

## FISHERIES ECOLOGY OF THE LOWER MEKONG RIVER: MYANMAR TO TONLE SAP RIVER

*Mark T. Hill\**

### ABSTRACT

The lower Mekong River is, in many respects, a pristine river, free of dams and large-scale water diversion projects, and the water quality is generally good. However, the need to develop electrical power, control flooding, improve dry-season agriculture, and a burgeoning population throughout the basin places new demands on the river which have potentially serious implications for the fishery resources. In this paper I present the current state of knowledge on the ecology of the fisheries in the lower Mekong River from the Myanmar (Burma) border to the Tonle Sap River in Cambodia. I use ecological stratification techniques to isolate distinct river reaches. The Mekong River supports numerous migratory fish species. Unfortunately very little is known about their stock composition, length of migration, spawning sites, or early rearing areas. It is quite likely that there are numerous subpopulations of the same species which have adapted to local conditions and follow life cycles in habitats that do not overlap. Non-migratory species may also exhibit subpopulations adapted to localized conditions. Preservation and management of Mekong fish faunas will depend upon incorporating spatial information into decisions about the permitting and locating of anthropogenic change. The first step in preservation and management must be the identification of stocks or subpopulations of fish species. Identification is best accomplished with broad ecological stratification to begin the process and to focus studies on localized habitat types to which subpopulations may have adapted. I recommend short term and long term studies which are needed to improve our understanding of the Mekong River fisheries and to evaluate future development projects.

### INTRODUCTION

The lower Mekong River Basin from the Myanmar (Burma) border to the Tonle Sap River in Cambodia (Figure 1) supports a diverse range of ecosystems with varied types of freshwater habitats. These habitats include inland waters, such as the large reservoirs on tributaries, the Great Lake in Cambodia, large rivers such as the Mekong, the Mun, the Tonle Sap, and the Bassac, intermediate tributaries and river branches, small streams and irrigation canals, large floodplains, swamps, irrigated rice fields, and one of the world's largest deltas (MEKONG SECRETARIAT, 1992). These diverse ecosystems contain productive and, for the most part, indigenous aquatic species.

The breeding, multiplication, and sustenance of tropical inland fish and prawn populations are intimately bound to the sequence of annual flooding (WELCOMME, 1985). The monsoon floods join the primary habitat types (rivers, canals, floodplains, ponds and lakes, and estuaries) of the inland open waters, and produce a single integrated biological

---

\*Ecosystem Sciences, 401 E. Iowa Dr., Boise, Idaho, 83706, USA

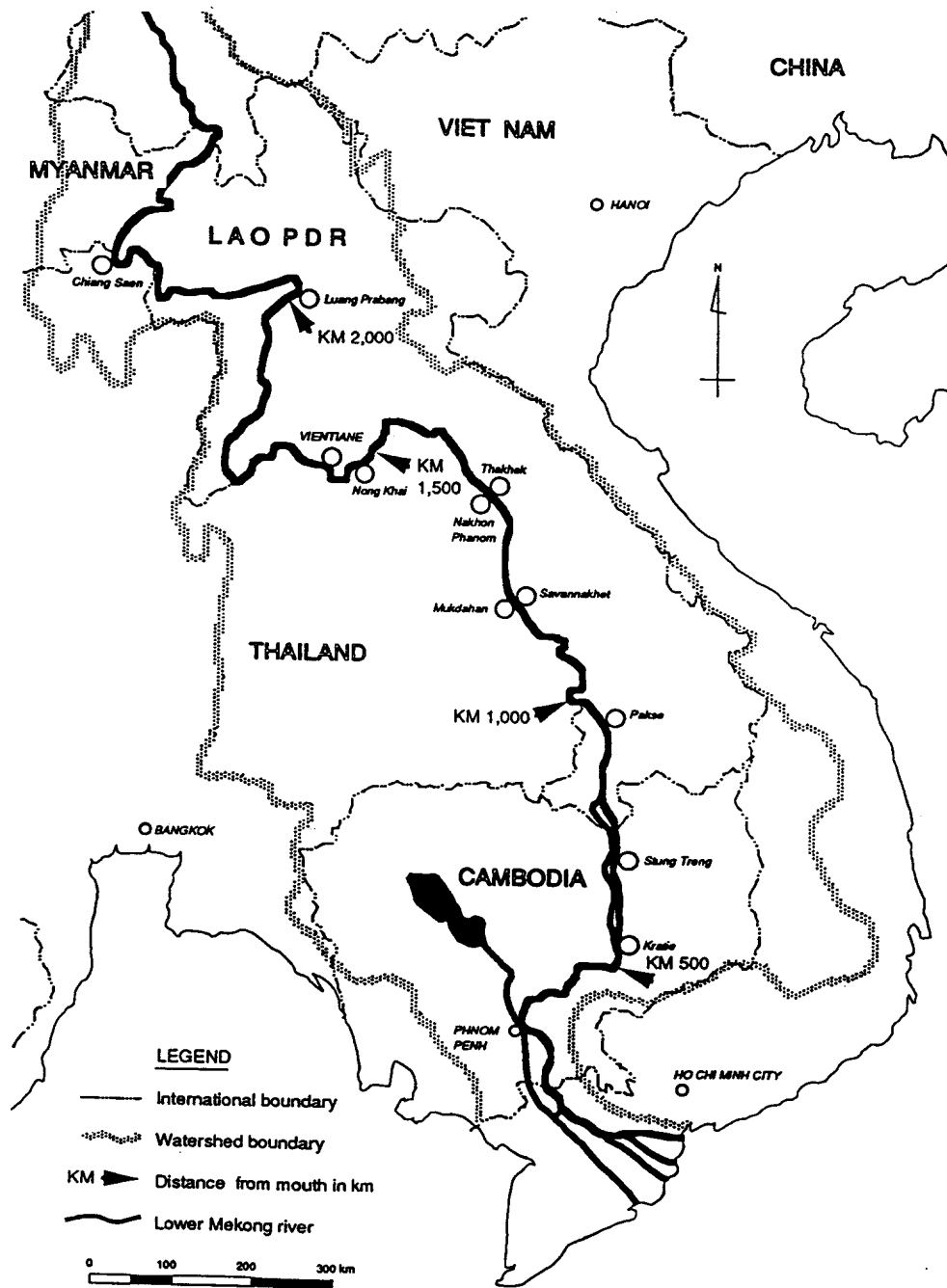


Figure 1. The lower Mekong River Basin.

production system which allows fish and prawn populations to breed, and to grow in numbers and in biomass. The inundated floodplains play the most significant role in this whole ecosystem (WELCOMME, 1985). The nutrient-rich and food-rich floodplains also provide nursery and feeding grounds for hatchlings, fry, and juveniles of a number of river-breeding, estuary-breeding and floodplain-breeding species (ROBERTS, 1993). Young fish may utilize floodplain-nursery and grow-out habitats for four to five months before entering riverine or estuarine habitats (ROBERTS, 1993).

The nature of the fisheries and the movement of fish are dictated by seasonal changes in water levels and discharge rates of extensive floodplain systems (WELCOMME, 1977). As the floodplains become inundated by rainfall and overbank flooding many species of fish begin a longitudinal migration upstream to spawn. Once the Mekong River and its tributaries begin to flood most fishes make lateral migrations into the many distributory channels of the rivers. From these channels fish move to the floodplains to exploit the food resources of the flooded area and to spawn. The productivity of a floodplain can be correlated with the area that is inundated (WELCOMME, 1977). The flood season represents the major period of growth for all sizes of fish; as the floodwaters recede, fishes migrate from the floodplains. The first to migrate are the adults, followed by large numbers of juveniles produced during the spawning season.

The open-water capture fishery of the Mekong River has been estimated to support over 60 percent of the annual production in the basin; aquaculture and marine catch contributes the remainder (MEKONG SECRETARIAT, 1992). The capture fishery, therefore, represents one of the single most important commercial and subsistence activities in the Mekong basin. Capture fishing is practiced on a range of scales—from rice-farming families fishing with small traps and nets in their fields, surrounding swamps, and irrigation canals—to large-scale operations involving substantial investment in technology and operation costs.

## ECOLOGICAL STRATIFICATION

The portion of the lower Mekong River included in this article (excluding the delta area) consists of eight broad ecological reaches which have been delineated with the classification system described in Table 1 (LOTSPEICH, 1980; LOTSPEICH & PLATTS, 1982; Platts 1988). The classification hierarchy for the lower Mekong, and the reaches which result from this classification at the valley bottom-type level, are shown in Figures 2 and 3, respectively. Ecological reaches are river lengths with similar geology, geomorphology, landtype, and landform which support a particular assemblage of fish species. It is the hierarchy of environmental conditions (from large scale to small scale) that results in specific fish habitat types within which discrete populations of fish live. Understanding the form, behavior, and historical context of landscapes is crucial to understanding ecosystems on several spatial and temporal scales (SWANSON ET AL., 1988). Landforms (such as floodplains and alluvial fans) and geomorphic processes (such as stream erosion and deposition) are important parts of the setting in which ecosystems develop, material and energy flows, and biological systems function.

Table 1. Ecological classification levels used to delineate reaches throughout the lower Mekong River.

Hierarchical Level	Description
Ecoregions	This is the first layer of classification. It is based on factors that cause regional variation in ecosystems or on factors that integrate the causes of regional variations (OMERNIK 1987). Principal factors that identify ecoregions are climate, land surface form, natural vegetation, and soils. Ecoregions are delineated with satellite imagery.
Geologic Districts	These are areas of similar rock types or parent materials that are generally associated with distinctive structural features and areas of similar hydrologic character. Structural features are the templates on which streams have etched drainage patterns (Swanson et al. 1988). The hydrologic character of landscapes is also influenced by the degree to which parent material is weathered and the water-handling characteristics of the parent rock and its weathering products. Geologic districts do not change in response to land uses, and they include both uplands and bottomlands. Geologic districts are delineated from 1:125,000 to 1:500,000 scale geologic maps.
Landtype Associations	These are identified by the dominant geomorphic processes responsible for shaping the landscape and influencing its functional character (LOTSPEICH & PLATTS 1982). Glacial, fluvial, alluvial, and lacustrine processes have shaped landscapes and continue to influence the manner in which water and sediments move through ecosystems. Landtype associations are subsets of geologic districts. Landtype associations seldom change in response to cultural practices, include both uplands and the valley-bottom, and are tens to hundreds of square miles in size. Landtype associations are delineated with 1:250,000 scale topographic maps and satellite photos, along with ground reconnaissance.
Landforms	These are components of a valley-bottom type. They are distinguished by form and position relative to the

Hierarchical Level	Description
Riverine-Riparian Complexes	<p>management perspective, landforms can be changed from one type to another. Landforms are mapped from aerial photos and 1:24,000 scale topographic maps.</p> <p>This is a precise map layer of vegetation types identified by physiognomic class (i.e., forested, shrub, herbaceous and woody), water regimes, and dominant plant species in overstory and understory canopies. Vegetation types tend to correlate with landforms; shrubs are common on levees while floodplains are typically herbaceous. Riverine-riparian complexes are mapped from 1:12,000 scale aerial photos coupled with on-site measurements with a global positioning system. Methods for assessing natural, existing and achievable states of riverine-riparian complex level of classification is the first level that directly expresses fisheries habitat.</p>
Channel Types	<p>ROSGEN (1993) identifies nine types of channels in relation to entrenchment, width-to-depth ratio, sinuosity, slope, and adjacent landform features. Channel types are subject to extreme modification by land and water uses. Channel types are identified and measured with 1:8,000 scale aerial photos and ground reconnaissance. At this level fisheries habitat is expressed as pool-riffle-run type habitat series.</p>
State Types	<p>These describe the present condition of the channel, streambank, and immediate landforms (e.g., eroded banks, laid-back banks, channelization, entrenchment) (PLATTS 1988). Streams change state types in response to both natural and artificial processes. State types are identified with 1:6,000 scale aerial photos and ground reconnaissance. This is the lowest level of classification that delineates fisheries habitat and is a direct function of anthropogenic activities and natural perturbations in the watershed.</p>

Natural gradients of fish community change have long been recognized (e.g., BURTON & ODUM, 1945) in streams with associated factors being habitat volume and diversity (SHELDON, 1968; SCHLOSSER, 1982) and environmental variability (RICKER, 1972; SCHLOSSER, 1990). The role of genetic factors in affecting intraspecific phenotypic variability has been more strongly recognized for fish than the majority of other wild or semi-domesticated vertebrates that are heavily managed (ALLENDORF ET AL., 1987). An obvious example is the fish "stock concept", demonstrating the general recognition of genetic differentiation coupled with phenotypic divergence among conspecific subpopulations of fish (see BERST & SIMON, 1981, and RICKER, 1972, for reviews).

Stocks or subpopulations (demes, metapopulations) of fish species evolve as a function of adaptation to local habitat created by higher order patterns. In a study of fish genetic variability and ecosystems, CHAKRABORTY & LEIMAR (1987) write:

"Genetic differences between subpopulations will evolve in the course of time if there is little or no gene flow between them. The amount of gene flow needed to prevent differentiation depends on the strength of the evolutionary forces responsible for differentiation among subunits. These differentiating forces are selection, genetic drift, and mutation. Selection pressure from the varying conditions under which the individuals of different subunits live results in adaptation to local conditions. The difference in allele frequencies and in the average values of quantitative characters accompanying such local adaptations constitute the genetic variation among subpopulations (stocks) that is of primary importance from the point of view of management and conservation."

This is the essential point in ecological stratification of the lower Mekong River. The Mekong supports numerous migratory fish species. Unfortunately very little is known about their length of migration, spawning sites, or early rearing areas. It is quite likely that there are several stocks or subpopulations of the same species which have adapted to local conditions and follow life cycles in habitats that do not overlap. Non-migratory species may also exhibit subpopulations adapted to localized conditions.

Preservation and management of Mekong fish faunas will depend upon incorporating spatial information into decisions about the permitting and locating of anthropogenic change. A hydropower dam might well block the migration of a stock of fish in a specific reach of the river, separating the stock from spawning grounds upstream or rearing habitat downstream. On the other hand, migration of a particular fish stock might not be affected if spawning and rearing habitat is contained between dams. (However, impacts other than migration blockage may occur). The first step in preservation and management must be the identification of discrete stocks of fish. This is best accomplished with broad ecological stratification (such as described in this paper) to begin the process of identification and to focus studies on localized habitat types to which subpopulations may have adapted. Future investigations of the river fisheries must not proceed willy-nilly', but must proceed within an organized framework that radiates out from broad scales to increasingly fine scales of study. Research, like the ecosystem itself, must be based on a hierarchical approach.

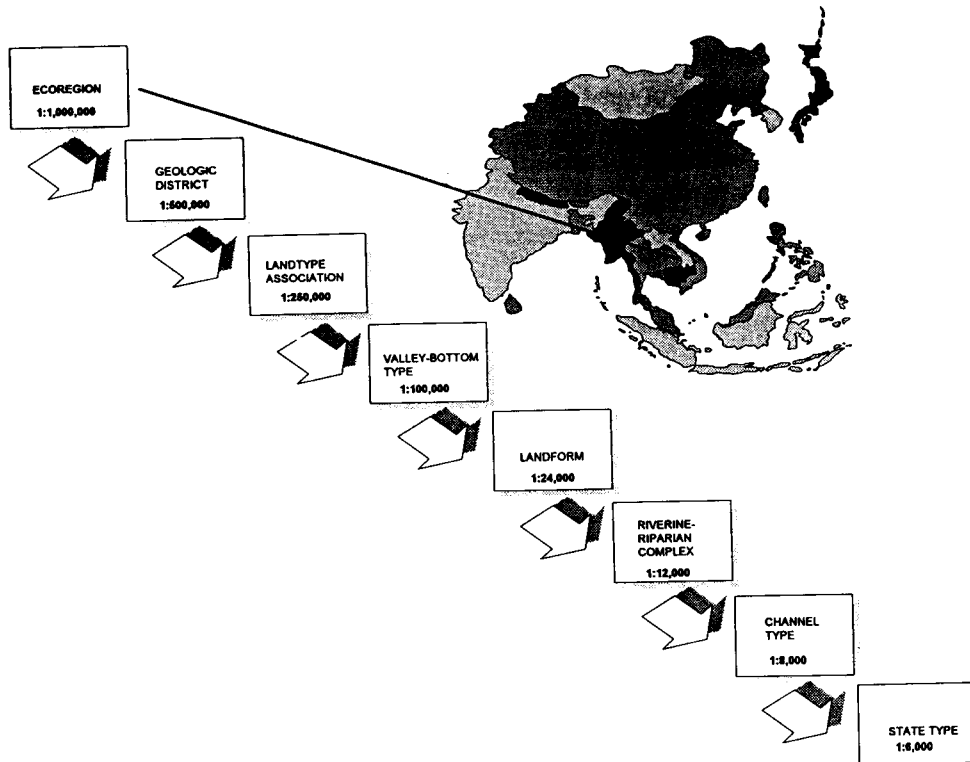


Figure 2. Hierarchical scale and classification of the Lower Mekong River Basin.

**Hierarchy Theory**—The premise of hierarchy theory is that higher levels of organization incorporate and influence phenomena at lower levels (O'NEILL ET AL., 1986). Hierarchical structuring simply means that, at a given level of resolution, a biological system is composed of interacting components (i.e., lower-level entities) and is itself a component of a larger system (i.e., higher level entities). Thus environmental hierarchies can be viewed as successively smaller habitats 'nestled' into one another (see Figure 2). At the lowest level of this nestling is the river and fish habitat; the culmination of all the higher level environmental conditions that form a unique landscape pattern.

Landscape patterns at the fish habitat level are expressed as unique physical attributes (e.g., streambanks, floodplain connectivity, littoral zones, substrate, depth, velocity), chemical attributes (e.g., temperature, ionic concentrations, carbon exchange, organic polymer composition), and biological attributes (riparian vegetation, benthic biota). The synergism between these attributes in one ecological reach is different from another reach because of the unique landscape patterns formed by higher-level entities within the hierarchy.

It would be convenient if nature followed Euclidian rules of space (e.g., perfect spheres, rectangles, and straight lines), but nature prefers conical space (parabolas and ellipses) (SHLAIN, 1991). Consequently a landscape is not made up of interlocking boxes but of implicit and explicit hierarchies of conditions that fill space with patterns (RISSER ET AL., 1984; FORMAN & GODRON, 1986). Landscape patterns can be strikingly different or very subtle, and the casual observer often cannot see the multiplicative interactions that make up unique ecological zones but which influence biological evolution and adaptation (EHRlich & RAVEN, 1964).

Delineation of river reaches is easily biased if the investigator chooses to associate patterns that do not fit into hierarchical classification or relies upon observation alone without reference to higher levels of organization (PLATTS, 1980). Watersheds cannot be isolated by political or social boundaries (SMITH, 1994), nor can they be isolated by arbitrary units of size. Whether a watershed is 50 km<sup>2</sup> or 100,000 km<sup>2</sup> is not as important as recognizing its ecological discreteness and accounting for stem and edge effects (HARRIS, 1984).

#### MAP SCALE CLASSIFICATION LEVEL

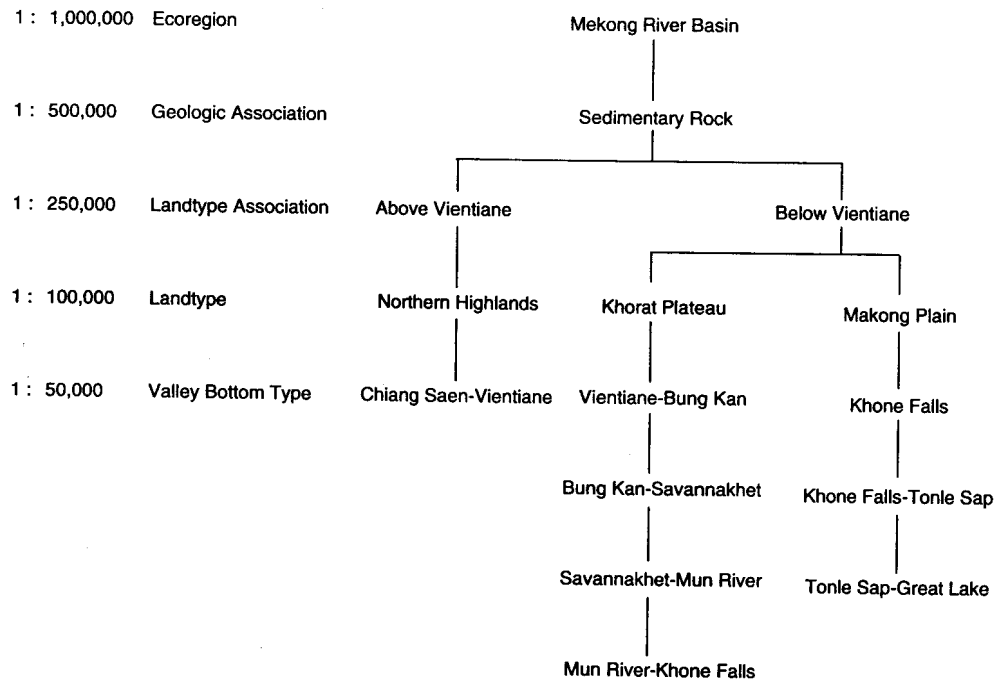


Figure 3. Ecological stratification of the lower Mekong River.



**Edge and Stem Effects**—When a delineated watershed exists as part of a larger landscape, edge and stem effects must be considered. For example, if a relatively pristine watershed with high biodiversity is classified out of a larger area that is subject to heavy anthropogenic alteration with a lower biodiversity, a much larger area for the internal watershed is needed to provide an unmodified interior environment (FRANKLIN, 1993; HARRIS, 1984). It should be recognized that edge influences can be extensive, and that the higher the contrast between watershed levels, the greater the effects (FRANKLIN, 1993).

Stem effects, on the other hand, are common to watersheds which include higher-order streams and migratory species (particularly anadromous and catadromous fish) (SMITH, 1994). Because migratory species use multiple watersheds as migration corridors, or for spawning or rearing, and fourth to eleventh order streams connect watersheds, the ultimate boundaries of a designated watershed must account for stem conditions. The boundary ends of the stratification to valley bottom type in the lower Mekong River (Figure 3) illustrate stem effects. The boundary ends of most of the ecological reaches are historically important fish collection areas. Fisherfolk have learned to focus catch effort in these areas because (1) resident fish tend to concentrate in habitats formed by transition zones (SCHLOSSER, 1982) and (2) migrating fish also congregate in these areas as they adjust to changing depth, velocity, temperature, and other physio-chemical cues (SHELDON, 1968). While classification delineates distinct ecological reaches in the lower Mekong River, one must also account for fish migration corridors between reaches and how subpopulations of fishes use them.

There are opportunities to incorporate edge and stem effects throughout the watershed hierarchy if adequate data are available to delineate the landscape to at least the channel type level. In the case of the lower Mekong River there are not adequate data at this time to allow for stratification below the valley bottom type level. Thus future investigations must account for stem effects on migratory fishes with more definitive stratification.

**Stratification**—The classification system I present in Figure 3 is described by BAILEY (1988) and PLATTS (1988) and consists of eight layers from the broadest to the smallest scale as described in Table 1. Stratifying the lower Mekong River into ecological reaches allows for a more detailed examination of the fisheries without the need for site specific information that is, for the most part, simply not available. Stratification also links one set of ecological conditions to another so that fish species that use more than one ecological reach can be evaluated on an interdependent level. I stratified the lower Mekong River into eight ecological reaches to the valley-bottom type level as follows (see Figure 3):

ECOLOGICAL REACH	REACH NUMBER
Chiang Saen to Vientiane	1
Vientiane to Bung Kan	2
Bung Kan to Savannakhet	3
Savannakhet to Mun River	4
Mun River to Khone Falls	5
Khone Falls	6
Khone Falls to Tonle Sap	7
Tonle Sap to Great Lake	8

The lower Mekong River can be divided into two main landtype associations—upstream mountainous and downstream plains. The section upstream of Vientiane is completely mountainous with relief ranging from a few hundred to over 1000 meters. In this landtype association the valley floor is commonly quite narrow (often only a few hundred meters wide) but in many places it is over 1000 m wide. The river gradient varies from place to place, and the river profile shows an average gradient of about 0.25 m/km for about 800 km of the river's length.

Downstream of Vientiane the terrain around the Mekong River is much more open with extensive plains and low hills along Thailand's side, but flanked by high mountains on the Laotian side. The river profile shows a drop in gradient to about 0.15 m/km for the next 250 km, beyond which the gradient is more variable. The Mekong River in the section below Vientiane is quite broad, 1000 m wide or more in most areas, but set within different landtypes and valley bottom types.

Below the landtype association level in the ecological stratification there are three distinct landtypes (Figure 3). These are described very well in the MEKONG SECRETARIAT report (1992). The Northern Highlands make up the northern part of the Lao PDR, the Loei province in northeast Thailand, and the mountains of Chiang Rai and Phayao Provinces in northern Thailand. The area is very mountainous and processes of erosion have carved a highly complex and dissected relief; topography is steep and rugged. Mountain ridges lying northeast-southwest rise up to between 1,500 to 2,800 m above relatively narrow valleys in this distinct landtype area. There are only a few larger plains where tributary streams join the Mekong in northern Laos—the Plain of Jars and, most notably, the Mae Kok and Mae Ing valleys of northern Thailand.

The Khorat Plateau constitutes one of two major areas of lowland in the lower Mekong Basin and covers the bulk of northeast Thailand and the adjacent lowlands of the Lao PDR around Vientiane and Savannakhet. The Khorat Plateau region is a low plateau with elevations of 160–200 m and is separated from the central plain of Thailand and from the Cambodian lake basin by a rim of hills to the west and south (the Dong Phraya Yen and Dong Rek Ranges). The plateau is generally of low relief, broken only by a low range of hills (the Phu Phan) running in a southeast-northwest direction across the northern part and by a series of table mountains in the west. The Khorat Plateau is drained by the Mun–Chi River system.

The Mekong Plain is the only true lowland area of the basin and covers most of Cambodia, the Mekong Delta in Vietnam, and small parts of adjacent Thailand and the Lao PDR. However, this area is by no means homogeneous and may be divided into several sub-units according to the criteria used. A basic distinction is conventionally made between the Tonle Sap lowland, which surrounds the Great Lake, and the deltaic track downstream of Phnom Penh, Cambodia.

The next level of ecological classification in the hierarchy is valley-bottom type (Figure 3). It is the lowest level of ecological stratification possible without more definitive channel mapping of the entire lower Mekong River.

The river reach extending from above Chiang Saen to Vientiane is a V-shaped valley with a moderate gradient streambed. Such valley bottom types are characterized by deeply incised drainage ways with steep, competent sideslopes which are very common in uplifted mountains. The river reach extending from below Vientiane to Bung Kan is also within

an alluviated, moderately bound, valley-bottom type characterized by an active floodplain and alluvial terraces which are bounded by moderate-gradient hillslopes adjacent to the immediate floodplain. Such valleys are typical of lowlands and foothills.

The next reach of the Mekong, extending from Bung Kan to Savannakhet, lies within a wide valley bottom of low gradient, and the floodplain is generally three times wider than the active channel width. This type of wide, low-gradient valley is alluvial, characterized by wide valley floors bounded by mountain slopes, and is generally associated with sloughs and cut-off channels. Below Savannakhet to the Mun River the valley bottom becomes narrower and the channel is restricted by adjacent geologic formations. This reach of the river is typical of an incised, U-shaped valley with a moderate-gradient. The river channel downcuts through deep, valley bottom deposits, and the immediate side-slopes are unconsolidated, and often unsorted, coarse-grained deposits. The next river reach of the Mekong begins below the Mun River and extends to Khone Falls; although this reach exhibits a wider floodplain and channel, it is similar to the Bung Kan to Savannakhet reach.

Khone Falls represents a unique ecological reach of the Mekong and is not duplicated anywhere else in the Basin; therefore it is selected as a distinct strata. Below Khone Falls and extending to the Tonle Sap River the valley bottom is characterized by an alluviated lowland with wide floodplains (usually more than 5 times the active channel width) (CHARLEY, 1984), which have been formed by present and historic rivers. The Khone Falls reach has flat to gently rolling landforms, sloughs, oxbows, islands, and abandoned channels.

The Tonle Sap River is also a unique area—it displays a similar valley-bottom type to the previous reach and its fishery is controlled by high flows in the Mekong River that reverse the Tonle Sap flow. The Great Lake of Cambodia, like Khone Falls, is a unique ecological area of the basin and is not similar to any other reach of the Mekong River.

The Mekong River reach below Khone Falls to Tonle Sap is an inland open-water fishing area which includes Kampong Cham, Kra Cheh, and Stung Treng (Stoeng Treng) Provinces. It lies entirely within the Kingdom of Cambodia. From Khone Falls to Phnom Penh the most important fishing activity of this reach takes place along a 150 km stretch of the Mekong River as it crosses Kra Cheh (Kratie) Province. Floodplains in this stretch of the Mekong dictate the biological cycle of fish migrations and reproduction and nearly all fish species migrate from the river into the flooded plains during the flood season, representing 30% of all production (MEKONG SECRETARIAT, 1992). According to information provided during a meeting with members of the Provincial Fisheries Office in Phnom Penh (KRATIE, 1994) this area is divided into two different sections: 1) an area which includes fishing areas on the Mekong River where fishing is permitted and is located 6 km above Kratie' city up to the border between Kampong Cham and Kra Cheh (Kratie) Provinces; and 2) an area extending from Chroy Ban Teay Commune to Stoeng Treng Province. The second area along the Mekong includes a number of deep holes which provide the habitat for "many fish species" (KRATIE AGRICULTURAL OFFICE, 1994).

This reach of the Mekong illustrates the need for more definitive stratification below the valley bottom type to the channel type level. It is one of the very few areas of the 1800 km of river included in this study where important fish habitats are known. The streambed below Kratie to above Stung Treng contains a series of deep holes (a partial list of these holes is shown in Table 2). Deep holes in the mainstem of the Mekong River appear to

Table 2. List of deep holes in the Lower Mekong River used by fish throughout the dry season in Kratie' Province, Cambodia (CMAFF, 1994).

NAME	LENGTH (m)	WIDTH (m)	DEPTH (m)
Kandol Moyroy	1000	200	40
Anglong Pra	500	150	40
Anglong Dam Rey	800	300	30
Anglong Preah Treal Lech	1000	100	20
Anglong Khach Mkak	200	200	
Anglong Achek	200	200	
Anglong Khach Soay	150		
Anglong Koh Knhe'	1000	500	20
Anglong Pheas Trea	1000	150	40
Anglong Tapeang	350	250	20
Anglong Chrak Tea	200	150	20
Anglong Kampong Prov	500	150	20
Anglong Ta Charr	200	200	10
Anglong Yeaymao	300	50	10
Anglong Veal Pronang	2000	600	40
Anglong Charr Pos Vek	300	200	30
Anglong Sre Kor	200	100	10
Anglong Tralok	150	100	
Anglong Kor Chlor	300	150	
Anglong Ueval	300	150	
Anglong Sang Kamkep	3000	300	40
Anglong Sang Kom	100		
Anglong Koh Cbar	300	150	
Anglong Koh Preng	300	150	20
Anglong Kantoy Koh Preng	700	100	15
Anglong Koh Real	100	50	10
Anglong Koh Pongear	800	150	40
Anglong Chroy Banteay	300	200	60

be primary rearing and dry-season holding habitat for large catfish and carp and would include target assemblage species for this ecological reach. Therefore, this reach of the river illustrates both the need to carry ecological stratification to at least the channel type level, as well as the unique hierarchy influences that resulted in numerous deep pools in this reach of the river.

It is likely that unique fish habitats, associated with distinct ecological reaches, occur throughout the river which could support subpopulations of important fish species. Stratification to isolate such critical fish habitats, in relation to the whole ecological reach and subpopulation life histories, is essential for future management and conservation efforts.

## FISHERIES ECOLOGY AND ASSEMBLAGE OF TARGET SPECIES

Fish species exploited in the Mekong River are a diverse group of more than 300 species; approximately 50 are of primary economic importance. A listing of the economically important species in each riparian country is shown in Table 3, which also indicates which species are migratory. This table should not be viewed as complete because no species surveys have been performed in most of the Mekong River since 1973. It is doubtful that the fisheries status shown in Table 3 is a complete list of species for the entire river, but work by the International Development Research Centre (IDRC), and work by T.R. Roberts at Khone Falls, has resulted in a reliable list of species for this ecological reach. While the species assemblage at Khone Falls is perhaps the most complete of any reach of the river, Roberts would argue that even this list is incomplete and that many species have not even been taxonomically identified. ROBERTS (1993) also argues that there is enough information on species assemblages for recognition that Khone Falls represents a biological barrier to some species (the magnitude of biodiversity is far greater below the falls than above). Typically most fish species separate themselves longitudinally within a river system and show different species upstream than downstream, and increasing biodiversity downstream (KINSOLVIN & BAIN, 1993).

Questions concerning stock separation, distance of migration, critical spawning areas, and key nursery habitat have not been answered for most resident and migratory fish species. While more is known about the timing and duration of migration in the Khone Falls reach, less is known in other reaches. This, of course, raises the possibility that numerous subpopulations of fish species are distributed throughout the mainstem and tributaries of the Mekong River Basin. To what degree subpopulations exist, interact, or are restricted to specific reaches is unknown. However, these are crucial questions which need to be addressed before sound management and conservation practices can be developed for the basin.

## FISH MIGRATION

Fundamental ecological issues related to river basin hydroelectric development are concerned with adverse effects of dams and impoundments upon migratory fish. Considerable research conducted upon large river systems has documented that reductions do occur in migratory fish stocks which result from dams as barriers to fish migration and turbine-related fish mortality (BROOKER, 1981; CASADO ET AL., 1989; CUSHMAN, 1985). Mekong River fishes migrate for reproduction, feeding, or dispersal and spreading of their populations (ROBERTS, 1993). Reproduction is clearly the primary biological motivation for migration of fish populations. Without annual recruitment of fish into the existing population there would be no further migrations. However, as ROBERTS (1993) states, all fish migrations in the basin are essential adaptations of the fishes (as self-regulating populations) to the linearity and seasonality of the riverine ecosystem.

The fishes of the Mekong basin are highly migratory and include two ecologically and commercially important groups (ROBERTS, 1993). The first group includes forage fishes (of critical importance to the food chain of many other species) which frequently make-

Table 3. List of economically important fish species in the Mekong River and their status by river reach (P = present, A = absent, R = rare, D = declining, U = unknown, M = migratory).

FAMILY and SPECIES		ECOLOGICAL REACH							
		1	2	3	4	5	6	7	8
CLUPEIDAE									
	<i>Tenualosa thibaudeaui</i>	A	A	A	A	A	R	R	R
NOTOPTERIDAE									
	<i>Chitala blanci</i>	U	U	U	U	U	U	U	U
	<i>Chitala ornata</i>	P	P	P	P	P	P	P	P
	<i>Notopterus notopterus</i>	P	P	P	P	P	P	P	P
DASYATIDAE									
	<i>Himantura chaophraya</i>	R	R	R	R	R	R	R	R
CYPRINIDAE									
	<i>Aaptosyax grypus</i>	M (?)	U	U	U	U	U	U	U
	<i>Bangana behri</i>		U	U	U	U	U	U	U
	<i>Catlocarpio siamensis</i>	M (?)	A	A	A	A	R	P	P
	<i>Cirrhinus microlepis</i>	M	P	P	P	P	D	D	D
	<i>Cirrhinus lobatus</i>	M	U	U	U	U	U	U	U
	<i>Cosmochilus harmandi</i>	M	A	A	A	A	U	D	D
	<i>Cyclocheilichthys enoplos</i>	M	A	A	A	A	A	D	D
	<i>Hampala macrolepidota</i>	M	A	A	A	A	A	P	P
	<i>Hypselobarbus spp.</i>	M	U	U	U	U	U	U	U
	<i>Labeo chrysophekadion</i>		U	U	U	U	U	U	U
	<i>Labeo pierrei</i>		U	U	U	U	U	U	U
	<i>Labiobarbus leptocheilus</i>	M	U	U	U	U	U	U	U
	<i>Leptobarbus hoeveni</i>		A	A	A	A	A	P	P
	<i>Mekongina erythrospila</i>	M	U	U	U	U	U	U	U
	<i>Osteocheilus melanopleura</i>		P	P	P	P	U	P	U
	<i>Osteocheilus hasselti</i>		P	P	P	P	P	P	P
	<i>Paralabuca typus</i>	M	P	P	P	P	P	P	P
	<i>Probarbus jullieni</i>	M	A	A	A	A	D	D	D
	<i>Probarbus labeamajor</i>	M	A	A	A	A	D	D	D
GYRINOCHEILIDAE									
	<i>Gyrinocheilus aymonieri</i>	M (?)	U	U	U	U	U	U	U
	<i>Gyrinocheilus pennocki</i>	M	U	U	U	U	U	U	U
COBITIDAE									
	<i>Botia modesta</i>	M	U	U	U	U	U	U	U
CLARIIDAE									
	<i>Clarias macrocephalus</i>		P	P	P	P	A	P	P
	<i>Clarias batrachus</i>		P	P	P	P	U	U	P

FAMILY and SPECIES		ECOLOGICAL REACH							
		1	2	3	4	5	6	7	8
<b>BAGRIDAE</b>									
	<i>Mystus microphthalmus</i>	U	U	U	U	U	U	U	U
	<i>Mystus nemurus</i>	U	U	U	U	U	U	U	U
<b>SILURIDAE</b>									
	<i>Wallago attu</i>	P	P	P	P	U	D	D	D
	<i>Wallago leerii</i>	P	P	P	P	U	D	D	D
	<i>Kryptopterus apogon</i> M	A	A	A	A	A	P	P	P
<b>PANGASIIDAE</b>									
	<i>Pangasius macronema</i> M	U	U	U	U	A	P	P	P
	<i>Pangasius larnaudii</i> M	U	U	U	U	A	P	P	P
	<i>Pangasius hypophthalmus</i> M (?)	U	U	U	U	U	U	U	U
	<i>Pangasius gigas</i> M	P	P	P	P	P	D	D	D
	<i>Pangasius sanitwongsei</i> M	U	U	U	U	A	D	D	D
	<i>Helicophagus waandersii</i> M	U	U	U	U	U	U	U	U
<b>CHANNIDAE</b>									
	<i>Channa micropeltes</i>	P	P	P	P	P	P	P	P
	<i>Channa striata</i>	P	P	P	P	P	P	P	P
<b>BELONTIIDAE</b>									
	<i>Osphronemus exodon</i>	U	U	U	U	U	U	U	U
	<i>Trichogaster trichopterus</i>	U	U	U	U	U	P	P	P
<b>SCIAENIDAE</b>									
	<i>Boesemanina microlepis</i> M	A	A	A	A	A	P	P	P
<b>ELEOTRIDIDAE</b>									
	<i>Oxyeleotris marmorata</i>	A	A	A	A	A	P	P	P

\* The list of economically and otherwise important native freshwater fish species was prepared for the Mekong Secretariat by Dr. Tyson Roberts. Presence/absence is based upon personal communications with representative of Thailand, Laos, and Cambodia fisheries agencies as well as Terry Warren (IDRC) and Ian Baird (Lao Community Fisheries and Dolphin Protection Program of Earth Inland Institute and the Lao PDR Department of Forestry). For the most part reliable catch data is lacking and most information is derived from fisherfolk and observations by the fisheries professionals listed above.

up the major portion of subsistence catches. These forage fish feed low on the food chain and are primarily cyprinid fishes such as *Cirrhinus* spp., *Labiobarbus leptocheilus*, and *Paralaubuca typus*, and the endemic Mekong freshwater herring *Tenualosa thibaudeaui*. The second group includes large migratory fishes (all economically important) of cyprinids and catfish from the families Siluridae and Pangasiidae.

Migrating species capitalize upon different seasonal environmental conditions within each long reach of the river. The motility of these migrating species places them in different reaches at different times of the year. During one season a certain river reach may provide rearing habitat while at another time the same reach is simply a passage corridor. As a result of these different uses of a river reach at different times of year, each stage of a migratory fishes' life history is a critical one for its continued survival. Fish may be denied passage upstream or downstream, and then become isolated from their spawning or rearing habitats and be unable to complete their life cycles.

Providing fish passage facilities as mitigation for dams as barriers to upstream migration is simply an unknown for the species common to the lower Mekong River (HILL & HILL, 1994). Specification of satisfactory water levels, in-stream flows, discharge regimes, attractant flows, and detailed criteria for passage facilities like fish-ladders are reasonably well developed for salmonid species (BELL, 1984; CRAMER & OLIGHER, 1964), but research and development of passage facilities for tropical fish species has rarely been performed. There is virtually no body of knowledge upon which to rely in making these decisions for tropical fish species.

### FISH ASSEMBLAGES

Assemblages of fish species can be identified within broad habitat types and within ecological gradients along the river. Species which are associated with the lower-basin main streams (just above the delta), and to some extent associated with the Great Lake, include species from families of marine (secondary-freshwater) origin which, in some cases, can migrate from brackish into freshwater: clupeids (*Hilsa* sp., *Ilish* sp., *Clupea thibaudeaue*), Sciaenidae (*Pseudosciaena soldado*) and Soleidae.

A group of species associated mainly with larger streams and the mainstem of the Mekong river, but undertake spawning migrations between these streams and flooded areas in the wet season (the 'white fish' of Cambodia), are primarily cyprinids (*Cirrhinus auratus*, *Hampala macrolepidota*, *Puntius altus*, *Leptobarbus hoevenii*, *Osteochilus melanopleura*, *Labeo chrysophekadon*), various *Pangasius* species, Siluridae (*Wallago attu*, *Kryptopterus apogon*), and Notopteridae (*Notopterus chitala* and *N. notopterus*). Several of these species undertake both lateral and longitudinal migrations.

Species able to survive in more adverse and varied environmental conditions (low-oxygen levels, some acidity, some salinity) and which are able to stay in the swamps and plains year around (the 'black fish' of Cambodia), include carnivores and detritus feeders. Some of these species are able to migrate over land, and several possess auxiliary organs for oxygen uptake from atmospheric air—this group includes members of the families Clariidae (*Claris batrachus*), Channidae (*Channa micropeltes*, *C. striata*), Bagridae (*Mystus nemurus*) and Anabantidae (*Anabas testudineus*, *Trichogaster trichopterus*).

Smaller, fast-growing, and prolific species (opportunists) are another ecological group that is able to utilize the flood period for prolific reproduction and growth—this group consists mainly of cyprinids (*Thynnichthys thynnoides*, *Dangila siamensis*, *Cirrhinus julleni*). Due to their unique biology this prolific group can exhibit very high abundance in a distinct seasonal pattern.



Different species groups exhibit very different migration patterns and production dynamics which, in turn, influence capture-gear technology and capture effort. At one extreme end of a continuum are the opportunist species—most efficiently harvested with a very high effort and unselective gear during the short time they are abundant. At the other end of a continuum are the largest of the white fish species which are unable to stand high-fishing pressure (especially as young-of-the-year) and are fished with highly selective gear and low effort. Opportunist species make up most of the total production of the ecosystem (especially in the floodplains) and are the primary focus of subsistence fishing. Commercial harvest consists primarily of large cyprinids and other catfishes.

From this ordering of biodiversity an assemblage of target species can be selected which exhibit the most sensitive response to changes in biotic and abiotic patterns. Target species assemblages appropriate for analysis of potential development project impacts on the Mekong River should not simply be the rarest species present in the watershed, or be selected from single taxonomic groupings or guilds (FRANKLIN, 1993); the assemblages should represent critical habitat types, trophic levels, behavior, and life histories.

NOSS (1990) identifies five categories of species that warrant intensive monitoring: (1) ecological indicators—species that signal the effects of perturbations on a number of other species with similar habitat requirements; (2) keystones—pivotal species upon which the diversity of a large part of the community depends; (3) umbrellas—species with large area requirements, which if given sufficient protected habitat area will bring many other species under protection; (4) flagships—popular, charismatic species that serve as symbols and rallying points for major conservation initiatives; and (5) vulnerables—species that are rare, genetically impoverished, of low fecundity, dependent upon patchy or unpredictable resources, extremely variable in population density, persecuted, or otherwise prone to extinction in human-dominated landscapes.

I recommend that an assemblage of target species by ecological strata for the lower Mekong River be used in the evaluation of proposed development projects. These target species assemblages must be based upon the presence/absence of species within the nine reaches (classified to at least the channel type level), and, as described above, represent a mix of ecological indicators, umbrellas, and vulnerables. Evaluation of development effects upon these species would then represent worst-case impacts within each ecological strata. Because the taxonomic list is incomplete, and there are inaccuracies inherent in the current state of knowledge of species presence and absence in river reaches, other investigators can and should develop a list of target species when evaluating potential development projects.

## LIMITING FACTORS

The single most important consequence of hierarchical structuring is embodied in the concept of constraint or “limiting factor”. This concept emphasizes that the behavior of an ecological system is limited by (1) the potential behaviors of its components, and (2) the environmental constraints imposed by higher levels (O’NEILL ET AL., 1989). Ecology generally recognizes that populations are usually limited by only one or two environmental factors at a time, but can be limited by several environmental factors over time (PITCHER & HART, 1982). The principal limiting factor referred to repeatedly in print (MEKONG

SECRETARIAT, 1992; ROBERTS, 1993), and in conversations about the lower Mekong River fisheries, is overfishing. Overfishing can certainly limit the Mekong fishery in time and over time. However, there is a paucity of data to support the argument that overfishing is the principal limiting factor throughout the Mekong River. It is reasonable to suppose that overfishing limits production of certain stocks in certain reaches of the Mekong river due to use of highly-efficient catch methods like lee traps, gill nets, and explosive devices. But there are still no data to indicate that overfishing is a limiting factor in more than local reaches of the river (CNMC, 1994; CMAFF, 1994; LNMC, 1994; LADF, 1994).

Fisherfolk observations would indicate that certain species are in decline, that total fish caught in the Khone Falls reach is also declining, and that fish catches downstream to the Great Lake are reducing (T. Warren, IDRC, personal communication, 1994). There are also indications that overfishing may be limiting total production in the reaches from Pakse to Khone Falls (LADF, 1994). Hard data on catch-through-time to confirm or to deny these suppositions is lacking in all reaches of the Mekong River.

ROBERTS (1993) has alluded to indications of decreasing stream flows in the Mekong River since 1970 as a potential limiting factor on the river fisheries. Figure 4 shows minimum and maximum flows in the Mekong at Vientiane (the upper reach) and Pakse (lower reach) for a 20 + year period-of-record beginning in 1970 (a 20-year POR is adequate to account for short-term and long-term hydrologic cycles) (MEKONG SECRETARIAT, 1993). This figure indicates that the trend in maximum annual flows is downward, but the 20-year trend for minimum flows has remained relatively constant. These trends were statistically tested and were found to be significant ( $p = <.05$ ) for all flows at both Vientiane and Pakse locations. The long term hydrologic record of the Mekong River reflects a number of cycles of both declining and increasing flows; the period of decline from 1970 to 1990 is not unique. This declining flow period represents a natural event cycle that influences the fish populations and the resulting catch rates.

If Mekong River flows have diminished during this 20-year period (1970–1990) as a consequence of damming tributaries to the Mekong or from irrigation diversions one would expect to see a similar downward trend in the minimum annual flows. However, since minimum flows have not changed significantly over time (maximum flows occur during the wet season and minimum flows during the dry season) precipitation fluctuations have been occurring (providing the data base from gaging stations are reliable) that contribute to declining stream flows as a natural cycle which limits the fishery throughout the Mekong Basin.

Reduced stream flows would then impose a limiting condition on fish production before limitations from overfishing take effect, but both limiting conditions operate over time by allowing overfishing and declining flows to act synergistically to affect the fishery.

Declining stream flows would naturally lead to a reduction in total habitat area in wetlands and floodplains which are essential for nursery and early rearing of fish (WARD & SANFORD, 1989). These declines would also reduce migration success and produce fewer spawners arriving at spawning sites—a condition which would be particularly critical at Khone Falls where large migratory catfish (the primary catch species) must negotiate narrow chutes (hoos) through the falls. Low high-flows would create passage difficulties, if not impossibilities, at many hoos. Fewer spawners means that annual recruitment would decline (SALE, 1995) and egg-to-fry survival would also decline with changes in incubation-

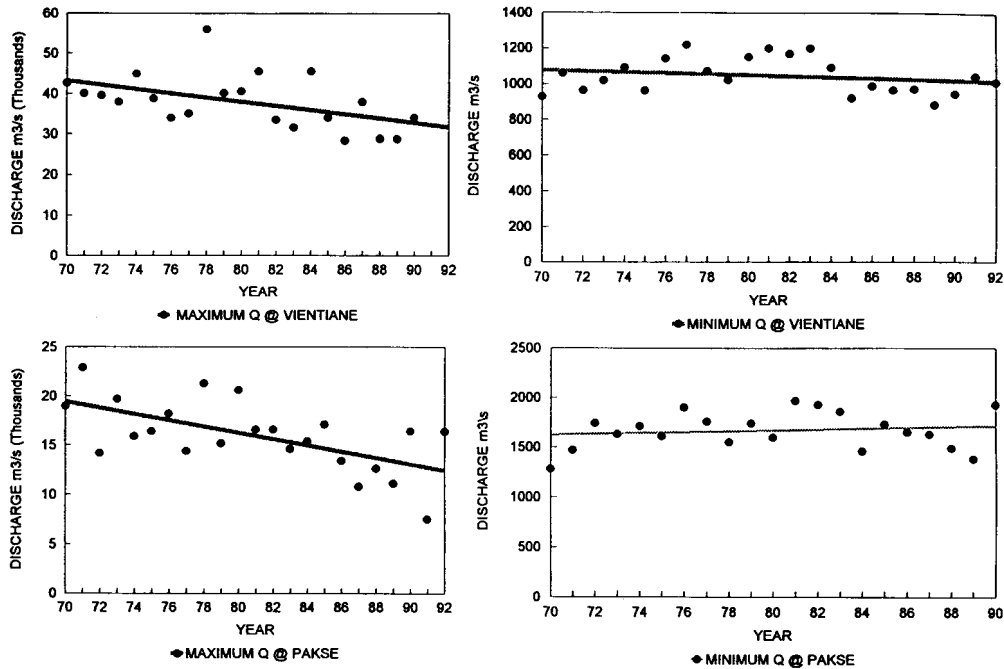


Figure 4. Trend analysis of flows in the lower Mekong River at Vientiane and Pakse, 1970–1992.

drift rate. A change in habitat space and quality would allow an increase in inter- and intraspecific competition for resources and would lead to changes in species composition and relative abundances as selective pressures favor more adaptable species (CHAPMAN, 1966). Subtle temperature changes, induced by lower maximum annual flows, could incrementally reduce growth rates of fish and vigor over time (ODUM, 1956; IRVINE, 1985). Migratory species might shift spawning sites to areas of easier access which leads to greater isolation of stocks and decreased genetic variability (HYNES, 1970). Most of these potential changes are individually subtle, but collectively such changes would manifest in changes in species abundance, or lowered overall biomass and productivity (ODUM, 1956). Subtle influences upon fish from reduced flows can be accelerated and magnified by overfishing (GRIFFITH, 1989).

Overharvest of adult fish further decreases recruitment of young-of-the-year, induces more rapid species shifts, decreases biomass, and reduces biodiversity as preferred species disappear and less desirable species expand into niches which have been left vacant (ODUM, 1956; HYNES, 1970).

Declines in catch typically induce fisherfolk to increase fishing efforts and to convert to more selective and efficient catch methods. The supply and demand of a market economy increases catch-effort and fish become more valuable when demand exceeds supply and fisherfolk recognize the opportunity to make more money. In time, diminishing catch and expanding effort creates a downward spiral of decline which is difficult to halt or correct.

It is important to recognize that any analysis of the fisheries of the Mekong River is speculative at this point due to the current lack of reliable data on fish production or actual effects of limiting factors within specific reaches. The temptation to draw conclusions from such speculation should be resisted because the conclusions could be wrong, leading to inappropriate actions to correct problems that have not been adequately identified. A simple assumption that the primary limiting factor on fish production is overfishing, without recognition that reduced stream flow impacts occur before overfishing, could lead to catch regulations which only reduce fisherfolk income and do very little to alleviate the real problems.

The additive cumulative impacts from all uses of the Mekong River, including natural cycles of change, overfishing, and possible multiple hydropower projects and large-scale water diversions, can result in a tremendous loss of biodiversity to the Mekong River fishery. Diversity of species (all aquatic species, not just fish) is the strength of any ecosystem. The variability associated with biodiversity allows biotic systems to tolerate natural environmental changes and to respond to extreme climactic fluctuations which affect populations. Loss of biodiversity is a loss of biological resiliency which weakens the entire riverine ecosystem, makes fish populations less capable of tolerating natural environmental changes, and less adaptable to cumulative anthropogenic uses. In time, as human demands and uses increase, incremental reductions in fish biodiversity will eventually create major losses in the Mekong River fishery.

## RECOMMENDATIONS

The central problem with this evaluation, as well as with other studies of the Mekong River fisheries, is a lack of data and information. Proposed development projects cannot be safely designed or adequately mitigated without a sound and reliable environmental data base. In the following section I recommend short-term and long-term studies which are necessary in order to describe specific development project impacts, mitigation, cumulative or combined impacts, and to suggest alternative project sites and dimensions.

Short-term studies focus on specific issues and data gaps that need to be studied and addressed in order to more accurately evaluate development projects; they are intended to answer the most pressing impact questions. Long-term studies are much more detailed and seek to provide not only background, but an environmental framework for sustainable development throughout the Mekong River watershed. An approach which combines short and long-term studies is relatively new, but is recognized in the international scientific community as the only plausible mechanism to develop resources and to maintain biodiversity in any river basin in the world.

### Short Term Studies

**Stock evaluation**—Fish stock information (size, location, life history) is one of the most critical gaps in the information base for the lower Mekong River. Development project impacts on migrating fisheries cannot be predicted accurately without more specific data on stocks in each of the ecological reaches. This fishstock study must focus upon

