of the Mekong, plus removal of synonyms this was updated to 1,393 species, of which at least 293 (21.0%) are considered truly migratory (Supplementary Table 1 – *Mekong Fish Species list*). This information was used to assign the status, distribution (zone, habitat type) and ecological traits (feeding, reproduction, migration) of each fish species in the database. These data were cross-checked for accuracy by national and regional experts.

To support the analysis, a classification system has been developed for the Mekong based on Welcomme et al. (2006) that categorizes fish species into ten broad guilds based on migration tactics and habitat associations (Table 1; Mekong River Commission (MRC) 2017a). The species guilds are broken into migratory (anadromous; catadromous; potamodromous, long-distance main channel and tributaries residents; potamodromous, short-distance main channel & tributaries spawners and potamodromous; floodplain spawners [grey fishes]), marine and brackish water species (estuarine resident and amphidromous; marine migrant) and non-migratory (rhithron resident; floodplain resident [blackfish] and eurytopic). An additional category is added for non-native species. The latter is because non-native species introductions and subsequent invasion is a pressure on the fisheries in its own right, and prominence of invasive species can indicate, amongst others, heavy fisheries exploitation, a deterioration of habitat quality or escapes from aquaculture systems. It should be noted that many of the new species are small endemics found in headwater and small streams (e.g. Kottelat 2001, 2016;; Rainboth 1996) and from the upper Lancang system in China (Li et al. 2019); and some of these have yet to be categorized into an appropriate guild.

Fish distribution in the Mekong River based on the MRC Fisheries Abundance and Diversity Monitoring (FADM) database for the years 2018–2022 (Mekong River Commission (MRC)) 2023a) exhibits a well-defined zonation pattern with different species assemblages in various zones along the river (Figure 4A). The zonation pattern is confirmed by average linkage cluster analysis based on the species assemblage in each zone using the Jaccard index, (Supplementary Figure 1), although Zones 2 and 3 supported similar species, as does the Tonle Sap system (Zones 6 and 7). Rhithron species dominate the species assemblages in the upper zones 1-4 followed by potamodromous species (both long and short-distance white and grey fishes), but generalists and black fishes become more prominent in the lower floodplain reaches of Cambodia and Vietnam (Zones 5, 6 and 7), and finally amphidromous and marine resident species predominate in the Mekong delta (Zone 8). By contrast, potamodromous species dominate the catches with the exception of the Mekong delta where amphidromous and marine resident species contribute the greatest part of the catch (Figure 4B). Of concern is the high proportion of

Table 1. Definitions of migratory patterns and guilds assigned to fish species inhabiting the Mekong River basin (a full species list is provided in Supplementary Table 1).

Guild name	Potential range of habitat used and typical characteristics	Number of species
Migratory		293
Anadromous	• Majority of life in marine or estuarine habitats: species migrate to fresh water mostly as adults (obligate or opportunistic) to breed. • Impacted by river dams that stop migration both upstream and downstream migration.	3
Catadromous	• Majority of life spent in fresh water: migrate to the sea to spawn. • Juvenile or sub-adult migration to freshwater habitats, often penetrating far upstream. • Vulnerable to overexploitation and tend to disappear when river is dammed preventing longitudinal upstream migration.	4
Potamodromous, long-distance main channel & tributaries resident	• Majority of life spent in main river and larger tributaries, migrating upstream to spawn. • Long distance migrations up to 1500 km within main channel; spawning in the main channel upstream.	20
Potamodromous, short-distance main channel & tributaries spawner	• Shorter distance migrations between 100 and 300 km within main channel and tributaries. • Spawn in the mainstream, in tributaries and around floodplains. • Adults and drifting larvae return to floodplains to feed. • May migrate to deep pools in the mainstream during the dry season.	146
Grey fish: potamodromous, floodplain spawner-	• Undertake migrations from floodplain feeding and spawning habitat to refuges (deep pools) in the main river channel during the dry season. • Differ from main channel spawner in that spawning occurs on the floodplain with main channel used as refuge during dry season. • Sensitive to damming and disconnection of floodplain habitat.	120
Marine brackish water		493
Estuarine resident amphidromous	• Limited migrations within the estuary in response to daily and seasonal variations in salinity. • Usually confined to the brackish part of system although some incursion into freshwater habitats • Includes stenohaline species that inhabit freshwater component of estuarine system.	178
Marine migrant	• Enter estuaries opportunistically.	315
Non-migratory		459
Rhithron resident	• Resident in rapids torrents, rocky areas and pools in the rhithron, mostly in upstream areas. • Generally insectivorous, algal scrapers or filter feeders, small in size, lithophilic or phytophilic with extended breeding seasons and suckers or spines to maintain position in the flow. • Limited migrations • Little or no impact from dams on migration, but potentially high impact from flow regulation due to exposure of riffle areas and inundation of upstream habitats.	357
Floodplain resident (blackfish)	• Limited migrations between floodplains, pools, river margins, swamps, and inundated floodplains. • Tolerant to low oxygen concentrations or complete anoxia. • Often repeat breeders, phytophils, nest builders, parental care or live bearers. • Vulnerable to loss of lateral connectivity and reduced flooding of floodplain	57
Eurytopic generalist	• Limited non-critical migrations in mainstream. • Highly adaptable, often tolerant of low oxygen concentrations. • May be semi-migratory often with sedentary local populations; may seek refuge in deep pools during dry season. • Often repeat breeders or breed during both wet and dry seasons sometimes with nests and parental care. • May undertake lateral migrations to floodplains to occupy habitats during flooding.	45
Non-native		49
Non-native	• Throughout river system, especially main channels and larger tributaries • Often introduced for aquaculture • Tolerant to habitat degradation and exploit modified habitats at expense of indigenous species.	49
Not allocated guild		99
Total species		1393

non-native species, mostly common carp (*Cyprinus carpio*), in the catch in the upper Lao PDR (Zones 1 and 2) of the LMB.

The diversity and zonation of fish species assemblages is largely due to the occurrence of a wide range of permanent and seasonal habitats, which result from the interaction of the hydrological cycle and complex geology of the basin. In particular, the vast floodplains (Figure 3; see Supplementary File 1_*Zonal species diversity in the Mekong River Basin* for detailed information on underlying characteristics of the fish zonation pattern) created by the annual flood-pulses are highly productive ecosystems, and support a wide diversity of fish and other aquatic animals. Most fish species depend on different habitats at different life stages and during different seasons, and thus should be considered migratory. During the flood season many fish species take advantage of the floodplains for feeding, breeding and rearing their young. Outside the flood season, fish stay in dry season refuge habitats, mainly in permanent lakes and deep pools (Figure 2) or within deeper river channels.

Characterizing migration patterns of fish species in the Mekong

Migratory species make up a substantial proportion of the fish assemblage in the Mekong basin (at least 293 of 1393 species; Table 1), with considerable differences in their contribution to biodiversity and yield

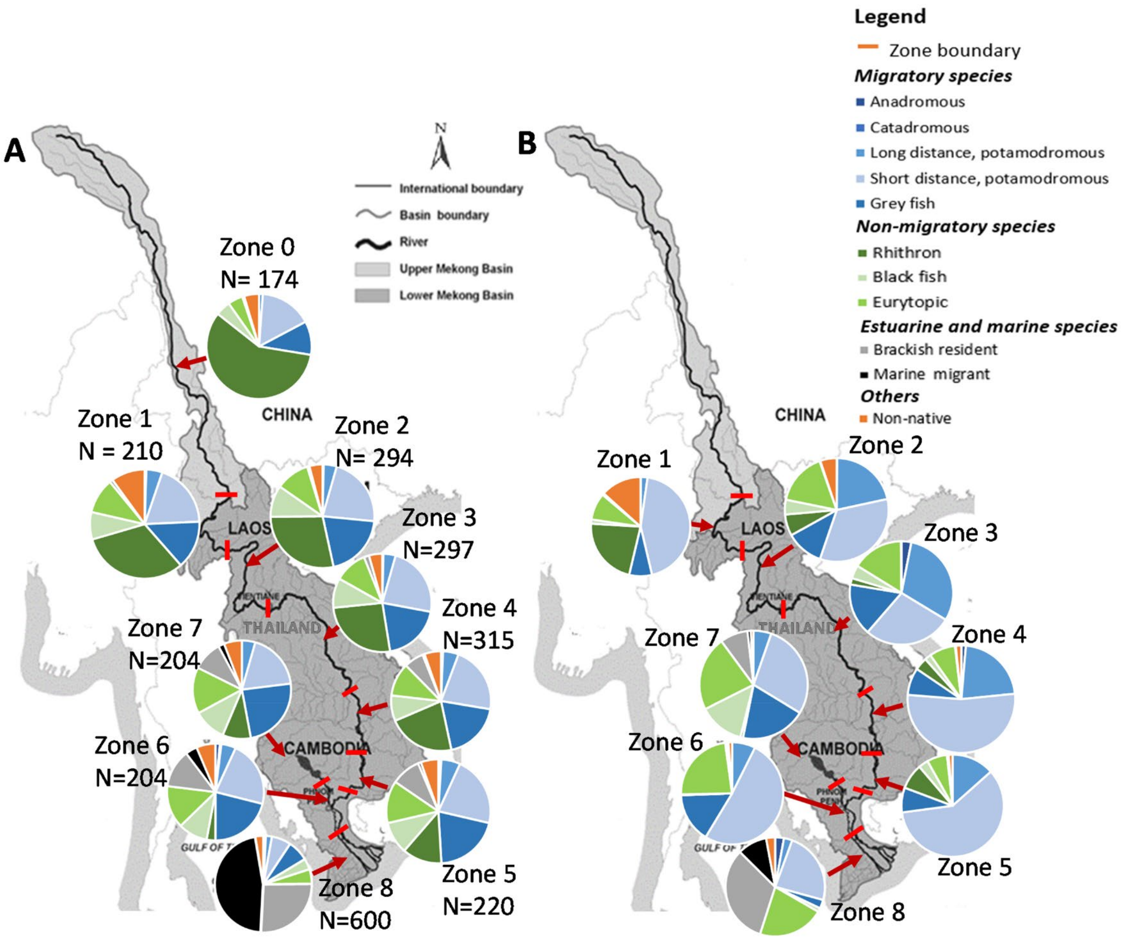

Figure 4. (A) Zonal distribution of fish species presence (*N*= number of species reported). (B) Contribution of different fish guilds by weight to catch in different ecological zones (b based on MRC catch monitoring surveys: MRC Council Study 2017a). Data provided in Supplementary Tables 2 and 3, respectively.

between different river zones (Figure 4A,B). The number of migratory species in the current assessment in different regions of the Mekong is considerably greater than enumerated under the Global Swimways project (see http://www.explorer.globalswimways.org/), which indicated 11–20 migratory species in the Lancang region (Zone 1), 21–30 species in the upper Lao PDR region (Zones1, 2 and 3) and 31–61 species in the lower reaches (Zones 4–8). This is likely because of the in-depth review of species ecological characteristics, and inclusion of potamodromous floodplain spawning species plus amphidromous migrants. The lower number of migratory species enumerated under the Global Swimways project and the Living Planet Index for Migratory Freshwater Fishes (Deinet et al. 2020, 2024; and listed under IUCN Redlist has considerable implications for protection of migratory species that are possibly the most vulnerable category of freshwater fishes in inland waters. There is an urgent need to undertake in-depth analysis of the prevalence and status of migratory freshwater fishes in major drainage basins of the world, such as carried out here for the Mekong or in the Amazon (Herrera-R et al. 2024).

Fish migration patterns in the Mekong are generally characterized into three main systems (Figure 5). The upper system, upstream from the Loei River, comprises mainly Zones 0 and 1. Here fish migrate upstream to spawning habitats both in the main channel and tributaries during the wet season to return later to their dry season habitats along the main river and larger tributaries (van Zalinge et al. 2004). The middle system stretches from the Loei River downstream to the Khone Falls (Zones 2, 3 and part 4). In this system, fish generally move upstream during the wet season on the rising water, and enter the tributaries and their associated flooded areas for spawning and feeding. During receding flows, they leave the tributaries and return downstream to dry season refuges in the main river channels. The lower system, downstream from the Khone Falls, includes the Tonle Sap River and Great Lake system in

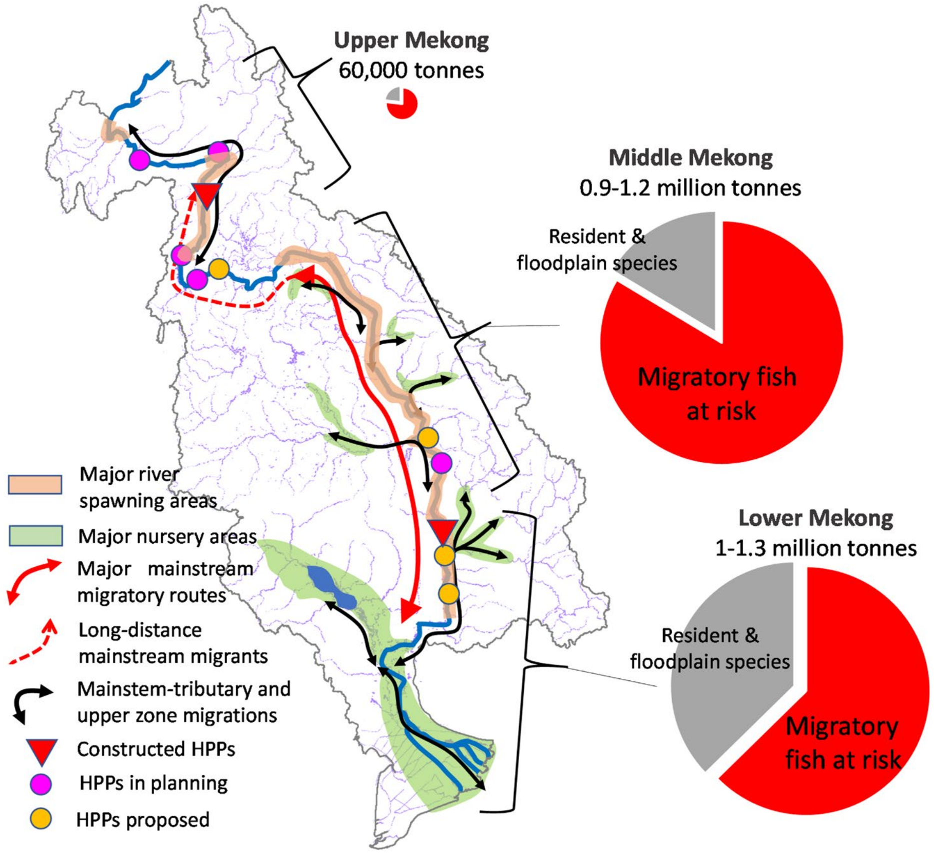

Figure 5. Map of fish migration systems in the Lower Mekong Basin. The pie charts present the proportion of migratory and non-migratory fish in the catches at risk from hydropower development in the three migration systems.

Cambodia and the Mekong Delta in Vietnam (Zones 4 [part], 5, 6, 7 and 8; also see Case Study on lower Mekong migratory super swimway). In this system, fish migrations are not just longitudinal movements upstream into the tributaries, including the Tonle Sap and 3S rivers, and then returning to the main Mekong River during the low flow periods, but include lateral movements onto the floodplains during the flood season. Further, a number of species spawn around dry season refuges, often in deep pools, at the onset of the wet season as water levels rise.

Timing of upstream and downstream migrations is variable depending on fish species life cycles, but importantly there is continuous spawning throughout the year with peaks during the spring (February-March) followed by onset of floods (June-July) and when flows are receding (November) (Supplementary Figure 2). Many of the abundant species caught in the Mekong floodplains spawn around the beginning of the flood season. Flood-related spawning results in fish larvae and fry growing at a favorable time, when available aquatic habitat is expanding and zooplankton (the essential food for most fish larvae) becomes abundant. These spawning periods are associated with continuous capture of larval and juvenile life stages in drift samples (although the main peaks are around the onset of the flood season) (Cowx et al. 2015), and therefore highlight the need to enable downstream drift of larvae throughout the year.

This behavior is strongly selected for in monsoonal ‘flood-pulse’ environments and onset of the flood pulse appears to be the cue for upstream migration (see case study on *Pangasius krempfi*). The primary cause for differences in timing of upstream migration is adaptation to changes in flow regime during each period of the year. Small- to medium-sized species (i.e. <50 cm total length, TL) are sensitive to discharge, and peak catches, hence movements, are between 2,000 and 4,000 m^3/s. Meanwhile large size species (>60 cm TL) are moderately sensitive to discharge at beyond 5,000 m^3/s, when catches are generally maximized (Baran et al. 2005). This characteristic should be taken into consideration when designing fish passage facilities, such that fish passes need to facilitate movement of fish of different species all year round and not just at the beginning of the wet season.

The classification of fish migration into three major zones hides many nuances about fish migratory pathways in the Mekong. Many species also migrate between these zones, and the majority are commercially important potamodromous and diadromous species (Poulsen et al. 2002, 2004; Vu, Baumgartner, Limburg, et al. 2022; Vu, Baumgartner, Mallen-Cooper, et al. 2022; Vu et al. 2023, 2024). Migration patterns for some species (e.g. *C. lobatus, H. siamensis*, *P. proctozystron*, *P. malcolmi*, *C. harmandi*, *P. conchophilus* and *Pseudolais pleurotaenia*) extend over long distances upstream, at least as far as Luang Prabang. *Pangasius krempfi*, an important commercial species, spends part of its life at sea and in brackish waters in the Mekong Delta before returning to spawn in fresh water (see case study on *Pangasius krempfi*). Other species, such as *Cirrhinus microlepis* and *P. larnaudii,* appear to undertake less-intensive migrations.

Linked to this, is an increasing awareness that many migratory species exhibit complex life cycles that involve a diversity of migration tactics (Vu, Baumgartner, Limburg, et al. 2022; Vu, Baumgartner, Mallen-Cooper, et al. 2022; Vu et al. 2023, 2024), and some species do not necessarily adopt a single migration pattern. These species, especially Pangasiid catfishes, can exhibit multiple tactics and potentially have sub-populations or genotypes (Duong et al. 2023). This is highlighted for *P. krempfi* in the case study, which has four migratory patterns, and potentially independent populations (Vu, Baumgartner, Mallen-Cooper, et al. 2022). These patterns are also found in, for example, *Plotosus canius, Polynemus melanochir* and *Hilsa kelee*, which appear to exhibit four, four and three migration patterns, respectively (Vu, Baumgartner, Mallen-Cooper, et al. 2022). Such plasticity in migratory patterns within different species was first recognized by Sokheng et al. (1999) who argued that they may represent different stocks or populations that occupy different zones in the river. This is highlighted using descriptions of migratory behavior of two species from different guilds, viz *Yasuhikotakia (Botia) modesta* (Eurytopic generalist) and *P. jullieni* (Potamodromous, short-distance main channel spawner) (Supplementary File 1_*Zonal species diversity in the Mekong River Basin*) coupled with the in-depth information provided in the case studies on *P. krempfi* and the lower Mekong migratory super swimway.

This existence of multiple stocks of the same species in different reaches of the LMB has been confirmed using molecular genetics techniques (Adamson and Hurwood 2016; Hurwood et al. 2006). For example, *Henicorhynchus siamensis, and Henicorhynchus lobatus* were believed to be from the same stock because they are morphologically similar, but mitochondrial DNA results indicate that three separate stocks of *H. lobatus* and four stocks of *H. siamensis* exist in different reaches or tributaries of the LMB. Such genetic diversity arises because mixing between stocks/populations is limited, either because of the coexistence of separate breeding populations or isolation between locations due to natural barriers such as water falls or artificial barriers (Adamson and Hurwood 2016; Raeymaekers et al. 2009). Consequently, it is likely that multiple swimways exist for these and other species, many of which have yet to be appreciated or fully understood.

Information on actual spawning habitats for migratory species in the Mekong Basin is described for only a few species, e.g. *Probarbus* spp. and *Chitala* spp., mainly because these species have conspicuous spawning behavior at distinct spawning sites. For most other species, in particular for deep-water mainstream spawners such as catfish species, spawning is virtually impossible to observe directly. Information about spawning is instead obtained through indirect observations such as presence of ripening eggs in fish and identification of spawning areas from larval drift studies (Cowx et al. 2015). Spawning habitats are generally believed to be associated with: (1) rapids and pools of the Mekong mainstream and tributaries; and (2) floodplains (e.g. among certain types of vegetation, depending on species). River channel habitats are, for example, used as spawning habitats by most large pangasiid catfishes and some large cyprinids, such as *Cyclocheilichthys enoplos, C. microlepis*, and *Catlocarpio siamensis*, which rely on particular hydrological conditions to distribute the offspring (eggs and/or larvae) to downstream nursery habitats (see Cowx et al. 2015). Floodplains are used as spawning habitats, mainly by laterally migrating potamodromous (grey) and floodplain resident species and eurytopic species (Poulsen et al. 2002). Fishes that spawn in main river channels are believed to occur in stretches where there are many rapids and deep pools, e.g. (1) the Kratie–Khone Falls stretch; (2) the Khone Falls to Khammouan/Nakhon Phanom stretch; and (3) from the mouth of the Loei River to Bokeo/Chiang Khong.

At least 23% of the freshwater fish assemblage (excluding estuarine and marine migrants and non-natives) in the Mekong Basin (Table 1) are considered non-migratory fish species. Nevertheless, it should be recognized that many of the adult forms of these species, which are represented by rhithron, eurytopic and floodplain resident fish species, undertake movements, albeit likely short distances. Rhithron species, for example, may move between fast-flowing riffle areas and deeper pools in the dry season to seek refuge habitat. Similarly, floodplain resident fishes inhabit permanently flooded wetland areas that may be disconnected from the river system for several years at a time, but will migrate onto the floodplain to spawn if the system floods (Welcomme et al. 2006). Also, eurytopic fish species adopt highly flexible life history strategies to adapt to changing environmental conditions in habitats they occupy. This may include making movements between habitats to survive stressful conditions or improve their reproductive capacity. Thus, they also potentially undertake movements, but are not necessarily linked to reproductive or feeding tactics. About 35% of non-migratory species in the Mekong are listed on the IUCN Red List (IUCN (International Union for Conservation of Nature) 2022; Supplementary Table 4), and most are rhithron species often found in upland areas and headwaters of tributaries. Considerable knowledge gaps remain for these species, especially about movement patterns of eggs and larvae. If these fish exhibit significant "drifting" phases during early life, then swimway management needs to protect these important, and fragile, life stages.

To summarize, the timing of upstream and downstream migrations is variable depending on fish life cycles, but appears to be driven mostly by the flood cycle (Supplementary Figures 2 and 4). Importantly, there appears to be continuous migration in the river throughout the year, with peaks during the pre-flooding season (February–March), followed by the onset of the flood (June–July) and then when the water is receding (November). To complete these migrations requires unobstructed passage upstream as well as the capacity for adults, larvae and juveniles to migrate or drift downstream, and maintenance of connection to floodplain habitats as nursery and refuge habitats.

Social and economic importance

Fish and other aquatic animals [OAAs] (e.g. amphibians and crustaceans) have been exploited for centuries in the Mekong Basin, and these natural resources are essential to livelihoods of 70 million people, where 70% of communities are rural, and rice farming and fishing are primary occupations. The LMB is considered the biggest and most valuable inland fishery in the world (So et al. 2015). Total fish catches in the LMB have exceeded 2.3 million tonnes annually (2010) worth up to USD 11.5 billion (So et al. 2015), but more recently (2020) have fallen to 1.51–1.71 million tonnes, valued at USD 7.1–8.4 billion (Mekong River Commission (MRC) 2023a). In addition, OAAs can contribute up to 20% of the aquatic products caught (Mekong River Commission (MRC) 2023a; Hortle 2007). Beyond the importance of these fish, fisheries and OAAs to global biodiversity, and to local communities and national economies, their value should also be judged by their replacement cost, profitability, contribution to food security and nutrition (Ainsworth et al. 2021; Beard et al. 2011; Mekong River Commission (MRC) 2010; Orr et al. 2012). The livelihood benefits of the resource, in terms of nutrition, income and employment, is vital, particularly for the rural poor, who have few other livelihood options.

Fisheries supply 49–82% of the animal protein consumed in the LMB depending on region. Average per capita consumption is estimated at 45.4 kg, with Cambodia having the highest level at 52.4 kg/capita/year, followed by Vietnam (49.5 kg/capita/year), Thailand (46.9 kg/capita/year) and Lao PDR (43 kg/capita/year). These are amongst the highest rates of fish consumption in the world, with other animal food sources assume comparatively lesser importance in regional diets (Hortle 2007). Fish also have high levels of essential minerals (i.e. calcium, iron and zinc) and vitamins essential to human health (Golden et al. 2019; Hicks et al. 2019).

As previously indicated, between 40 and 70% of the catch is dependent on fish species that migrate long and short distances along the Mekong mainstream and into its tributaries (Figure 5; Barlow et al. 2008), and these fish stocks are especially vulnerable to dams built in the middle and lower Mekong basin. Of particular importance are the small-sized fishes that migrate throughout the Tonle Sap, Cambodian floodplain, Mekong Delta system (see case study on Mekong Super-highway).

Conservation status

Many native Mekong fish species (113; 15.0% of fish evaluated) are listed as threatened based on the IUCN Red List (IUCN (International Union for Conservation of Nature) 2022). This includes 24 Critically Endangered species, 32 Endangered and 57 Vulnerable (Supplementary Figure 3; Supplementary Table 4); and many are iconic species, such as the Mekong giant catfish (*Pangasianodon gigas*) and giant barb (*C. siamensis*). The majority of species inhabit the middle and lower reaches of the LMB (Zones 3–7), whilst those found in Zone 8 are mostly of marine origin. Thirty species (2%) are Near Threatened and 609 (49%) of Least Concern; the remainder are either Data Deficient (228 – 18%) or Not Evaluated (262 – 21%).

Of particular concern are the large number of migratory species amongst the threatened species (Figure 6; Supplementary Table 4): 35% threatened in the Red List compared with 23% diadromous and potamodromous migratory species [i.e. not including marine migrants and amphidromous estuarine species as migrants] in the Mekong fish assemblage. These species need free movement in both upstream and downstream directions to complete their life cycles.

Threats to migratory fishes and disruption of swimways

It is well established that the Mekong fish assemblage and fisheries are intrinsically linked to the hydrological cycle (Kummu and Sarkkula 2008a), and that fish of different species groups (guilds) migrate up and downstream or laterally on to floodplains during different periods of the flood cycle, while others occupy permanent floodplain habitats and wetlands (Table 1). Maintaining these longitudinal and lateral migratory swimways and the river hydro-geomorphological characteristics are critical to protecting the aquatic biota in this biodiversity hotspot (Cooke et al. 2024). It is important that the diversity of migratory tactics among and within species and life stages are considered. Migration is not simply an 'adult' life stage trait in the Lower Mekong. There are complex requirements to access spawning, feeding and nursery habitats across the entire life cycle – see case studies to understand these complexities of individual species migration patterns. Many species also have drifting egg and larval stages that need protection (Cowx et al. 2015). These are all important considerations when conceptualizing swimways in biodiverse and hydrologically variable systems, typically found in large tropical rivers. The fish and fisheries and other aquatic animals are, however, under heavy pressure from rapid economic development, especially agriculture, hydropower, industrial expansion and mining, and a growing human population (Mekong River Commission (MRC) 2019a), all of which are already impacting on the complex Mekong swimways network (see cases studies). In addition, climate change is beginning to have profound effects on the Mekong ecosystem, the implications of which have yet to be fully explored (Mekong River Commission (MRC) 2022b).

Hydropower

Hydropower development is considered one of the biggest threats to fisheries in the Mekong River basin (Dugan et al. 2010; Winemiller et al. 2016; Mekong River Commission (MRC) 2017a). There are six dams in the Upper Mekong with a further seven in commission or under construction, plus a further seven dams in the middle-lower Upper Mekong in Yunnan Province. As of 2019, there were 89 completed hydropower projects in the LMB, with the majority in Lao PDR (65), plus two in Cambodia, seven in Thailand and 14 in Vietnam. A further 44 are in construction or at the planning stage (Mekong River Commission (MRC) 2022a).

The ecological impacts of dams in the LMB have been well documented in the context of hydropower (e.g. Baird and Hogan 2023; Campbell and Barlow 2020; DHI and HDR 2015; Dugan et al. 2010; Mekong River Commission (MRC) 2017a; Ziv et al. 2012). The immediate impact is the barrier created by the dam infrastructure and impoundment, preventing migratory fishes from completing their life cycles, usually because they are isolated from their spawning and nursery areas.

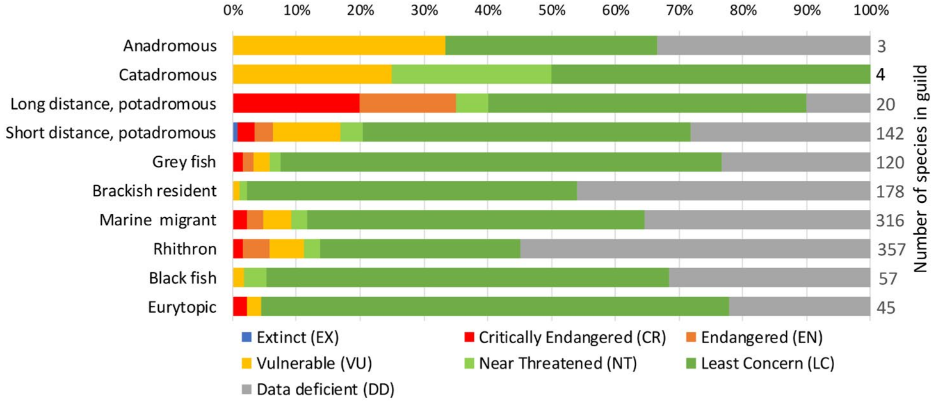

Figure 6. Breakdown of contribution of each IUCN Red List status in different guilds (values to right of bars are the number of fishes in each guild).

Movement of fish past dams is particularly critical because fish passes are rarely integrated into large dams in the LMB, and current fish passage technology is not considered practicable to cope with either the volume of fishes or diversity of species required to bypass the larger hydropower dams in the LMB (Mekong River Commission (MRC) 2019b). Whilst ongoing research is being carried out to test this precept at Xayaburi and Don Sahong where fish passage solutions have been constructed or channels modified to facilitate passage (Mekong River Commission (MRC) 2022a), the insurmountable problem in the LMB is that most dams have not been fitted with fish passage facilities. Consequently, most of the major tributaries are disconnected from the mainstem river. For example, the Nam Ou has two hydropower dams completed and a further four in planning or construction and none has a fish pass fitted. This will completely disconnect the Nam Ou, a major tributary in northern Lao PDR, from the mainstem Mekong. Even where fish passes have been incorporated into the dam, e.g. Pak Mun and Lower Sesan 2 [LSS2], they are poorly designed. This fragmentation is illustrated by the WWF flowing rivers modeling for the LMB (Grill et al. 2014, 2019, 2022) (Figure 7), where the upper reaches (Zones 1, 2 and 3, and major tributaries) are severely fragmented and effectively block migratory routes.

Impounding the river will also have a range of impacts on aquatic biota and fisheries immediately upstream, especially because impoundments extend considerable distances upstream (≈98 km for Xayaburi hydropower dam). Impoundments potentially drown out spawning and nursery habitats of migratory species, which tend to disappear if other suitable spawning habitats are not available further upstream or in adjacent tributaries. Perhaps the most profound effect arises from the shift from a riverine to lacustrine environment. This inundation changes the hydraulic conditions of the river environment and results in loss of rapids and fast flowing sections of river, as well as deep pools. Of particular concern is the impact on rhithron, potamodromous (both long and short distance migrators) and floodplain spawning [grey] species, which make up the majority of the catch. Flooding of the fast-flowing sections and regulation of flows downstream (see below), plus disruption of migration pathways, can be catastrophic, as was predicted by the MRC Council Study (Mekong River Commission (MRC)) 2017a) and elsewhere (e.g.

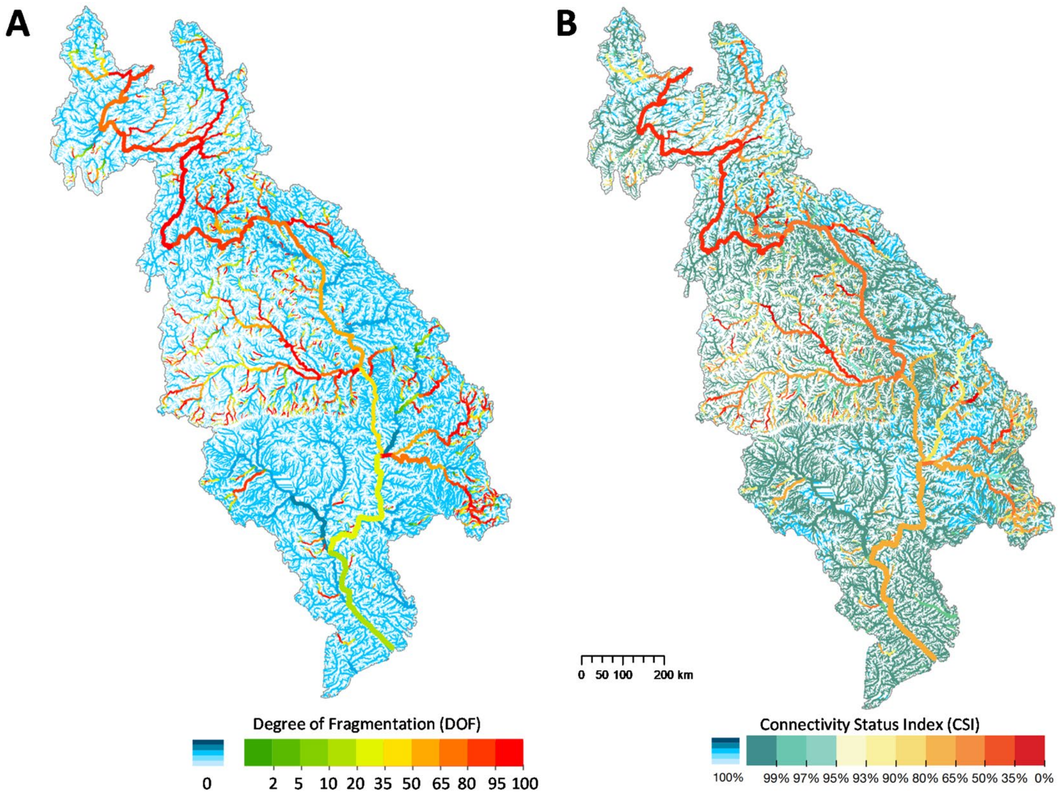

Figure 7. (A) Degree of fragmentation (DOF) caused by barriers in the LMB and (B) Connectivity Status Index (CSI) at the reach scale combining indices of Degree of Fragmentation, Degree of Regulation, Sediment trapping, Consumptive water use, Urban areas, and Road density (*Source*: Grill et al. 2022).

Mekong River Commission (MRC)) 2016). For example, fish catches are predicted to decline by up to 40%, mostly of migratory species, if the 11 mainstem dams on the LMB are constructed (Mekong River Commission (MRC)) 2017a). Rhithron species will be lost from impounded areas as these species require flowing water habitats (Birnie-Gauvin et al. 2017). In addition, individual species, such as the iconic and Critically Endangered Mekong giant catfish (*P. gigas*) and Jullien's carp (*P. jullieni*), and the anadromous species *P. krempfi* (see case study) are vulnerable to dam development. Mekong giant catfish migrate from the lower Mekong Basin to spawn in the Upper Mekong Basin at Ban Had Krai, Chiang Khong District, Chiang Rai Province, Thailand and northern Lao around Luang Prabang between the end of April to May, and construction of hydropower dams would obstruct this migration. Also, of concern is the proliferation of non-native species, particularly common carp, which comprise a high proportion of the catch in impacted areas (Figure 4B). It is likely these species will benefit from altered environments and expand further, possibly eliminating native species.

Impoundments also present problems to downstream migrating fishes. Many species (e.g. Pangasiid catfishes) are multiple spawners and need to migrate both up and downstream. Adults must bypass the impoundment and dam infrastructure in a downstream direction. They are impacted because they lose their migration stimulus of directed flow through large reservoirs and get stranded. They can also suffer considerable injuries and mortality passing through turbines, and be subjected to increased predation in stilling basins below dams. For hydropower dams, mortality from passage through turbines alone is especially significant; turbine losses of juveniles of 10-40% have been widely reported and mortality of large-bodied fish can be up to 100% (Mekong River Commission (MRC)) 2017a). Such factors are in addition to the imposed changes in discharge and water quality, particularly gas supersaturation, which affect all fishes within the riverine section below dams. In addition, Mekong fish species rely on drifting of eggs, larvae and juvenile life stages to downstream nursery and feeding areas to complete their life cycles (Cowx et al. 2015). A flow of >0.3 m/s is required to maintain larval fish in the water column as they drift downstream (Mekong River Commission (MRC)) 2017a, 2022b), but this water velocity is rarely maintained throughout the impoundment, especially in the middle sections of the large impoundments associated with mainstem hydropower schemes.

Below the dams, the effects are varied and usually relate to the manner in which the hydrology of the river is regulated in terms of timing and duration of flooding and low flow events as a result of the dam operation. All LMB mainstem dams are classed as run-of-river schemes generating power based on the natural flow regime, with inflows roughly matching outflows. The upstream impoundments only tend to hold sufficient water for 3–5 days generation (Mekong River Commission (MRC)) 2019c) but these schemes appear to operate a hydropeaking regime to meet peak demand (Mekong River Commission (MRC)) 2021b). As a consequence, rapid rises and falls in water level can occur over relatively short time periods (minutes), especially in the morning and evening, thus rapidly flooding or drying up critical habitat with little opportunity for aquatic biota to respond. By contrast, the majority of hydropower schemes in the tributaries and upper Mekong Lancang typically store large volumes of water for release during the dry season. Here the hydrograph is heavily modified, such that elevated flows are experienced in periods of naturally low water level conditions and reduced under flood conditions. The net outcome is that erosion and deposition processes are altered and seasonal flooding patterns modified; both resulting in deterioration of downstream habitat and disruption of longitudinal and lateral migrations. These effects may be transmitted considerable distances downstream.

In some cases, longitudinal migration of fishes is also compromised because environmental cues for migration (trigger floods) are lost, and passage over rapids, falls and other natural, partial obstructions to fish for considerable distances downstream are disrupted. Indeed, fishers downstream of Xayaburi hydropower report that some species, such as *P. jullieni*, are being caught at different times of the year than previously (N. Sukumasavin, pers. comm.), and this may be due to disruption of environmental cues for migration caused by the altered hydrological regime. Also, floodplain resident fishes that rely on floodplain inundation for breeding and replenishment of stocks are constrained and do not recruit successfully. Generally, the downstream fish community structure and population dynamics are altered and the fishery moves toward lesser catches of smaller, non-migratory species of lower economic value, as is being reported now by fishers downstream of Xayaburi and Don Sahong. This results in the need to change fishing methods, and reduction in catch and value of the fishery, leading to social and economic disruption, especially in rural fishing communities.

In addition, modification of river flows caused by hydropower developments is coupled with significant interruption to sediment and nutrient transport, undermining the general productivity of downstream reaches (Kondolf et al. 2018). Predicting the impact of such developments on fisheries is complicated because of problems discriminating the impacts of dams from other exogenous factors such as irrigation schemes, isolation of floodplains by embankments and water gates, especially for rice production, aggregate excavation, and heavy fishing pressure. Indeed, loss of sediment and associated nutrients is estimated to be equally responsible for declining fish populations as direct barrier effects (Mekong River Commission (MRC)) 2017a; DHI and HDR 2015). One other aspect of intercepting sediments by dams is the loss of nutrient delivery to the ocean. River sediment in the Mekong has been recognized as a key driver of ecosystem productivity in coastal areas of the South China Sea (known locally as the East Sea), which produces between 500,000 and 726,000 tonnes of fish per year, and can result in coastal erosion, loss of mangrove forests and declining fish stocks in coastal areas (DHI and HDR 2015).

Predictions indicate that basin-wide development of 77 dams in the Mekong would result in the loss of 550,000–880,000 tonnes of capture fisheries (ICEM 2010; Lymer et al. 2016), or 23%- 39% of the LMB catch reported in 2010. Estimates of fish loss in Cambodia and Vietnam from the 11 mainstem dams indicate that yield would be reduced by 238,377 tonnes and 358,514 tonnes respectively, which is equivalent to more than 40% of the catch in each country (DHI and HDR 2015).

Unsustainable exploitation of the fish and fisheries

Capture fisheries have grown rapidly in the LMB over the last 30 years, driven mostly by population growth, improved access (roads and boats) and the availability of low-cost fishing gears (e.g. monofilament gill nets). As a result, many fishers are now complaining about declining catches, change in fish species and sizes of fish caught, with the more valuable large potamodromous fish species becoming less common in the catch, and some species have become rare at some locations (Mekong River Commission (MRC)) 2019b, 2021a, 2023a). This is in part caused by fishing in deep pools (typically established as sanctuaries) in the Mekong mainstream and major tributaries all year round, in particular in the dry season when fish aggregate in these pools, coupled with illegal fishing activities, such as electrofishing, poisoning and explosives (Chan et al. 2020; Mekong River Commission (MRC) 2023a; Ngor et al. 2018c). Underpinning this problem is a massive increase in fishing effort to meet market demand, economic pressures on rural poor people who resort to fishing as a livelihood, and weak or ineffective enforcement of fisheries laws leading to declining fish catches and yield. In addition, changes in river geomorphology and functioning caused by development projects (navigation, sand mining, hydropower) and climate change, are impacting fish and aquatic production (Friend et al. 2023). This intensification of fishing effort, both legal and illegal, is targeting migratory fishes as they move throughout the river systems, ultimately disrupting recruitment processes and sustainability of these species.

Land use change and wetlands degradation

The third main pressure is linked to loss of wetlands, which has a profound impact on fisheries as they provide essential habitat for fish feeding, spawning and nursery grounds. Agricultural expansion, urbanization and other types of construction have caused a radical loss of wetlands or disconnection from the main river channels.

The most damaging change is from irrigated agriculture, especially for floodplain rice. This has disconnected critical floodplain habitats from fish production through the construction of flood control gates, mostly built without fish passage facilities, and levees, which isolate large areas of floodplain from the main river and tributaries (Figure 8). These development activities constrain lateral flooding and isolate floodplain lakes and other water bodies. They interfere with lateral nutrient interchanges and reduce overall productivity of aquatic and terrestrial systems. Flood control gates and levees also block lateral movements and migrations onto the floodplain and into major tributaries in the Mekong, as few are built with fish passage facilities or are operated to promote fish movements (Baumgartner et al. 2014, 2018, 2019). Flood control gates are particularly prevalent in the Mekong region of Thailand, and levee construction is widely distributed across the floodplain regions of Lao PDR, Cambodia and Vietnam (Figure 8). All have been associated with declines in stocks and catches (Vu et al. 2021).

Deforestation contributes to this process, resulting in proliferation of local erosion processes causing siltation of wetlands, choking of substrates, loss of food organisms and degradation of spawning sites for psammophilic and lithophilic fish species. Deforestation

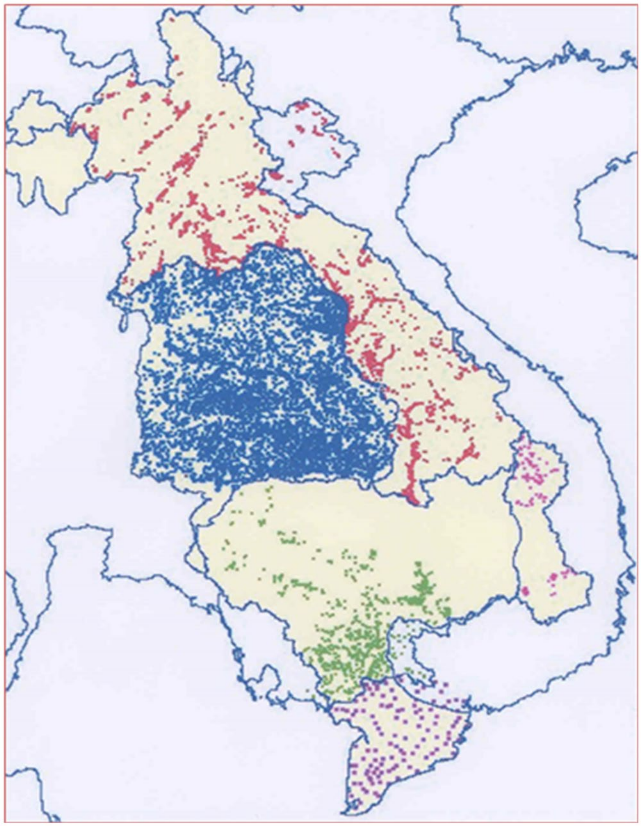

Figure 8. Location of water control structures across the LMB illustrating the scale of issues related to water resource management (*Source*: MRC 2019a).

also increases the amplitude between high and low water discharges, which may lead to drying out of portions of the river channel, making habitats unsuitable for some or most fishes. Deforestation is particularly notable around the Tonle Sap Lake flooded forest, which is being harvested for fuel wood and converted to agriculture land, including to produce low value products such as millet (Mekong River Commission (MRC)) 2022b). This is degrading critical habitat for many Mekong fish species, including migratory species, which use the flooded forest area as breeding and nursery areas.

Aggregate extraction

A hidden pressure on the fisheries resources is the large-scale extraction of aggregates (sand and gravel) from the river channel for construction. This problem is being exacerbated by sediment trapping by dams, especially in the Chinese portion of the Mekong (Lancang). Prior to dams being constructed on the Mekong mainstream (Lancang) in China, annual suspended sediment loads were estimated to be 60–100 Mt/yr. Since 2008, these loads have decreased to 10–20 Mt/yr (Mekong River Commission (MRC) 2022b), meaning that much less sediment is delivered to the lower reaches. This is compounded by large-scale river sand and gravel mining, with some 55 Mt removed annually, considerably more than is naturally transported in the system under the current damming regime (Hackney et al. 2021). This has caused channel incision, river bank collapse, and increased salt water intrusion, all of which reduce availability of key fish habitats, destroy spawning habitats and diminish lateral connectivity (Cooke et al. 2024). Of particular concern is the heavy aggregate extraction in Cambodia around the confluence of the Tonle Sap River (Hackney et al. 2021), which is having profound effects on the seasonal flooding patterns in the Tonle Sap Lake, and in the Vietnam area of the LMB, the latter causing the delta to sink and erosion of the coastal areas (Kondolf et al. 2022; Schmitt et al. 2017). Both are likely to negatively affect seasonal migration patterns that are linked to the flood pulse.

Climate change

Climate change is predicted to increase vulnerability of freshwater ecosystems in the Mekong region due to changes in precipitation, more frequent severe weather events, and prolonged droughts (Mekong River Commission (MRC) 2019a). Temperatures in the LMB are expected to increase by 3 to 5 °C by the end of the century (ICEM 2013). Rates of change in temperature are highest in the 3S catchment of Eastern Cambodia and in the Cambodian floodplain and Mekong Delta, where increases of 2 to 3 °C could be reached before 2050. Precipitation is projected to increase between 3 and 14% (35–365 mm) throughout the basin. Projections also indicate climate change will alter the Mekong hydrological seasons, with the wet season starting 1–2 wk earlier but also finishing 1–3 wk earlier. These stressors will further diminish the ability of the river to function, resulting in a loss of ecosystem integrity and fish production. Changes in extremes, including floods and droughts, are projected to disrupt fish recruitment and production, and exacerbate the decline in fisheries in the region. Capture fisheries are likely to be buffered to some extent against climate change by the large ecosystem diversity. Some species may benefit from changing conditions possibly maintaining fisheries productivity, while other less tolerant species may decline. This is likely to lead to a decline in overall biodiversity (ICEM 2013), although the more extreme floods could potentially increase productivity in large floodplain systems in Cambodia and Vietnam (Mekong River Commission (MRC)) 2017a). Higher flows during the wet season could benefit fisheries, but changes to flows in response to temporal changes in precipitation could disrupt the movement of migratory species (Mekong River Commission (MRC)) 2010).

Cumulative effects of environmental change on fish migration pathways

The impact of development in the LMB on fisheries has been well described in the context of hydropower (Campbell and Barlow 2020; Dugan et al. 2010), but less well developed with respect to other drivers, such and agricultural development (Vu et al. 2021), mining, pollution or climate change. The MRC Council Study (Mekong River Commission (MRC)) 2017a) has explored the impacts of multiple drivers on ecosystem functioning and aquatic biota across the LMB and explored the cumulative and transboundary impacts of different sectors, but especially hydropower and climate change. The Vietnamese Delta study (DHI and DHR 2015) further examined the impact of multiple drivers on the Vietnamese Delta area and Cambodian floodplain, but less has been done with respect to the impacts in Lao PDR and Thailand.

Case studies

The following case studies and an additional case study on the 3S river system (Supplementary File 2_*Sekong case study*) are provided to illustrate the complexities of individual species and multi-species migration patterns in the Lower Mekong Basin. They highlight the need to maintain both longitudinal and lateral connectivity as well as natural flow regimes in the basin to protect these valuable natural resources and ensure their contribution to food security and livelihoods is sustained.

Pangasius krempfi

Anadromous fish species, those that spend most of their life in marine waters but migrate considerable distances upstream into freshwater habitats to spawn, make good case studies to understand the impact of an array of pressures on swimways, not least the impacts of dams that block pathways to and from the ocean. Until recently, *P. krempfi* (Fang & Chaux) was the only species confirmed as anadromous from the Mekong River Basin (Hogan et al. 2007), but Vu et al. (2022a), using otolith microchemistry and review of available information, identified another anadromous species, *Pangasius mekongensis*, with similar migration patterns to *P. krempfi*.

Pangasius krempfi is an economically important species that is considered to spend most of its life in marine waters and then migrates to the Khone Falls and beyond to spawn. Its distribution has been mapped from fisher knowledge (Poulsen et al. 2002), fisheries assessment surveys carried out by the Mekong River Commission and associated agencies in the LMB riparian countries (Mekong River Commission (MRC)) 2022b), and from literature sources (Figure 9). The distribution *P. krempfi* is widespread across the LMB, including, importantly, in major tributaries, and the Mekong Delta and coastal areas, and as far upstream as Luang Prabang in northern Lao PDR. This distribution of *P. krempfi* in the mainstem Mekong and larger tributaries highlights the anadromous status of the species in the LMB. The migration patterns, however, are not a simple linear function from the marine environment to upstream spawning areas.

Using otolith microchemistry, Vu et al. (2022a) found *P. krempfi* exhibited at least three migration strategies, all based on spawning in freshwater riverine habitats (Figure 9). These were: (1) growing mainly in brackish waters (lower Mekong Delta) with little or no movement in either marine or freshwater areas (81% of individuals examined); (2) growing in brackish water within the estuary but with periodic movements into fresh water (15%); and (3) growing mainly in marine waters (4%) before returning to fresh water to spawn. These sub-populations spawn in the mainstem Mekong between Phnom Penh and Nong Khai (Tran et al. 2021), although they may also spawn as far upstream as Luang Prabang. Irrespective of migration strategy, most *P. krempfi* migrate upstream for a relatively short time for spawning, although some remain in the river for up to 2 years (Vu et al. 2022a). The length of time larvae and juveniles stay in fresh water before moving to brackish and marine environments is also variable with some larvae remaining in fresh water for about six months, before

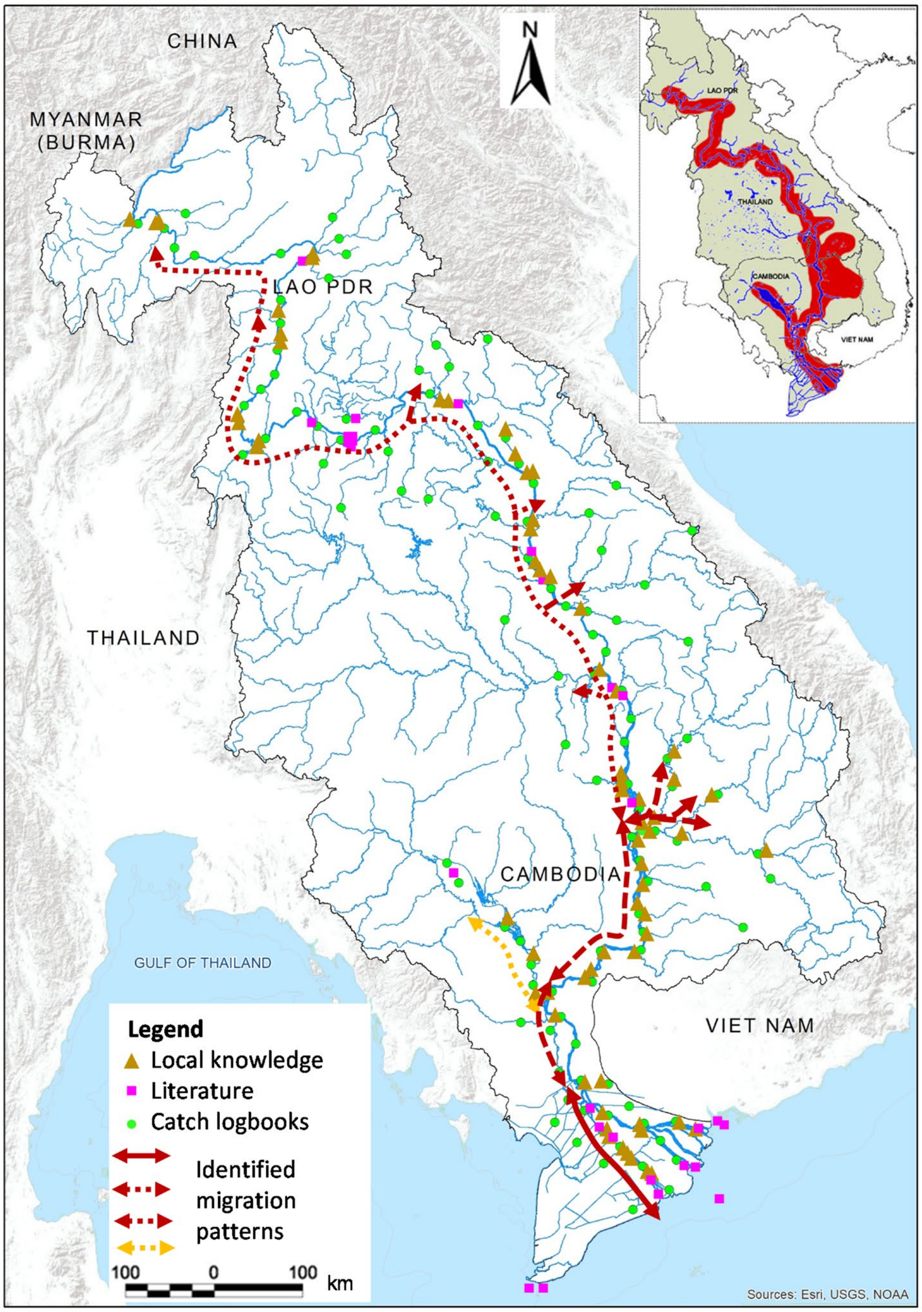

Figure 9. Reported distribution of *Pangasius krempfi* based on fisher knowledge, fisheries assessment surveys and published literature. Different colored arrows show different migration strategies of *P. krempfi* based on Vu et al. (2022a): growth is mainly in the Mekong estuary but some occupy coastal waters; all migrate long distances upstream into the Mekong River to spawn. Red lines represent main patterns: i.e. predominantly between the sea and delta (solid line); dashed between sea, delta and upstream to Cambodia-Lao boarder including 3S system; dotted upstream to northern Lao. Yellow dotted line represents minor migratory route into Tonle Sap system. Insert shows modeled distribution based on known records (after Poulsen et al. 2002).

moving to the Mekong estuary as a nursery habitat. This suggests their migration pattern is not just driven by larval drift in the early life stages and later upstream migration to spawn. Indeed, Duong et al. (2023) indicated that there are multiple genetic lineages of *P. krempfi* in the LMB, although they found no genetic differences between populations sampled in different parts of the LMB. These findings would support the conclusions on diversity of migratory pathways. In all cases, however, Duong et al. (2023) also stressed these patterns exhibit a long migratory pathway that needs to be protected to maintain the diverse genetic origins and complexities in the lineages of the species in the LMB.

Analysis of MRC fisheries monitoring data reveals a preponderance of *P. krempfi* in the catch in the Mekong Delta and coastal areas, the Cambodian floodplain system, including the Tonle Sap system, and the Champassak and Savanakhek areas (Zone 3) of southern Lao PDR. The numbers of *P. krempfi* caught in the Mekong declines the further upstream the species is distributed, but critically the species is caught in substantial numbers in the floodplain systems of southern Lao PDR and the main tributaries, especially the Sekong River (Supplementary File 2). There is a general increase in catches in Zones 2 and 3 at the start of the flood season (June-July), but also a consistent catch in the dry season in Zone 3.

The contribution of *P. krempfi* to the catches reflects the known distribution of feeding and breeding areas for the species in the LMB, but crucially highlights the importance of major tributaries to the life cycle of the species. Understanding the life history and migration patterns of *P. krempfi* provides valuable insights into the impacts of development activities on sustainability of the species. *Pangasius krempfi* is largely restricted to main channel habitats in the Mekong mainstem and major tributaries between the coastal region offshore from the Delta as far upstream to Luang Prabang, although there is a predominance in the Tonle Sap system and delta region. Thus, the species is vulnerable to pressures acting on the main channels rather than floodplain habitats. As a consequence, any modification or blocking of the main river channels through construction of hydropower or irrigation infrastructure, sediment extraction and modification of the channel for navigation, and modification of flow regimes brought about by these pressures, are likely to impact on *P. krempfi* populations. Of particular concern is the construction of large dams on the mainstream and major tributaries along its migration routes. These will likely see populations of *P. krempfi* collapse in the LMB, and extirpated from the middle and upper reaches of the Mekong in Lao PDR and Thailand. It is unclear whether climate change impacts on flows and the sinking of the delta will have any notable impact other than perhaps reducing the available habitat for individuals using the delta region for feeding and growth.

Lower Mekong migratory super-swimway

The Lower Mekong downstream from the Khone Falls to southern Cambodia, including the Tonle Sap system, 3S tributaries and the Mekong Delta in Vietnam (Figure 10), probably represents one of the most complex migration systems globally (Ngor et al. 2018a). This large-scale migratory network is in response to the spatial and temporal separation of feeding and rearing habitats during the annual flood cycle (Arias et al. 2013; Campbell et al. 2006; Kummu and Sarkkula 2008a; Ngor et al. 2018d; Sor et al. 2024). Fish typically migrate between upstream dry-season refuge habitats and fertile floodplain habitats in southern Cambodia and the Mekong Delta in Vietnam when they become available for feeding (Poulsen et al. 2004; Figure 10). As water levels on the floodplains, including the Tonle Sap/Great Lake system, start to recede, usually between mid-October and January, fish migrate toward refuge habitats, including deep pools (Figure 2) in the main channel along the Kratie to Stung Treng reach and the Sekong River (Lee et al. 2023). This epic migration comprises billions of fish, mostly small cyprinids, but also includes two of the largest and most endangered freshwater fish in the world: the Mekong giant catfish *Pangasianodon gigas* and the giant barb *Catlocarpio siamensis* (Hogan et al. 2001). Migration peaks around January and is associated the highest catch rates in the Dai fishery, a specialized, large-scale bag-net fishery, on the Tonle Sap river. As water levels begin to rise again, usually in April/May, fish initiate their upstream migrations toward spawning habitats located in the main channel of the river and its tributaries, including the 3S rivers (Figure 10; Supplementary File 2). Other species migrate laterally to spawn on or near the floodplain areas. Spawning of fish typically occurs in June or July. This timing corresponds with the flow reversal in the Tonle Sap when water backs up from the Mekong to fill the Great Lake, as well as the start of floodplain inundation. During this period, fish eggs and larvae, usually drifting passively with the flow of the water, and adults return to downstream floodplain habitats (Figure 10). Over a 10-year period, larvae and juveniles of 168 species belonging to 107 genera, 40 families, and 11 orders were recorded from larval drift

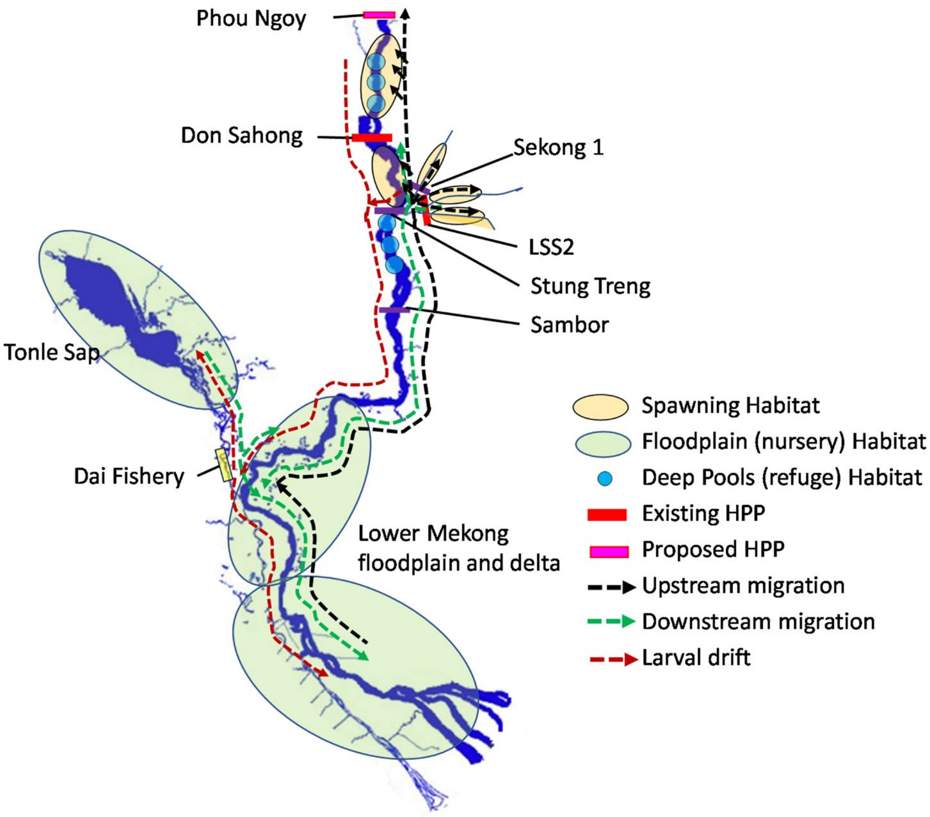

Figure 10. Graphic showing the transboundary lower Mekong migratory super swimway in Cambodia and Vietnam. Different colored lines represent upstream and downstream active migration and larval drift patterns.

nets set in the Mekong near Phnom Penh (Chhuoy et al. 2023). This drift and downstream migration facilitates colonization of downstream floodplain areas. The reversal of flow from the Mekong to the Tonle Sap also allows fish larvae and juveniles to enter the Tonle Sap and assists the movement of larval and juvenile toward the floodplain rearing areas. Once the drifting larvae and adults colonize downstream floodplain habitats, they begin to feed and grow (July - October). This growth phase continues until water levels start to fall again around October. Some fish species may, however, remain resident in the main channel or on the floodplain throughout the year. Others may exhibit migratory behavior, but over shorter distances. Additionally, eurytopic species adapt their behavior opportunistically according to the prevailing environmental conditions and exploit flooded areas similar to potamodromous species.

One of the most important fish species that contributes massively to this ‘super swimway’ linking the Tonle Sap, delta, 3S system and the Cambodia floodplain is *H. siamensis*. This species is considered a eurytopic species yet exhibits considerable migration tendencies. Upstream migration occurs throughout the year, but mainly from November to April, peaking in December, although migration occurs later, from February to March, around the Khone Falls. It migrates laterally into streams and flooded areas during the flood season and uses the habitat for nursery and grow purposes. This is particularly true of the Tonle Sap system that is a primary area for production of the species and contributes massively to the Dai fishery catch. As flows in the Tonle Sap recede, they move out of the flooded areas into the Tonle Sap River and migrate downstream into the Mekong before moving north toward 3S rivers and above the Khone Falls. They spawn in May June in the floodplain systems of Savannakhet-Mukdahan and the larvae drift downstream to populate the Tonle Sap system and delta where they grow on.

Overall, this case study highlights the intricate relationship between the Mekong River hydrological dynamics, the Tonle Sap/Great Lake system, and the super swimway system in the region. The migration of fish between the different habitats is vital for their survival and contributes to the overall ecosystem health of the Mekong River basin. Yet, despite the critical importance of this migratory system to fish production in the LMB, the river is under considerable pressure from intensive fishing and a plethora of external economic development activities in the last 20 years that are disrupting the migratory pathways.

First and foremost is the construction of hydropower dams (Arias et al. 2012, 2014), notably Lower Sesan 2 at the confluence of the Sesan and Sre Pok on the 3S system and Don Sahong on the Hou Sahong channel that was recognized as the most important fish bypass route over the Khone Falls. There have been considerable declines in fish catches in Zones 4, 5, 6 and 7 of lower Mekong since both were closed in 2020 (Mekong River Commission (MRC) 2011; Chevalier et al. 2023). These declines were most notable for potamodromous, long- and short-distance main channel and tributary spawners and potamodromous floodplain spawners. The construction of numerous other hydropower dams in the 3S rivers system and tributaries of the Tonle Sap, plus future closure of Sekong 1 on the Sekong (see Supplementary File 2: *Sekong case study*), also contribute by isolating large areas of spawning habitat. Further problems are likely to arise from disconnection of the floodplains for rice farming (Vu et al. 2021), aggregate mining lowering the river bed level in the Cambodian main channel region (Hackney et al. 2021), and alteration to the hydrological cycle through flow regulation by upstream dams (Arias et al. 2012, 2014) and the adverse effects of climate change causing prolonged periods of low flows (Arias et al. 2012, 2014). These barriers to migration and dispersal along this super swimway together with other forms of flow modification will result in potentially catastrophic declines in fish stocks and probably extinction of several fish species that are already critically endangered.

Challenges to maintaining swimways in the Mekong River

Improving understanding of migratory pathways

Considerable information is available on the distribution and ecology of fish species in the Mekong River basin. Species have been categorized into ten ecological guilds based on their habitat use and migratory behavior, but information on the actual migration patterns remains largely inferred from distribution mapping, although tagging and tracking studies are now ongoing for a limited number of species in specific areas. Most migratory species are potamodromous, short-distance main channel (and major tributary) spawners (146 species), potamodromous, floodplain spawners (grey fish) (120), or amphidromous estuarine resident (178) and marine migrant species (315), with just a small number of anadromous (3), catadromous (4) and potamodromous, long-distance, main channel spawners (20) (Table 1). By far the best-represented group is the rhithron species (357) that occupy riffle areas, often in upland streams and fast-flowing sections of the main river. Little is known about the migratory pathways of these species, no matter how short a distance, to complete their life cycles (Birnie-Gauvin et al. 2017) and this needs further investigation. Critically, however, some 35% of migratory species are threatened according to the IUCN Red List and thus it is fundamental that the migratory pathways of these species are maintained, and in many circumstances need improvement or intervention measures.

The main movements observed in the Mekong system are up and downstream longitudinal migrations within the mainstream Mekong and major tributaries, and lateral movements to and from floodplains, tributaries, streams and rice fields (Poulsen et al. 2002, 2004). These movements are mainly to find suitable habitat in the main river and tributary channels and on the floodplains to breed when flows are high, and then dispersal as the flows in the rivers and wetlands recede. The direction of movements varies between regions and there are no consistent upstream movements at a particular time of the year or downstream movements at another. The timing of the movements also varies between the lower floodplain reaches and the areas where the river is more confined to the channel (Zones 1 & 2). For example, downstream migration from the tributaries occurs at the onset of dry season as the river flow quickly recedes, but it is slightly later for fish occupying the floodplains.

Several factors are probably responsible for this variability, of which flow is the main driver (Supplementary Figure 4; Baran 2006), but natural features like the Khone Falls are also implicated. These falls can act as a barrier to upstream migration, especially when flow characteristics are unfavorable, e.g. extreme low or high flows (Baran et al. 2005). Nevertheless, some species bypass the falls at specific times of the year, especially at the end of the dry season and onset of the wet season, to coincide with major migrations in the Mekong. For example, *Y. modesta* and *H. siamensis* bypass the Khone Falls in the dry season, a timing that matches that in the upstream reaches of the Mekong River (Hori 2000), but these species also exhibit contrasting movements between populations living up and downstream of the Khone Falls. Those populations that persist below the Khone Falls migrate down the Mekong into Cambodia and Vietnam, while their counterparts upstream of the falls exhibit opposite movements at the same time. This illustrates the complexity of the migratory patterns of these species, and that simple, unidirectional movements at well-defined times are not necessarily the case.

Despite considerable work on fish migratory pathways and critical habitats for fisheries in the LMB since the 1990s, much of this information is fragmented and not used systematically in planning processes to maintain and promote swimways as an important ecological function. There is no doubt the principle migration zones outlined by Poulsen et al. (2002) are appropriate, but many more species make long distance migration throughout the catchment than originally thought. Thus, understanding of migratory pathways needs to go beyond mapping species presence and timing of migration, and move toward more empirical knowledge about functional pathways, such as determined by Vu et al. (2022a) for Pangasiid species or Vu et al. (2024) for Ariid catfishes (also see case study for *P. krempfi*) using otolith microchemistry or tagging and tracking research. These are expensive tools and will rely on development funding, such as the Wonders of the Mekong project, although the hydropower developers should be encouraged to invest in such studies to improve understanding and the actions that can be taken to maintain and improve swimways. In addition, any studies should consider the entire suite of ecological needs of all species, but migratory species in particular (Loury et al. 2021), and not just their distribution ranges, to maximize the effectiveness of fisheries conservation measures. Such information is provided in the updated Mekong species database (Supplementary material Table 1) but remains incomplete. Beyond this, there is also a need to improve knowledge of the multiple migration strategies identified by Vu et al. (2022b); Vu et al. (2024), using tools such as otolith microchemistry, and linking them to genetic discrimination of sub-populations (Duong et al. 2023) within the river system. Only when such outputs are available, will the full impact of disruption of migratory pathways be understood. Unfortunately, novel approaches such as eDNA, while having the potential to improve this knowledge, suffer from limited reference sequences available in GenBank (Durand et al. 2022) and currently is unable to quantify the abundance of fish or define migratory pathways without intensive sampling.

Linked to this analysis about migration routes for individual species is a better understanding of the critical habitats required to meet their life cycle requirements. These include the precise location of spawning, nursery areas and growth and refuge areas, and crucially the pathways between these habitats. Knowing the location of such habitats will contribute toward maximizing the effectiveness of conservation measures, especially promoting freshwater protected areas, and help identify key habitats for restoration. This will be particularly important where both longitudinal and lateral connectivity have been disrupted and help focus on solutions to reestablish swimways.

Within this context, there is the need to better understand the role tributaries play in the life history strategies and sustainability of fish populations of both the individual and different fish species in the LMB. Tributaries have been recognized as having 'High Significance' regarding water use, but potentially also having been considerably impacted (Vogel 2012) in some way or form by either dam development or agricultural expansion. Very few rivers remain free-flowing (exceptions include the Songkhram), while others have been, or will eventually be, developed into a cascade of hydropower dams or irrigation barriers (e.g. Nam Ou and Nam Kam, respectively). Nonetheless, there are opportunities to open up migratory pathways and improve the contribution of tributaries to productivity. Hanpongkittikul et al. (2024), showed the efficacy of retrofitting fish passage facilities on water control gates in the Nam Kam and found fish were able to access all areas of the river if the gates were managed in an effective manner to enable migration at critical times of the year related to their main upstream migration period around the onset of the flood season.

Managing environmental pressures

Hydropower, agricultural intensification, heavy fishing pressure, and urban and industrial development pose major threats to fisheries in the LMB, especially at the transboundary level through disruption of flows and sediment dynamics, and isolation of key habitats (Baird and Hogan 2023; Campbell and Barlow 2020). The social and economic benefits of capture fisheries have been consistently undervalued, due in part to lack of reliable data on fish catch and nutritional importance, resulting in little attention to water-food-energy tradeoffs (Friend et al. 2023; Pittock et al. 2017; Ziv et al. 2012). Conversely, the economic benefits of dams, irrigation systems, and other capital-intensive projects are easy to quantify and can be quickly realized. This has arguably resulted in an overinvestment in energy and agricultural projects that often conflict with countries' commitments to biodiversity, environment and sustainable development goals (IFC (International Finance Corporation) 2021).

As a consequence of these pressures, the status and catches of migratory species are now in decline and predicted to be 40–60% lower than catches in 2000 if the full development of mainstem hydropower schemes comes to fruition (Mekong River Commission (MRC) 2017a). Coupled with agricultural development, the prognosis for fisheries is worrying. There is an urgent need to prioritize actions to protect and restore critical transboundary fish habitats and migratory pathways and agree, at the regional level, measures that address these fundamental problems, such as improving the design of low-head passage facilities at in-channel water control structures (Hanpongkittikul et al. 2024) and reconnecting wetland and floodplain habitats (Baumgartner et al. 2014, 2018, 2021), designing environmental flows to protect key flooding periods (Bunn and Arthington 2002), manage sediment dynamics for fisheries and aquatic production (Cooke et al. 2024; Koehnken et al. 2020), and promote sustainable fish-rice systems (Loury and Ainsley 2020; Vu et al. 2021).

Managing migratory fish and fisheries

Information on migration patterns and pathways is important for management of migratory fish species. It identifies when various species are most vulnerable to exploitation and those most impacted by river development. The large main river deep pools are refuge areas in the dry season, but also easily exploited by gillnets. Similarly, reproductive migrations of fish at higher flows enable the fishers to target adult stocks as they pass obstacles (e.g. by using traps). This information on the most vulnerable stages of the life cycle can be used to formulate management measures, such as closed seasons or areas, and thus regulate when and where fish can be exploited. Although basin and fisheries management plans have been developed (Mekong River Commission (MRC) 2017b), these mostly highlight key threats to ecosystem functioning and aquatic resources that are dependent on them, and there has been limited investment in conservation of aquatic biodiversity, or protection and management of wild capture fisheries. There is a clear need to fully integrate fisheries and exploitation of other aquatic animals into wider basin planning processes and ensure their contribution to food security and livelihoods is sustained and, where practical, enhanced.

This is particularly problematic because there is limited experience with transboundary fisheries management that is required for the migratory fishes of the LMB. The 1995 Mekong River Agreement provides the legal basis for managing aquatic resources across the LMB, but there are weaknesses from a transboundary perspective. Each country has legislation and regulations to manage fisheries, but these are not harmonized into specific agreements on fisheries between countries. This compromises the ability to manage highly migratory, and most valuable, fisheries components that are reliant on multiple aquatic habitats in different regions across the basin to sustain the stocks. It also precludes an upstream-downstream thinking approach to management of these resources.

In addition, there is a need to manage fish stocks in a more sustainable manner. This is probably best achieved by strengthening community-led fisheries management and enforcement initiatives, as well as engaging with communities to help restore degraded habitats and reestablish the ecosystem structure and functions that existed prior to the initiation of development activities. (KC et al. 2020).

Conservation actions

Without doubt the rich aquatic biodiversity of the LMB is under threat from an array of pressures. There is an urgent need for affirmative actions to improve, protect and conserve these valuable assets for future generations, because of their social, economic and cultural importance. This will require measures both directly targeting the fisheries but also actions targeting ecosystem form and functioning.

Beyond traditional fisheries management and restoration measures, there are a number of actions that need to be considered to protect and conserve the rich aquatic biodiversity of the Mekong Basin. Maintaining ecological connectivity, reconnecting freshwater habitats and restoring natural flows should be a primary focus, but these actions will need to be accompanied by other effective area-based conservation measures (OECMs), habitat improvements and refuge creation that benefit from the restored hydrology and opening up of fish migratory pathways (Mekong River Commission (MRC) 2023b, 2023c). Actions also need to consider transboundary perspectives, where changes brought about by economic development activities in one country or region can have considerable and damaging impacts in other areas. Consequently, any initiatives to protect and conserve fish and fisheries in the LMB should move beyond construction of fishways on smaller barriers in tributary rivers or reconnection of irrigated agricultural areas in floodplain systems to include establishment of protected or conservation areas that are dedicated to supporting fisheries and aquatic biodiversity (Acreman et al. 2020; Kura et al. 2023; Loury and Ainsley 2020), habitat rehabilitation in degraded wetlands, improved agricultural practices in catchments and better management of land use, at least in the immediate, perhaps 15-km, corridor either side of the main river and tributaries (Mekong River Commission (MRC) 2021c).

Establishing protected areas, conservation zones and sanctuaries within the Mekong requires specific dialogue because there are already a several protected areas and numerous fish conservation zones (FCZs) defined under religious beliefs, typically deep pools throughout the mainstem Mekong (Baird 2006; Baird et al. 2005). Whilst these protected areas may contribute toward supporting fisheries and aquatic resources, most are not set up with migratory fishes in mind. Instead they are based on local beliefs or have been established where there is a willingness or desire to help protect specific habitats, the functionality of the river or specific species of conservation value, support improved productivity from the system, or a combination of these (Kura et al. 2023; Loury and Ainsley 2020). Thus, any actions should first explore the existing network of protected areas, FCZ and sanctuaries, and determine whether they are suitable for meeting the needs of migratory fish management, fisheries conservation objectives or improved yield/production. Additional commitments to maintain or restore connectivity of the most important migratory pathways or swimways will be a critical, novel additional level of protection.

To achieve this, existing protected areas should be reviewed in the context of whether they are providing critical pristine habitat, protecting habitats of importance to ecosystem functioning or protecting/conserving priority species. Once carried out, the protected areas should be checked to see if they meet all the habitat needs of the species of conservation concern and whether the pathways between the protected areas have been disrupted. The minimum distribution range of migratory species should be delineated from historical information on fish species in the basin and the relationships to various habitat needs for the target species (Poulsen et al. 2002, 2004). The latter habitat requirements can be derived from spatial data sources and related to species habitat quality and critical habitats mapped from indigenous knowledge and other ongoing monitoring activities, e.g. Mekong River Commission Fisheries Abundance and Diversity Monitoring (Mekong River Commission (MRC) 2021a). In doing this, it should be recognized there are multiple species migrating through the whole of the Mekong and within sub-basins, thus connectivity assessments should also take place on multiple scales covering the entire LMB.

In effect, there will be a shift away from just solely focussing on iconic, often commercially important, long-distance migratory fish, such as the Mekong giant catfish, toward protection of aquatic biodiversity and enhancement of fisheries of greater importance for subsistence and small-scale fisheries. This does not mean that the conservation of the incredible biodiversity supported by the Mekong is not enhanced. Rather, it is a co-benefit from the actions proposed. Non-fish aquatic biodiversity and dependent species will also benefit from healthier wetlands and floodplains. It is not just the fisheries that will improve but wildlife that depends on robust and prolific fish stocks, such as the Critically Endangered Irrawaddy dolphin.

Further, regional efforts to protect or restore key ecosystems and reconnect swimways will need to be embedded in regional energy planning (Friend et al. 2023). There will be a need to prioritize significant critical habitats within the framework of existing and new transboundary fisheries management projects, and ensure the support of local communities in the design and implementation of transboundary management plans/agreements, establishment of fish conservation areas and seasonal closures, coupled with sustainable financing and mechanisms to improve value chains to maximize the benefits from healthy and sustainable fisheries and aquatic biodiversity.

Further development of the global swimways concept in tropical rivers

Global swimways was inspired by the flyways concept for birds, which emphasizes the value of protecting long-distance migration routes. Global swimways are also underpinned by long-distance migration routes and, at present, longitudinal migrations are the focus. In large tropical floodplain rivers two additional key migrations stand out as essential for ecosystem functioning: (i) long distance downstream migration or "drift" of larvae, which is an active life history strategy to optimize survival; and (ii) short distance lateral migrations on and off floodplains. The obligate nature of these migrations is less obvious in many temperate streams, but critical in tropical systems. Consequently, as the swimways concept develops in large tropical rivers, these migration strategies should be given equal weighting alongside large longitudinal upstream migrations. Accounting for these species groups and also considering short-distance movements may be present in many species considered "non-migratory" is critical to get a better understanding of the complexities of migratory traits in fish species. It will also help better enumerate the true number of migratory species in aquatic systems and address the apparent underestimates of migratory species reported in global assessments such as the The Living Planet Index for Migratory Freshwater Fish (Deinet et al. 2020, 2024).

The first implication of this improved understanding is that upstream fish passage at dams, which is often seen as mitigating the impacts on migration, needs to give equal weighting to downstream drift of larvae where the hydraulic barrier caused by the lentic habitat of the impoundment can be potentially more devastating to fish populations than the more obvious upstream barrier at the dam wall.

The second implication is appropriate effort and resources need to be given to downstream movement of adult and sub-adult fish that spawn multiple times over their life cycle and must negotiate dam infrastructure, especially spillway gates and hydropower turbines, on their downstream return journey to feeding and refuge areas.

The third implication is that modernization of irrigation and flood prevention infrastructure is isolating floodplains from the river channel and preventing lateral migrations, which leads to declining fisheries in rice fields and wetlands, causing food security issues, poorer nutritional outcomes, and poorer incomes for fishers. There is thus a need to improve understanding of the importance of tributary systems and lateral migrations onto floodplain systems to enhance the protection of all migratory species groups.

Aligned with maintaining these migratory swimways is the need to protect, and nowadays rehabilitate, critical habitats to ensure the long-term sustainability of fish populations. These include identifying and reconnecting key habitats used during critical life stages, such as deep pools or floodplain areas in the LMB. This is particularly important for threatened species of high conservation value such as the mega fishes, which can act as models for promoting long-term sustainability of ecosystem functionality.

Acknowledgements

We thank Chavalit Vidthayanon, Kenzo Utsugi and Chaiwut Grudpan for reviewing the species identification and guild structure under the Mekong River Commission Council Study, and Michele Thieme for comments on an early draft of the manuscript.

Ethical approval

There are no ethical considerations as the research reviews existing information.

CRediT authorship statement

Ian G. Cowx: Conceptualization, methodology, formal analysis, writing – original draft, editing. An Vi Vu: Analysis, review & editing, VALIDATION. Martin Mallen Cooper: review & editing, validation. Lee Baumgartner: review & editing, validation. Quan Lai: review & editing, validation. Zeb Hogan: Conceptualization, writing, review & editing. Gunther Grill: Analysis, review, Validation Catherine Sayer: Conceptualization, review & editing,

Disclosure statement

The authors declare no conflicts of interest in conducting and reporting the results of this study. All research was carried out in an objective and unbiased manner to ensure accurate and reliable findings. The authors are solely responsible for the content of this manuscript and have no financial or personal relationships that could influence the interpretation of the data.

Declaration of generative AI in scientific writing

There is no parts or sections of the manuscript written with the assistance of AI or using AI-assisted technologies.

MRC data disclaimer

The Mekong River Commission make no warranties about this data and disclaim all responsibility and liability for all expenses, losses, damages and costs which may be incurred as a result of the data being inaccurate or incomplete in any way and for any reason. The data contained herein do not imply the expression of any opinion whatsoever on the part of the Mekong River Commission concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delineation of its frontiers or boundaries.

Funding

This report was funded by the USAID 'Wonders of the Mekong' Cooperative Agreement No: AIDOAA-A-16-00057' through IUCN.

Data availability statement

The data that support the findings of this study are openly available from open sources or and are presented in the Tables and Supplementary files.

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