FISH BIOECOLOGY IN RELATION TO SEDIMENTS IN THE MEKONG AND IN TROPICAL RIVERS

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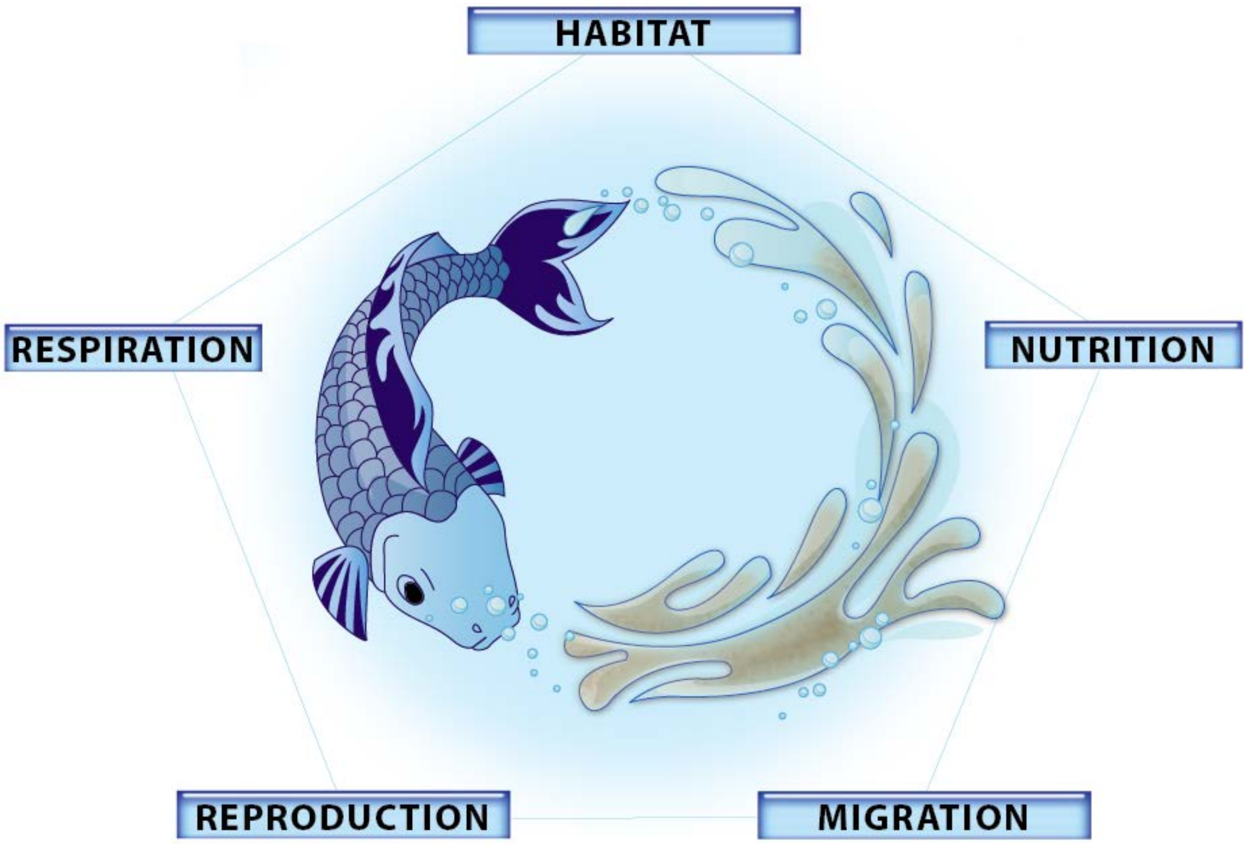

Project
"A Climate Resilient Mekong: Maintaining the Flows that Nourish Life"
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EXECUTIVE SUMMARY

The Mekong Basin is experiencing rapid development, including plans for the construction of 88 hydropower projects by 2030, which will have a very substantial impact on the river's sediment load (sediment trapping by dams). The current report reviews the interactions between sediments and fish in tropical rivers and in the Mekong, and focuses more specifically on a reduction of sediment loads following dam construction.

In the Mekong, the total annual sediment discharge is about 160 million tonnes per year on average, with a wide range of intra-annual as well as inter-annual variability. Sediments in rivers are found in two main forms (suspended and bedded sediments) and they consist of a variety of particle sizes (roughly categorized as gravel, sand, clay and silt). Most of the sediment load in the Mekong is suspended.

One property of sediments is that they adsorb and thus facilitate the transport of nutrients (in particular phosphorus and nitrogen) and organic particles. As dissolved nutrients in the water are generally low, the main nutrient load is associated with sediments. The dominant sediment categories in the Lower Mekong Basin are fine sands, silts and clays; the proportion of organic particles represents 6-8% of the total sediment load, which is considered high by global standards.

The Mekong is a place of exceptional fish biodiversity. Fish biodiversity increases downstream and the 3S system is a hotspot. The Mekong produces about 18% of the world's freshwater fish yield. Mekong fish resources are essential to food security in the basin. Fish migrations are an essential feature of the Mekong. Sediments influence fishes' biological functions, particularly respiration, nutrition, reproduction and migration, but also their habitat. Nutrient load is also a dominant factor explaining the overall productivity of tropical river ecosystems (including floodplains, estuaries and coastal areas).

Respiration. The organic component of sediments has a direct negative impact on dissolved oxygen through its Oxygen Demand. Suspended sediments and adsorbed nutrients also influence the amount of dissolved oxygen in the water through their interference with plant photosynthesis.

Nutrition. Sediments are the basic input for the food chains and trophic webs that fish are part of at a higher level, and thus are an essential component of fish nutrition. Suspended sediments and the turbidity they cause reduce photosynthesis and thus decrease primary production. Suspended sediments also play a role in predator-prey relationships. In the Mekong, a reduction of sediment loads is likely to result in decreased primary production, which might in turn change the dominant fish species and drive down fish productivity. But the relative influence of nutrients loads and turbidity on primary production must be clarified for this potential impact to be assessed.

Reproduction. The main relationship between fish reproduction and sediments is through spawning grounds. In estuaries high turbidity is favorable to the larvae of many coastal fish species. There is little information in the literature about the relationship between tropical fish reproduction and the impact of a *reduced* sediment load.

Migrations. Changes in turbidity or water color are a migration trigger for at least nine of the migratory species in the Mekong. Fish migrations can play a significant role in the nutrient distribution in the river basin. In the Mekong fish constitute a nutrient transfer from nutrient-rich downstream floodplains towards more oligotrophic upstream tributaries.

Habitat. Sediment load plays a major role in river geomorphology and in the riverbed and riverine habitats. Blocking sediment load will degrade the river bed downstream and will therefore affect the aquatic organism communities adapted to these specific habitats. In the Mekong, deep pools, an essential habitat for the survival of numerous fish species during the dry season, could be affected by modified water flows that result in an infilling of these pools, though this impact remains to be clarified. Water pH is also a characteristic of fish habitats that is related to suspended sediment concentrations.

The river flood pulse concept explains the exceptionally high productivity of rivers and their associated floodplains. It has been widely accepted as describing the exceptional productivity of the Mekong. Dam development is expected to reduce `the flood pulse as well as downstream sediment concentrations; this combination may have a synergetic and negative effect on the overall productivity of the river downstream, leading to its oligotrophication. This process of nutrient rarefaction, poorly studied, changes food web structures and decreases fisheries resources. Oligotrophication is most commonly related to phosphorus deficiency, but the nitrogen/phosphorus ratio is also to be considered. Ongoing hydrodynamic and physical modelling will also clarify the retention rate of dams and the fate of sediments, but the coupling between sediments and nutrients and the role of the amount of nutrients that are independent of sediments remain to be addressed.

1 INTRODUCTION

Sediments are an essential component of rivers and of their biological functioning. In addition to their influence on river geomorphology (maintenance of river forms and habitats such as pools and sand bars), sediments also include nutrients, detritus and organic debris of various sizes which interact with the river's different life forms, including fish (USEPA, 2003). The interaction between sediments and aquatic organisms, directly or indirectly through the effects of sediments on physical habitats, unquestionably influences the biodiversity and productivity of a river.

The Mekong is the second river in the world after the Ganges for its load in suspended solids[1], and is also the second richest river in the world in terms of fish biodiversity (Carling 2009; Baran 2010). Its average sediment discharge is estimated at 160 million tonnes per year, i.e. 12% more than the Amazon River (Wolanski and Nguyen Huu Nhan 2005, Sarkkula *et al.* 2010).

The Mekong Basin is experiencing rapid development, including plans for the construction of 88 hydropower dams by 2030, which will have a very substantial impact on the river's sediment load: when river flows enter a dam reservoir they decrease in velocity, which results in a fraction of the transported sediment being deposited in the dam reservoir (Palmieri *et al.* 2003, Lu and Siew 2005, and Figure 1). Thus, the Strategic Assessment of Mekong mainstream dams predicts a 75% reduction of the sediment load at the mouth of the Mekong by 2030 if all planned dams are built (ICEM 2010).

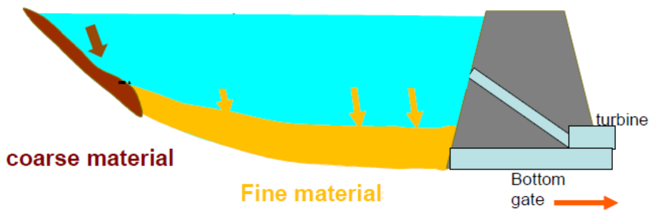


Figure 1: Accumulation of sediment behind dams. Source: Fruchart 2009

An abundant literature covers the effects of increased sediment and nutrient concentrations caused by reservoir sediment flushing or organic pollution on fish; however, very few studies detail the consequences of reduced sediments or nutrients for fish communities and production. This might be explained by visibility and timing issues: while flushing operations are spectacular and their impact immediately measurable, the effects of reduced sediment loads on ecosystems involve long-term processes such as modification of the river morphology over

[1] These figures are somewhat disputed since Welcomme (1985) indicates 190 and 406 million tonnes of suspended load for the Mekong and the Amazon respectively, but 560, 812 and 1625 million tonnes for the Yangtze, Brahmaputra and the Ganges respectively. The Yangtze, Brahmaputra and Amazon are not part of Carling's comparison.

decades (as a consequence of sediment loss) and oligotrophication (resulting from nutrient loss) whose impacts on fish communities are gradual, over several years. The consequences of these processes might also be buffered and thus hidden for a while by the resilience capacity of the river (nutrients released by the floodplain and sediments released by erosion to overcome the losses in upstream inputs).

TEXT BOX 1

MRC State of the Basin report, 2003 (excerpts)

At present the MRC monitors chemical water quality once or twice per month at 98 sites. Sampling has been conducted since 1985 in three LMB countries, and since 1992 in Cambodia. The data collected under the MRC sampling programme are taken just below the water surface, and give no indication of the bedload transport of sediment. Nevertheless, the measure should act as a reasonable indicator of the amount of sediment in the water.

The concentrations of TSS showed a decrease at 23 sites and an increase at six. Notable regions where TSS concentrations decreased were the entire set of Mekong mainstream sites between Chiang Saen and Pakse in Lao PDR, and eight of the 13 sites in northeastern Thailand. The trends in phosphorus and nitrogen were similar [except in the Delta]..

The most prominent change at mainstream sites was the decrease in TSS which extended from Chiang Saen downstream. At the Chiang Saen site, the decline in TSS concentrations is likely to be due to changes that have occurred in China. The most likely dam that could have influenced the river is the Manwan Dam. Regression analyses on data before and after the dam started filling in 1992 demonstrate that the decrease in TSS in the downstream sites has been caused by the entrapment of suspended sediment by the dam.

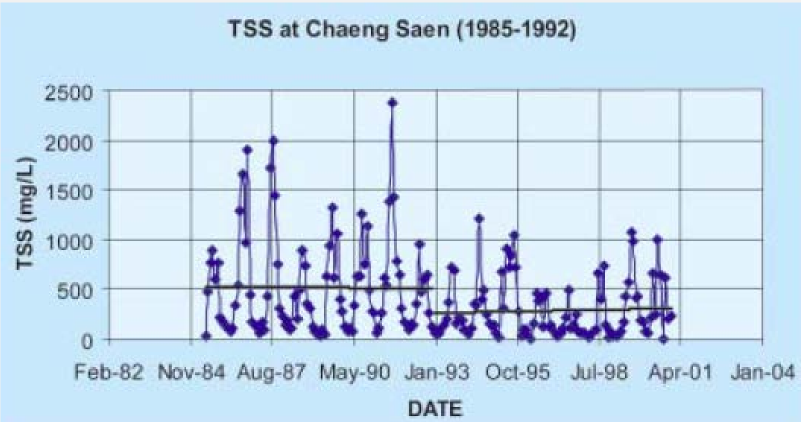


Figure: Suspended solids concentrations in the Mekong River at Chiang Saen, with linear regression lines fitted for the periods before and after the Manwan Dam commenced filling in 1992

The current report reviews the interactions between sediments and fish in tropical rivers and in the Mekong, and focuses more specifically on a *reduction* of sediment loads following dam construction. Sediment loads increase due to reservoir flushing and the impact of flushing on fishes are reviewed in another report (Reservoir sediment flushing and fish resources). The second and third sections of the present report (respectively “Sediments” and “Mekong fish”) introduce some core notions related to sediments and fish in the Mekong. In Section 4 (“Sediments and fish bioecology”) we review the interactions between sediments and i) fish biological functions (respiration, reproduction, etc.) and ii) fish habitat (biotope and water quality). In sections 5 the role of sediments in fish productivity is reviewed, before reviewing in the conclusion the main findings and knowledge gaps identified.

2 SEDIMENTS: CORE NOTIONS

Sediments in rivers are found in two main forms: suspended and bedded sediments (SABS). This distinction is based on the sediments’ size, nature and mode of transportation by the water. *Suspended sediments* are made of “particulate organic and inorganic matter that suspend in or are carried by the water” while *bedded sediments* or bedload “accumulate in a loose, unconsolidated form on the bottom of natural water bodies” (USEPA, 2003)[2]. Thus, coarse material, gravel and pebbles are transported by the bed load at the bottom of the river bed, while fine materials, sand and silt, are transported in suspension (Fruchart 2009).

A major property of sediments is their ability to adsorb small organic or inorganic compounds (i.e. these compounds stick to the sediment particles); thus the transportation of organic or inorganic matter in the hydrosystem is largely facilitated by sediments. This means that sediments are actually a combination of mineral, inorganic and organic compounds with different properties. It also means that sediments largely facilitate the transportation of organic or inorganic matter in the hydrosystem. We summarize in Figure 2 the main components of sediments and detail these components below.

[2] Castro and Reckendorf (1995) detail further the components of the bedload: « **Framework bedload** refers to the larger particles that are moved only during large flow events. They create the structure of the bed. The **matrix bedload** refers to that part of the bed material that is small enough to be frequently entrained by low to moderate flows but is large enough to settle out of the water column in lower velocities. This also includes sediment deposited by intragravel flow. This would incorporate the sand and silt size material. The **matrix bedload** is often referred to as "sediment" by fisheries biologists and is the size class that is of most interest and concern in fisheries studies”.

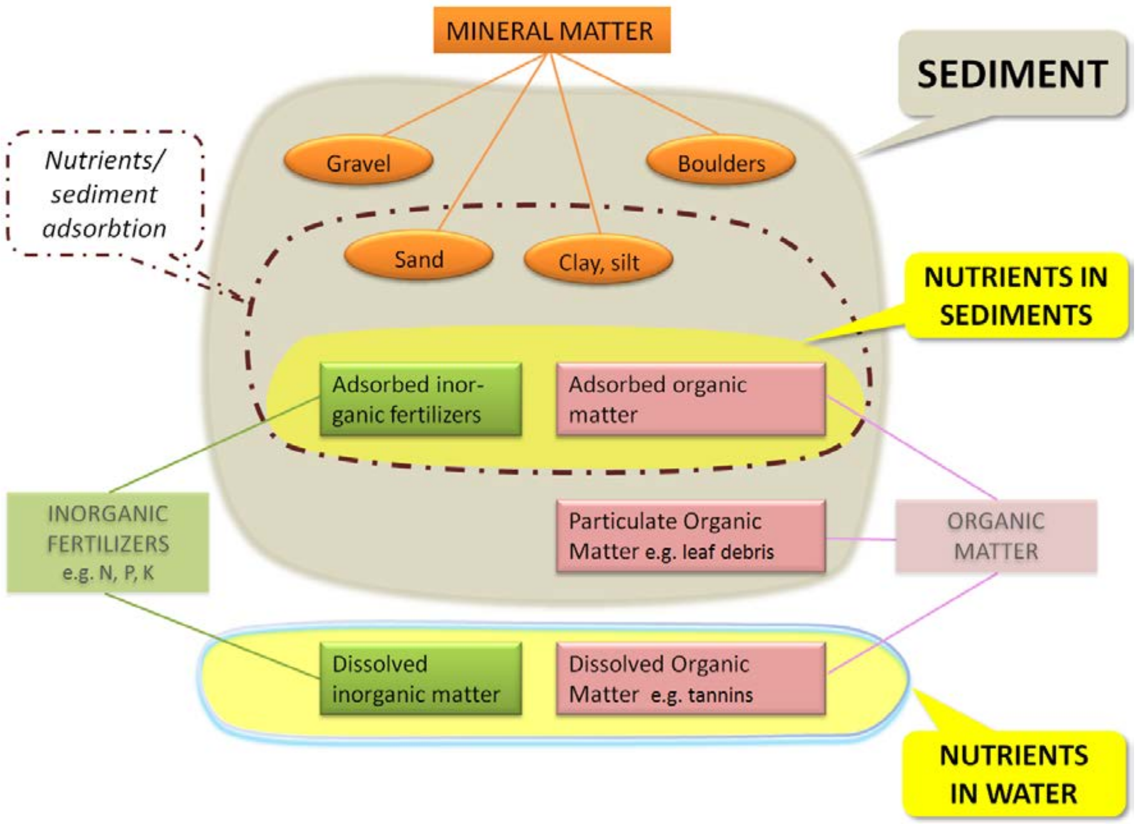


Figure 2: Main components of river sediment

2.1 Sediment particle size

A standard classification of mineral sediments based on particle size is detailed in Table 1.

D grain size range	Type of sediment
> 256 mm	boulder
64–256 mm	cobble
32–64 mm	very coarse gravel
16–32 mm	coarse gravel
8–16 mm	medium gravel
4–8 mm	fine gravel
2–4 mm	very fine gravel
1–2 mm	very coarse sand
0.5–1 mm	coarse sand
0.25–0.5 mm	medium sand
125–250 µm	fine sand
62.5–125 µm	very fine sand
3.9–62.5 µm	silt
1-3.9 µm	clay
<1 µm	colloid

Table 1: Conventional grain size ranges for different sediment types. Source: Ketelsen and Ward 2010

Welcomme (1985) gives a relationship between current speed and size of the sediment particles moved by the flow (Figure 3)

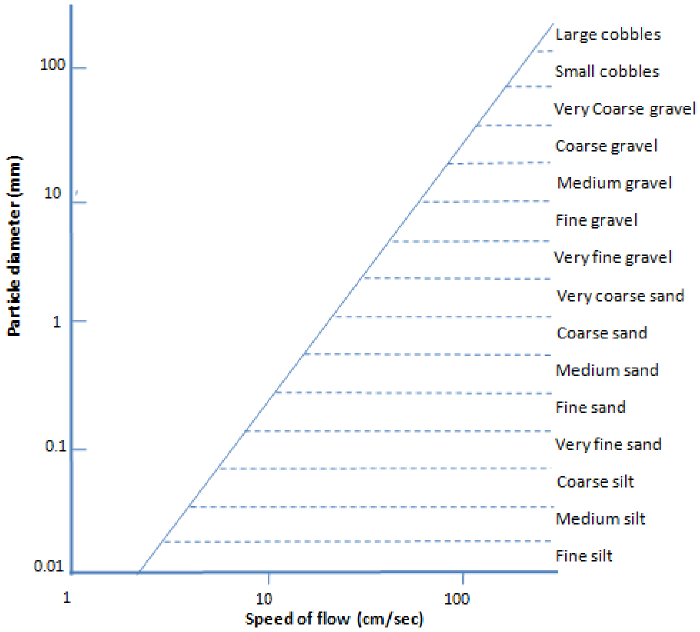


Figure 3: Relationship between flow speed and size of particles moved. Source: Welcomme 1985.

For the purpose of this report, we adopt a simplified classification reduced to three categories that are significant in the case of fish bioecology (Rowe *et al*. 2003):

- *Coarse sediment*, defined as particles larger than 0.95 or 1 mm. Being the main component of the river bed, affect the morphology of the river, shape fish habitats or spawning sites, and constitute the main biotope of several macro invertebrate species that fish feed upon;
- *Sand* or fine sediment, consisting of particles smaller than 0.85 mm which can be either bedded sediments or the suspended sediments depending on the river velocity (Figure 4).
- *Silt and clay*, i.e. particles smaller than 0.063 mm suspended in flowing water (thus creating its turbidity) or deposited into mud beds.

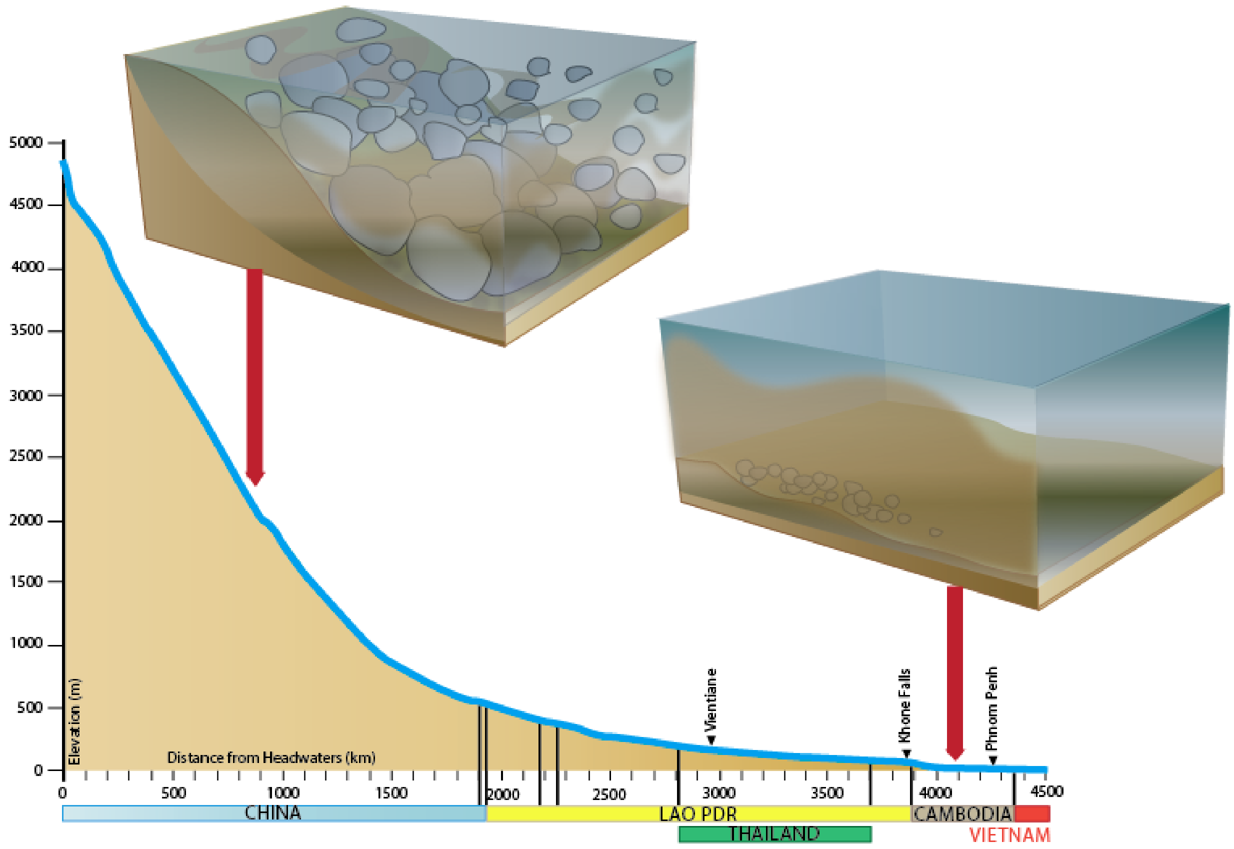


Figure 4: Nature of sediments depending on location, slope and current speed

In the case of the Mekong, a review of sediment-related information and data (Ketelsen and Ward 2010) led to the conclusion that "*considerable skepticism surrounds Mekong sediment data, which has been collected with inconsistent methods, measuring different parameters and has often yielded widely divergent estimates*".

Yet several authors agree that the dominant sediment categories in the Lower Mekong Basin are fine sands, silts and clays (Irvine *et al.* 2007, Sarkkula *et al.* 2009, Carling 2009). One of the few reliable sediment distribution curves available (cited in Ketelsen and Ward 2010, Figure 5) shows that in Pakse 99% of the sediment has a grain size smaller than fine gravel (>4.75 mm) and that 41% of the distribution is finer than coarse sand (>0.45 mm). In the Tonle Sap, silts and clays are the dominant grain size (Sarkkula *et al.* 2010). The latter authors conclude that the Mekong probably transports proportionally less sand and more silt/clay than other large rivers, and that clay and cohesive sediments seem to remain in suspension until the Mekong enters the Cambodian floodplain and the Mekong Delta.

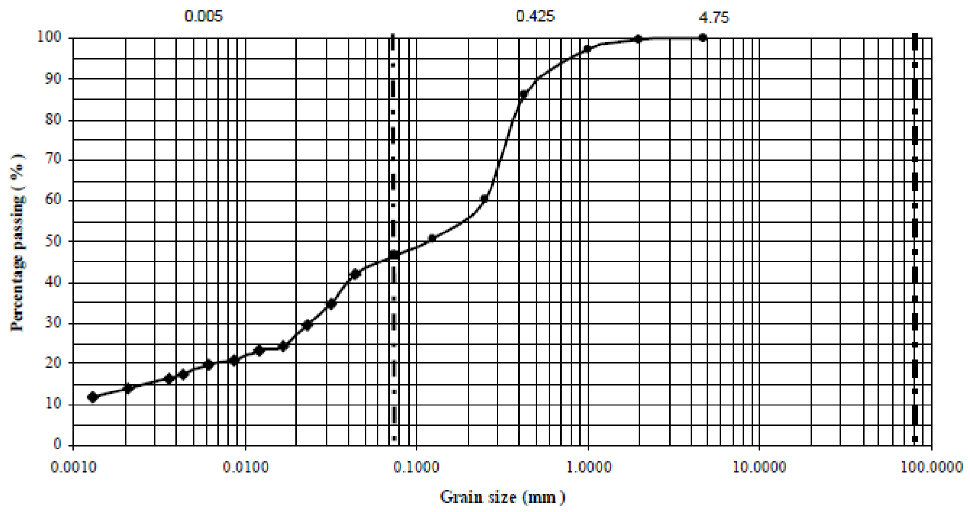


Figure 5: Sample grain size distribution curve for Pakse (cited in Ketelsen and Ward 2010)

In this context, sand is, by contrast and considering its limited abundance, an important component for the ecology of the Mekong. Sand and sandy islands are a typical component of the wetland zone stretching between Pakse and Kratie (MRC BDP 2 zone 4, including the Siphandone wetlands) and an essential habitat for the biodiversity of the Mekong, as detailed for instance in Baird 2001, Bezuijen *et al.* 2008, Allen *et al.* 2008 or Meynell 2010. Sand transportation and dynamics (resuspension, movements of sand bars or in-channel consolidation) are directly dependent upon hydrodynamic conditions (Sarkkula *et al.* 2010), which implies that changes in these conditions may have a disproportionately large impact on the sandy habitats in the Mekong. More generally coarse materials are very important for the stability of the river bed as they constitute a carpet protecting the bottom of the river from incision by water-driven erosion; unfortunately coarse materials settle completely when entering dam reservoirs (see Figure 1), and cannot be flushed downstream (Fruchart 2009).

2.2 Sediments and organic matter

Sediment loads also include an organic component of great importance for the biological productivity of the river. This organic component is made of i) dissolved organic matter (e.g. degraded proteins from vegetal or animal origin, tannins) and ii) particulate organic material transported from the watershed slopes (pollen, leaves, branches, trees) and subject to biological degradation and size reduction (Welcomme 1985). Dissolved Organic Matter (DOM) is part of the water flow but is not sediment, whereas Particular Organic Matter (POM) is a part of the sediment load of rivers.

Importantly, a fraction of the organic matter is adsorbed onto sediment particles, which facilitates the transport of such matter but also influences their chemical dynamics: this adsorbed organic matter may be stored within deposited sediments, or may be reincorporated into the flow through erosion. (Welcomme 1985).

In the case of the Mekong, the organic content amounts to 6-8% of the total sediment load (Pantulu 1986), which is seen as a large percentage and which contributes to the considerable productivity of the river.

2.3 Sediments and inorganic matter

River sediments serve as a major carrier and storage agent for inorganic nutrients such as phosphorus, nitrogen or potassium, but also pesticides and metals (Yang Xiaoqing 2003, Yi *et al.* 2008). As water contains low concentrations of dissolved nutrients, a river's main nutrient load actually consists of nutrients associated with—or adsorbed on—sediments. Thus, measurements in North America and Europe showed that about 90% of the total phosphorus flux in rivers was associated with suspended sediment (Ongley 1996). The pattern seems to be similar in the Mekong (Meynell 2010).

The most important sediments for the transportation of nutrients are the very small size sediments such as clay and colloids. The sediments that are chemically active are those that are smaller than 63 mm (i.e. silt and clay), in particular for phosphorus, a nutrient highly attracted to ionic exchange sites that are associated with clay particles and with the coating common on these small particles (Ongley, 1996). In South America, rivers with high sediment loads and high alkalinity have higher concentrations of nitrogen and phosphorus—and thus are more productive—than rivers with clear water (Forsberg *et al.* 1988). Unlike phosphorus, the transport and fate of organic sediments or organic matter attached to sediments is complicated by microbial degradation.

In the Mekong, the nutrients associated with sediments are responsible for the fertility of the floodplains and the delta (Meynell 2010). In particular, Sarkkula and Koponen (2010) showed that the high productivity of the Mekong floodplains is based on the nutrient loading associated with the sediments from upstream areas and that phosphorus is often the limiting nutrient. More specifically, 31-42% of the bioavailable phosphorus is transported into the floodplain with the sediment influx, which equates to 21,500 t/yr of bioavailable phosphorus (Sarkkula *et al.* 2010). Suspended inorganic material from the mainstream channel is often seen as more important to productivity than dissolved and particulate organic material (Vannote *et al.* 1980, Junk 1999).

The Mekong River Commission has defined quality classes for the main water parameters (MRC 2007). These water quality classes are based on thresholds defined by French water-basin authorities and are detailed in

Table 2: Parameters and thresholds used to classify the water quality in the Mekong. This table focuses on mineral and organic matter found in sediments. Source: MRC 2007

Class of water quality	Very good	Good	Fair	Bad	Very bad
Organic matter and other matter that can be oxidized					
DO (mg/l)	≥8	≥6	≥4	≥3	<3
COD (mg/l O_2)	≤5	≤7	≤10	≤12	>12
NH_4^-(mg/l NH_4)	≤0.5	≤1.5	≤2.8	≤4	>4
Nitrogenous matter					
NH_4^-(mg/l NH_4)	≤0.1	≤0.5	≤2	≤5	>5
Phosphorous matter					
TP (mg/l)	≤0.05	≤0.2	≤0.5	≤1	>1
PO_4^{3-} (mg/l PO_4)	≤0.1	≤0.5	≤1	≤2	>2
Suspended matter					
TSS (mg/l)	≤5	≤25	≤35	≤50	>50

2.4 Sediment loads

The amount of sediment transported by a river is another important factor in relation to fish biology and productivity.

In the case of the Mekong there is limited knowledge and great uncertainty about the suspended sediment load and its variability. There is data—whose quality is disputed—on the suspended load, but there is no reliable data on bed load. This means that an ecologically important type of sediment transport that is affected by dams is not part of current analyses. (Kummu and Varis 2007, Ketelsen and Ward 2010).

It is now largely agreed that the total annual sediment discharge of the Mekong amounts to about 160 million tonnes per year (range 140 -180 Mt/y), which is high in comparison with other major rivers of the world (Meade 1996, Wolanski and Nguyen Huu Nhan 2005, Sarkkula *et al.* 2010, Ketelsen and Ward 2010). The total load of the Mekong is about the same as the Mississippi, 85% of that of the Yangtze River and 12% larger than that of the Amazon (Carling 2009, Sarkkula *et al.* 2010,)[3]. Under natural conditions, 50% to 60% of the sediments originate from China, the 'Three S' catchments contributing about 17 Mt/yr (i.e. about 10% of the total load) and the remainder of tributaries in the Lower Mekong Basin providing about 30% of the total load (Ketelsen and Ward 2010).

The Mekong's sediment load is characterized by large intra-annual and inter-annual variability (Welcomme 1985, Ketelsen and Ward 2010 and Figure 6). On the seasonal level, water is heavily charged with silt during the rising flood, then deposits its suspended sediments

[3] These figures are somehow disputed since Welcomme (1985) indicates 190 and 406 million tonnes of suspended load for the Mekong and Amazon respectively, but 560, 812 and 1625 million tonnes for the Yangtze, Brahmaputra and Ganges respectively. The Yangtze, Brahmaputra and Amazon are not part of Carling's comparison.

over floodplains during the flood, and then becomes clear during the dry season (Welcomme 1985). From an interannual-perspective, LMB tributaries contribute a greater proportion of the annual load during wet years, while in dry years the amount of input from China is higher than normal (Ketelsen and Ward 2010).

The Mekong's sediment load is also characterized by strong geographical variability, the total suspended load increasing farther downstream. Thus, the annual total suspended load has been estimated as 67, 109 and 132 million tonnes per year at Chiang Saen, Vientiane and Khone Falls respectively (Carling 2009). Overall the Cambodian floodplains and Mekong Delta receive 95% of the total suspended sediment flux from upstream (Kummu and Varis 2007) and 80% of the suspended sediments that enter the Tonle Sap Lake get deposited in its floodplain (Lamberts 2006), which makes these intensive fishing grounds directly dependent on the flow conditions of the Upper Mekong (Baran *et al.* 2007a).

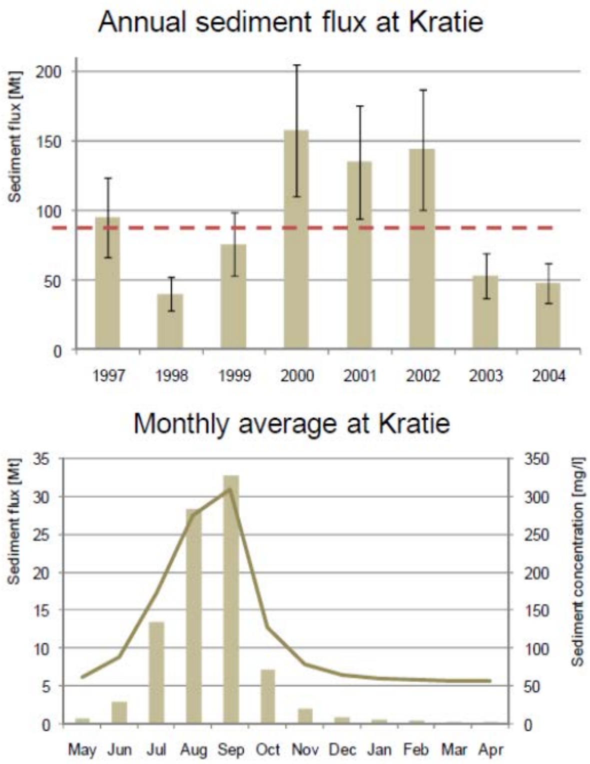


Figure 6: Annual average sediment load (1997-2004) at Kratie. Source: Kummu *et al. in* Ketelsen and Ward (2010)

3 MEKONG FISH: CORE NOTIONS

The exceptional features of the Mekong fish resources have been detailed in several publications (e.g. Lagler 1976, Pantulu 1986, van Zalinge *et al.* 2003, Baran *et al.* 2007b, Hortle 2009). We briefly review them here before focusing on the fish features related to sediments.

The Mekong is a place of exceptional fish biodiversity. The Mekong River is the world's second richest river after the Amazon. The Tonle Sap is the lake with the highest fish biodiversity in the world after the East-African Great lakes. An analysis of lists of species and endangered species among 302 countries or territories worldwide shows that Lao PDR, Thailand and Viet Nam are among the top 5% for their number of freshwater fish species and number of threatened fish species.

Fish biodiversity increases downstream and the 3S system is a hotspot. Like the sediment load, the Mekong River mainstream is characterized by a gradient of increasing species richness from the headwaters down to the sea, with 24 species in Tibet and 484 species in the Mekong Delta. A recent study (Baran *et al.* 2011) showed that within the Mekong Basin, the 3S system (Sekong, Sesan and Srepok watersheds) is home to 42% of the total Mekong fish biodiversity (i.e. 329 fish species out of 781), though the surface area of the 3S represents only 10% of the 800,000 km^2 of the Mekong watershed area. The 3S Rivers are also characterized by 17 endemic species found nowhere else in the world.

The Mekong produces about 18% of the world's freshwater fish yield. The fish catch, estimated to be between 755,000 and 2.6 million tonnes (the most reliable assessment being 2.1 million tonnes), comprises about 18% of the global freshwater fish catch (range 6-22%), making the Mekong the largest inland fishery in the world.

Mekong fish resources are essential to food security in the basin: Cambodia, Lao PDR and Thailand are the top four countries in the world for their freshwater fish consumption: fish consumption ranges between 24.5 and 34.5 kg/person/year. Thus, fish contributes 81% of the population's protein intake in Cambodia and 48% in Laos. The economic value of Mekong capture fish is up to USD 2.2-3.9 billion per year.

Fish migrations are an essential feature of the Mekong. Of the 189 migratory fish species known, 165 are long-distance migrants and these species represent more than 37% of the total yield, i.e. more than 770,000 tonnes per year. At the end of the dry season, more than 100 migratory species (Ziv *et al.* 2012) migrate up tributaries to lay eggs in a riverine environment characterized by clear water and its associated seasonal flora and benthofauna.

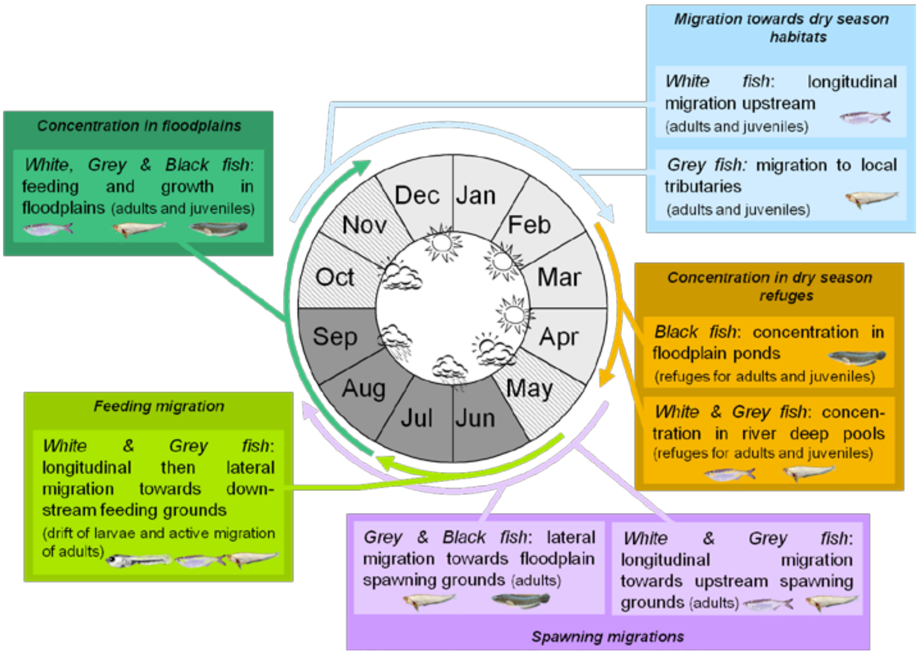


Figure 7: Fish migration patterns in the Mekong. Source: Baran and Un, *in press*.

The exceptional abundance of Mekong fish resources is explained by a combination of high fish biodiversity, high productivity linked to high sediment load and flooding, and a high exploitation rate (Baran and Un, *in press*).

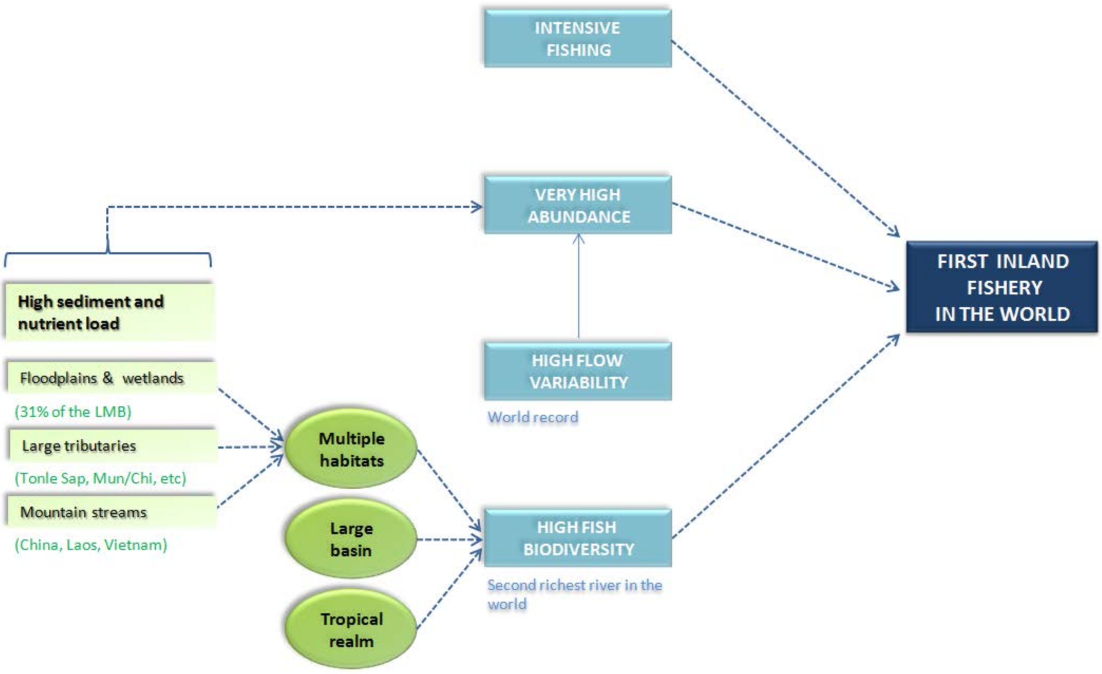


Figure 8: Factors explaining the size and importance of Mekong fisheries. Source: modified from Baran and Un (in press).

4 SEDIMENTS AND FISH BIOECOLOGY

Sediments constitute an important environmental factor in fish bioecology. Fish species inhabiting a river body are either adapted to specific sediment characteristics which are not constants (e.g. seasonal and inter annual variations) or tend to leave the area subject to excessive sediment load before returning after the event (flush flood, seasonal flood). Thus, from a fish ecology viewpoint, the presence of sediments is normal; it is variation outside of the normal range that is detrimental to species, and there is no specific level at which all species of fish would be equally affected (Sanderson 2009).

Among rivers of the world there is a relationship between energy availability and sediment availability (Welcomme *et al.* 1989); in the Mekong the hydropower potential of the Lower Mekong Basin is estimated at 53,000 MW (ICEM 2010), with 30,000 for the Lower Mekong Basin alone (MRC 2001). The impact of such power extraction on the river nutrient availability deserves being studies in more detail.

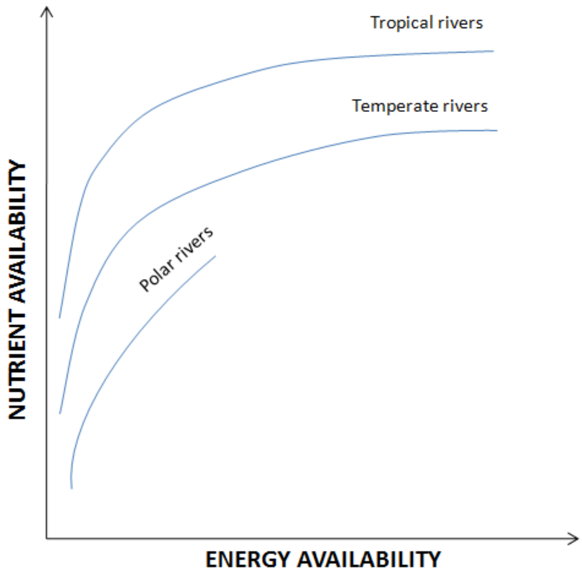


Figure 9: relationship between energy availability and sediment availability. Source: Welcomme 1989

4.1 Sediments and fish respiration

Note: the issue of sediment overload and fish gill clogging is not detailed here since it is covered in the report "Reservoir sediment flushing and fish resources" also produced for the current project.

There are two main sources of oxygen in the aquatic environment: the atmosphere and photosynthesis by plants. Oxygen from the atmosphere is diffused in the water through the air/water interface and this process is accelerated by wind and wave action; photosynthesis by aquatic plants, algae and phytoplankton is the most important source of dissolved oxygen in aquatic environment (Francis-Floyd 2011).

The organic component of sediments has a direct negative impact on dissolved oxygen through its Oxygen Demand. These organic compounds consume oxygen for oxidation processes, which reduces the amount of dissolved oxygen available in the water column (Welcomme 2001). WUP-FIN studies mentioned this phenomenon in the case of the Tonle Sap floodplain where sediment carried by the rainy season freshwater pulse can dramatically change dissolved oxygen levels and subsequently impact fisheries (Sarkkula and Koponen 2003, Koponen *et al.* 2005).

Suspended sediments also influence the amount of dissolved oxygen through their interference with photosynthesis. Two opposite pathways can be noted (UTAH State Water Plan 2010): i) turbidity reduces the amount of sunlight reaching the aquatic vegetation and thereby reduces its oxygen production (negative effect); ii) nutrients associated with suspended sediments favor plant growth and thereby increase their oxygen production (positive effect). Thus, dam development reducing sediment concentration would have opposite effects by simultaneously promoting and reducing plant-driven oxygen production (the release of hypoxic or anoxic reservoir water being ignored here). The combination of these different factors makes it difficult to predict the overall impact of sediment load reduction on oxygen concentration in water (Figure 10).

In the Mekong mainstream the average dissolved oxygen concentration in running waters ranges between 5.5 and 8.5 mg.l^{-1} (1985-2005 data; MRC 2009). Dissolved oxygen concentrations below 5 mg.l^{-1} may be harmful to fish and piping (gulping air at the surface) is observed when DO falls below 2 mg.l^{-1} (Francis-Floyd 2011).

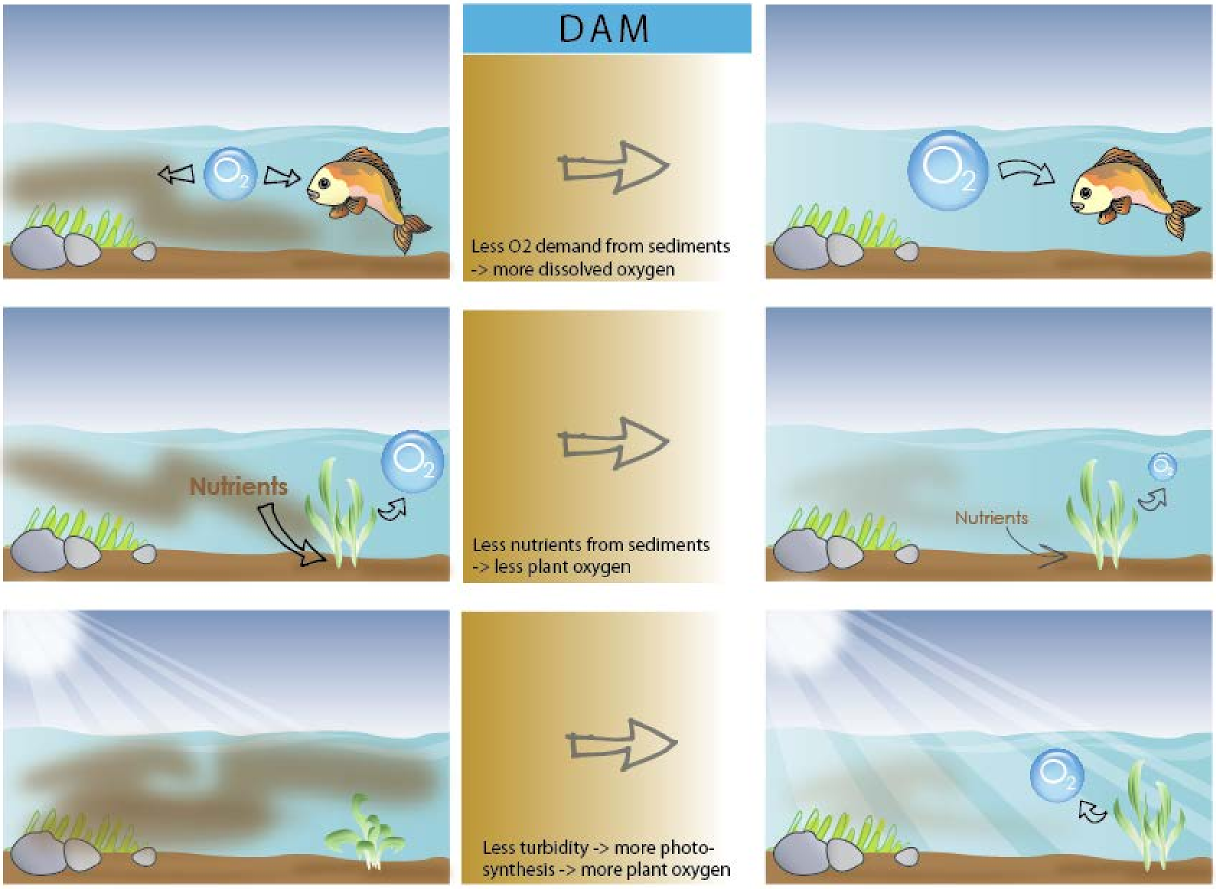


Figure 10: Influence of suspended sediment on oxygen content in water

4.2 Sediments and fish nutrition

In the Mekong, there is not enough information to establish a detailed connection between sediment classes and the feeding of fish species. We reviewed for the present report the feeding of Mekong species in relation to sediments, as compiled in a literature review of 296 Tonle Sap species (period covered: 1938-2003; Baran *et al.* 2007c) and detailed in FishBase (*www.fishbase.org*) and the Mekong Fish Database (MRC 2003)**.** The information on diet contained in these two databases refers to the following food items and all their combinations: Detritus, Algae, Plants, Plankton, Zooplankton, Zoobenthos, Nekton, Animals and Insects. Although some of these categories (e.g. detritus, zoobenthos) reflect to some extent a sediment-related feeding mode, they are not explicit about the type of sediment involved. Alternatively, Valbo-Jorgensen *et al.* (2009) review, from unspecified data, the food items of Mekong fish species, and find that mud feeders constitute 1% of Mekong fish species and that 69 species are detritivores (Figure 11).

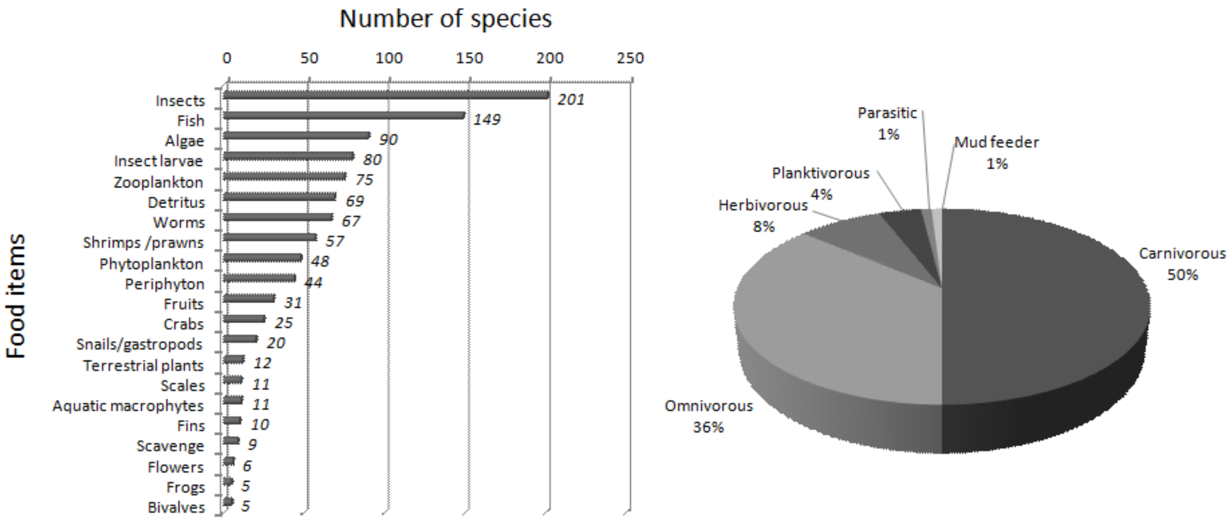


Figure 11: Number and percentage of Mekong fish species feeding on various food sources. Source: Valbo-Jorgensen *et al.* 2009.

Evidence from other tropical rivers shows that sediment concentration influences i) the trophic food chains that fish are part of or depend upon, ii) the predator-prey relationship, and iii) the dominance of species in fish assemblages. We detail these aspects in the following paragraphs.

Fish nutrition and growth depends on the concentration and composition of sediments in the river. Fish sometimes feed directly on sediment (e.g. mullets), but more importantly sediments condition the presence and abundance of fish prey. The carbon component of sediments is the main food source of zooplankton and benthic invertebrates, and nutrients adsorbed on sediments are the main input for phytoplankton, algae and aquatic plant development. These first levels of the trophic pyramid constitute the diet of many fish species and are essential to fish productivity. Although the details of these very complex food webs are not well known, there is ample evidence that fish nutrition and productivity ultimately depends on the concentration and composition of sediments (in particular nutrients and organic particles) available in the river (Gray and Ward 1982, Ward 1992, Power *et al.* 1996, Ongley 1996, USEPA 2003)**.**

Although the overall positive role of sediments on fish nutrition is clear, detailed processes are complex and sometimes in opposition: a decrease in sediment loads—and attached nutrients—might result in a reduction of primary production (UTAH State Water Plan 2010) but can also be favorable to primary production through increased irradiance (Lloyd *et al*. 1987). The latter phenomenon was observed on the Nile River, where a significant reduction in water turbidity (from 3000 to 15-40 mg-l^{-1}) following sediment trapping by the Aswan dam resulted in increased phytoplankton density (Dubowski 1997); yet, the Nile fishery gradually collapsed (Bebars *et al.* 1996). In the coastal zone, maximal phytoplankton production is often found at some distance from the mouth of a river, in a zone of lower nutrient concentration, and this is related to increased light availability (Parsons 1977, Randall and Day 1987). Yet in the Mekong, Wyatt and Baird (2007) note a paradoxical effect: the sediment retention by the Yali Falls dam on the Sesan River resulted in increased sediment load and turbidity downstream due to increased riverbank erosion; this phenomenon in turn “*reduced the light available for algal growth, or smothered bottom-growing algae, which are an important food source for some species*”.

In the Mekong the link between upstream nutrients and fish abundance was already noted in 1933 by Chevey: “A remarkable concentration of fish can be noticed at the mouth of the Bassac and Mekong Rivers at the beginning of the dry season. The fish are attracted by the enormous concentration of nitrogenous material coming from the Mekong” (Chevey 1933). In the South China Sea fish relying on Mekong river nutrients are found as far as 500 km from the river mouth (MRC 2003).

Overall, permanently reduced sediment loads modify food webs and result in a change in fish communities and dominant species. Following the closure of the Tucurui Dam (Brazil) and the downstream reduction in sediment load, the biomass of piscivorous fishes increased while that of planktivores diminished, and some species changed their diet (e.g. de Merona 2001). More generally Welcomme (2001), summarizing the impact of human interventions on fish, indicates that a decrease in suspended silt load results in changes in the fish community, with in particular a reduction in the number of non-visual predators and carnivores, and that a lack of sediment downstream of dams changes the nutrient cycle and causes a loss of illiophages (mud feeders).

Permanently reduced sediment loads also alter the fish community structure and dominant species by altering fish predation patterns. Turbidity determines underwater visibility conditions, and it is now well established (review in Kerr 1995) that this in turn influences the predation efficiency of visually oriented fish species. Unlike species located at the bottom of the trophic pyramid, who usually filter water (planktivores) or forage at random (detritivores, bottom feeders), piscivorous predators mostly depend on their vision to catch prey. Turbidity subsequently influences the predator-prey relationship and ultimately the progressive dominance of specific predators and prey. Thus, de Melo *et al.* (2009) showed that in the Bananal floodplain (Mato Grosso, Brazil) changes to water transparency influence the composition of fish assemblages and dominant species among Cynodontidae. In estuaries Blaber *et al.* (1985) also report that predation, usually low due to high turbidity, can increase under specific conditions of clear and deep water. However, the relationship is not clear: reduced turbidity following retention of sediments by dams might favor top-level predators, but also the survival rate of prey that would better perceive predators. Overall, the literature review does not lead to clear conclusions about the impact of sediment retention on changes in trophic levels or the overall productivity of the fishery.

4.3 Sediments and reproduction

The main relationship between fish reproduction and sediment is through spawning grounds. The reproductive guilds[4] of fishes formalized by Balon (1975, 1981) and encompassing all the 30,000 fish taxa are based on three main criteria: forms and functions in early development stages, features of reproductive behavior, and preferred spawning grounds. The latter makes extensive reference to the nature of the substratum where eggs are laid (Table 3).

Table 3: Main fish reproductive guilds. Guilds whose spawning is dependent on river sediment classes are highlighted in grey. Source: Balon 1981.

Ethological section	*Ecological group*	*Guild*	*Meaning*	*Notes*
NON-GUARDERS	**Open substratum spawners**	Pelagophils	Pelagic spawners	Numerous buoyant eggs
		Lithopelagophils	Rock and gravel spawners with pelagic larvae	Embryos pelagic by positive buoyancy or active movement
		Lithophils	Rock and gravel spawners with benthic larvae	Early hatched embryo hides under stones
		Phytolithophils	Nonobligatory plant spawners	Adhesive eggs on submerged items
		Phytophils	Obligatory plant spawners	Adhesive egg envelope sticks to submerged live or dead plants
		Psammophils	Sand spawners	Adhesive eggs in running water on sand or roots over sand
		Aerophils	Terrestrial spawners	Small adhesive eggs scattered out of water
	Brood hiders	Aeropsammophils	Beach spawners	Spawning above the waterline of high tides
		Xerophils	Annual fishes	Eggs and embryos capable of survival for many months in dry mud
		Lithophils	Rock and gravel spawners	Eggs buried in gravel depressions called redds or in rock interstices
		Speleophils	Cave spawners	
		Ostracophils	Spawners in live invertebrates	
GUARDERS	**Substrate choosers**	Pelagophils	Pelagic spawners	Non-adhesive, positively buoyant eggs
		Aerophils	Above water spawners	
		Lithophils	Rock spawners	Strongly adhesive eggs, attached at one pole by fibers
		Phytophils	Plant spawners	

[4] "A guild is defined as a group of species that exploit the same class of environmental resources in a similar way" (Root 1967)

Ethological section	*Ecological group*	*Guild*	*Meaning*	*Notes*
	Nest spawners	Aphrophils	Froth nesters	
		Polyphils	Miscellaneous substrate and material nesters	Adhesive eggs attached singly or in clusters on any available substratum
		Lithophils	Rock and gravel nesters	Eggs always adhesive, free embryos
		Ariadnophils	Gluemaking nesters	
		Phytophils	Plant material nesters	
		Psammophils	Sand nesters	Thick adhesive chorion with sand grains gradually washed off or bouncing buoyant eggs
		Speleophils	Hole nesters	
		Actiniariophils	Anemone nesters	
BEARERS	**External bearers**	5 guilds		
	Internal bearers	4 guilds		

This table illustrates the importance of sediments in river fish reproduction, and the very specific role of different sediment classes in fish spawning.

For their reproduction some river fish species are dependent upon bedload while others are dependent upon washload. A number of fish species, in particular in upstream environments and in floodplains, spawn on the bottom and deposit their eggs in the empty spaces between gravel (e.g. croakers, lithophils) or on fine sediment and vegetation debris (e.g. some snakeheads). They may use their fins to create a microenvironment within the streambed with optimal water current and thus egg oxygenation (e.g. tilapias). Egg development requires a fine balance between discharge, velocity, and bed material for spawning to be successful. As opposed to this strategy, other species release their eggs in the water column (e.g. freshwater clupeids), and in this case egg development requires a fine balance between egg buoyancy and water/sediment density.

There is little information in the literature about the relationship between tropical fish reproduction and the impact of a reduced sediment load. If there is substantial information about sediments and fish in temperate rivers (in particular those with salmonids subject to sediment flushing), and about the spawning behaviors and preferences of East African lake fish species (in particular tilapias), overall the relationship between fish and sediments in tropical rivers is not well known, and reproduction as a physiological and behavioral process remains largely understudied in environments characterized by a high number of species, a diversity of life strategies and few fish biologists. Thus, no substantial information has been generated at the crossing of two limited fields of research.

Furthermore, a considerable body of information details the impact of an *increased* sediment load (mainly due to erosion following deforestation, mining, etc.) on spawning, spawning sites, egg development and overall reproduction success in clear temperate streams (Kerr 1995, Castro and Reckendorf 1995[5]), but very little information is available about the impact of a *reduced* sediment load on fish reproduction (i.e. the main focus of this report).

Freshwater fish at younger life stages are more vulnerable and more severely impacted by sediment variations than those at adult life stages (Alexander and Hansen 1986, Appleby and Scarratt 1989, Newcombe 1994). The most sensitive stage is the larval stage, more sensitive than the egg or juvenile stages (Appleby and Scarratt 1989, Isono *et al.* 1998).

In estuaries, high turbidity is favorable to the larvae of many coastal fish species. These species tend to spawn in the coastal zone, and then larvae drift or actively migrate towards river estuaries where they find turbidity caused by a high concentration of suspended organic matter decreases the efficiency of predators and increases their survival rate (Blaber and Blaber 1980, Cyrus and Blaber 1987a&b, Baran 1995, Lévêque and Paugy 1999).

A reduced sediment load tends to impact the reproduction success of species laying their eggs on river beds. In particular, when bedload transport is reduced, the riverbed's sediments are not replaced by upstream sediments, which results in "armoring" of the riverbed. The resulting rockier riverbed is less suitable for the fish species that require specific substrate compositions for reproduction (Bizer 2000). Fish eggs directly exposed to water friction are also generally more vulnerable than eggs buried in the substrate (Newcombe 1994, Kerr 1995).

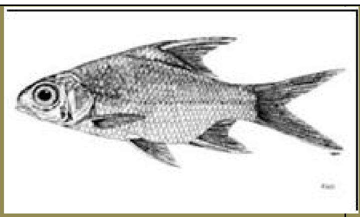
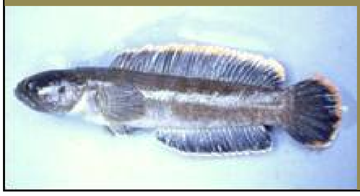
A reduced sediment load may impact the reproduction success of some species spawning in the water column (pelagophils). The eggs of these species must stay near the oxygenated water surface, which implies that their buoyancy matches the water density in the river at the time of spawning, the latter being driven by the water's silt content. When oocytes are released and fertilized, they get hydrated, which increases egg volume several times and reduces their specific weight, prompting flotation and drifting (Carolsfeld *et al.* 2003). However, in the case of reduced silt content, eggs lose their buoyancy, sink and die. This phenomenon, relatively undocumented for river fish, is now well known for marine fish; e.g. Griffin *et al.* 2009, Ospina-Álvarez *et al.* 2012; it was flagged by Baran *et al.* (2007) as possibly having large-scale implications for the Tonle Sap fish resources. This buoyancy issue can also be significant in the case of juvenile fish (Pavlov *et al.* 1995, 2008)

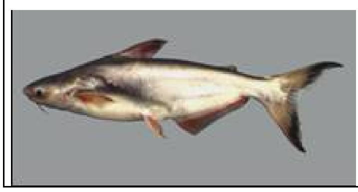
[5] In their review, Castro and Reckendorf note that "Researchers have consistently found that the introduction of excess matrix bedload can have disastrous results for the spawning habitat of fish that require gravel substrate for spawning."

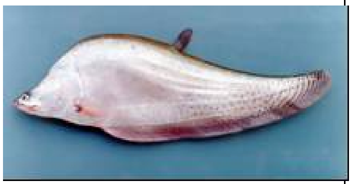
In the Mekong, the spawning grounds and the nature of these grounds have not been identified for the large majority of species (Chea Tharith *et al.* 2005). However, we reviewed for the present report the reproduction of Mekong species in relation to sediments, as compiled in a literature review of 296 Tonle Sap species (period covered: 1938-2003; Baran *et al.* 2007c) and detailed in FishBase (*www.fishbase.org*) and the Mekong Fish Database (MFD 2003). Findings are detailed below (Table 4)

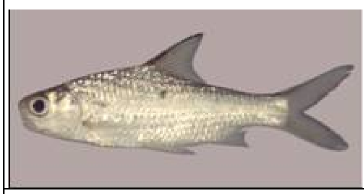
Table 4: Tonle Sap species whose reproduction is or is not dependent on sediments.

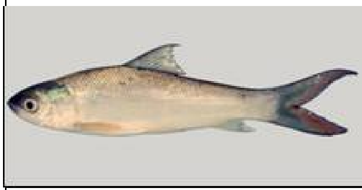
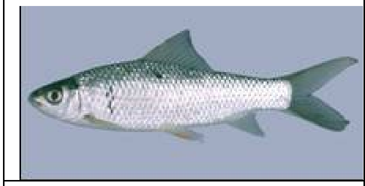
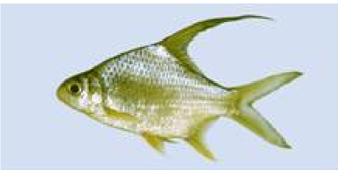
Species whose reproduction is dependent on sediments			
	Probarbus jullieni	Falling water and atmospheric temperatures, together with decreased turbidity, may be important factors in controlling the arrival time of Probarbus to its spawning grounds. The eggs are buoyant or semi-buoyant, but slightly heavy and adhesive. Generally intolerant of habitat alterations, it has disappeared from areas affected by impoundments. Large dams in Stung Treng and Kratie provinces would eliminate most of the rapids habitat that are important for the spawning of this species.	Baird and Flaherty 2000; Ukkatawewat 1999; Amatyakul *et al.* 1995; Rainboth 1996; Roberts 1992
	Pangasius macronema	It spawns in rapids in the beginning of the rainy season.	Schouten *et al.* 2000
	Boesemania microlepis	The identified spawning areas are characterized by being over 20 m deep, with hard rock or pebble and silt or sand substrate, and having slow to moderate counter-current eddies in the dry-season, and with steep rock sides descending into the pools.	Baird *et al*. 2001
	Probarbus labeamajor	Large dams on the mainstream in Stung Treng and Kratie provinces, would eliminate most of the rapids habitats that are important for its spawning.	Roberts 1992
	Puntioplites proctozystron	Spawning occurs in slow moving water areas with muddy bottom. The eggs are of the semi-buoyant type.	Watanadiroku and Murada 1985; Banyen *et al.* 1989a; Banyen *et al.* 1989b; Duangsawasdi *et al.*

			1988; Banyen 1988
	Channa gachua	Spawns in shallow water with a silt or gravel substrate.	Talwar and Jhingran 1992

Species whose dependence on sediments for reproduction is unclear			
	Datnioides pulcher	Spawns in March, the eggs are buoyant and approximately 0.8 mm in diameter.	Rithcharung and Mahawong 1993
	Labeo chrysopheka dion	It is reported to spawn in swamps, flooded areas, or just upstream from shallow sandbars that line long river bends (Rainboth 1996). The eggs are semi-buoyant.	Smith 1945; Poulsen and Valbo-Jørgensen 2000; Baird *et al.* 1999
	Osteochilus melanopleur us	It is a pelagic spawner which produces semi-buoyant eggs.	Warren 2000; Watanadirokul *et al.* 1983;
	Osteochilus hasseltii	Spawning occurs in floodplains in areas covered with submerged vegetation and gravel bottom. The eggs are buoyant or semi-buoyant.	Warren 2000; Pholprasith and Janesirisak 1972; Warren 2000; Pennapaporn *et al.* 1991
	Pangasius conchophilus	It seems likely that the species spawns at various times of year. An important spawning ground appears to be the Mekong mainstream somewhere between Kompong Cham and Khone Falls and in rapids and riffles of the Mun River.	Baird and Phylavanh 1999; Poulsen and Valbo-Jørgensen 2000; Schouten *et al.* 2000

	Chitala blanci	Spawning takes place within the main river channel in areas with submerged wood and rocks, and the female guards the fry.	Poulsen and Valbo-Jørgensen 2000
	Chitala chitala	Lays eggs usually on stakes or stumps of wood, male fans them with tail, keeps them aerated and silt-free, guards them against small catfish and other predators.	MFD 2003

Species whose reproduction is not dependent on sediment			
	Clupeichthys aesarnensis	It spawns pelagically probably in the upper water column close to the water surface although earlier reported to spawn at stumps, plant roots and grasses.	Scott and Crossman, 1973; Soemarwotto and Costa-Pierce 1988
	Corica laciniata	It probably spawns at regular intervals throughout the year in the upper water column close to the water surface.	MFD 2003
	Tenualosa thibaudeaui	It spawns pelagically in open water. Developed eggs occur in March-June. In the Middle Mekong along the Thai-Lao border, young of 40 to 50 mm total length were first encountered in the middle of April, but the abundance of juveniles increases during the onset of the rising water levels when the suspended solids increase.	Poulsen and Valbo-Jørgensen 2000; Rainboth *et al.* 1975; Rainboth 1996
	Amblyrhynchichthys truncatus	Pelagic spawner, spawns in floodplains and mainstreams of large rivers during the wet season.	Warren 2000
	Barbonymus altus	It spawns pelagically in floodplains and flooded forests, or among flooded vegetation, and has buoyant or semi-buoyant eggs, with an initial diameter of 0.74 mm.	Warren 2000; Baird *et al.* 1999; Duangsawasdi *et al.* 1988

	Cirrhinus microlepis	It is a pelagic spawner and the eggs are buoyant or semi-buoyant.	Warren 2000; Pinyoying 1970
	Cirrhinus molitorella	It is a pelagic spawner, which produces buoyant or semi-buoyant eggs.	Warren, 2000
	Cyprinus carp io	Open water/substratum egg scatterers with a fecundity of 281,936 eggs/kg.	Skelton 1993
	Labeo dyocheilus	This fish species spawns in August-September. It spawns pelagically in the mainstream in the wet season.	Baird *et al.* 1999; Warren 2000
	Puntioplites falcifer	The spawning season is protracted with eggs reported in the period from March-December (with most reports from May-June), and 2 cm long juveniles reported all year (although in highest occurrence is from May to November). It is a pelagic spawner which lays buoyant or semi-buoyant eggs.	MFD 2003
	Monopterus albus	A bubble nest builder at the water surface near the shoreline during the rainy season.	Rainboth 1996; Talwar and Jhingran 1992

4.4 Sediments and migration

Changes in turbidity or water color are a migration trigger for at least nine of the Mekong migratory species. In the Mekong, 87% of the species whose migration status is known (i.e. 135 species) are migratory species characterized by longitudinal or lateral migrations; out of these, more than 100 species are long-distance migrants (Ziv *et al.* 2012). Changes in turbidity or water color at the beginning of the rainy season are a migration trigger for at least nine of these species, which makes these species possibly sensitive to changes in sediment concentration. These species are: *Pangasius polyuranodon, Pangasianodon gigas* and *Pangasius bocourti* (three catfishes, including a critically endangered species), *Cyclocheilichthys enoplos* and *Paralaubuca typus* (two cyprinids very dominant in catches), *Bangana behri, Labeo chrysophekadion, Mekongina erythrospila* and *Tenualosa thibaudeaui* (Baran 2006).

Fish migrations can play a significant role in nutrient distribution in a river basin. In South America, some “black water” hydrosystems are poor in nutrients (i.e. oligotrophic) with a limited in situ primary production, and yet they are characterized by a high fish biomass (Goulding *et al.* 1988, Polis *et al.* 1997). In fact, migratory fishes are the main vector of nutrient transfer from nutrient-rich turbid whitewater hydrosystems to nutrient-poor clear blackwater systems in South America (Kern and Darwich 1997, Winemiller and Jepsen 2004) and this system of "foodweb spatial subsidy" also characterizes mainstream-floodplain exchanges (Junk 1999), temperate streams (Schuldt and Hershey 1995, Bilby *et al.* 1996) and estuaries (Deegan 1993)

In the Mekong a similar process of nutrient transfer from nutrient-rich downstream floodplains towards more oligotrophic upstream tributaries via fish migrations is expected. Thus at least 35% of the fish biomass is made of migratory species (Baran 2010) and the 3S system for instance is characterized by at least 89 migratory fish species representing 60% of the fishermen’s total catch (Baran *et al.* 2011); in the Tonle Sap River, more than 2000 tonnes of fish are harvested per day during the migration peak[6]. If this process is confirmed, then a reduced sediment and nutrient load due to dam construction would result in a lower productivity of downstream floodplains, reduced fish migrations, and subsequently reduced nutrient transfer towards and productivity of the tributaries that are not directly subject to dams (Figure 12).

[6] Common catch rates during the days preceding the January full moon: 350 kg per haul, one haul every 15 mn for each “dai” net, 64 nets, 24 hours a day.

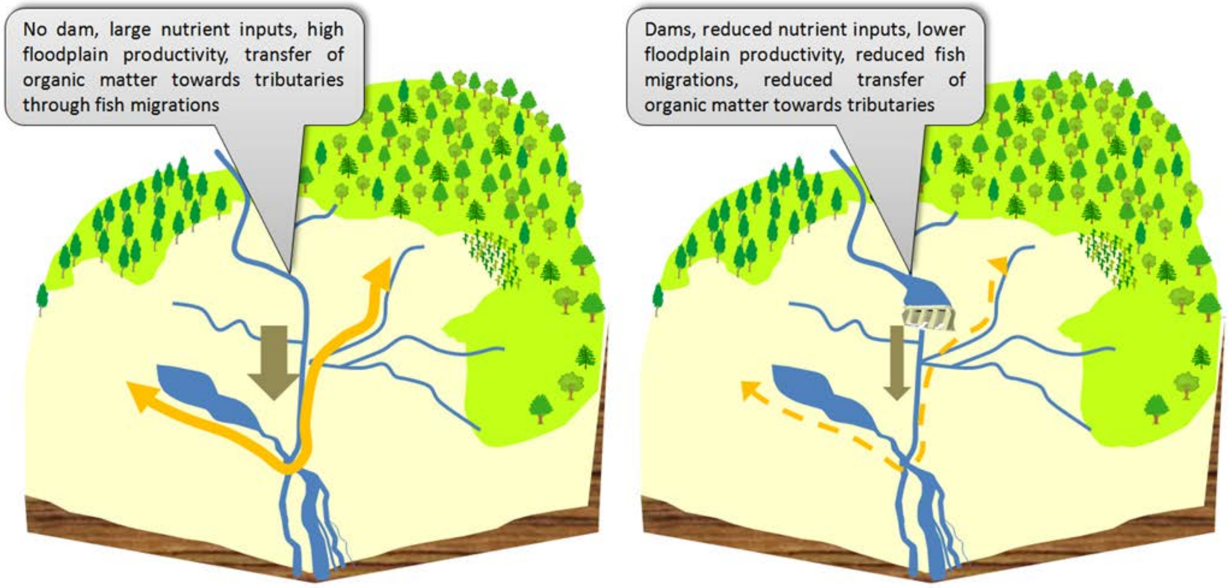


Figure 12: Reduction of nutrient transfers between river systems through reduced fish migrations.

4.5 Sediments and fish habitat

Fish habitat in tropical rivers should not be seen as a unique geographical area, but as groups of physically separated biotopes (feeding, spawning and nursery areas, dry season refuges) (Poulsen and Valbo-Jorgensen, 2001, Hortle 2009), plus the water quality inherent to these biota. Sediment plays a role in the characteristics of these habitats:

- geomorphology and bed substratum are determined by sediment loads;
- water turbidity is directly correlated with suspended sediment;
- pH of the water can be influenced by sediment.

Sediment load plays a major role in the geomorphology of river banks and river beds, two drivers of aquatic organisms' communities, in particular fish. The composition of aquatic organism assemblages basically reflects i) the nutrient inputs and ii) the physical form of the river system (Welcomme 1985). The reduction of the upstream sediment load results in large-scale changes in the downstream riverbed, the latter being a dynamic system in which sediments removed from the channel are replaced by the inflow of sediments from upstream. This sediment reduction in turn makes river microhabitats less suitable for aquatic organisms that require specific substrate compositions for reproduction and/or foraging (Bizer 2000, Osmundson *et al.* 2002). Thus, the long-term ecological consequences of dams and other stream disturbances are related to such geomorphological changes (Trush *et al.* 1995, Pitlick and Van Steeter 1998).

A modification of the Mekong sediment concentration may affect deep pool fish habitats. In the Mekong, deep pools constitute a critical habitat for many fish species, especially during the dry season (Poulsen *et al.* 2002a, Baran *et al.* 2005, Viravong *et al.* 2006, Baird 2006). Hydropower development on the Mekong would result in reduced flows in the rainy season and therefore less flushing of the sediments accumulated each year in the deep pools, i.e. increased sedimentation of deep pools (Conlan *et al.* 2008). However, dam construction would also reduce sediment concentrations and downstream bedload waves, resulting in a slower or reduced sedimentation process in pools. The balance of these two phenomena and the overall impact on deep pools as fish habitats is not well known.

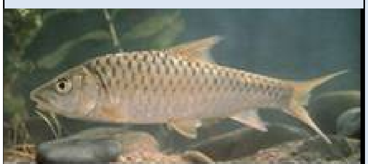
Turbidity influences the distribution and abundance of fish in the main habitats of tropical rivers including river streams, floodplains, estuaries and river plumes. Several studies conducted in tropical floodplains have indicated that water transparency is a good predicator of fish assemblage composition and distribution (e.g. Tejerina-Garro *et al*., 1998; Pouilly and Rodríguez 2004). Turbidity is one of the parameters that strongly influences the distribution and abundance of communities in estuarine waters (Kennish 1990, Lévêque and Paugy 1999); thus Diouf (1996) based on a review of 50 studies in estuarine areas, shows that in 75% of the cases turbidity is one of the structuring factors of fish communities.

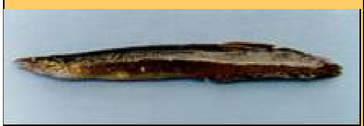
The community structure and abundance of fish species adapted to naturally turbid regimes can be affected by reduced sediment loads and flow regime regulation. Studies in South American floodplains showed seasonal changes in the relative abundance of visually and non-visually oriented fish groups following water turbidity fluctuations (Tejerina-Garro *et al*. 1998). In the Missouri River fish populations declined following the degradation of their habitats by river flow stabilization and sediment load reduction (Cross and Moss 1987, Pfleiger and Grace 1987, Hesse *et al.* 1993).

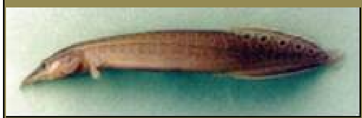
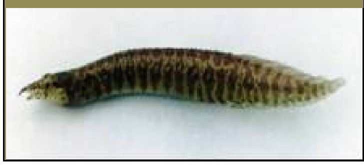
Sediment concentration influences water pH. In most tropical rivers, the ionic composition of the water derives primarily from the rain and the rock or sediments over which river flows. (Welcomme 1985). Fine sediment particles adsorb and neutralize dissolved humic acids (Ertel *et al.* 1986) and help maintain pH at values compatible with fish survival. Modifications in water pH can affect reproduction and other biological processes of fish. Extreme pH values, i.e. those below 4.5 or above 9.5, alter aquatic organisms' ionic regulation and are usually lethal (Gonzalez, 1996, Val *et al.* 1999)

In the Tonle Sap there are only 20 fish species whose ecological dependency on sediment is known. We reviewed for the present report the ecology of Mekong species in relation to sediments, as compiled in a literature review of 296 Tonle Sap species (period covered: 1938-2003; Baran *et al.* 2007c) and detailed in FishBase (*www.fishbase.org*) and the Mekong Fish Database (MFD 2003). Findings are detailed below (Table 5).

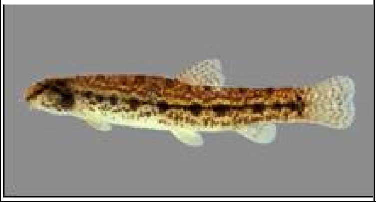
Table 5: Tonle Sap species that are ecologically dependent on sediments.

Species whose ecology is dependent on sediments			
	Hypsibarbus lagleri	May migrate into flooded forests immediately adjacent to rivers, but does not occur over fine-grained sediments, preferring rocks instead.	Rainboth 1996
	Homaloptera smithi	Adults are found in high gradient streams over fast bedrock, cobble runs, and rapids, and juveniles occur in slower stretches of gravel and exposed tree roots.	Rainboth 1996; Krachangdara 1994; Rainboth 1996
	Crossocheilus atrilimes	Usually associated with clear, relatively fast waters with gravel or boulders.	Kottelat 2001
	Opsarius koratensis	Found over gravel substrate in clear, swift, small streams on rapidly flowing stretches of large rivers, especially areas with many rocks.	Rainboth, 1996; Baird *et al.* 1999
	Tor sinensis	Occurs in pools and runs over gravel and cobble in clear rivers in forest areas.	Rainboth 1996
	Schistura pellegrini	Inhabits shallow, clear, fast-flowing water over rocky bottoms in upland streams.	Rainboth 1996
	Garra fasciacauda	Inhabits rocky bottoms in fast flowing water of all sizes of rivers and streams.	MFD 2003
	Garra cambodgiensis	Inhabits rocky bottoms in swiftly moving water of small and medium-sized streams.	MFD 2003

	Setipinna melanochir	Becomes abundant in the Middle Mekong when the water levels rise and turbidity increases. Inhabits shallow, clear, fast-flowing water over rocky bottoms in upland streams.	Rainboth 1996
	Macrognathus maculatus	Found in lowland streams and peats. Often occurs in clear water over rocky bottoms in flowing streams.	Vidthayanon 2002
	Mystacoleucus marginatus	Found at bottom depths of rivers and streams. Inhabits areas with sand or gravel from small streams to large rivers.	Rainboth 1996
	Hypsibarbus malcolmi	Found in large rivers in the dry season and moves to medium-sized rivers in the wet season. Usually found over coarse substrate.	MFD 2003
	Glossogobius aureus	Found in rivers in clear to turbid water, usually over sand or gravel bottoms and mud.	Allen 1989; Allen *et al.* 2002
	Mastacembelus favus	Inhabits flowing waters. Most often found over gravel substrates where it buries itself during the day.	MFD 2003
	Tuberoschistura cambodgiensis	Inhabits sandy-bottomed streams. Previously found in a flowing stream with sandy bottom between Siem Reap and Kompong Thom near the Great Lake. Also found in sandy bottomed streams south of Phnom Penh.	Rainboth 1996

	Hemibagrus nemurus	This species occurs in most habitat types, but most frequently in large muddy rivers, with slow currents and soft bottoms.	Kottelat 1998
	Channa striata	Survives the dry season by burrowing into the bottom mud of lakes, canals and swamps as long as skin and breathing apparatus remain moist.	Davidson 1975
	Pangio anguillaris	Found near the bottom over sand or silt substrate in debris and decaying vegetation. Spends much of its time buried in the sand or slowly foraging across the surface.	Rainboth 1996; Kottelat 1998
	Macrognathus siamensis	Spends much of its time buried in the silt, sand, or fine gravel with only a part of its head protruding from the bottom, but it emerges at dusk to forage for food.	Rainboth 1996
	Macrognathus taeniagaster	During the daytime, it spends much of its time buried in silt, sand, or fine gravel with only its snout and eyes protruding from the bottom, but it emerges at night to forage.	Rainboth 1996

Species whose dependence on sediments is unclear			
	Syncrossus helodes	Found in small upland streams with fast currents, as well as at bottom depths of the Great Lake	Rainboth 1996
	*Cyprinus carp io*	Feeds mainly by grubbing in sediments, whereby it often uproots aquatic plants and stirs up mud.	Scott and Crossman 1973; Rainboth 1996

	Lepidocephalichthys hasselti	Inhabits slow-moving, shallow waters of canals and inundated floodplains, usually on or in muddy substrates. Lives in swamps and rivers including peats. Also found in mountain streams, preferring sandy or gravelly bottom.	Rainboth 1996; Kottelat 2001; Vidthayanon 2002
	Pseudobagarius filifer	This species is present in the Mekong Basin, living in turbid, sandy-bottom lakes with moderate current.	Ng and Rainboth 2005
	Nemacheilus pallidus	This species is known to congregate in areas receiving direct sunlight such as shallow depths of small streams and rivers with sandy to muddy bottoms. It is found over sandy substrates with slow current.	Rainboth 1996; Kottletat 2001
	Polynemus aquilonaris	Found on sandy or muddy bottoms of freshwater rivers and estuaries.	Motomura 2003

Species whose ecology is not dependent on sediment			
	Parachela oxygastroides	This species and P. siamensis seem to be more tolerant of high amounts of suspended solids than *P. maculicauda* or *P. williaminae* and are more common in habitats disturbed by farming activities.	Rainboth 1996

5 SEDIMENTS AND FISH PRODUCTION

Nutrients transported by sediment loads are essential to fish productivity in tropical rivers. Nutrients are essential to vegetation growth (phytoplankton, algae and plants), which constitutes the primary production level of aquatic food webs and determine the productivity of higher trophic levels. In tropical rivers, the majority of these nutrients are transported by the suspended sediment load. We detail in this section the linkages between sediments, flood pulses and fish production, and the consequences of reduced sediment load (oligotrophication) on river productivity.

The exceptionally high productivity of the river and its associated flood plains is explained by the river flood pulse. The flood pulse concept developed by Junk (Junk *et al.* 1989, Junk and Wantzen 2004) and based on the Amazon hydrosystem focuses on the lateral exchange of water, nutrients and organisms between a river or lake and the connected floodplains. This concept argues that the annual flood pulse is the most important aspect and the most biologically productive feature of a river ecosystem. The flood pulse is typically characterized by three main components: amplitude, duration and timing. Dam development results in reduced sediment concentration downstream, but also in reduced amplitude of the flood and in a delayed flood (change in timing due to the filling of the dam reservoirs at the beginning of the rainy season). This combination of sediment retention and reduced hydrodynamic pulse may have a synergetic and negative effect on the overall productivity of the river downstream.

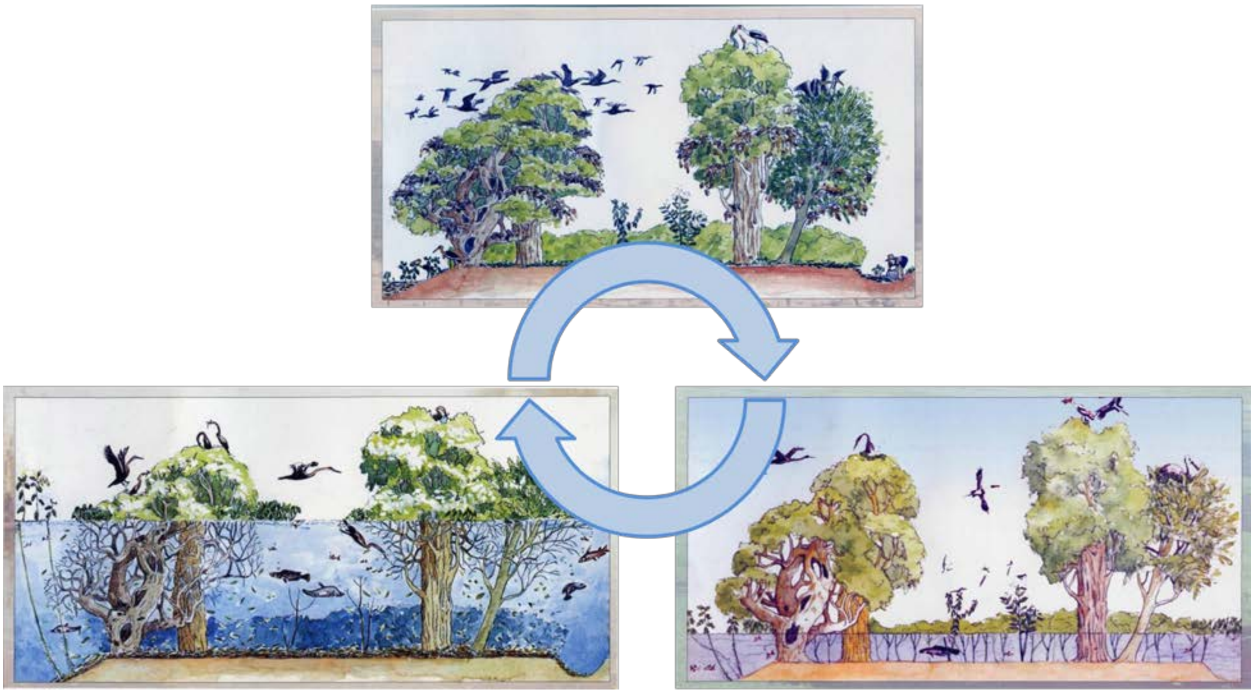


Figure 13: Flood pulse in the Tonle Sap Lake. Source: Osmose NGO, Cambodia.

The flood pulse concept is widely accepted as an explanation for the exceptional productivity of the Mekong floodplains and, in particular, the Tonle Sap, yet the Mekong system has some unique characteristics. Multiple authors have referred to the flood pulse as the driver of the productivity of the Mekong floodplains (e.g. Lamberts 2001 and 2006, Poulsen *et al.* 2002b, Sverdrup-Jensen 2002, Sarkkula *et al.* 2004, Davidson 2006, Baran *et al.* 2007a, Kummu *et al.* 2008, TKK and SEA-START RC 2009, Hortle 2009). Campbell *et al.* (2009) are the only authors who reject this explanation, without providing many details. The relationship between the flood pulse and fish production has been underlined in particular for the Tonle Sap Lake (Sarkkula and Koponen 2003, Lamberts 2006, Halls *et al.* 2008, Lamberts and Koponen 2008, Kummu *et al.* 2008, Sarkkula and Koponen 2010). However, the Mekong system is distinct from South American hydrosystems; in particular, the Mekong floodplains are covered with rice fields and are home to 11.3 million people, resulting in the release of local nutrients via artificial fertilizers, untreated sewage (60 million people, MRC 2003) and livestock (24 million heads, Nesbitt *et al.* 2004). However, it remains unclear whether these new sources of nutrients can compensate for those lost due to sedimentation behind dams. Furthermore, these expected additional nutrient inputs, in particular the phosphorus inputs, have to be analyzed in the context of the upcoming supply crisis expected at the global scale in the medium term (Roberts and Stewart 2002, Vaccari 2009, Cordell *et al.* 2009, *http://phosphorusfutures.net*)

If an abundant literature exists on *eu*trophication or *naturally* oligotrophic hydrosystems, very few studies have addressed dam-driven *oligo*trophication. Oligotrophication is the process by which a hydrosystem becomes nutrient-deficient and less productive, i.e. the opposite of the more common "eutrophication". While eutrophication was considered in the last decades as one of the major environmental issues for hydrosystems under human influence, oligotrophication was perceived as an aesthetic improvement resulting in "clean" water, though from a fishery perspective, it also implies low productivity (Stockner *et al.* 2000).

Oligotrophication is mainly related to phosphorus deficiency, but the nitrogen/phosphorus ratio is also an important factor. Since phosphorus is much less soluble than nitrogen and leaches from the soil at a much slower rate, it is a more limiting nutrient of plankton and vegetation growth in aquatic systems than nitrogen. Consequently, oligotrophication most often results from a decrease in phosphorus, in particular in temperate systems. However, in some tropical aquatic systems nitrogen could also be the limiting factor (Moss, 1969, Guildford *et al.* 2003, Lehman and Branstrator 1993)

Oligotrophication results in changes to the food web structure (Stockner 1987, Tonn 1990, Mann 1993 in Stockner *et al.* 2000). Nutrient-rich and productive hydrosystems (e.g. coastal upwellings, eutrophic lakes) are usually characterized by short food chains and productive fish resources (Cushing 1989, Ware and Thomson 1991). In hydrosystems that are becoming nutrient-poor, primary production declines and food chains become less energy efficient and become longer (Pomeroy 1974, Stockner and Porter 1988, Weisse and Stockner 1993).

Oligotrophication results in declining fisheries resources. Marked declines in yields from inland fisheries over the last 20–30 years in Europe and North America have largely been attributed to oligotrophication (Hartmann and Quoss 1993, de Bernardi *et al.* 1995, Ashley *et al.* 1997, Hess *et al.* 1982). Oligotrophication following dam construction also impacts fish production in the coastal zone (Marmulla 2001). Thus, in Cuba the reduction in sediment flow following the combination of river damming and reduced fertilizer use caused a dramatic decrease in the catches of estuarine species (Baisre and Arboleya 2006). In Brazil, a cascade of dams on the Sao Francisco river trapped 95% of the suspended sediment, reduced the nutrient concentration in the river plume by 90% and caused the estuary to become transparent, oligotrophic and unproductive (Knoppers *et al.* 2012). In Egypt, oligotrophication due to sediment trapping by the Aswan Dam has had a catastrophic effect on coastal fisheries at the mouth of the Nile River (El-Sayed and van Dijken 1995, Bebars *et al.* 1996)

In the Mekong the impact of oligotrophication on fish resources remains to be assessed. In particular, the role of phosphorus as a possibly constrained and limiting nutrient has not been established in the Mekong (Ongley 2009). Overall dam-driven oligotrophication is expected to significantly affect primary production and consequently the fish productivity of the Mekong; this correlation has been clearly established in the case of the Tonle Sap Lake (Sarkkula and Koponen 2010). However fish productivity decline is expected to be relatively more important in the Mekong Delta and in the sea area than in the Tonle Sap Lake (Sarkkula and Koponen 2010).

Overall, fish production in the Mekong is a multifactor phenomenon. It is clear that dam development will reduce the downstream sediment concentration, but will also minimize the flood pulse, alter water quality and block fish migrations. Fishery productivity resulting from these four drivers will be affected in multiple ways that cannot be related to sediments only (Figure 14). Overall, our literature review confirms the major role—previously underappreciated—played by sediments and the need for new research to better assess the impact of oligotrophication on fisheries productivity. Ongoing hydrodynamic and physical modeling will clarify the retention rate of dams and the fate of sediments; however, what has not yet been addressed is the coupling between sediments and nutrients, and the amount of nutrients independent of sediment.

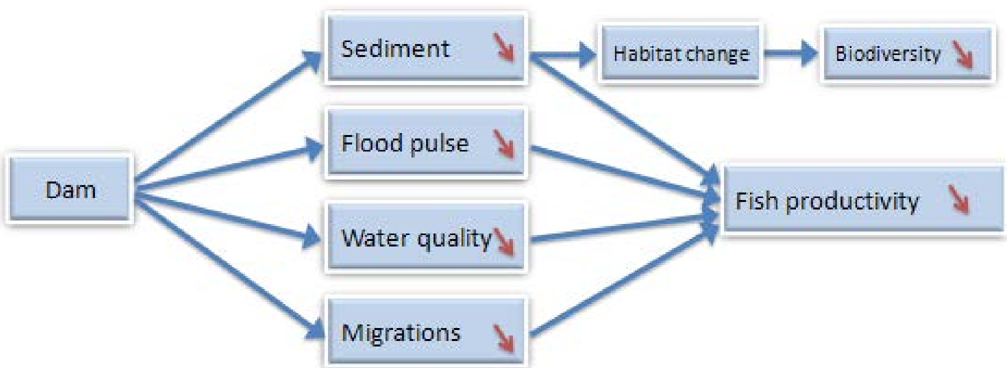


Figure 14: Relationship between dams, environmental or biological impacts and fish productivity.

6 CONCLUSIONS

In the Mekong, the total annual sediment discharge is about 160 million tonnes per year on average, with a wide range of intra-annual as well as inter-annual variability. Sediments in rivers are found in two main forms (suspended and bedded sediments) and they consist of a variety of particle sizes (roughly categorized as gravel, sand, clay and silt). Most of the sediment load in the Mekong is suspended.

One property of sediments is that they adsorb and thus facilitate the transport of nutrients (in particular phosphorus and nitrogen) and organic particles. As dissolved nutrients in the water are generally low, the main nutrient load is associated with sediments. The dominant sediment categories in the Lower Mekong Basin are fine sands, silts and clays; the proportion of organic particles represents 6-8% of the total sediment load, which is considered high by global standards.

The Mekong is a place of exceptional fish biodiversity. Fish biodiversity increases downstream and the 3S system is a hotspot. The Mekong produces about 18% of the world's freshwater fish yield. Mekong fish resources are essential to food security in the basin. Fish migrations are an essential feature of the Mekong. Sediments influence fishes' biological functions, particularly respiration, nutrition, reproduction and migration, but also their habitat. Nutrient load is also a dominant factor explaining the overall productivity of tropical river ecosystems (including floodplains, estuaries and coastal areas).

Respiration. The organic component of sediments has a direct negative impact on dissolved oxygen through its Oxygen Demand. Suspended sediments and adsorbed nutrients also influence the amount of dissolved oxygen in the water through their interference with plant photosynthesis.

Nutrition. Sediments are the basic input for the food chains and trophic webs that fish are part of at a higher level, and thus are an essential component of fish nutrition. Suspended sediments and the turbidity they cause reduce photosynthesis and thus decrease primary production. Suspended sediments also play a role in predator-prey relationships. In the Mekong, a reduction of sediment loads is likely to result in decreased primary production, which might in turn change the dominant fish species and drive down fish productivity. But the relative influence of nutrients loads and turbidity on primary production must be clarified for this potential impact to be assessed.

Reproduction. The main relationship between fish reproduction and sediments is through spawning grounds. In estuaries high turbidity is favorable to the larvae of many coastal fish species. There is little information in the literature about the relationship between tropical fish reproduction and the impact of a *reduced* sediment load.

Migrations. Changes in turbidity or water color are a migration trigger for at least nine of the migratory species in the Mekong. Fish migrations can play a significant role in the nutrient distribution in the river basin. In the Mekong fish constitute a nutrient transfer from nutrient-rich downstream floodplains towards more oligotrophic upstream tributaries.

Habitat. Sediment load plays a major role in river geomorphology and in the riverbed and riverine habitats. Blocking sediment load will degrade the river bed downstream and will therefore affect the aquatic organism communities adapted to these specific habitats. In the Mekong, deep pools, an essential habitat for the survival of numerous fish species during the dry season, could be affected by modified water flows that result in an infilling of these pools, though this impact remains to be clarified. Water pH is also a characteristic of fish habitats that is related to suspended sediment concentrations.

The river flood pulse concept explains the exceptionally high productivity of rivers and their associated floodplains. It has been widely accepted as describing the exceptional productivity of the Mekong. Dam development is expected to reduce `the flood pulse as well as downstream sediment concentrations; this combination may have a synergetic and negative effect on the overall productivity of the river downstream, leading to its oligotrophication. This process of nutrient rarefaction, poorly studied, changes food web structures and decreases fisheries resources. Oligotrophication is most commonly related to phosphorus deficiency, but the nitrogen/phosphorus ratio is also to be considered. Ongoing hydrodynamic and physical modelling will also clarify the retention rate of dams and the fate of sediments, but the coupling between sediments and nutrients and the role of the amount of nutrients that are independent of sediments remain to be addressed.

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