Mekong River Commission

Fish migration triggers in the Lower Mekong Basin and other tropical freshwater systems

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Meeting the Needs, Keeping the Balance

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TECHNICAL ADVISORY
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Summary

Nature and objective of the study

This report reviews the factors that trigger fish migration in the Mekong River and other tropical freshwater river systems. It aims to provide a basis for understanding the consequences of human intervention to the natural flow regime of the river system on fish migration and thereby on the fisheries of the Lower Mekong Basin.

The report comprises two parts. It begins with a systematic review of the published information on migration triggers and cues in the Mekong River system and in other tropical rivers worldwide. This part includes a discussion of other associated issues, such as spawning triggers, which should also be taken into account when dealing with Mekong fish migrations and management.

The second part of the report presents a quantitative analysis of the environmental factors that trigger the migration of Mekong species. This section is based on a merger of FishBase 2004 with the Mekong Fish Database, and covers the entire population of 768 Mekong species held within FishBase. The merged data set includes biological data and coded ecological information for all of these species. The results are supplemented by an analysis of data from a recently published study of migration patterns and hydrological triggers at the Khone Falls (Southern Lao PDR).

Summary of the findings

Literature review: migration triggers in the Mekong and in other tropical systems

Literature on the migration of tropical freshwater species (as opposed to freshwater temperate and marine species) is scarce and there are few documented studies that deal specifically with migration triggers.

The literature cites water-level and current, discharge, precipitation, the lunar cycle, water colour and turbidity and the apparition of insects as key migration triggers for tropical freshwater fish worldwide.

- Water level is the environmental parameter most often cited as a migration trigger; this parameter correlates closely with discharge and water current. Thresholds, or changes, in water level, discharge or current are known to trigger the migration of 30 Mekong fish species. In the case of many, it is the *variation* of water level, rather than particular water-level thresholds, which acts as the trigger.

- The first rainfalls of the wet season also trigger breeding and reproductive migration in the tropics. In the Mekong River system, 11 species are known to be triggered by

early rainfalls. In several river systems, the migrations cued by the first rains are also associated with the lunar cycle.

- Changes in turbidity, or in water colour, are recorded as migration triggers for nine species in the Mekong River system. However, these criteria do not discriminate between changes caused by increasing or decreasing sediment load, and those caused by blooms of algae or other planktonic organisms.

- The apparition of insects triggers the migration of five Mekong fish species.

The literature also cites the lunar phase as an environmental trigger. The influence of the moon on several Mekong species is well documented, however it is unclear which lunar phase is the trigger, as this seems to vary depending upon species and location. However, in the Mekong River system the migration of large numbers of fish across the Khone Falls at the time of the second new moon after the winter solstice (at the time of the Chinese New Year), is well known. Indeed, similar spectacular migrations corresponding to the lunar phase have also been recorded in Africa, but the importance of the moon in migration, in general, remains far from clear.

Additional issues highlighted by the literature review

The literature review presented in this report targeted those environmental factors that trigger migration; however the review also brought to light three other important points, namely:

- Fish density as a complementary *biological* migration trigger.

- The need to consider *spawning triggers* in addition to migration triggers. These reproduction triggers are equally crucial to the sustainability of fish populations and also concern non-migrant species.

- The *multiplicity* and *interaction* of triggers and the role they play at different times and in different physiological mechanisms, mean that triggers cannot be reduced to a single parameter such as 'discharge'.

Data analysis: quantification of Mekong migration triggers

Status of knowledge on migration of fish species

- The migration status (that is whether a given species is migratory or non-migratory) is known for only 165 (24%) Mekong fish species.

- There is no information about the migratory behaviour of the remaining 579 (76%) Mekong species.

- Of the species whose migration status is known, 135 (87%) are migrant species and 30 (13%) are non-migrant species.

Status of knowledge on migration triggers of fish species

- The merged data set cites five environmental factors that trigger or cue migration: i) variation in river discharge; ii) variation in water level; iii) first rainfalls after the dry season; iv) change in water turbidity or colour; and v) apparition of insects.

- Environmental factors are known to trigger migration of at least 30 (18%) of the 165 migratory species; 12 of these are sensitive to more than one trigger.

- The migration cues of the remaining 135 (82%) migratory species are unknown.

Classification of factors triggering fish migration

Of the species for which migration cues are known:

- ninety per cent respond to variations in water level or in discharge;

- thirty per cent respond to the first rainfalls at the end of the dry season;

- thirty per cent respond to change in turbidity or water colour;

- ten per cent respond to the apparition of insects.

Fish families most sensitive to triggers

The pangasiid family (catfishes) appears to be the most sensitive to migration cues; 11 of the 19 species in this family (58%) respond to one or more environmental trigger. The next most sensitive families are silurids (3 species, 9% of the species of this catfish family) and Cyprinids (9 species, 3% of the family). Thus catfish species are the most sensitive to migration triggers.

Correlations between environmental cues in the Mekong.

Analysis of available qualitative ecological records shows no statistically significant correlations between any of the environmental triggers. However, a quantitative analysis of environmental variables of a three-year data set shows that water level and discharge are closely correlated and should be considered as a single cue. The other environmental parameters are independent.

Quantitative relationships between discharge and migrations

Eight distinct waves of fish migration occur annually at Khone Falls in southern Lao PDR. These have been studied and recorded in great detail over a number of years. An extensive analysis combining six years of fishery data from Khone Falls and corresponding hydrological measurements from gauges at Pakse (the nearest monitoring station) shows:

- That the most diverse catch is taken when the discharge is low.

- That 96% of the fish is caught at discharge rates of between 2000 and 8000 cumecs (cubic metres per second), and that the most important discharge for fisheries is between 2000 and 3000 cumecs. Additional results show that five species make almost half of the catch. These species are all known to be sensitive to hydrological triggers.

- An analysis of the relationship between the abundance of the 47 most common taxa in catches and discharge shows that 13 taxa are very sensitive to (low) discharge, 17 taxa are sensitive to discharge, 13 taxa are not sensitive to this variable, and the relationship is unknown for 4 taxa.

These results all converge to highlight the extreme importance of low water-levels and discharges to the richness and production of Khone Falls fisheries, and to the Lower Mekong in general, at a time when fish are dense and fisheries very intensive.

With regard to flow modifications, the most important negative impacts on fisheries will be those that increase dry season flows (impact on ecology and catchability of fish), and those that delay the onset of the flood. Flow modifications in the transitional or rainy seasons are likely to have much smaller impact. The importance of Mekong fisheries (which, at 2.6 million tonnes per year, are 7 times greater than the whole Northern American inland fisheries sector) to the lives and livelihoods of the basin's inhabitants calls for additional thorough analyses of the impact of flow modifications on fisheries, in order to integrate this essential sector in plans and policies for the development of the Mekong's water resources.

KEY WORDS: Mekong River; fish migration triggers; fisheries; Khone Falls

1. Introduction

Scope of the study

The objective of this report is to review literature on the factors that trigger, or cue, fish migrations in tropical freshwater systems, particularly the Mekong River system, in order to better understand the possible impacts of flow changes induced by water-related developments (primarily dams) on fish migrations and ultimately on the fisheries of the Mekong.

The demand for this study was driven by the members of the Technical Advisory Body for Fisheries Management (TAB)[1], who identified a 'knowledge gap' on this subject. Despite the fact that a large portion on the Mekong's fish migrate (particularly the commercially important species), very little hard information seemed to exist about migration and specifically the environmental factors that trigger migration. Clarification was needed, and it was also considered useful incorporate information from studies on other tropical freshwater systems.

The bibliographic review focused on river fishes and migrations; marine and estuarine systems were not included. Their exclusion is justified because brackish environments account for only three per cent of the area of the lower Mekong River system.

Within the freshwater realm, the review concentrated on potadromous fishes, fishes that migrate entirely within freshwater systems. However, the data analysis also included anadromous and catadromous Mekong species.

The review was also focused on tropical systems, as major migration triggers in cold and temperate countries are large-scale seasonal temperature and photoperiod variations (up to 20^{0}C and 8 hours of light per day), which do not occur in tropical environments. However, temperature and photoperiod variations were included in the review of fish migration triggers.

Methodology

To identify relevant articles, the literature search used two large bibliographic resources (Cambridge Scientific Abstracts – CSA and Aquatic Science and Fisheries Abstracts – ASFA) that cover the majority of journals dealing with fish and fisheries worldwide. Selected articles were acquired through the Agora, Science Direct and SwetsWise portals.

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1 The TAB comprises senior representatives from the fisheries ministries and departments of the four riparian countries, Cambodia, Lao PDR, Thailand and Viet Nam in the Lower Mekong Basin. SIDA, (Swedish International Development Assistance) and Danida (the international development agency of the Danish government) fund to the body through Mekong River Commission (MRC) which also provides additional logistical and operational support.

The literature search was supplemented by the resources of WorldFish Center library in Malaysia, access to the IRD on-line library[1] and the use of Library of the Museum National d'Histoire Naturelle in Paris, which is a source of scientific colonial publications from Indochina and Africa. Researchers from the IRD (Institut de Recherche pour le Développement, formerly ORSTOM, France) and from the Tropical Ecology working group at the Max Planck Institute for Limnology (Germany) provided additional information on freshwater fish migration in Africa and South America.

In addition to this literature review, the author undertook a systematic screen of the two main databases that cover all Mekong fish species: the Mekong Fish Database (MFD) produced by the MRC (MRC 2003), and FishBase, the repository of all published information on fish maintained by the WorldFish Center (Froese and Pauly, 2000, see www.fishbase.org). The MFD provides detailed ecological information, while FishBase provides a number of published life history parameters, such as age at first maturity, food items and estimated life span, for each species.

This overview confirmed the earlier conclusions of Lucas and Baras (2001), who recognised that while a large amount of information is available on migrant species in riverine and marine environments in cold and temperate latitudes, much less literature exists on the migration of tropical freshwater species, despite the huge diversity of this fish fauna. In the Mekong Basin for instance, where migrations are known to be an essential ecological feature (e.g. Pantulu, 1986; van Zalinge *et al.,* 2004), there is no information on migration for 76% of the species.

In this context of limited knowledge about the migration of tropical freshwater fishes, the particular issue of migration triggers, if often mentioned in ichthyology, has very seldom been the object of specific studies. In the Mekong Basin, no specific study of migration triggers has been attempted, although Baran *et al.* (2005) do address the migration of 47 species in their broader review of fisheries bioecology at Khone Falls.

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1 http://www.bondy.ird.fr/pleins_textes/index.htm. 35,000 documents online, including most of the French ichthyologic research in West Africa and in South America

2. Definitions and Context

Migrations, triggers and cues

According to dictionaries, to migrate consists of passing, usually periodically, from one region to another for feeding or breeding[1]. However several definitions of the term 'migration' have been proposed with a particular reference to fishes (e.g. McKeown, 1984; Sparre and Venema, 1992; Lucas and Barras, 2001). The concept of migration starts with clear-cut long range journeys between distant localities, but as scientists started acknowledging that short-distance movements could also be crucial in the life history of a species, the challenge was to sort out in one sentence the difference between 'significant' moves and random movements of a species.

In their studies of Mekong fish migration, Singhanouvong *et al*. (1996a) define migrations as 'any purposeful, seasonally regular type of movement of individuals from one ecologically distinct zone to another'. The most simple, clear and comprehensive definition is probably that of Northcote (1984), who defines migration as, 'movements that result in an alternation between two or more separate habitats, occur with a regular periodicity, and involve a large proportion of the population'.

A trigger is commonly defined as a factor that initiates a process or reaction, by analogy to the metallic part of a gun moved by the finger to fire. In the case of Mekong fish migration, triggers are understood as environmental factors that provide a sudden signal for fish to start actively migrating.

Similarly, a cue is 'a signal to a performer to begin a specific action'. The term is considered in this study as a synonym of trigger. Referring to reproductive cues, Helfman *et al*. (1997) distinguish *predictive cues* (that trigger, for example, gonadal maturation before any migration), *synchronizing cues* that signal appropriate environmental conditions, and *terminating cues* that indicate the end of the appropriate period.

Types of migration

From a spatial perspective fish migration can be lateral, longitudinal or vertical, and the movements can be either active or passive (in particular in the case of eggs and larval drift).

Longitudinal migrations[2] take place up and down the main river-channel whereas lateral migrations are movements from the main river channel into the floodplain, and back again when the water recedes (examples in Welcomme, 1979). However, lateral migrations are

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1 More generally, the study of the timing of recurring biological events and the causes of their timing is called phenology (Lieth, 1974).

2 Longitudinal migrations can be either anadromous, i.e. ascending rivers from the sea for breeding, like salmons, or catadromous, i.e. living in fresh water and going to the sea to spawn, like eels, or potamodromous (migratory within freshwater). According to Gross *et al*. (1988), catadromous species predominate at tropical latitudes where rivers productivity exceeds that of marine waters, and conversely in temperate latitudes.

often followed by longitudinal migrations within the main river channel (Bao *et al*. 2001). As pointed out in Jorgensen *et al.* (1998), lateral migrations, if less spectacular, are at least as important as long-distance longitudinal migrations in terms of fish production.

Vertical migrations of adult fish have not been detailed in this study as only two Mekong species are known to undertake such migrations: *Clupeichthys aesarnensis* and *Corica laciniata* (Warren, 2000).

From an ecological viewpoint, Baker (1978; in McKeown, 1984) identifies two main types of fish migration: obligatory and facultative. Obligatory migrations refers to movements following a series of physiological modifications in fishes, these modifications being themselves triggered by environmental parameters such as moon phase or temperature. This physiological response to triggers is thus age and size specific. On the contrary facultative migration refers to movements made response to degrading living conditions, such as de-oxygenation, food scarcity or high predation pressure.

> ### *Why do fish migrate?*
>
> *Animals migrate because key habitats essential for their survival in terms of reproduction and food availability are separated in time and space (Poulsen et al., 2002). For example, in a tropical floodplain river like the Mekong, breeding migrations upstream ensure that newly hatched fish larvae and juveniles can drift with the rising flows down to floodplains when they become most productive and accessible to fishes, i.e. at the beginning of the rainy season (Bao et al., 2001). In this respect these migrations contribute to increased growth and survival of a species, and thus to increased productivity of a system (Fernandes and de Merona, 1988). It is generally considered that these movements have evolved with, and thus are finely tuned to, the environment within which they occur (Poulsen, 2003). Some authors also consider those migrations as a way for species to minimize predation on their juveniles in confined areas; they also allow the dispersion of juveniles all over a river system, thus maximizing the expansion and survival chances of the species (Fryer, 1965). Some carnivorous species also follow shoals of their migrating preys, and thus undertake similar migrations, as highlighted by Daget (1957) in Africa.*

Migrations are a remarkable feature of South American fishes. As in the Mekong they involve commercially important species and stocks, can be observed on a large scale, and occur over hundreds of kilometres. They have been described in a number of books and studies (reviews in Welcomme, 1985; Barthem and Goulding, 1997; Winemiller and Jepsen, 1998; Carolsfeld *et al.,* 2003). In contrast, migrations do not appear prominently in the literature on African freshwater fishes. They are of course mentioned in a number of studies, in particular in relation to floodplains (e.g. Niger River, Lake Chad), but for instance a comprehensive review such as that of Lévêque and Paugy (1999) only dedicates a few pages out of 500 to migration issues. This could be due to a limited number of focused or precise studies as suggested by Lévêque (1999) despite the large number of potamodromous species in Africa. The low emphasis put on fish migrations in Africa could also be explained by partitioning of fish bioecology into specialties dealing with breeding, nutrition, growth or

competition; multipurpose migrations are partly addressed in each discipline thanks to a high number of detailed studies, but do not constitute a field of research *per se*.

Floodplain fish ecology in a nutshell

'In floodplain rivers, floods may increase the size of aquatic environment up to 50% annually, and also bring in nutrients which stimulate rapid growth of micro-organisms, invertebrates and plants, giving abundant food and cover for the fish during the high water season. The high water season is the main feeding and growing time for the fish which then lay down fat stores to last through the ensuing dry season, when they have to retreat to the main rivers where there is little food, or remain in floodplain pools. Mortality is very high as the water recedes.

On the floodplain, losses due to eggs being stranded, deoxygenation and predation are very great, providing great pressures for rapid development and growth. Many of these floodplain fishes mature in one or two years.

Both the intensity of flooding (height and duration of flood) and amount of water retained at low water many affect fish numbers in subsequent years. The dependence of these fishes on the arrival of floods for spawning and the effects of floods on growth rates of individual fish, was well shown.'

Lowe McConnell, 1979

Migration in the Mekong River

Poulsen *et al*. (2002) distinguish three major migration systems in the Lower Mekong Basin: the Lower Mekong (altitude 0–150 masl[1]), the Middle Mekong (altitude 150–200 masl) and the Upper Mekong (altitude 200–500 masl) (Figure 1).

In the Lower Mekong migration system the migrations are basically movements out of the floodplains and tributaries, including the Tonle Sap, to and up the Mekong River at drawdown period. A number of species spawn around their dry season refuges usually at the onset of the monsoon and beginning of water level rise.

In the Middle Mekong migration system, fish move upstream during the wet season and associated rising waters, and enter the tributaries and their associated flooded areas for feeding. During drawdown they leave the tributaries and return to dry season refuges downstream in the Mekong (Poulsen, 2003).

Finally in the Upper Mekong migration system the fish migrate upstream to spawning habitats during the wet season to return later to their dry season habitats also along the main river (van Zalinge *et al*., 2004).

It is important to note that the systems are not closed but are strongly interconnected, and many species are known to migrate from one system to another.
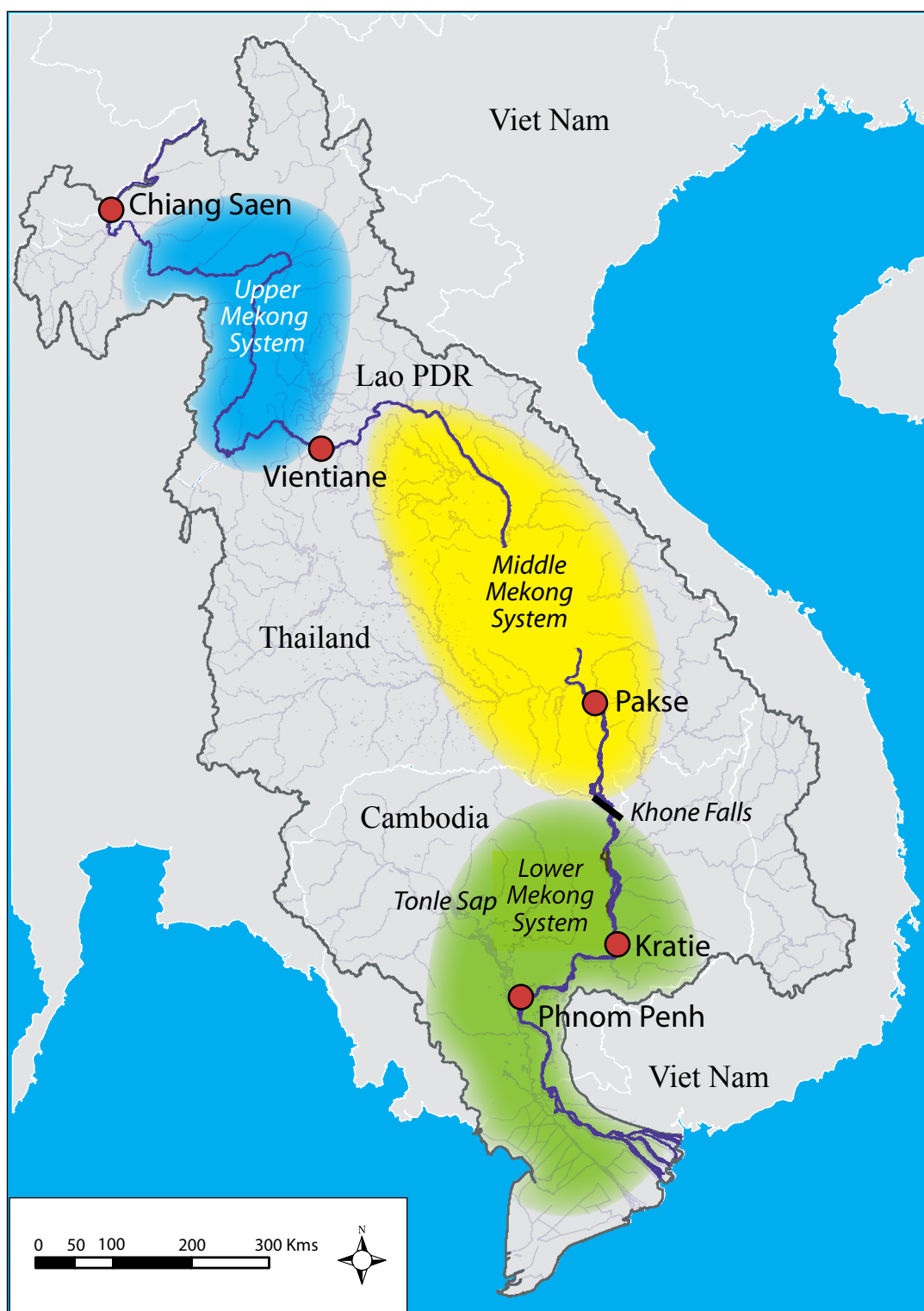
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1   masl = metres above sea level

Figure 1. Migration systems in the Lower Mekong Basin (after Poulsen *et al.*, 2002)

3. Review of Migration Triggers

For a migration to be successful it must be initiated at the appropriate time. Thus migration cues play an essential role in tuning up the response of a species, allowing a coordinated breeding or feeding strategy among individuals, that will maximize the chances of survival at the scale of a population[1].

> *'One postulated function of cyclical behaviors is the opportunity that it affords individuals to synchronize their behaviours with that of conspecifics. Nowhere is such synchronization more obvious and necessary than in reproduction. Not only must both sexes aggregate at the same locale to release gametes, but preparatory events of gametogenesis (gamete production) and secondary sex character development must also occur with similar timetables that converge on the same small time window.'*
>
> *Helfman et al., 1997*

In this context, a better understanding of the factors that initiate migrations is important for the sustainable management of capture fisheries, in particular in a system such as the Mekong where fish production is exceptional (Baran *et al*., in press) and where migrations play an important role. The sections below present a synthesis of the literature reviewed. This synthesis is based on the following sources:

Baird (1998); Baird and Flaherty (2001, 2002, 2004); Baird *et al*. (2001a, 2003, 2004); Baird and Phylavanh (1999); Bardach (1959); Chan (2000); Chan *et al*. (1999); Chomchanta *et al*. (2000); Heng *et al*. (2001); Hortle *et al*. (2005); Ngor *et al*. (2005); Poulsen and Valbo-Jørgensen (2000); Poulsen *et al*. (2004); Rainboth (1996); Roberts (1993); Roberts and Baird (1995); Roberts and Warren (1994); Sao-Leang and Dom-Saveun (1955); Schouten *et al*. (2000); Singanouvong *et al*. (1996a and b); Sukumasavin and Leelapatra (1994); Viravong *et al*. (1994); and Warren *et al*. (1998).

Discharge, water level and current

Water level is the environmental parameter most often cited in the literature as a migration trigger. This parameter is however also correlated to discharge and current speed, as will be demonstrated in Chapter 4. But the latter variables are less easy to observe and quantify than water level, which might explain the higher occurrence of water-level in records of migration triggers. The correlation between these environmental cues leads Poulsen *et al*. (2004) to simply say, for a number of Mekong species, that 'the arrival of the monsoon season triggers the fish to migrate'.

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1   Hence the notion of involving 'a large proportion of the population' highlighted in Northcote's definition of migration.

Mekong River

In their study of Mekong fish migrations, Poulsen (2000) and Bao *et al.* (2001) found that in the case of all species, a change in water level was the most important factor associated with both longitudinal and lateral migration. Fishers from Khone Falls also say that at the beginning of the rainy season the change in water level is the single most important factor determining the catch of migrating fish (Viravong *et al.,* 1994). However, it is also noted that the dry season migration seems to be less under the influence of changing water levels and climatic conditions than the May-June migration that proceeds the flood.

Baird *et al.,* (2004) and Singhanouvong *et al.* (1996a and b) argue that the *variation* of water level, rather than a particular water level threshold, is the factor that triggers migration (this was demonstrated later by Baran and Baird (2003) and Baran *et al.,* (in press)). This phenomenon has been illustrated in particular with *Pangasius krempfi*.

According to FishBase and MFD, 26 species are known to be triggered by thresholds or changes in discharge, water-level or current; they are:

Cyprinidae: *Bangana behri; Barbonymus gonionotus; Cyclocheilichthys enoplos; Cyprinus carpio carpio; Labeo chrysophekadion; Macrochirichthys macrochirus; Parachela oxygastroides; Paralaubuca typus*.

Pangasidae: *Pangasius conchophilus; Pangasianodon hypophthalmus; Pangasius krempfi; Pangasius kunyit; Pangasius larnaudii; Pangasius macronema; Pangasius polyuranodon; P. sanitwongsei.*

Siluridae: *Micronema bleekeri; Wallago leerii; Hemisilurus mekongensis.*

Others: *Hemibagrus filamentus* (Bagridae); *Tenualosa thibaudeaui* (Clupeidae); *Botia modesta* (Cobitidae); *Lycothrissa crocodilus* (Engraulidae); *Pristolepis fasciata* (Nandidae)*; Chitala blanci* (Notopteridae) and *Osphronemus exodon* (Osphronemidae).

Some other species can be added to this list: *Pangasius bocourti* (Chhuon, 2000), *Puntoplites falcifer* and the southern population of *Pangasius sanitwongsei* (Poulsen *et al.,* 2004), to some extent *Morulius chrysophekadion* (Heng *et al.* 2001) and *Henicorhynchus siamensis* (Bao *et al.*, 2001). The latter case is not clear as: i) the taxonomy of the genus *Henicorhynchus* is confused (in particular with *Cirrhinus*); ii) the number of species in this genus is not fixed; and iii) the identification of most species of the genus is almost impossible in the field.

In contrast, van Zalinge *et al.* (2002) report that it is the *spawning* of *Pangasianodon hypophthalmus*, that is triggered by a rapid rise in the Mekong water levels, and Singhanouvong (1996b) refers to occasions when *Pangasius conchophilus* has not migrated despite considerable increases in flow volumes. Finally, Baird *et al.* (2001a) highlight considerable uncertainty in the literature about which factors trigger *Pangasius macronema* migrations.

Other tropical rivers

The influence of seasonal water level changes on fish ecology and migrations in South America has been discussed in a number of publications, in particular by Fernandez and Merona (1988) and Gercilia *et al.* (2000) for the Amazon, by Winemiller and Jepsen (1998) for the Orinoco systems, Sato and Godinho (2004) for São Francisco River, Agostinho *et al.* (2004) for Upper Paraná Basin and Watkins *et al.* (2004) for the Iwokrama forest in Guyana.

Fish movements in these systems are associated with changes in water level during the cyclical seasonal flooding. Fishes occupy these flooded areas during rainy season, then move to more permanent water bodies when water recedes (de Oliveira and Garavello, 2003). The genus *Prochilodus* provides an alternative example of species undertaking a long distance spawning migration in the dry season, so that they arrive before, or at the same time as, the rising flood (Fuentes and Espinach Ros, 1998).

However, in all these cases fish migrations seem to occur gradually as the water-level changes (either progressing or receding), and no specific thresholds or triggers are identified, in particular at the scale of the whole fish community. Thus in the Upper Paraná Basin, Paraguay, migration and spawning occurs over a large period of time, between October and January for *Characiforms* and between December and March for *Siluriforms*. However, if the flooding is delayed, spawning is also delayed, and most migratory species then start during February. A failure of fish reproduction was reported in the Upper Paraná as a consequence of the absence of flooding during the spawning season (Agostinho *et al.,* 2004). Pavlov *et al.* (1995) confirm, in their study of ichthyoplankton of the Amazon, that migration is accelerated by rising waters (however, migration of juveniles is also recorded at lower water levels because a portion of the adult community spawns all year round).

In Nigeria, Ezenwaji (1998) shows that the migration of the juveniles of the catfish *Clarias albopunctatus* is triggered by current speed (no migration below 0.08 ms^{-1}). In the Niger Inner Delta, Benech *et al.* (1994) and Benech and Penaz (1995) show that migrations out of the floodplain back to the mainstream start immediately after the water starts to descend.

In the Murray Darling system of Australia, the results of Reynolds' studies (1983) suggest strongly that the migration of a number of species is related to changes in water level and reproductive behaviour. For instance, Golden and Silver perch undergo long-distance upstream migrations initiated by water-level rises at the onset of major flooding. However, according to Humphries and Lake (2000), in this system 'the generalisation that all river spawning behaviour is linked to the hydrological regime may be incorrect'. As a matter of fact, Reynolds (1983) also found that unlike perches, catfishes, which are nest builders and lay demersal eggs, do not undergo long-distance movement. These observations lead to the conclusion that long distance migration triggered by a rise in water level is necessary for non-guarder species, so that their drifting eggs and larvae do not get washed into the sea but arrive at fertile floodplains at the right time.

Precipitation

Precipitation, at the onset of the rainy season, seems to trigger breeding and reproductive migration in the tropics in conjunction with associated rises in water level. Lowe-McConnell (1987) provides details of this phenomenon.

Mekong River

In the Mekong Basin, heavy monsoon rains begin in May–June and continue till October. Fishers along the Lao–Thai stretch of the Mekong often mention that the first rains after the dry season trigger fish to migrate upstream (Poulsen, 2000).

According to our review, ten species are known to be triggered by early rainfalls; they are:

Cyprinidae: *Barbonymus gonionotus; Cyclocheilichthys enoplos; Mekongina erythrospila; Paralaubuca typus*

Pangasidae: *Pangasianodon gigas; Pangasius pleurotaenia; Pangasius polyuranodon*

Others: *Micronema bleekeri* (Siluridae) and *Tenualosa thibaudeaui* (Clupeidae)

Poulsen *et al.* (2004) also say that the migration of *Micronema apogon* (Siluridae) is triggered by the first rain at the end of the dry season and by water-level changes. These migrations are under the additional influence of the moon (in Cambodia, migrations out of floodplains occur on, or immediately before, the full moon).

Other tropical rivers

In the Amazon strong rains, as well as lunar rhythms, seem to be important stimuli for schooling of *Semaprochilodus insignis* and *S. taeniurus* during their spawning season (Ribeiro; 1983, in Fernandes and de Merona, 1988).

Similarly, the preliminary results of Silva and Davis (1986) from Sri Lanka suggest that nine species of indigenous fish actively migrate upstream to spawn before the onset of the north east monsoonal rains.

Pre-monsoon migration dominates in the Ganges, especially with catfish and Cyprinids, but the peak can vary as snow melt also induces migration (Payne *et al.,* 2003). This suggests that changes in water level of rivers and lakes, rather than rainfall, is the direct trigger of migration.

Benech and Dansoko (1994) conclude that in the inner Niger Delta both flooding and raining can trigger reproduction; however closer analysis shows that flooding triggers species that breed in running waters, whereas raining triggers species that breed in calm waters.

Lunar cycle

At particular times of the year, migrations of certain species are known to be in tune with the lunar cycle. The moon can then, directly or indirectly, act as a fish migration trigger. Fish may sense the lunar cycle through gravitational force, visual cues or indirectly, via tidal inferences. As Helfman *et al.* (1997) note, the new moon is the primary time when elvers (juvenile eels) migrate upstream and maturing adult eels migrate downstream, but the underlying mechanisms of this periodicity remain unknown.

Mekong River

Blache and Goosens (1954) provide the first records in Cambodia of migrations that are triggered by the moon. These authors also showed that falling atmospheric pressure and storms could disrupt the migration process.

According to Poulsen (2000), the lunar phase influences the migratory behaviour of many Mekong fish species. This was demonstrated previously at Khone Falls (e.g. Warren *et al.*, 1999; Baird and Flaherty, 2001) and in the Tonle Sap (Lieng *et al.,* 1995) where during the migration period (November to March) the catches of the *dai* fishery (in particular those of *Henicorhynchus* spp.[1]) vary strongly with lunar periodicity. Deap (1999) found for this fishery a peak period of 4–6 days before full moon and a low period during the rest of the month. The full moon is said to initiate the migration of certain fish such as *Morulius chrysophekadion*, *Paralaubuca typus*, *Belodontichthys dinema* (Heng *et al.,* 2001) *Tenualosa thibaudeaui*, and *Cirrhinus microlepis* (Phallavan and Ngor, 2000). The migration of *Pangasianodon hypophthalmus*, which is triggered mainly by variations of water level, is said by Poulsen *et al.* (2004) to be also under lunar influence, since migration of this fish occur normally just before, and during, the period of the full moon. At Khone Falls, Baird *et al.* (2003) demonstrate that between January and March there is a very clear correlation between overall catches of a fishery[2] and the new moon. The bulk of the catch (78.6%) at this time comprises small cyprinids, *Henicorhynchus lobatus*[3] and *Paralobuca typus*. Conversely, Baird and Flaherty (2001), working on a different fishery[4], and thus on a diversity of medium-sized cyprinids, conclude that no significant correlation can be found between peak catches and lunar phases.

Chomchanta *et al.* (2000) highlight the crucial role of the new moon of the second lunar cycle after the winter solstice (the time of the Chinese New Year) in the dry season migrations. The spectacular intensity of the phenomenon was first reported by Roberts (1993) and later confirmed by Roberts and Warren (1994) and Viravong *et al.* (1994). The latter also note large movements of fish during the first lunar cycle after the winter solstice. However, the importance of new moon of the second lunar cycle as a migration cue, if striking at Khone Falls, was not witnessed further up or down the Mekong at Pakse or at Stung Treng (Roberts and Warren, 1994).

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1 Representing 40% of the yield according to Baran *et al.* (2001).
2 The 'tone' or fence-filter trap fishery.
3 Recorded as *Cirrhinus lobatus* or under *Henicorhynchus spp.* in other studies.
4 4-9 cm meshed gillnet fishery.

Also, over the years, migratory activity at this time seems to be lowest when water temperatures were highest, and vice versa (Viravong *et al.*, 1994). In Cambodia, Bao *et al.* (2001) observe that in the Tonle Sap *Henicorhynchus siamensis* migrates just before full moon, but a little upstream the Mekong near Kratie it migrates during the full moon, and further up at Sambor, it migrates immediately after the full moon. This probably reflects the time needed for the species to swim upstream (Baird *et al.*, 2003), and emphasises the need to clearly identify the starting location when evaluating with migrations triggered by the moon (and this certainly also applies to the other cues).

Among the species apparently triggered by the Chinese New Year new moon are *Labiobarbus leptocheilus*, *Botia modesta*, *Scaphognathops stejnegeri* and *S. bandanensis* (Roberts and Warren, 1994), although Singhanouvong *et al.* (1996a) conclude from their observations that *S. stejnegeri* and *S. bandanensis*, unlike other species, migrate during the period from the full moon to the last quarter. Warren *et al.* (1998), acknowledging the contradicting conclusions of Welcomme (1985), Lieng *et al.* (1995) and themselves, suggest that response to lunar influence might be site-specific, the phase when the moon is obscured being preferred in confined environments where predation pressure is high.

Other tropical rivers

In the Lago do Rei, South America, the migratory movement of fishes out of the lake coincides with the maximum flood-peak that occurs between the new moon and the full moon (Fernandes and de Merona, 1988). However, no long-term trend in migration and lunar cycle was detected in their study.

In Africa, Daget (1949, 1952, 1957) showed that the Tineni (*Brycinus leuciscus*[1], Characid) undertake massive migrations out of the floodplain at the end of the rainy season. These slow and long migrations (1 to 1.5 km/h sometimes over 400 kilometres), even if they are triggered by receding waters, are also driven strongly by the lunar phase, with three migration pulses corresponding to the October to December moons. In fact, each time the peak of migration occurs during the first half of the lunar month. Interestingly, Daget observed that *B. leuciscus* congregate and migrate cohesively under the moonlight, and that the shoals disaggregate at the end of each lunar month; unlike the moonlight, the sunlight does not affect the fish migration. He also noted that a slight rise in water level will suffice to bring migration to a halt. Supplementing Daget's results with their studies in Lake Chad, Benech and Quensiere (1983) reach the general conclusion that the influence of the moon is not predominant, that it plays only a secondary role after hydrology[2], and that only a few species are regularly and repeatedly influenced by the moon.

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1   Formerly *Alestes leuciscus.*
2   This was confirmed in the inner Niger Delta by Benech *et al.* (1994, 1995), who conclude that the moon only influences lateral migrations that were originally triggered by hydrological variations.

Other migration triggers

Apparition of insects

Poulsen (2000), found that fishers working along the upper stretch of Mekong River believe the appearance of certain insects, in particular dragonflies and mayflies, is one of the most important indications that fish are about to begin migrating. The small pangasid *Pangasius pleurotaenia*, is a good example as it appears in high numbers when these insects (dragonflies in particular) are abundant; on these occasions fish are observed appearing at the surface and feeding on the insects.

Data held in FishBase and MFD, shows that the migration of *Pangasius macronema* and *Pangasius polyuranodon* (Pangasidae) and *Paralaubuca typus* (Cyprinidae) correlates with the apparition of insects. Upstream of Khone Falls the migration of *Pangasius conchophilus* also coincides with blooms of insects (Chhuon, 2000).

Water colour and turbidity

A change in turbidity or in the water colour is mentioned as a migration cue in the Mekong by several authors. It should be noted that sediment load is synonymous of turbidity but not necessary of water colour, as the latter term can also include algal developments such as that of green algae noticed annually in Khone Falls.

According to FishBase and MFD, nine species are known to be triggered by a change in water colour; they are:

Cyprinidae: *Bangana behri*; *Cyclocheilichthys enoplos*; *Labeo chrysophekadion*; *Mekongina erythrospila*; *Paralaubuca typus*

Pangasidae: *Pangasianodon gigas*; *Pangasius bocourti*; *Pangasius polyuranodon*

Others: *Tenualosa thibaudeaui* (Clupeidae)

However, the notion of change in turbidity or water colour is imprecise as it does not discriminate between increasing sediment load at the beginning of the rainy season, decreasing sediment load in the dry season and algal or planktonic development.

Temperature and photoperiod

In their extensive review of fish diversity, Helfman *et al.* (1997) note that seasonality among tropical freshwater fishes is defined more by rainfall than by temperature, as seasonal temperature fluctuations are not very strong. Pavlov *et al.* (1995) also note that there is no relationship between migration of Amazon ichthyoplankton and water temperature. According to McKeown (1984), what seems to be more important than the length of the photoperiod is the change from light to dark.

In an observation that applies to most tropical river systems, Daget (1957) concludes that migration responses to 'sidereal and meteorological influences' in the Niger River are very

specific and that species belonging to the same genus can have very different responses. This shows that a significant analysis of migration triggers must go beyond a collection of anecdotal observations, and requires a numerical approach, as detailed for the Mekong River in the following section.

Issues raised by the literature review

The literature review brought to light a number of associated issues that may be of importance in the study of the Mekong fish migrations and for the sustainable management of the fishery resources.

Importance of fish density as a complementary biological trigger

Helfman *et al.* (1997) stress that variability of migration cues can arise from secondary parameters such as water quality, presence of predators or social interactions, which can contribute to blur the effect of triggers. According to Singhanouvong *et al.* (1996b), Khone Falls is a bottleneck where fish gather in the mainstream below the rapids before undertaking the ascent of the falls. Singhanouvong *et al.* hypothesize that 'the migratory response to both absolute and changes in flow-volume also depends on the overall stage of the migration', the fish undertaking their migration only if 'there are sufficient numbers of fish waiting below the fault line'. Baird and Flaherty (2001) support this theory, which also echoes Daget's work in Africa.

Importance of spawning triggers in addition to migration triggers

In their review of Amazon catfishes and their migrations, Barthem and Goulding (1997) provide details of large scale migrations, often over hundreds of kilometres, but do not mention clear migration triggers. However, the first flood is mentioned as a *spawning* trigger for some catfish species of the Paraguay Basin (spawning taking place one day after the first heavy floods). 'Most of the species depend absolutely on the cues associated with flooding, for it is these cues that trigger reproduction' (Harvey and Carolsfeld, 2003).

The role of first strong rains as a recurrent trigger of spawning for African river fishes is illustrated by Lowe-McConnell (1987), Ochumba and Manyala (1992) and Ezenwaji (1998). Likewise, Fuentes and Espinach Ros (1998) show that rising water levels and temperature act as spawning synchronizers in South America. In the inner Niger Delta, Benech and Dansoko (1994), using flooding/production correlations, demonstrated that intense flooding induces a higher breeding effort.

However, a clearer distinction between migration triggers and spawning triggers, if necessary on the scientific ground, might not be of great use to river managers. Scott (1979) stresses the diversity of the physiological processes and stages in fish reproduction that are sensitive to external cues, and the multivariate nature of spawning triggers. According to him, 'it seems to be only the final stage of the reproductive cycle, spawning, which is associated with flooding, and the questions remains of how such species regulate the earlier stages of their cycle so that they are physiologically ready for spawning when the flood comes'.

Finally, the role of environmental triggers vis-à-vis reproduction highlights the need to consider the role of these triggers on the reproduction of fishes that do not migrate. The alteration of some environmental factors, for instance through hydropower development or river management, may also influence reproduction process or success even among non-migrant species. This issue is not explored in this current study.

Multiplicity of triggers

A number of tropical species migrate in floodplains to spawn, whereas others, like large characids, migrate upriver to headwaters in anticipation of seasonal rains. In tropical rivers throughout the world, predatory species often spawn earlier than their prey, thereby assuring a food source for their offspring (Helfman *et al.,* 1997). This diversity of requirements helps to explain the number of migration triggers that come into play for different species and in different time windows.

Singhanouvong *et al.* (1996b) were the first authors to provide a summary of the factors likely to trigger migrations and to present a critical analysis of possible migration cues in the Mekong Basin. According to them, water level, *variations* in water level, flow volume and local rainfalls are important stimuli at Khone Falls, whereas water velocity, temperature and turbidity are possible stimuli. The lunar phase and cloud cover play a role when in conjunction with water level and flow volume, but pH, oxygen concentration, water hardness and alkalinity have a negligible effect.

The bi-directional migration movements across Khone Falls (upstream and downstream) 'appear to be dependant on local hydrological conditions, […] and triggered by channel flow-volume, although water depth and current velocity might be the actual factors involved'.

The diversity of triggers also reflects the interactions among environmental factors and the fact that fish production cannot be summarized nor controlled by a single parameter. The complexity highlighted in the various studies of migrant species also expresses a diversity of physical and ecological processes occurring at different spatiotemporal scales, and interactions among scales. For instance, Labbe and Fausch (2000) showed that for darter (a small American perch), spring rains trigger reproduction but also increase groundwater levels, which in turn connects stream reaches. This increased connectivity allows the darter 'metapopulation' to persist at landscape scale. As Poulsen (2000) puts it, the high fisheries productivity of the Mekong Basin is not so much determined by a certain amount of water containing a certain number of fish but rather by the annual rise and fall of the Mekong waters. Fausch *et al.* (2002) conclude that, 'to provide useful information for managers, stream fish ecologists will need to embrace the complexity of these ecological systems at multiple scales, not force simplicity upon them'.

4. Quantitative Analysis of Mekong Fish Migration Triggers

The two main repositories of information about fishes, and Mekong fishes in particular, are FishBase and the Mekong Fish Database (MFD, 2003). FishBase is based on a strict academic approach and was used as a taxonomic reference for Mekong species; MFD containing much more than FishBase about Mekong fishes (in particular unpublished information) was used as the main reference (supplemented by FishBase) for information on the ecology and migrations of species.

FishBase (web version, www.fishbase.org, June 2005) holds records on 768 species that have been clearly identified and documented as living in the Mekong Basin[1]. These species belong to 62 families.

Methodology

The analyses done and detailed in this section are based on the following approach:

- creating a matrix of life history parameters for all Mekong species from FishBase;

- adding bioecological information from MFD to the matrix;

- adding complementary information from FishBase—in particular about those species on which there is information on migration triggers or cues;

- identifying migration triggers and cues in the enlarged matrix;

- coding migration triggers and cues;

- analysing the matrix—results of these analyses are presented below.

The FishBase team, on the author's request, created a specific module[2] to generate a matrix of all Mekong species and a number of life-history parameters of these species. The quantitative information available in this matrix is summarised in Table 1. This table details the life-history variables proposed by FishBase matrix, the number and proportion of species in the table for which a value is available for a given variable, and ultimately whether this variable was kept for further analyses. The variables selected are detailed in Table 1 below

Among the reasons for putting this information together are:

- the need for an overview of available knowledge on Mekong fish species;

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1 MFD, with less selective criteria, identifies 924 species.
2 See: www.fishbase.org, Information by ecosystem / Species ecology matrix.

- the need, given the high diversity of species and of specific strategies, for a quantitative approach to species ecology;

- the need to identify of guilds (= groups or clusters) of species that behave similarly and will respond similarly to environmental modifications.

This approach was used by Winemiller (1989) who, working on Venezuelan floodplains, quantitatively analyzed 10 life history traits from 71 species. He was able to recognise three major life strategies and corresponding guilds of species, and could demonstrate that seven life history traits correlated significantly to body length.

Table 1. *Life history variables detailed for Mekong species*

Variable	Abbreviation (unit)	Meaning	Measured or calculated	Number of records ($\neq 0$) available and % of 768 species
Maximum length	Lmax (cm)	Maximum length ever reported for the species in question	Measured	716; 93%
Life span	tmax (year)	Approximate maximum age that fish of a given population would reach	Calculated (estimated from Linf., K and to.)	762; 99%
Age at first maturity	tm (year)	Average age at which fish of a given population mature for the first time	Calculated (estimated from Linf., K and to.)	631; 82%
Length at maturity	Lm (cm)	Average length at which fish of a given population mature for the first time	Calculated (estimated from Linf.)	762; 99%
Length for max. yield	Lopt (cm)	Length class with the highest biomass in an unfished population	Calculated (estimated from Linf.)	762; 99%
Trophic level		Rank of a species in a food web, calculated from food items, weighted by the contribution of the various food items to the diet.	Calculated	390; 51%

For each species in the life history matrix, information on migration was automatically extracted from the MFD in MS Access format. For species listed in FishBase, but not present in the MDF, a synonyms correspondence table was used to search for all possible synonyms, and the relevant information was then extracted from the synonym species.

In the resulting expanded matrix, species were sorted according to the 'migration' criteria present in MDF. Information on migration was available for only 189 of 768 Mekong fish species listed in the database[1].

A multivariate approach of the available data was performed following the example of Benech and Dansoko (1994). However, the nature of variables (both qualitative and quantitative) requires sophisticated statistical methods and the limited number of species

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1 In either fields 'Migration Type' or 'Migration' of the database.

in the matrix on which migration data was available, did not justify the use of complex analyses or permit the author to draw strong quantitative conclusions. As a result, a simple presentation of the main trends was preferred, and is discussed below.

Migration and triggers of the 768 Mekong fish species

Status of knowledge on migration of fish species

The table below summarises the information currently known about migration of fishes basinwide:

Table 2. *Information available on migration of Mekong species*

	Number of species	% of total species
Migrant	165	21
Non-migrant	24	3
No information	579	76

Thus:

- the migration status (whether the fish is migratory or non-migratory) is known for only 189 (24%) of the 768 Mekong fish species;

- there is no information on migration status of three-quarters of Mekong species;

- of the species whose migration status is known, 165 (87%) are migrant species and 24 (13%) are non-migrants.

Status of knowledge on migration triggers of fish species

Information was read, synthesized and coded for each of the 189 species for which information on migration is available.

- The databases list five environmental factors that act as migration triggers:

    − variation in river discharge;

    − variation in water level;

    − first rainfalls after the dry season;

    − change in the turbidity or colour of the water;

    − apparition of insects, in particular dragonflies.

    In principle, all these factors are somehow correlated, as the water level varies with the discharge, high turbidity is correlated to rainfall (due to runoff) and thus to

high discharge, and insects appear in the air after the first rainfalls. The correlations between these variables on the basis of their trigger effect will be analysed in a next section.

- Thirty of the 165 migratory species are known to be sensitive to an environmental migration trigger. Of these, 12 species are sensitive to more than one trigger.

  These thirty species are:

  Pangasiidae (shark catfishes)

  Pangasianodon gigas, Pangasianodon hypophthalmus, Pangasius polyuranodon, Pangasius macronema, Pangasius bocourti, Pangasius conchophilus, Pangasius krempfi, Pangasius kunyit, Pangasius larnaudii, Pangasius pleurotaenia, Pangasius sanitwongsei (11 species)

  Cyprinidae (minnows or carps)

  Paralaubuca typus, Cyclocheilichthys enoplos, Bangana behri, Barbonymus gonionotus, Labeo chrysophekadion, Mekongina erythrospila, Cyprinus carpio carpio, Macrochirichthys macrochirus, Parachela oxygastroides (9 species)

  Siluridae (sheatfishes)

  Hemisilurus mekongensis, Micronema bleekeri, Wallago leerii (3 species)

  Bagridae (bagrid catfishes)

  Hemibagrus filamentus

  Clupeidae (herrings, shads, sardines, menhadens)

  Tenualosa thibaudeaui

  Cobitidae (loaches)

  Botia modesta

  Engraulidae (anchovies)

  Lycothrissa crocodilus

  Nandidae (Asian leaffishes)

  Pristolepis fasciata

  Notopteridae (featherbacks or knifefishes)

  Chitala blanci

  Osphronemidae (gouramies)

  Osphronemus exodon

The summary information, extracted from FishBase and the Mekong Fish Database, on the 30 species sensitive to migration triggers is presented in Annex 1.

Migration cues have been documented for 30 (18%) of the migratory species. Migration cues are unknown for the remaining 135 species (82%) (Figure 2).
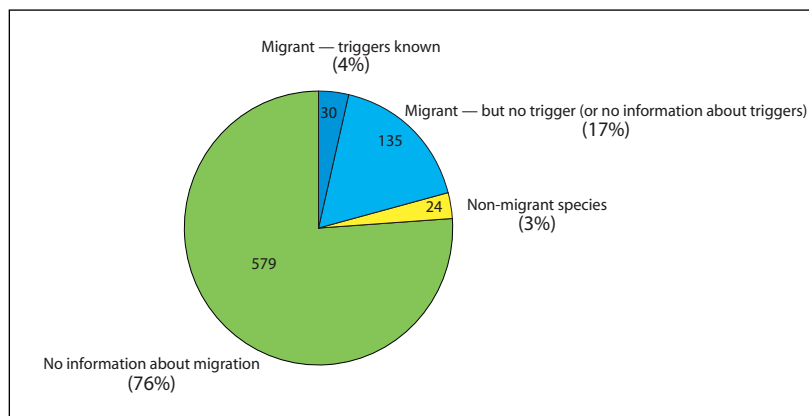
Figure 2. Migratory behaviour and sensitivities to triggers among 768 Mekong species

For the 76% of fish species for which migration patterns are not documented, there are undoubtedly a number of migrant species, and in particular species sensitive to environmental cues which trigger migration, but these have yet to be identified.

Classification of factors triggering fish migration

An analysis of the factors that trigger migrations shows (Figure 3) that 80% of species for which migration cues are documented respond to a variation in water level. This variation can be either when the water is rising (e.g. *Pangasius krempfi*) or when it is receding (*Pangasius polyuranodon* in northern Cambodia), or in both cases (*Pangasius larnaudii, P. pleurotaenia,* most white fishes migrating temporarily into floodplains).
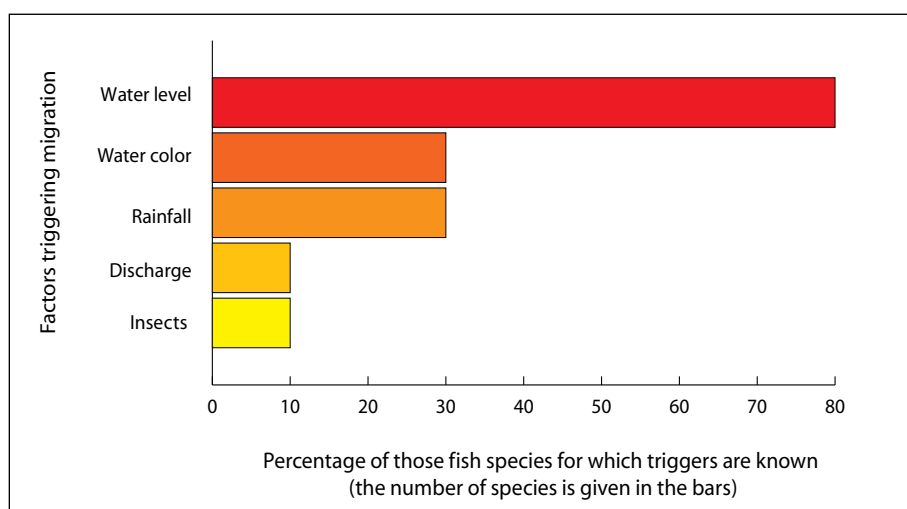
Figure 3. Percentage of species sensitive to migration cues
that respond to a given triggering factor

The second and third most frequent triggering factors are a change in water colour and the first rainfalls at the end of the dry season, both affecting nine (30%) of the species sensitive to environmental cues. Discharge and the apparition of insects each count for three (10%) species known to be sensitive to environmental cues.

As statistical analysis shows (see the section below—Correlation between environmental variables) that water level and discharge are closely correlated parameters, and should be considered as a single environmental cue. This means that 90% of species sensitive to migration cues are sensitive to variations, or thresholds, in water level/discharge.

*Fish families most sensitive to triggers*

From a taxonomic viewpoint, the pangasiid catfishes stand out as the family most sensitive to migration triggers. Eleven (58%) of the 19 species of the family that live in the Mekong respond to environmental triggers. Silurids (another catfish family) follow next with three species (9% of the species belonging to the family), then cyprinids with nine species, representing 3% of the 285 species of this family found in the Mekong (Figure 4).

Thus among the 18% of migratory fish for which the triggers have been documented, catfishes, with 15 species listed, are by far the group most sensitive to triggers, particularly bearing in mind that many of these species are sensitive to several triggers at once (see Annex 1 for details).

Figure 4. Species sensitive to migration triggers, per family
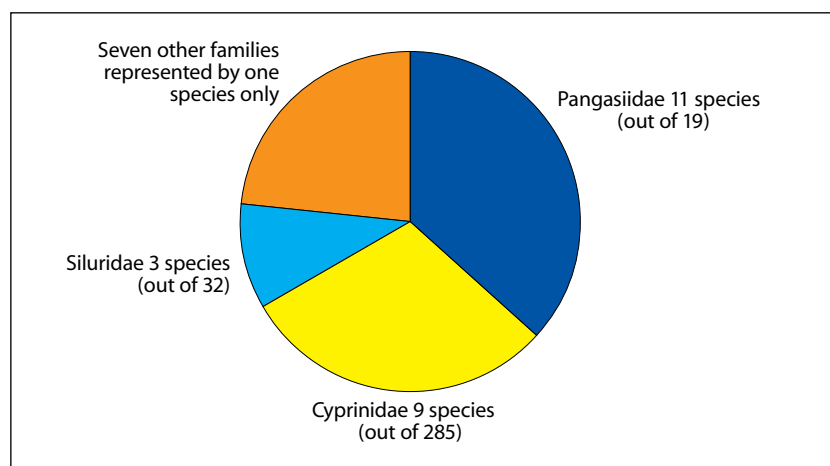
Correlation between migration cues

Correlation between triggers of fish migrations

Of the thirty species sensitive to migration cues, twelve species are sensitive to at least two triggering factors, and four species are known to respond to either three or four cues. The fact that triggering factors (discharge, water level, etc) may be inter-correlated has been

highlighted above. In order to clarify the interactions between triggering factors, a principal component analysis was performed on the table of triggers to calculate the correlation coefficient between all factors (30 rows = species, 5 columns = triggers; Table 3).

Table 3. *Correlation coefficient between migration triggers (from the Annex 1)*

	Discharge	Water level	Rainfall	Water colour	Insects
Discharge	1				
Water level	-0.389	1			
Rainfall	-0.218	-0.218	1		
Water colour	-0.218	-0.218	0.524	1	
Insects	0.259	-0.111	0.267	0.267	1

The correlation matrix shows that according to this data set based on qualitative ecological records, none of the triggers correlates significantly with another. Thus according to these data, variation in discharge, water level and water colour, the apparition of insects and early rainfalls are not triggering factors systematically recorded together.

Correlation between environmental variables

As noted previously, changes in water levels, turbidity and the first rains anticipate the arrival of the annual monsoon. Some fishers say that it is the combination of the three factors that triggers migration (Poulsen, 2000). The possibility that a combination of different factors triggers migrations has also been documented in South America. Sato and Godinho (2004), working in the São Francisco River, note that fishes migrate mainly from October to January, when the water levels tend to rise, temperatures are higher and the days are longer.

In order to assess the possible correlations between environmental variables mentioned in the previous sections, we combined hydrological data from the MRC with environmental data from the Department of Hydrology in Lao PDR (Ministry of Water Resources and Meteorology). Data from Pakse (the gauge station closest to the Khone Falls) over the period from July 1995 to June 1998 (n = 36 months) was used. The matrix of correlation coefficients is given in Table 4.

Table 4. *Correlations between environmental parameters in Pakse*

	Temperature	Rainfall	Water level	Discharge
Temperature	1			
Rainfall	0.13	1		
Water level	0	0.25	1	
Discharge	0	0.26	0.99	1

This analysis, although limited in the time covered, shows clearly that in Pakse:

- discharge correlates strongly to water level;

- other environmental parameters do not correlate.

Although data on total suspended solids was available, correlations between turbidity and other environmental variables has not been calculated here because of a bias: the relationship between discharge and water quality varies between the rising and falling stages of the flood. The phase of the moon, which is also available in data set, does not, of course, correlate with any of these environmental factors.

These results show that in further analyses of environmental cues, water level and discharge should be considered as a single trigger, and other parameters can be considered as independent.

Quantitative relationships between discharge and migrations

Baran *et al*. (2005) present the most detailed study of the relationship between triggers and discharge in the Mekong Basin. This study, which was based on six years of monitoring data recorded from a multi-gear fishery situated just below Khone Falls in Southern Lao PDR (Figure 1), reviews the response of fish species to hydrology. The study combined daily fishery records complied by I.G. Baird with MRC daily hydrological records collected at Pakse, located about 130 km upstream of Khone Falls.

A general description of the migration patterns in Khone Falls is given below, then the results of Baran *et al*. (2005) are reviewed and deepened.

Overview of migration patterns at Khone Falls

Baird (2001) provides a precise description of the succession of migrant fishes below Khone Falls. The following list is a summary of his observations:

- The fishing year begins at the end of the monsoon season, in late September or October. Villagers then target short distance migrators ('black fishes') that move from seasonal streams and wetlands back to perennial water bodies.

- By the end of October, fish begin migrating up the Mekong River from Cambodia, starting with medium and large-sized cyprinids.

- Between November and early January, three spawning cyprinids are abundant in catches, in particular *Probarbus jullieni* (65% of the catch of large-meshed gillnet fishery). These species are supplemented by about 30 other species of large fishes, mostly cyprinids.

- Around mid-December, a wave of small cyprinids arrives, starting with *Henicorhynchus* spp.

- They are followed by a wave of medium-sized migrating cyprinids, comprising about 100 species, whose fishing season lasts from December to January.

- Early February important schools of small cyprinids begin arriving at Khone Falls from Cambodia. Their movements are closely associated with lunar cycles.

> *Henicorhynchus* spp. and *Paralaubuca typus* are the two most abundant taxa, making up to 80% of the catch. The migration generally ends around March.

- In April, schools of large sized *Cirrhinus microlepis* (cyprinds) migrate up-river from Cambodia, at the height of the dry season.

- By the end of April, still during the dry season, the first schools of small migratory catfishes arrive from Cambodia.

- By May, when the monsoon rains begin to fall and the Mekong River rises dramatically, many species of medium to large pangasid catfishes and other large cyprinids arrive from Cambodia. This is a time of intensive fishing targeting in particular large pangasiids.

- Between June and July the catch is made of small and medium-sized cyprinids that migrate downstream from Lao PDR to Cambodia.

- By July, the water levels are high and fishing becomes difficult. It is thus difficult to determine possible migratory patterns at this season, but it is believed that most species then migrate downstream.

These patterns are illustrated in Figure 5.

The combination of fishery catch data with hydrological records by Baran *et al*. (2005) shows that:

- the highest species diversity in catches correspond to the lowest water levels;

- as much as 96% of the Khone fishery yield is made of fish taxa sensitive to discharge.

Representativeness of the Khone Falls studies

The fact that almost the entire catch, in terms of biomass, is made of fish taxa sensitive to discharge highlights the dramatic impact that flow modifications may have on the fish harvest at Khone Falls and possibly in the whole Lower Mekong Basin. However, one might question the representativeness of conclusions drawn from this study in the Khone Falls, and the validity of inferring from this area to the whole LMB.

Representativeness of sampling

The fact that the overall catch results from 32 distinct fishing methods targeting all species and operated during six years at all hydrological levels ensures an extensive sampling (of 666,000 individual fishes), much superior to any 'scientific' sampling that would necessarily be more limited in time and in scope.

This sampling however is driven by fishers, not by scientists, which may create a bias towards valuable commercial species. In fact, fishers deploy an exceptional diversity of gears and strategies (detailed in particular in Roberts and Baird, 1995; Claridge *et al*., 1997) to maximize their yield: they catch all species and all sizes, fish year round and harvest resident
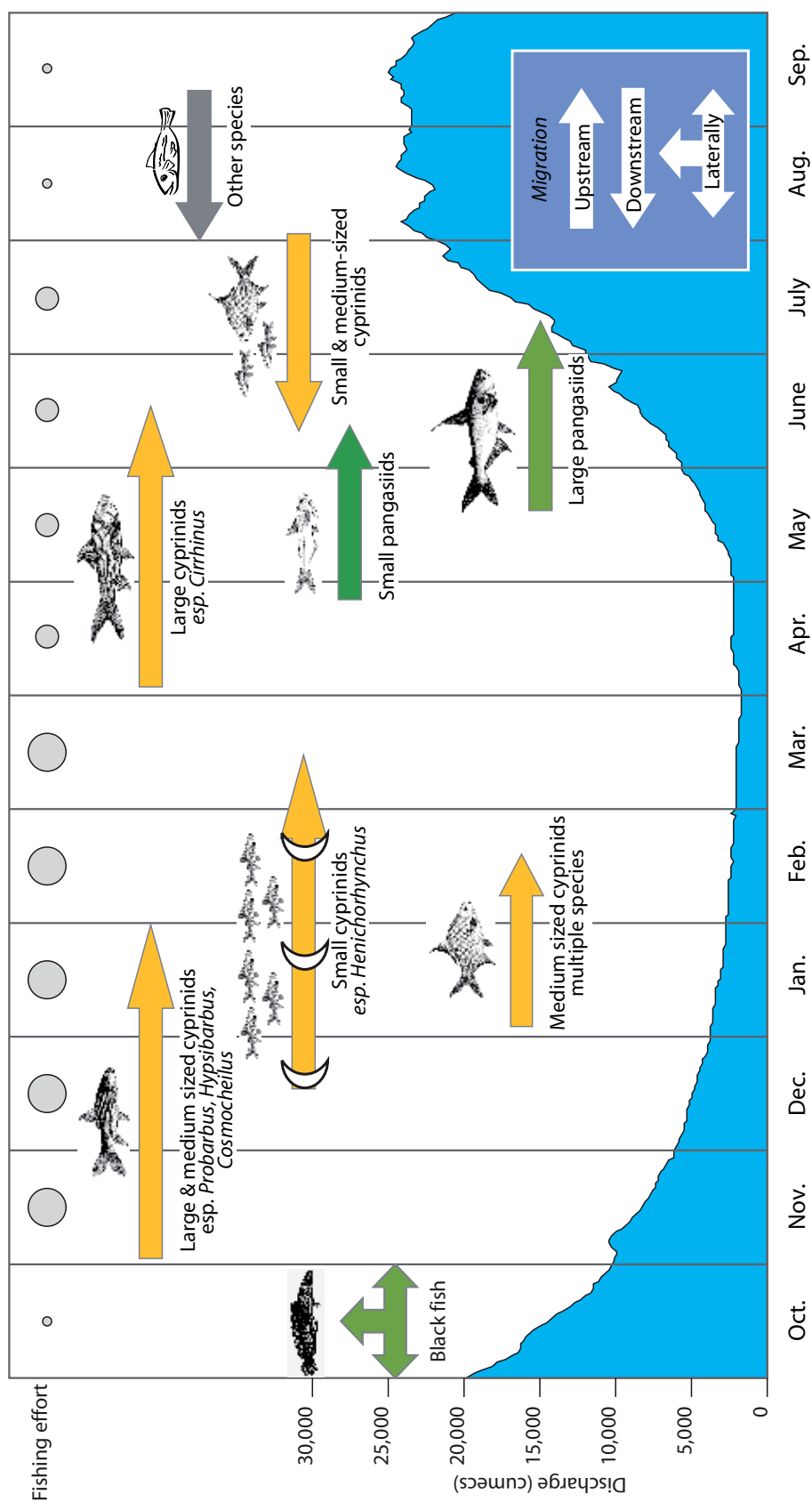
Figure 5. Major migration patters just below Khone Falls (figure based on Baird, 2001)

fishes as well as migrant ones (although migrants form the bulk of the catch). Thus the bias in sampling is minimal, certainly not higher than that of a more limited scientific sampling using only a few gears.

However, it should be acknowledged that in this particular stretch of the river system, the share of migrant fishes could be slightly overestimated when picturing the local river fish community, as not all species force their way through this natural bottleneck where they get caught.

Spatial representativeness

The results detailed in the above study and below are specific to Khone Falls, i.e. of the middle part of the lower Mekong River. The corresponding fish community includes a number of species that are found upstream but not far downstream, and this community is significantly different from that found, for instance, in the Delta.

However, the species that make the bulk of the catch are the same as in Cambodia as they migrate between both countries (see MRC 2001 for details). The top-ten species in the Khone Falls fisheries are detailed in Table 5; a comparison with the top-ten catches in Cambodian fisheries (van Zalinge *et al*., 2000) shows that the four taxa common to both fisheries (namely *Henicorhynchus* spp., *Paralaubuca typus*, *Pangasius* spp. and *Cyclocheilichthys enoplos*) constitute 36% of the total catch in Cambodia, i.e. about 245,000 tonnes in this country alone, according to van Zalinge *et al*. (2004).

Thus, the conclusions drawn from the Khone Falls study largely apply to Cambodia. If Lao PDR contributes only about 7% of the Mekong fish harvest, Cambodia contributes, with 682,150 tonnes, one fourth of this total harvest. Therefore, the conclusions regarding the relationship between discharge and migrations drawn from the Khone Falls area, i) are significant to a large share of the catch of the whole Mekong, and ii) apply to more than two hundred thousand tonnes of fish contributing to food security basinwide.

Catches, species richness and discharge: global patterns

We propose below a detailed analysis of the relationship between daily catches in Khone Falls and corresponding discharge levels. All gears have been lumped together (the reasons why this is the least dissatisfying option are detailed in Baran *et al*. 2005, chapters 4 and 6), species have been identified, biomasses expressed in kilograms, and discharge levels (cubic metres per second, i.e. cumecs) have been rounded to the closest thousand. Figure 6 shows the response of the Khone Falls fish community, in terms of biomass and species richness, to the various discharge levels.
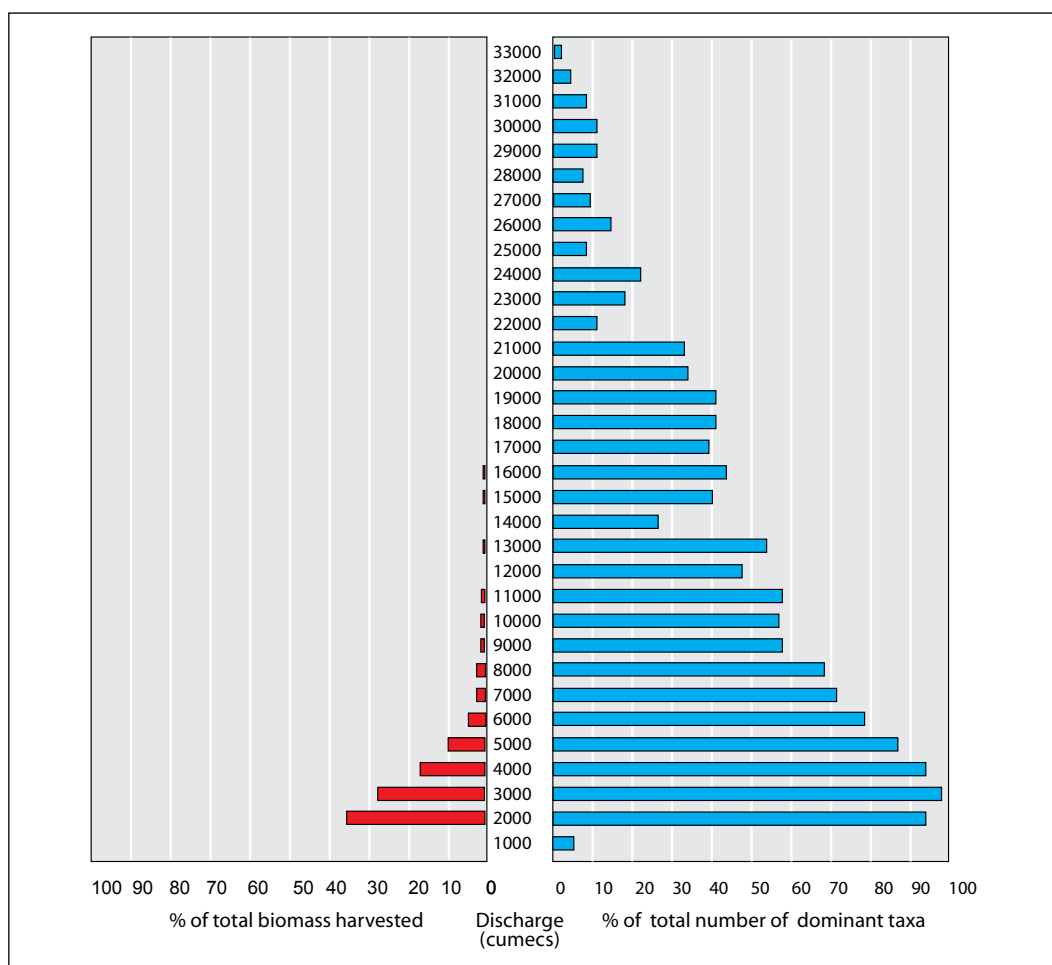
Figure 6. Percentage of the total biomass and of the dominant taxa harvested at each discharge level.
(Out of 201 fish species recorded in Khone Falls, 110 taxa are defined as dominant.)

This figure shows that:

- the discharge levels that correspond to the most diverse catch are the low discharge levels, in particular between 2000 and 8000 cumecs;

- very low discharges, between 2000 and 4000 cumecs, correspond to the maximal diversity in catches, with more than 90% of all dominant taxa recorded caught at these discharge levels;

- almost ALL the biomass (precisely 95.7% of it) is caught between 2000 and 8000 cumecs.

These results highlight the extreme importance of low water-levels and discharges in the richness and production of the Khone Falls fisheries.

Catches and discharge: detailed patterns

In Figure 7, the global patterns outlined above are detailed for each of the 110 taxa dominant in catches.
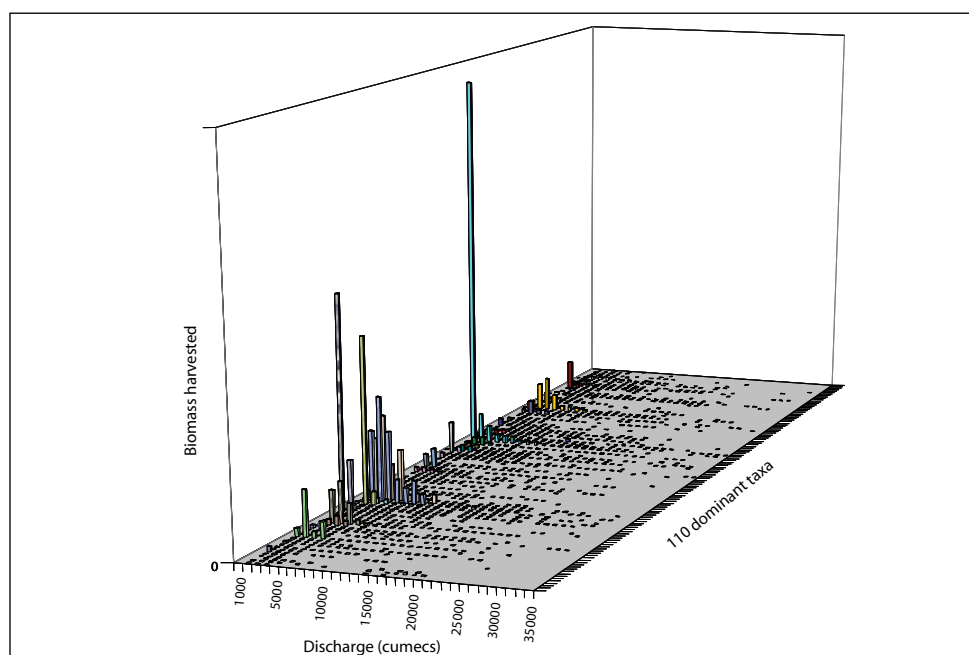
Figure 7.   Catch of 110 dominant taxa in Khone Falls, in relation to discharge levels

This figure, intentionally simplified to illustrate major patterns, shows that most catches are realized at low discharge levels (between 2000 and 8000 cumecs), with scattered but very minor catches are higher rates, and that the bulk of this catch is actually due to a few species or taxa. There results also show how sharp the migration peaks of these dominant species can be.

The catch of the top-ten species as a function of discharge is detailed in Table 5.

Table 5.   *Top-ten species or taxa in Khone Falls catches, and percentage of the total catch of this species/taxon for a given discharge range*

		Discharge ranges (cumecs) and corresponding % of the specific catch						
Species or taxon	% of the overall catch	1000-5000	6000-10 000	11 000-15 000	16 000-20 000	21 000-25 000	26 000-30 000	31 000-35 000
Henicorhynchus spp.	20.0	94	5	1	0	0	0	0
Pangasius krempfi	14.4	76	23	1	1	0	0	0
Pangasius conchophilus	11.8	70	29	1	0	0	0	0
Paralaubuca typus	11.7	100	0	0	0	0	0	0
Pangasius macronema	8.1	100	0	0	0	0	0	0
Probarbus jullieni	4.5	93	7	0	0	0	0	0
Cosmochilus harmandi	4.5	83	15	2	1	0	0	0
Scaphognathops bandanensis	3.5	99	1	0	0	0	0	0
Labiobarbus leptocheilus	1.8	95	4	1	0	0	0	0
Botia modesta	1.5	100	0	0	0	0	0	0

This table, which complements Figure 7, confirms how the bulk of the catch is correlated to low discharge levels, and shows that this relationship is due to a handful of species only.

Among the top-ten species listed in Table 5, five (*Pangasius krempfi, Pangasius conchophilus, Paralaubuca typus, Pangasius macronema* and *Botia modesta*) have been identified earlier in this review as triggered by thresholds or changes in discharge, water level or current. These five species alone represent 47% of the total annual catch at Khone Falls.

Response of 47 fish taxa to discharge

Baran *et al.* (2005) give individual relationships between abundance and discharge for 53 taxa. Data being gathered on a daily basis over six years, abundance is expressed in terms of biomass of a taxon in daily catches of the overall multi-gear fishery, and discharge is taken from gauge records measured at Pakse, located about 130 km upstream of Khone Falls.

Out of the 53 taxa studied, 6 were discarded as being rare and 47 have been kept as 'dominant taxa', for which at least 50 individuals were caught per year. Out of these 47 dominant taxa, the sensitivity to discharge is nil or unclear for 14 of them: *Hemipimelodus borneensis, Hemisilurus mekongensis, Kryptopterus* spp*., Lobocheilos melanotaenia, Opsarius* spp*., Osteochilus* spp*., Pangasius pleurotaenia, Pangasius polyuranodon, Pristolepis fasciata, Pseudomystus siamensis* and *Rasbora* spp*. The sensitivity to discharge can be thus quantified for 36 remaining fish taxa, as detailed in Annex 2 and illustrated in Figure 8. These results show that four groups of species can be identified:

- very sensitive species caught during an extremely narrow discharge range (e.g. *Paralaubuca typus*);

- sensitive species whose peak abundance corresponds to a narrow discharge range (e.g. *Pangasius macronema*), but that can also be caught, in lesser abundance, at other discharge values;

- non-sensitive species, whose catches do not exhibit a peak in relation to discharge;

- species whose response or lack or response vis-à-vis discharge cannot be characterised.

These results also show that low discharge levels (between 1000 and 5000 cumecs) are important to several species, and correspond to the peak in the catch of these species.
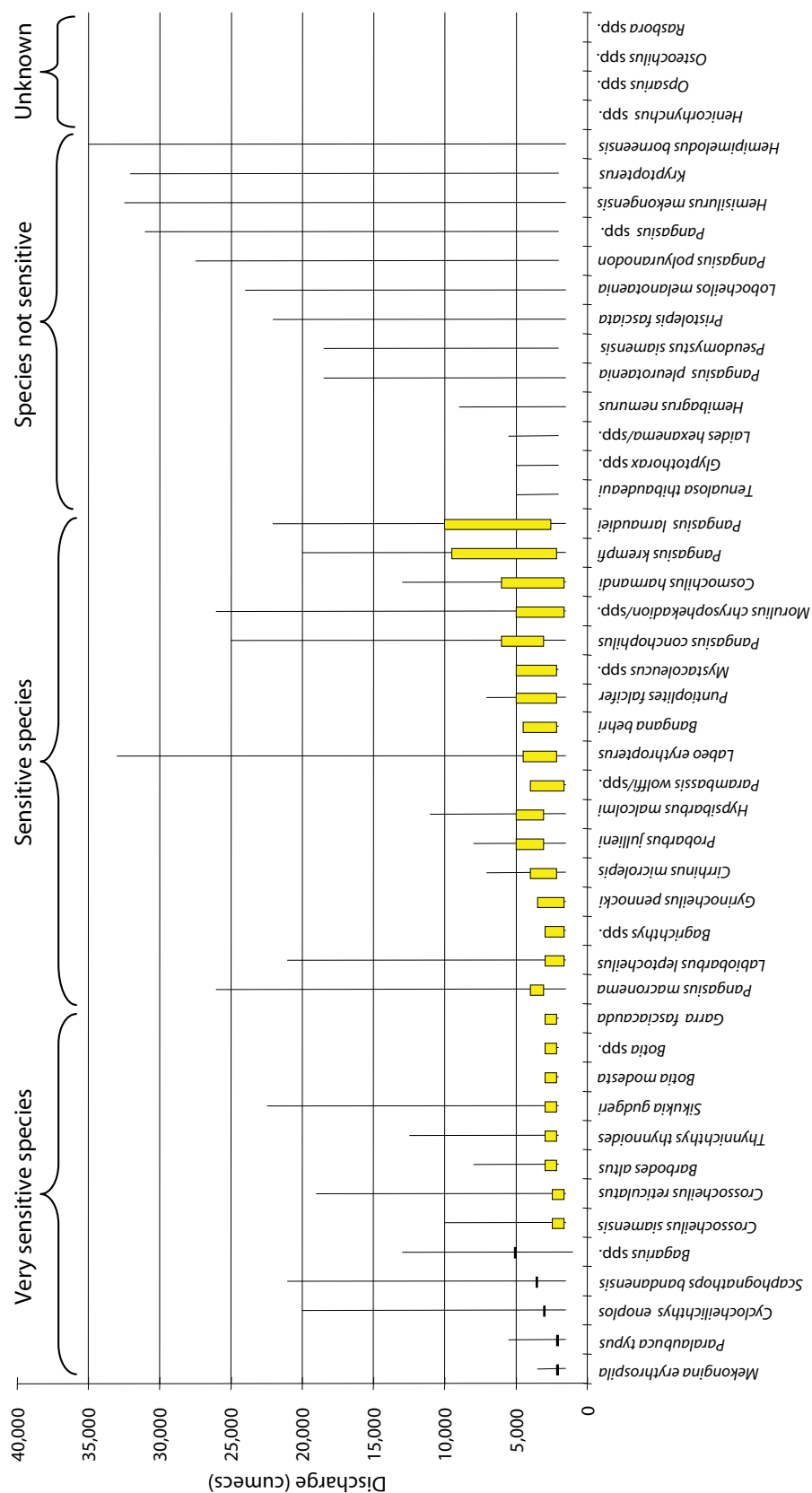
Figure 8. Discharge and fish migration at Khone Falls. Lines represent the distribution range of a taxon in catches as a function of discharge, and yellow boxes highlight peaks within the distribution range

5. Conclusions

Migration and triggers

The first point highlighted by the literature review is that relatively few studies focus specifically on the migration of tropical freshwater species. In the 40 publications on this topic the Mekong figures prominently as a river where fish migrations play an essential role in the ecology of the system and sustainability of the fisheries.

Fish migration triggers have only been addressed in a handful of publications worldwide, and the very dominant share of Mekong-related publications among those dealing with this topic confirm the special importance of migration triggers in the Mekong Basin.

However, this study also shows that given the rich biodiversity of the Mekong River (768 fish species documented scientifically), knowledge of migration patterns is available for only 24% of the fish species. Lack of information about the possible migratory behaviour of three-quarters of Mekong species calls for an increased effort in bioecological studies in order to better assess the behaviour, requirements and response to environmental changes of the large majority of Mekong fish species.

The literature review identified five major migration triggers in tropical rivers worldwide, as well as in the Mekong; they are i) discharge, water level and current; ii) rainfalls at the end of the dry season; iii) changes in water colour and turbidity; and iv) the apparition of insects. The fifth possible trigger, the moon, is also often considered important, but its role (in particular that of a given lunar phase) remains unclear.

Of the 165 Mekong fish species known to migrate, migration cues have been documented for 30 species; i.e. for 18% of them. Migration cues are unknown for the remaining 82% of these migrant species.

Water-level is the environmental parameter most often cited in the literature as a migration trigger. Literature and our data show a close correlation between this parameter and discharge and water current, and that they are best considered as a single trigger.

In the Mekong Basin, 26 species are known to be triggered by thresholds or changes in discharge, water level or current.

The first rainfalls marking the end of the dry season also trigger breeding and reproductive migration of fishes in the tropics, and of nine species in the Mekong Basin.

The migration of nine Mekong fish species is known to be triggered by a change in turbidity or in the water colour. The latter terms include increasing sediment load, decreasing sediment load and algal or planktonic development.

Finally, the migration of three Mekong fish species is triggered by the apparition of insects, in particular at the beginning of the rainy season.

Ninety per cent of Mekong fish species for which migration cues are documented respond to a variation in water level or in discharge. The second and third most frequent triggering factors are a change in water colour and the first rainfalls at the end of the dry season, both affecting 30% of species sensitive to migration cues. The apparition of insects is a trigger for 10% of species known to be sensitive to environmental cues. As mentioned above, the moon is widely acknowledged as playing a role in the migration of several Mekong species, but is it unclear whish phase of the moon is a trigger, as this seems to vary depending upon species and locations. In the Khone Falls area, spectacular migrations occur at the new moon of the second lunar cycle after the winter solstice, the time of the Chinese New Year.

Data analysed showed that the pangasiid family (catfishes) is the most sensitive to migration triggers, that affect 58% of the families 19 species. The other sensitive families are silurids (another catfish family, with 3 species, i.e. 9% of its species) and cyprinids (9 species; i.e. 3% of the family). Thus among documented species, catfishes, with 15 species, are by far the group most sensitive to migration triggers. Catfishes are highly appreciated on markets, as attested by their market price that is among the top three highest prices per kilogram (US$2 to 2.16/kg in Cambodia according to Rab *et al.,* 2005). Catfishes also play a major role in the regional aquaculture sector, the fingerlings being caught in the wild to be raised in cages[1]. So beyond capture fisheries catches, a modification of triggers and of the reproductive success of catfishes might result in diminished supply for the whole aquaculture sector in Cambodia and southern Viet Nam.

Among the ten dominant taxa in Cambodia listed by van Zalinge *et al.* (2000), four are sensitive to migration cues: *Cyclocheilichthys enoplos, Pangasius* spp*., Barbonymus gonionotus* and *Paralaubuca typus.* They represent 18% of the total catch and 14% of the commercial value respectively, not to mention *Henicorhynchus* sp. (21 additional per cent of the catch) that is sensitive to water current and lunar phase without being listed in this review as a species whose migration is clearly *triggered*.

Discharge, catch and diversity

The current study, based on Khone Falls fisheries and hydrological data whose representativeness has been demonstrated, shows clearly that 96% of the total fish biomass harvested year round in the Khone Falls is harvested between 2000 and 8000 cumecs (discharge measured in Pakse). The most 'productive' discharge levels are 2000 and 3000 cumecs, as they total more than 60% of the annual yield.

This dependence of catch on low, dry season, discharge levels is due, i) to the multiple fish migration waves that occur during low water levels (see Figure 5); ii) to the dominance of

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1 In Cambodia, the aquaculture production of species whose cycle is mastered represents less than 5.5% of the total freshwater fish production. Ninety four per cent of the fish production thus originates from capture fisheries and from wild fingerlings –including catfishes- grown in cages.

a few fish taxa in catches, most of these taxa being sensitive or very sensitive to discharge levels (see Figure 8), and iii) to the catchability of fish at these discharge levels.

The results also show that the diversity in catches is also higher at low discharge levels (in particular between 2000 and 8000 cumecs) and decreases progressively as discharge increases. However in tropical fish communities, the biodiversity is made of a small number of very dominant species and a long tail of rare species. Thus the impact of dry season flows alterations will be much more dramatic for fishers and food security than an ecological analysis encompassing all species might tell.

The crucial importance of the dry season low discharge levels for the ecology of dominant fish species and, in particular, for the overall fishery harvest and food security should be strongly emphasized. This importance makes it a priority area of research to better inform development options. The water allocation rules being developed by the MRC and the Mekong riparian countries should also integrate the information regarding fisheries and its dependence upon low discharge levels.

Consequences of flow modifications on fish

A recurrent question is that of the consequences of flow modifications, due to damming or water abstraction, on fish migrations and ultimately on fish production. Several conclusions can be drawn from the above results.

Dry season flow modifications

Dry season flow modifications will be those having the strongest impact on fish ecology and catches.

- Increased dry season flows (possibly due to water released by dams)

  – The biological implications of increased dry season flows would be that dry season migration thresholds or cues are never reached, thus possibly inhibiting the migration of species sensitive to these low flows. These species and their level of sensitiveness are detailed in Figure 8. As most migrations occurring in the dry season have a reproductive purpose, the biological impact of increased dry season flows might be on reproduction success.

  – The fisheries implications of increased dry season flows would be that most gears designed to catch species migrating at low water levels cannot be operated any longer or are less efficient at higher water levels, hence a loss of catch and productivity even in presence of fish.

- Decreased dry season flows

  A reduction of dry season flows, for instance due to water abstraction for irrigation, would have dramatic consequences if the discharge in Pakse goes below 2000 cumecs,

as shown by Figures 6, 7 and 8 where no catches are recorded for such low discharge levels.

- Delayed flood onset

  Delayed flood onset might have a significant negative impact on the fish abundance as this factor is playing a strong trigger role in the migration of a majority of commercially important species. Several reports based on fishers' observations have also documented a positive relationship between an early flood and a productive fishing year, as early floods generally correspond to long flooding periods that allow a longer growth period for fish and thus a bigger annual fish stock. Welcomme and Halls (2003) also highlights the fact that in a system where the upstream movement of adult compensates the downstream drift of larvae, a natural or artificial variation of the flow regime is likely to result in a very different distribution of fry and thus in a fluctuating production in downstream regions, as illustrated by the *Prochilodus* genus in the Parana River (South America).

Impact on fish migration and production

The literature review did not identify any study having focussed specifically on the impact of dams on migration triggers. However the broader issue of the impact of dams on fish migration and production has been detailed in several extensive reviews (including Jackson and Marmulla, 2001, Welcomme and Hall 2003 or Arthington et al. 2004). Among the most documented assessments of the impact of dams on floodplains rivers are those from the Niger Basin (Laë, 1994; 1995; 1997; Laë et al., 2003). These results show a close correlation, over 25 years, between the decline of catches and that of annual average discharges (the latter being due to a combination of droughts and dam construction). In the Niger Central Delta, a reduction of 75% of the area of floodplain resulted in a 50% loss of the fish harvest, the two dams of the system contributing 10% of these losses (Laë, 1992). However these results also highlighted the fact that a declining natural fish production can be blurred by an increased concentration of fishes (hence a higher catchability) and an increased fishing efficiency due to new gears and fishing methods.

The increased production of reservoir fish following the creation of a dam is often cited as a natural compensation for the loss of capture fish. However out of 160 families living in freshwater, only 17 are fully lacustrine or able to live in lakes at all stages of their life cycle (Fernando and Holcik, 1982), most species having to return to free-flowing rivers to breed. An analysis of the information available in the Mekong Fish Database shows that in the Mekong Basin, nine species only are known to breed in reservoirs such as those that could be created behind dams: Cirrhinus jullieni*;* Cirrhinus molitorella*;* Clupeichthys aesarnensis*;* Cyclocheilichthys apogon*;* Hampala macrolepidota*;* Oreochromis niloticus niloticus*;* Oxyeleotris marmorata*;* Pristolepis fasciata *and* Puntioplites proctozysron.

Rainy season flow modifications

The impact of rainy season flow modifications would be minor compared to dry season flow changes.

- Decreased flood peaks in the rainy season might slightly improve the catchability of fish but not necessarily in a significant way, the harvest being very limited anyway in that season (the bulk of the catch is made in the dry season).

- Delayed flood peaks might not have a major impact on the catch and food security, as flooding is mainly a period of growth for fish, without noticeable migration nor breeding patterns.

Methodological points

Most of the literature in the above review uses information supplied by fishers. This fact has two consequences.

The first consequence is that information is biased towards commercially dominant species, i.e. the relatively small fraction of species numerically abundant that are typical of tropical fish assemblages (Gaston, 1994). Given this bias, only a fraction of the full biodiversity spectrum is considered (i.e. large knowledge gap from a conservation perspective). Conversely the knowledge gathered is the one that matters most to the livelihood and food security of riparian communities.

The second consequence is that the documented migration triggers and cues are mainly those fishers can, and choose, to record. This approach based almost exclusively on traditional ecological knowledge ignores the variables that are not visually perceptible, and results in the total absence of information on some variables, for instance chemical, that are known to cue migrations in temperate rivers.

Thus changes to water chemistry and sediment load, among other factors that might result from development activities, may also be important but remain totally undocumented.

The literature review has also highlighted three points to be considered in future studies:

- The importance of fish density as a complementary biological trigger of migrations, fish undertaking their migration only if there is a sufficient density of individuals in a given place.

- The importance of spawning triggers in addition to migration triggers, as reproduction is a phenomenon that itself requires appropriate coordination among individuals and thus coordinating triggers. These reproduction triggers are crucial to the sustainability of a fish population and also concern non-migrant species.

- The multiplicity of triggers, that play a role at different times in different physiological mechanisms; they result from a sum of ecological processes and cannot be reduced to a single parameter such as discharge at time *t*.

Despite a remaining share of uncertainty this study highlights, with quantitative arguments, the possible impact of water level/discharge alterations on fish migrations in a river system that generates 2.6 million tonnes of capture fish per year (van Zalinge *et al*., 2004) and produces four times as much fish per square kilometer than the North Sea (Jensen, 2001), Cambodia alone harvests more freshwater fish than the whole Northern America. Subsequently, basin development plans should definitely include a strong component focusing on the impact of flow modifications on inland fisheries, so that trade-offs are adequately assessed and that sound development options are chosen, integrating the fact that millions of basin dwellers currently depend on Mekong aquatic resources for their food security and livelihood.

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Annex 1. Life history, migration and triggers of Mekong fish species

Life history parameters, migration pattern and migration triggers of the 30 Mekong fish species known to have environmental migration cues (after FishBase 2005 and Mekong Fish Database 2003)

Scientific Name	Family	Common name	Max. length (cm)	Life span (year)	Age at first maturity (year)	Length at maturity (cm)	Length for max. yield (cm)	Trophic level	Migration season	Migration Trigger				
										Discharge	Water level	Rainfall	Water colour	Insects
Pangasius polyuranodon	Pangasiidae	Shark catfishes	80	31.6	0	44	52.9		Dry and Rainy		Yes	Yes	Yes	Yes
Paralaubuca typus	Cyprinidae	Minnows or carps	18	8	2.2	11.8	11.4	3.3 s.e. 0.43	Dry and Rainy		Yes	Yes	Yes	Yes
Cyclocheilichthys enoplos	Cyprinidae	Minnows or carps	74	28.7	6.4	41.1	48.8	3.2 s.e. 0.43	Dry and Rainy		Yes	Yes	Yes	
Tenualosa thibaudeaui	Clupeidae	Herrings, shads, sardines, menhadens	30	7.3	1.8	18.5	19.4	2	Dry and Rainy		Yes	Yes	Yes	
Bangana behri	Cyprinidae	Minnows or carps	60	20.4	4.7	34.1	39.4	2	Dry and Rainy		Yes		Yes	
Barbonymus gonionotus	Cyprinidae	Minnows or carps	40.5	14.2	3.4	24.1	26.3	2.4 s.e. 0.13	Dry and Rainy		Yes	Yes		
Hemisilurus mekongensis	Siluridae	Sheatfishes	80	2.6	0	44	52.9	3.3 s.e. 0.44	Dry and Rainy	Yes	Yes			
Labeo chrysophekadion	Cyprinidae	Minnows or carps	90	28.7	6.2	48.8	59.7	2	Dry and Rainy		Yes		Yes	
Mekongina erythrospila	Cyprinidae	Minnows or carps	45	19	4.5	26.5	29.3	2	Dry and Rainy			Yes	Yes	
Micronema bleekeri	Siluridae	Sheatfishes	60	3.4	0	34.1	39.4	4.5 s.e. 0.80	Dry and Rainy		Yes	Yes		
Pangasianodon gigas	Pangasiidae	Shark catfishes	300	7.3	0	141.4	205.1	2.3 s.e. 0.17	Dry and Rainy			Yes	Yes	
Pangasius macronema	Pangasiidae	Shark catfishes	30	2.6	0	18.5	19.4	3.2 s.e. 0.40	Dry and Rainy	Yes				Yes
Botia modesta	Cobitidae	Loaches	25	13.5	3.5	15.7	16.1	3.4 s.e. 0.43	Dry and Rainy		Yes			
Chitala blanci	Notopteridae	Featherbacks or knifefishes	120	24	5	62.9	80.2	3.7 s.e. 0.56	Dry and Rainy		Yes			
Cyprinus carpio carpio	Cyprinidae	Minnows or carps	120	27	5.3	75.2	98.5	3.0 s.e. 0.32	Dry and Rainy	Yes				

| Scientific Name | Family | Common name | Max. length (cm) | Life span (year) | Age at first maturity (year) | Length at maturity (cm) | Length for max. yield (cm) | Trophic level | Migration season | Migration Trigger | | | | |
										Discharge	Water level	Rainfall	Water colour	Insects
Hemibagrus filamentus	Bagridae	Bagrid catfishes	50	9.9	2.3	29	32.7		Dry and Rainy		Yes			
Lycothrissa crocodilus	Engraulidae	Anchovies	30	5.9	1.5	18.5	19.4	3.7 s.e. 0.59	Dry and Rainy		Yes			
Macrochirichthys macrochirus	Cyprinidae	Minnows or carps	100	32	6.8	53.5	66.5	3.7 s.e. 0.57	Dry and Rainy		Yes			
Osphronemus exodon	Osphronemidae	Gouramies	60	10.5	0	34.1	39.4	2.7 s.e. 0.29	Dry and Rainy		Yes			
Pangasius bocourti	Pangasiidae	Shark catfishes	120	17.5	0	62.9	80.2	3.2 s.e. 0.47	Dry and Rainy				Yes	
Pangasius conchophilus	Pangasiidae	Shark catfishes	120	24	0	62.9	80.2	2.7 s.e. 0.34	Dry and Rainy		Yes			
Pangasianodon hypophthalmus	Pangasiidae	Shark catfishes	130	10.8	0	67.5	87	3.1 s.e. 0.46	Dry and Rainy		Yes			
Pangasius krempfi	Pangasiidae	Shark catfishes	120	2.6	0	62.9	80.2	2	Dry and Rainy		Yes			
Pangasius kunyit	Pangasiidae	Shark catfishes	70.2	3.4	0	39.2	46.2	2.8 s.e. 0.38	Dry and Rainy		Yes			
Pangasius larnaudii	Pangasiidae	Shark catfishes	130	2.7	0	67.5	87	3.3 s.e. 0.52	Dry and Rainy		Yes			
Pangasius pleurotaenia	Pangasiidae	Shark catfishes	35	2.4	0	21.2	22.7	2.4 s.e. 0.26	Dry and Rainy			Yes		
Pangasius sanitwongsei	Pangasiidae	Shark catfishes	300	7.3	0	141.4	205.1	4 s.e. 0.66	Dry and Rainy		Yes			
Parachela oxygastroides	Cyprinidae	Minnows or carps	20	8.8	2.4	12.9	12.8	3.3 s.e. 0.43	Dry and Rainy		Yes			
Pristolepis fasciata	Nandidae	Asian leaffishes	20	4.4	0	12.9	12.8	3.1 s.e. 0.45	Rainy		Yes			
Wallago leerii	Siluridae	Sheatfishes	180	4.4	0	90	121.5	4.1 s.e. 0.69	Dry and Rainy		Yes			

Annex 2. Response of fish taxa to discharge at Khone Falls

Response of fish taxa to discharge at the Khone Falls (modified after Baran et al., 2005)

Taxon in the Khone Falls fisheries database	Family	Abundance in relation to discharge	Sensitivity to discharge
Parambassis wolffi/spp.	Ambassidae	Peak between 1,500 and 4,000 cumecs	High
Bagrichthys spp.	Bagridae	Sharp and dense peak between 1,500 and 3,000 cumecs	High
Tenualosa thibaudeaui	Clupeidae	Species caught between 2,000 and 5,000 cumecs	High
Botia modesta	Cobitidae	Very sharp and dense peak between 2,000 and 3,000 cumecs	High
Botia spp	Cobitidae	Very sharp and dense peak between 2,000 and 3,000 cumecs	High
Bangana behri	Cyprinidae	Peak between 2,000 and 4,500 cumecs	High
Barbodes altus	Cyprinidae	Species caught between 2,000 and 8,000 cumecs, with a peak between 2,000 and 3,000 cumecs	High
Cirrhinus microlepis	Cyprinidae	Species caught between 1,500 and 7,000 cumecs, concentrated between 2,000 and 4,000 cumecs	High
Crossocheilus reticulatus	Cyprinidae	Species caught between 1,500 and 19,000 cumecs, with a sharp peak between 1,500 and 2,500 cumecs	High
Crossocheilus siamensis	Cyprinidae	Species caught between 1,500 and 10,000 cumecs, with a sharp and intense peak between 1,500 and 2,500 cumecs (but 10 data points only)	High
Cyclocheilichthys enoplos	Cyprinidae	Species caught between 1,500 and 20,000 cumecs, with a sharp peak around 3,000 cumecs	High
Garra fasciacauda	Cyprinidae	Sharp peak between 2,000 and 3,000 cumecs, but few data points	High
Henicorhynchus spp.	Cyprinidae	Pattern species-specific	High
Hypsibarbus malcolmi	Cyprinidae	Species caught between 1,500 and 11,000 cumecs, with a peak between 3,000 and 5,000 cumecs	High
Labeo erythropterus	Cyprinidae	Species caught between 1,500 and 33,000 cumecs, concentrated between 2,000 and 4,500 cumecs	High
Labiobarbus leptocheilus	Cyprinidae	Species caught between 1,500 and 21,000 cumecs, with a concentration between 1,500 and 3,000 cumecs	High

Taxon in the Khone Falls fisheries database	Family	Abundance in relation to discharge	Sensitivity to discharge
Mekongina erythrospila	Cyprinidae	Very sharp and dense peak between 1,500 and 3,500 cumecs, in particular around 2,000 cumecs	High
Mystacoleucus spp.	Cyprinidae	Peak between 2,000 and 5,000 cumecs	High
Paralaubuca typus	Cyprinidae	Species caught between 1,500 and 5,500 cumecs, with a sharp and intense peak around 2,000 cumecs	High
Puntioplites falcifer	Cyprinidae	Species caught between 1,500 and 7,000 cumecs, with a concentration between 2,000 and 5,000 cumecs	High
Scaphognathops bandanensis	Cyprinidae	Species caught between 1,500 and 21,000 cumecs, with a peak around 3,500 cumecs	High
Thynnichthys thynnoides	Cyprinidae	Species caught between 2,500 and 12,500 cumecs, with a sharp peak between 2,000 and 3,000 cumecs	High
Gyrinocheilus pennocki		Sharp and dense peak between 1,500 and 3,500 cumecs	High
Pangasius krempfi	Pangasiidae	Species caught between 1,500 and 20,000 cumecs, concentrated between 2,000 and 9,500 cumecs	High
Pangasius macronema	Pangasiidae	Species caught between 1,500 and 26,000 cumecs, with a sharp and intense peak between 3,000 and 4,000 cumecs	High
*Laides hexanema/*spp.	Schilbeidae	Species caught between 2,000 and 5,500 cumecs	High
Hemibagrus nemurus	Bagridae	No clear pattern but concentration around 1,500 - 9,000 cumecs	Medium
Cosmochilus harmandi	Cyprinidae	Species caught between 1,500 and 13,000 cumecs, concentrated between 1,500 and 6,000 cumecs	Medium
Morulius chrysophekadion/ spp.	Cyprinidae	Species caught between 1,500 and 26,000 cumecs, concentrated between 1,500 and 5,000 cumecs	Medium
Probarbus jullieni	Cyprinidae	Species caught between 1,500 and 8,000 cumecs, with a peak between 3,000 and 5,000 cumecs	Medium
Sikukia gudgeri	Cyprinidae	Species caught between 2,000 and 22,500 cumecs, with a sharp peak between 2,000 and 3,000 cumecs	Medium

Taxon in the Khone Falls fisheries database	Family	Abundance in relation to discharge	Sensitivity to discharge
Pangasius bocourti	Pangasiidae	Species caught between 2,000 and 31,000 cumecs; no clear pattern	Medium
Pangasius conchophilus	Pangasiidae	Species caught between 1,500 and 25,000 cumecs, concentrated between 3,000 and 6,000 cumecs	Medium
Pangasius larnaudiei	Pangasiidae	Species caught between 1,500 and 22,000 cumecs, concentrated between 2,500 and 10,000 cumecs	Medium
Bagarius spp.	Sisoridae	Species caught between 1,000 and 13,000 cumecs, rather around 5,000 cumecs	Medium
Hemipimelodus borneensis	Ariidae	No clear pattern	Nil
Pseudomystus siamensis	Bagridae	No pattern	Nil
Lobocheilos melanotaenia	Cyprinidae	Species caught between 1,500 and 24,000 cumecs; no clear pattern	Nil
Pristolepis fasciata	Nandidae	No pattern	Nil
Pangasius pleurotaenia	Pangasiidae	No pattern	Nil
Pangasius polyuranodon	Pangasiidae	No pattern	Nil
Hemisilurus mekongensis	Siluridae	No pattern	Nil
Kryptopterus spp.	Siluridae	No pattern	Nil
Opsarius spp.	Cyprinidae	Insufficient data	Unknown
Osteochilus spp.	Cyprinidae	Pattern species-specific	Unknown
Rasbora spp.	Cyprinidae	Unclear response, probably species-specific	Unknown
Glyptothorax spp.	Sisoridae	Species caught between 2,000 and 5,000 cumecs, but few data points	Unknown