

Why Thai River Fish Occur Where They are Found

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Abstract

Diversity of freshwater fishes is spatially heterogeneous but, for the most part, the reasons remain poorly understood in Thailand. This review attempts to promulgate factors linking freshwater fishes and habitats, particularly morphological, physiological and ecological, drawing on principles and information from elsewhere but with the focus being Thailand. The review identifies areas in need of improved understanding with an assurance in the future of generous dividends for the investment.

Keywords: distribution; morphology; physiology; fish associations; S.E. Asia

1. Introduction

The easy answer to the question of why fish are where they are found is simply because they cannot live elsewhere. This review attempts to expand on this although it provides no more than an introduction to a full understanding of the current distribution of fish in the rivers of Thailand. It relies to a considerable extent on principles and information assembled in other regions of the world and concludes with the identification of important abiotic factors to species associations in regions of central Thailand. This review is also an attempt to provoke discussion and, ideally, enthusiasm to provide relevant information for the conservation of this magnificent national natural resource.

Diversity of fish is spatially heterogeneous within and among geographical regions of the world. There are doubtless many regions where species might well exist but from which they are absent (Beaufort, 1951). The reasons for this are many. The global landscape has been and continues to be in transition, a consequence of plate tectonics and other processes within the earth's crust. Landscape changes resulting from geological activity determine where water may and may not flow. The current global distribution of freshwater fishes is thought to relate to historical land bridges that are now submerged beneath the ocean surface (Golanka *et al.*, 1994; Moyle and Cech, 2000). To this, evolutionary processes and natural extinctions continually modify species complexity and numbers. In recent years distribution patterns of fish have been impacted additionally

along with a number of extinctions through the mostly thoughtless actions of humankind in terms of intentional and non intentional plant and animal introductions as well as through improper water use and channel modifications.

Patterns of diversity are generally described by scales of space and time in river systems and within each by abiotic and biotic processes. This review examines diversity from the perspective of ecological processes with implicit recognition of biogeographic processes (Gaston and Williams, 1996; Cornell and Lawton, 1992). Understanding diversity includes both patterns and mechanisms. The former are well known in some regions and little known in others. The latter is fraught with contention. Reasons for diversities involve many factors, physical, chemical and biological. For some species these factors are, again, quite well understood but for the vast majority they are not.

Globally, diversity tends to vary inversely with latitude (Rosenzweig, 1995; Leveque *et al.*, 1988) and directly with watershed size and elevation (Swift *et al.*, 1986). However, these patterns are sometimes far from clear (Love and Taylor, 2004) and can be affected by other processes such as might be initiated or accelerated by changes in climate or that might involve rates of evolutionary speciation and dispersal (Livingston *et al.*, 1982; Hugueny, 1989). Large rivers generally contain more species than small rivers. Indeed the largest rivers of the world are known to support or to have supported very large numbers of species. Number of species in the Amazon River in South America is listed at 804 in

Fish Base (Sistrom *et al.*, 2009; Froese and Pauly, 2010) although some suggest the number may be as high as 5000. A review of species diversity in African rivers by Livingstone *et al.* (1982) summarizes the trend of increasing species diversity with river size as well as the inconsistencies. Thus, species numbers in the Nile River, 6650 km in length and >3,000,000 km² in area, was reported as 115 (Greenwood, 1976) while the shorter Zaire River at 4,700 km in length but of similar area was said to contain 669 species.

The niche concept precludes more than a single species occupying the same habitat. Even the view of many species sharing a similar habitat runs contrary to expectations that might be drawn from the concept of competitive exclusion (Gilpin and Justice, 1972; McGehee and Armstrong, 1977). This concept applies under conditions of habitat stability and uniformity and for species dependent on the same resources. In contrast, physical and chemical conditions, predation and other factors are continually imposing their influence on population sizes and the nature of competitive interactions, making it likely that competitive equilibrium rarely occurs, if at all (Wiens, 1977; Huston, 1979). Even if competitive equilibrium is never fully achieved, the expected outcome of competition might be an eventual predominance of only a few competitors. Recent theoretical evidence suggests this need not occur where life history, morphological, physiological or behavioral variations differ such that they confer differential advantages (McCann *et al.*, 1998). Without these, increasing intensity of competition should result in a decrease in species evenness and, eventually species number. Intense competition should result in low diversity among competing species and high diversity might be expected where competition has yielded to resource sharing. But diversity is not simply a measure of competition but also how well species are able to perform in environments that vary in their chemical, physical and biological properties and to accommodate the successful outcomes of natural selection operating within a watershed.

2. Habitat and Thailand's Freshwater Fishes

Thailand's aquatic ecosystems are supported by six major watersheds, Salween, MaeKlong, Chao Phraya, Mekong, Peninsular and Southeast (Vidthayanon *et al.*, 1997). Within each watershed are many smaller rivers or tributaries. Northern Thailand lies between the Salween and Mekong rivers and water in most of this area is guided by landscape irregularities from two northern mountain ranges to larger rivers and, ultimately, the Chao Phraya River and the Gulf of Thailand after passing through the large city of Bangkok. The

northeast area drains mostly into the Mekong River while central Thailand is drained by the MaeKlong and Chao Phraya rivers and their many tributaries. Much of the MaeKlong River system in western Thailand is within the Tanao Sri mountain range that forms a boundary between Thailand and Myanmar. These systems are probably among the least disturbed lotic ecosystems in Thailand, although some have not been spared the effects of dam construction and other forms of human activity. The Peninsular watershed refers to the area south from the Isthmus of Kra and includes six short river systems, four that discharge into the Gulf of Thailand and, in the southern portion of the watershed, two that discharge into the Andaman Sea. The Southeast watershed is bounded by the Cardamom mountain range that divides Thailand and Cambodia and to the west, by the Gulf of Thailand and includes three comparatively short river systems.

Number of freshwater fishes in Thailand is in excess of 600 species (Smith, 1945; Vidthayanon *et al.*, 1997). While general distributions of many species have been described, quantitative estimates of actual species numbers within rivers have not, until now, been available. Recently, a quantitative estimate of species numbers was undertaken for nine rivers in Thailand. The rivers, all of medium and small size are located in western, southeastern and southern Thailand. Species richness was estimated from samples captured by electrofishing at sites selected according to a randomized stratified sampling program and analyzed by the Jackknife method (Krebs, 1989). Richness varied from 19 in the smallest river of only 8 km to 55 species in a river of approximately 40 km. The largest river, 82 km in length was estimated to contain 49 species. Generally, species numbers in the rivers increased with length and area. Of considerable conservation interest, but not surprising, is a suggestion of differences in species richness among the three regions, being highest in western Thailand. With the few rivers sampled the reasons can be no more than tentative but appear to be at least partly related negatively to regional anthropogenic activity.

Species packing or crowding is thought to be affected to a large degree by three major resources, habitat, food and time (Pianka, 1970; Schoener, 1974), particularly the availability and quality of each. Important also are competitive or sharing mechanisms (Ross, 1986; Piet, 1998). Closely related species tend to segregate in relation to at least one major resource with the degree possibly related to intraspecific genetic variations (Castillo-Rivera *et al.*, 1996; Mookerji *et al.*, 2004). Some closely related species differ morphologically, for example, in mouth size so that they feed on dissimilar prey allowing them to share the same habitat

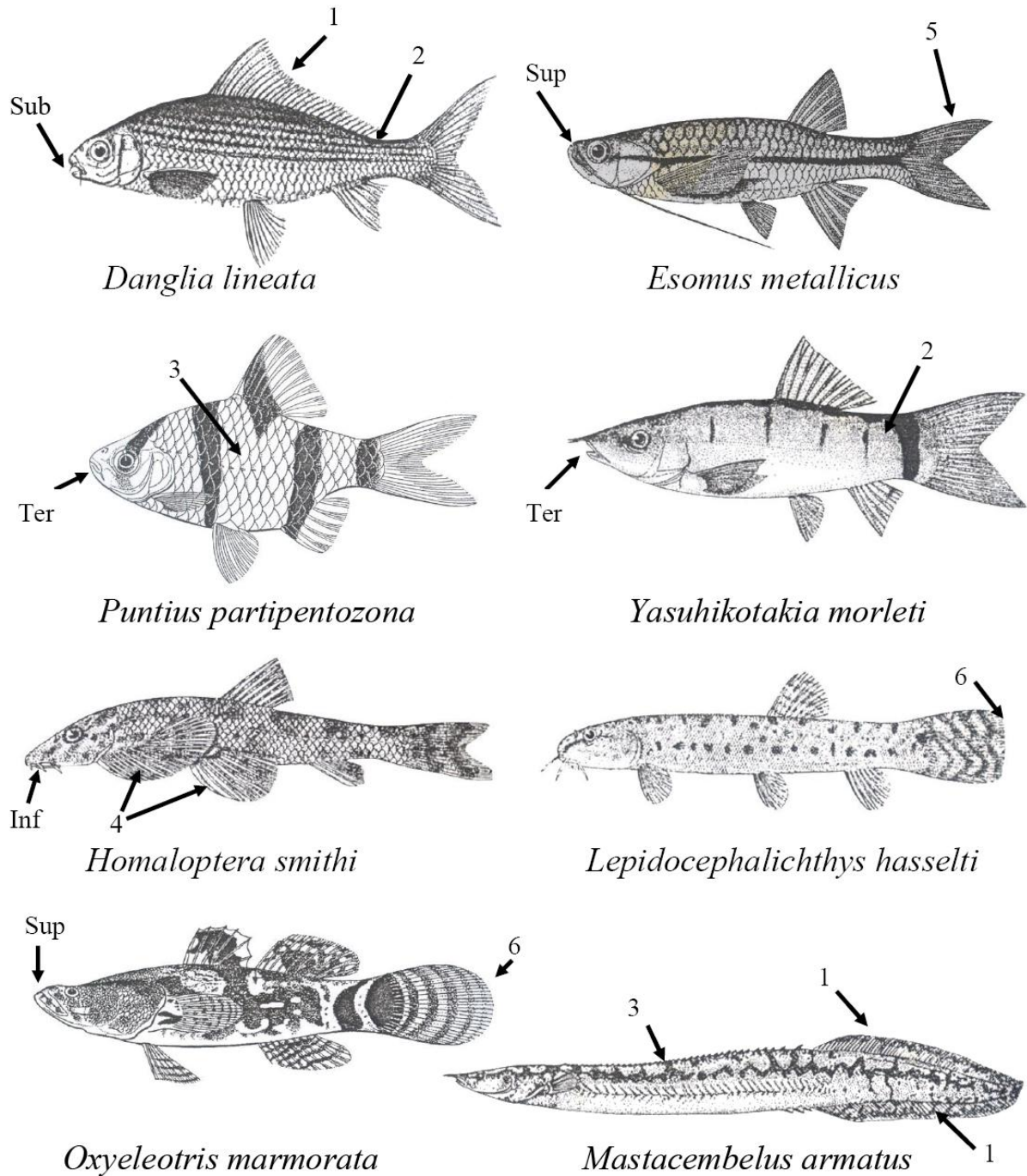


Figure 1. Variations in body shape, mouth position and fin shape, size and location (Rainboth, 1996). Sup or superior refers to a mouth designed to feed on prey above; Ter or terminal refers to a mouth located at the anterior end of the head and is commonly found on fish that feed within the water column. Sub, subterminal and Inf, inferior refer to mouth positions of fish that feed on benthic organisms. Arrows identify morphologies important in swimming, maneuvering or station holding; 1, long or short median fins; 2, narrow or deep caudal peduncle; 3, short or long body; 4, large pectoral/ pelvic fins station holding; 5, forked tail, sustained swimming; 6, truncate or rounded tail, strong but slow swimming speeds.

(Matthews *et al.*, 1982). Food availability and its nutritional qualities are also products of species-related physiological (Pierce and Wissing, 1974; Ogino, 1980), morphological (Wikramanayake, 1990; Wainwright and Richard, 1995) and behavioral characteristics (Werner and Hall 1974; Scott *et al.*, 2005). Greenfield *et al.* (1983) suggest this may be particularly characteristic of a tropical, species-rich assemblage, thereby allowing

for greater species packing potential. Competition among species sharing a similar habitat may be reduced through partial or full reductions in diet overlap (Page and Schemske, 1978) as well as temporal differences in feeding schedules (Nithirojapakdee *et al.*, in press). The importance of competition in assemblage structure within any or all of the resource axes is characterized by uncertainty, even contradiction.

Table 1. Fin areas, mm², of benthic fish of 25 and 50 mm total length calculated from significant linear regressions (Beamish, unpublished information).

Total length, mm	Tail		Pectoral		Pelvic		Dorsal	
	25	50	25	50	25	50	25	50
<i>Amblyceps mucronatum</i>	18	80	7	22	6	15	8	26
<i>Balitora sp</i>	22	58	15	47	13	34	10	27
<i>Channa gachua</i>	12	59	9	40	7	14	8	43
<i>Glyptothorax platypogonoides</i>	16	69	14	47	20	48	9	31
<i>Homaloptera smithi</i>	20	63	12	43	9	64	13	24
<i>Schistura kohchangensis</i>	27	84	18	38	13	30	15	38

A distinct linkage between morphology and distribution through the environment began to emerge in the 1940s (Goldschmid and Kotrschal, 1989) and became widespread as recently as the 1970s (Bock, 1990). The fundamental concept that morphology will predict distribution is based on the assumption that it influences performance and through this, resource use (Wainwright, 1994; Wainwright and Richard, 1995). Studies in ecomorphology attempt to identify relationships between variation in form and in ecology with respect to resource use within and among species and assemblages (Motta *et al.*, 1995). The major goal of functional morphology is to determine the potential functional role of structures (Liem, 1991). Functional morphology in conjunction with ecomorphological studies, play an important role in identifying the causal relationship between an organism's form and performance (Wainwright, 1994). Functional morphology thereby acts as a tool, a priori, in identifying the potential niche of species. Whether or not a species is able to fully utilize a potential niche is due to other factors.

Species distributions and habitats within biogeological confines can be expected to be largely dictated by evolved adaptations. Some support has been expressed for the view that locomotor morphological features define the subset of fishes that live in certain habitats but a more common view is that morphological features act in concert with other factors, physiological, behavioral and environmental to define a species' habitat. Swimming styles or gaits differ with species. Morphologies of importance in flowing water can be inferred largely from the shape and size of the body and fins (Wiehs, 1973; Daniel and Webb, 1987). Probably the majority of species are of fusiform shape and oblong to round in cross section, examples including most species of *Rasbora*. A second category includes species that are laterally compressed with a deep body such as species of *Pristolepis* or *Nandus*. The third category includes mostly benthic species with a dorsally compressed body that is oblong in cross section, examples being species in the family Gobiidae. Fish use the body, paired fins and

median fins for propulsion. Some fish swim largely or even exclusively with an individual or limited number of fins such as *Notopterus notopterus*. However, most fish swim using several propulsors working in concert, especially at low speeds. Forward movement, particularly at faster speeds is usually provided by lateral body undulations driven by muscles in the caudal peduncle resulting in forward thrust from the caudal fin. Cyprinids with a wide and deep caudal peduncle and a flexible body such *Osteochilus vittatus* and *Mystacoleucus marginatus* have these adaptations allowing them to swim where water currents are high.

Fish morphology is often specialized, adapting the recipients for specific habitats and activities. Thus, maneuverability or agility is advantageous in habitats congested with plants or debris when food is available. Maneuvering at fast speeds requires high rates of centripetal acceleration which is best achieved by fish with a short body length in which body mass and depth are centrally concentrated as in *Puntius partipentozona* (Fig. 1). This body shape helps minimize the turning radius and increase agility of high speed turns (Webb, 1998). Low speed maneuverability requires the ability to orient thrust in many directions using large or long and flexible fins, capable of independent motion at different places along its length. A deep body as occurs in *Cyclocheilichthys apogon* provides maneuverability but not fast speeds where they occur in their debris-cluttered slow flowing habitat. An alternative morphology for low speed maneuvering uses shorter based pectoral, pelvic, anal, dorsal and caudal fin propulsors distributed around the center of body mass as in *P. partipentozona*. This morphology may be accompanied by fin embellishments or attachments that increase drag and further facilitate low speed turns.

Regions of high water velocity often have large, benthic populations of immature insects as well as other fauna that constitute a rich food source for fish. This can also be an energetically hostile environment for fish. However, not all species that live in habitats characterized by fast currents are strong swimmers. At

this point it is useful to point out that swimming performance has yet to be measured for a single fish species indigenous to Thailand (Beamish, 1978; Sfakiotakis et al., 1999). One approach to live in fast water is to avoid the energy demands of swimming by seeking refuge within or amongst the substrate. Efficient substrate refuge requires maximizing effective weight and friction coefficients and minimizing drag and lift (Webb, 1998). Drag is minimized with a flat body shape but this increases lift. A fusiform body reduces lift but increases drag. Successful benthic species have compromised their shape so that it is partially dorso-ventrally flattened providing for both lower drag and lift. This shape is common among Thai benthic species within the families Cyprinidae, Balitoridae, Gobiidae, and the order Siluriformes.

Many of the benthic species that live in lotic regions move by creeping along the substrate aided by large paired pectoral and pelvic fins (e.g. *Homaloptera*

smithi, Fig. 1) that serve as depressors. Paired fin areas differ widely among benthic fishes (Table 1) suggesting different efficiencies or tactics. As fish increase in size, relative surface area and hydrodynamic drag in flowing water can be expected to decline in contrast to a disproportionate increase in area of paired and median fins. It is tempting to suggest that size related morphometric differences such as these may impose spatial habitat separation during ontogeny. Some benthic species also have a large caudal fin that can provide ample forward thrust in flowing water to capture prey as well as avoid predation (Table 1). Thoracic adhesive adaptations in *Glyptothorax plectilis* (Ng and Hadiaty, 2008), ridges (Hora, 1930) or adhesive pads on the ventral surface of pectoral and pelvic fins (Roberts, 1982) may serve as friction devices further facilitating station holding in flowing water. Bottom dwelling benefits also from fish densities that typically exceed that of water and are generally above those of pelagic species (Table 2).

Table 2. Density of river fishes by habitat depth. Density was measured by displacement on fish freshly killed by an overdose of methane tricaine sulfonate. The relationship between density and total length was not significant for any species at $P > 0.05$.

Habitat	Species	Sample	Total Length, mm		Density	
Surface		Size	Mean	SD	Mean	SD
	<i>Dermogenys pusilla</i>	41	44	19	1.0059	0.0954
	<i>Xenentodon cancila</i>	10	122	42	1.0154	0.0151
Pelagic						
	<i>Danio acrostomus</i>	47	62	20	0.9799	0.1147
	<i>Mystacoleucus marginatus</i>	29	88	13	1.0157	0.054
	<i>Neolissochilus stracheyi</i>	7	101	51	1.0235	0.0732
	<i>Osteochilus vittatus</i>	26	93	26	1.0005	0.0496
	<i>Puntius binotatus</i>	59	72	19	1.01	0.0478
	<i>Puntius orphoides</i>	7	106	19	1.0081	0.0328
	<i>Rasbora borapetensis</i>	16	40	6	1.0247	0.0823
	<i>Rasbora paviana</i>	50	66	21	0.9951	0.0449
Benthic						
	<i>Acanthocobitis zonalternans</i>	10	45	3	1.0202	0.0771
	<i>Channa gachua</i>	55	114	54	1.0628	0.0671
	<i>Garra sp.</i>	10	85	20	1.0158	0.0711
	<i>Glyptothorax laosensis</i>	5	86	13	1.0863	0.0609
	<i>Homaloptera smithi</i>	37	52	13	1.0639	0.0815
	<i>Lepidocephalichthys berdmorei</i>	10	117	60	1.0735	0.0643
	<i>Macrogynathus circumcinctus</i>	20	125	50	1.0456	0.0712
	<i>Mastacembelus armatus</i>	28	165	55	1.0569	0.0768
	<i>Monopterus albus</i>	10	221	89	1.0591	0.0711
	<i>Oxyeleotris marmorata</i>	13	68	14	1.0493	0.0911
	<i>Schistura sexcauda</i>	22	51	11	1.0779	0.0975

Many benthic species of Siluriformes, Balitoridae and Cobitidae have reduced swimbladders that contribute to their higher densities (Knaepkens *et al.*, 2007). Finally, habitat associations are supported by buoyancies which are higher and lower in pelagic and benthic species, respectively (Table 3).

Current understanding of the lateral line systems of fish, while incomplete, is revealing other adaptations for specific habitats in rivers. Fish differ in the number and distribution of sensory pores in their lateral line system. While not yet experimentally investigated, the lateral line system of free swimming fishes may play an important role in monitoring water movement over their bodies and providing muscular feedback for efficient swimming in quiet as well as turbulent water (Coombs, 2001). Fish seem able to monitor boundary layer flow around their bodies (Anderson *et al.*, 2001) and, with this information, synchronize tail beat frequency and amplitude to capture energy from vortices produced when swimming (Triantafyllou *et al.*, 1993; Wolfgang *et al.*, 1999).

The abundance of cephalic pores on some benthic species such as the balitorids may provide assistance to detect nearby prey and discriminate between the hydrodynamic signatures of different animals and forms of movement (Bleckmann *et al.*, 1991). Stationary obstacles also create distortions in the currents of surrounding water, which could be passively imaged by fish. Indeed, the lateral line system seems to be important to station-holding behaviors of fish that maintain their position behind rocks in a stream (Sutterlin and Waddy, 1975). Vortices shed by these obstacles may even be exploited by fish to conserve energy against the downstream forces of the current.

Morphological adaptations associated with swimming or station holding are not the only determinants of habitat. Other morphological adaptations in conjunction with specific behaviors and physiologies have been linked with diet and feeding ecology among co-existing fish species and are indicative of why they occur where they are found (Hartman, 1958; Labropoulou and Eleftheriou, 1997; Xie *et al.*, 2001). Morphological features of the head and feeding apparatus are indicators of the type of prey eaten. Carnivorous fish tend to have large mouth gapes and sharp, conical teeth (Keast and Webb, 1966; Winemiller, 1991) with short relative intestine lengths (Ribble and Smith, 1983; Kramer and Bryant, 1995). Detritivorous and herbivorous fish on the other hand, tend to have smaller mouth gapes, an increased incidence of pharyngeal teeth, and much greater relative intestine lengths (Ribble and Smith, 1983; Kramer and Bryant, 1995). Position of the mouth (superior, supraterminal, terminal or inferior, (Fig. 1) indicates the position in the water column where fish generally feed (Gatz, 1979; Felley, 1984; Winemiller, 1991).

A study on five Thai fishes, *Rasbora caudimaculata*, *Schistura desmotes*, *Dermogenys pusilla*, *Xenentodon cancila* and *Monopterus albus* that commonly occur together in the riffle regions of headwater rivers in Thailand found strong correlations between those morphological features associated with feeding and their diet (Ward-Campbell *et al.*, 2005). While this was the first such study on Thai fishes a subsequent study has also linked morphological features to diet, feeding ecology and habitat in co-existing species within the family Cyprinidae.

Cyprinids are well represented in the rivers of

Table 3. Buoyancy values for river fishes. Benthic species are indicated by an asterisk No attempt was made to remove gas from the swimbladder of fish before making measurements

Species	Sample Size	Buoyancy % wt in water/air
<i>Amblyceps mucronatum</i> *	9	11.72
<i>Channa gachua</i> *	9	7.15
<i>Glyptothorax laosensis</i> *	5	10.1
<i>Glyptothorax major</i> *	4	10.18
<i>Gobiidae</i> *	7	24.19
<i>Homaloptera smithi</i> *	12	13.13
<i>Macrognaathus circumcinctus</i> *	12	13.34
<i>Mastacembelus armatus</i> *	2	11.91
<i>Mystacoleucus marginatus</i>	20	8.03
<i>Osteochilus vittatus</i>	12	2.2
<i>Poropuntius deauratus</i>	11	3.93
<i>Puntius binotatus</i>	9	3.74
<i>Schistura kohchangensis</i> *	4	12.12

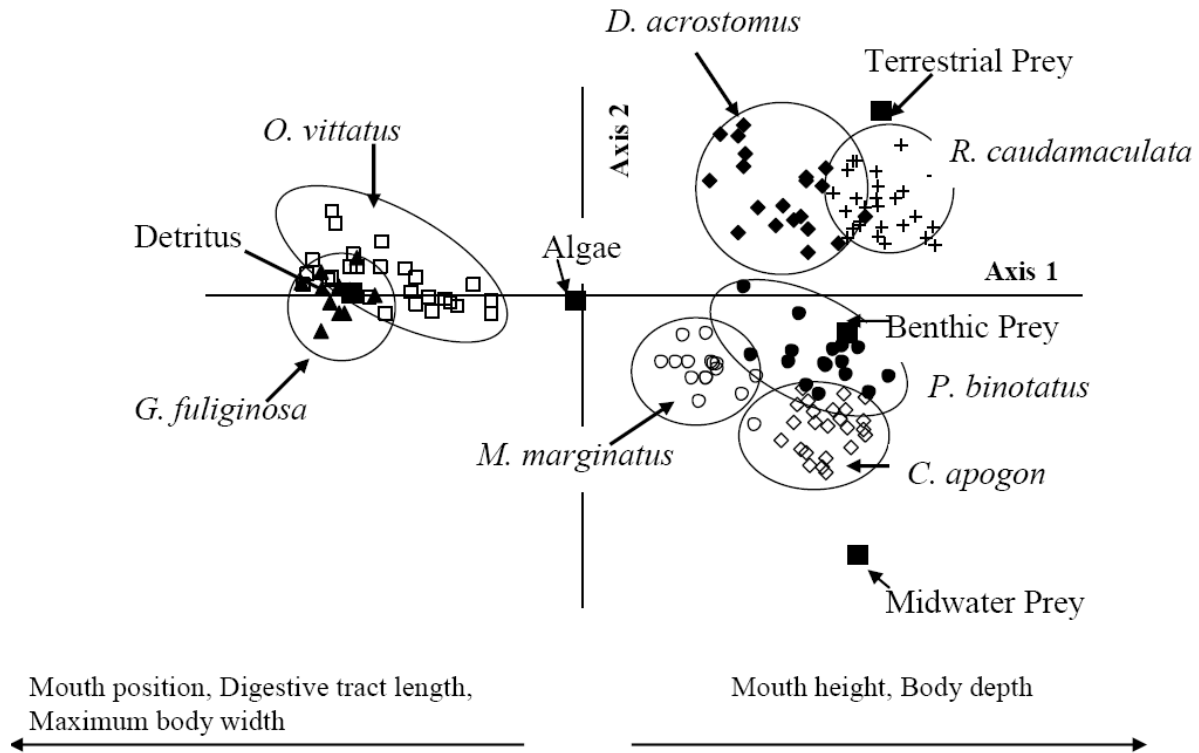


Figure 2. Canonical correspondence analysis (CCA) for seven species of cyprinids coexisting in the same environment and diet items projected onto the first two axes. The first axis was correlated positively with increasing mouth height and body depth and correlated negatively with increasing gut length, total length, body depth and mouth position. The second axis correlated positively with caudal peduncle width and depth. Species scores were obtained from CCA on the morphological attributes for each of the seven species as well as their diets, grouped into four categories, terrestrial, benthic, midwater, detritus and algae.

Thailand with many species coexisting in the same or similar habitats, sometimes with overlapping diets. Ward-Campbell (2004) examined the morphology and diet of seven species of cyprinids commonly found in the fast flowing or riffle regions of Thai rivers. She found a clear dietary separation of two of the species, *O. vittatus* and *Garra fuliginosa*, that feed mainly on detritus. Larvae of benthic macroinvertebrates, particularly mayflies or ephemeroptera constitute an important but not exclusive dietary component of the other five cyprinids. Other major prey items in the diets of *R. caudimaculata* and *Danio acrostomus* include terrestrial hymenoptera and, in *C. apogon*, include trichoptera and a midwater arachnida or mite. Ephemeroptera is also an important item in the diet of *M. marginatus*, however, it is supplemented with algae. *G. fuliginosa* and *O. vittatus* feed extensively on detritus and algae with detritus being more dominant in the diet of the latter species.

Important morphological characters associated with feeding, obtained with Canonical Correspondence Analysis (CCA) included position and height of mouth, length of digestive tract, body width and caudal peduncle width and depth. Digestive tract length was

positively associated with the presence of detritus in the diet and clearly separated *G. fuliginosa* and *O. vittatus* from the other five species (Fig. 2). Caudal peduncle length and depth on axis 2 was associated positively with the presence of terrestrial insects in the diet of *R. caudimaculata* and *D. acrostomus*. All species, with the exception of *O. vittatus* and *G. fuliginosa*, exhibited overlap with *M. marginatus*. The functional aspect of an increased digestive tract length in these species relates to the greater time and surface area required for digestion and absorption of nutrients from the comparatively poor food quality of detritus and algae.

An inferior or downturned mouth (Fig. 1), long digestive tract and wide body is of importance to species such as *O. vittatus* and *G. fuliginosa* that feed primarily on benthic detritus and algae attached to hard surfaces such as rocks and submerged wood. For those species feeding on invertebrates, a relatively short digestive tract, a more narrow body width and large mouth gape are of greater significance. *C. apogon* had the greatest body depth among the seven species. Body depth is associated with increased maneuverability, due to the reduction of the moment of inertia around the turning axis (Alexander, 1967). This is certain to be an advantage

to *C. apogon*, the only one of the seven species to consume mites. These invertebrates inhabit regions of marginal aquatic vegetation where maneuverability is a distinct advantage to the predator. Conversely, in the two detritivorous species, body depth was low relative to body width, sacrificing maneuverability, which is of less importance when feeding on algae and detritus from the substrate or other hard surfaces.

Superior or up-turned mouths are indicative of surface feeding. As fish feeding on terrestrial insects have less opportunity to meet their prey “head-on”, a greater mouth height enables fish to initially grasp prey from the surface. Terrestrial prey, of the order hymenoptera, are of greater importance in the diet of *D. acrostomus* than *R. caudimaculata*, and so it follows that this species should also have the most upwardly turned mouth of all seven species, followed by *R. caudimaculata*.

The diverse array and high abundance of cyprinids relative to other species in small rivers in central Thailand is, not surprisingly, consistent with that throughout their world distribution (Howes, 1991). In Thailand, >35% of the described freshwater fishes are cyprinids (Smith, 1945; Vidthayanon et al., 1997) with similar proportions reported elsewhere in Southeast Asia (Inger and Chin, 1962; Roberts, 1989; Zakaria-Ismail and Sabariah, 1994). Broad morphological, physiological and behavioral adaptations, described mostly for temperate cyprinid species, have allowed cyprinids to occupy physically, chemically and biologically diverse habitats. For example, some cyprinids such as the European *Carassius carassius* are tolerant of much lower ambient oxygen than are many other species, through adaptations in their hemoglobins or anaerobic capacity particularly when temperature is low (Blazka, 1958) allowing them to occupy habitats unavailable to many other species but where food may be abundant and, predators scarce. There is evidence among temperate and tropical cyprinids of genetic adaptations and phenotypic plasticity in growth rate as well as in their ultimate size, the former accommodating to cohabiting species, the latter, a range of habitats (Mann, 1991). Some species display adaptive modifications in their digestive tract such as a reduction of stomach size and increased intestine length allowing them to survive on the typically more abundant plant material when animal material is scarce (Persson, 1991). The success of cyprinids may also be linked with their wide range of family life histories and reproductive styles (Balon, 1975; Mills, 1991). Many cyprinids, particularly the smaller species, have high reproductive efforts (Gale and Buynak, 1982; Mills, 1991) contributing to their abundance and, perhaps easing colonization of unstable environments (Cambray and Bruton, 1985).

A classification of environmental factors based on

how they broadly impact fish physiology and behavior with respect to a species’ potential distribution and habitat was proposed by Fry (1947; 1971) and, elaborated by Brett (1979). Fry (1971) considered fish as an open system, walled from the external environment, and through which energy flows. Energy comes from the environment which also largely sets the conditions under which assimilated energy is used and includes both obligatory and voluntary activities, the former included largely within basal metabolism. Fish are able to regulate their activities with a portion of their assimilated energy, the extent seemingly being under genetic control (Perry et al., 2005). Fry (1947) classified the environment into five categories based on the manner in which factors affected fish metabolism, integrity and other activities. He called the categories lethal, controlling, limiting, masking and directive and stressed that the same factors can exercise their effect under more than a single category.

Environmental factors may act as a lethal agent at high and low values or concentrations (Howarth and Sprague, 1978; Jiraungkoorskul et al., 2007; Rani et al., 2011). Perhaps the best understood lethal factor is temperature, although disappointingly little information is available for Southeast Asian freshwater fishes. However, upper incipient lethal temperatures for several marine species from the Gulf of Thailand thermally acclimated to about 23°C have been reported as 32.0, 34.0 and 37.0°C for *Ostorhinchus aureus*, *Halichoeres nigrescens* and *Therapon theraps*, respectively (Menasveta, 1981). Similarly, lethal responses to heavy metals, xenobiotics and other substances are known to vary widely among species thereby restricting their distribution and habitat (Howarth and Sprague, 1978; Kumaraguru and Beamish, 1981; Prashanth et al., 2010).

Two other categories, controlling and limiting factors represent environmental identities that govern metabolic rate. For example, temperatures within the non lethal range for a species act as a controlling factor by governing both basal and maximum metabolic rates (Brett, 1979) while a limiting factor such as carbon dioxide (Beamish, 1964b) acts only on maximum metabolic rate within its non lethal range. A limiting factor may cause metabolic rate to change directly with its concentration in some species while in other species metabolic rate may become independent of concentration beyond a critical or threshold concentration. The difference between basal and maximum metabolic rates represents the amount of metabolism or energy available to a fish to perform its various activities beyond those required for basal responsibilities. When an environmental factor reduces a fish’s metabolism so also is its capacity to perform other activities. Controlling and

limiting factors are cumulative in restricting a species' capacity to perform within a habitat and, where the appropriate information is known, they can help to explain the occurrence, absence or substandard performance by a species within what may appear as a suitable environment or habitat (Beamish, 1964a; 1964b; Brett, 1979). It appears no quantitative measurements of any controlling or limiting factor have been made on any indigenous Southeast Asian species.

Directive and masking factors act to modify each others actions. For example swimming capacity of a euryhaline species such as *Oreochromis niloticus* may vary with salinity, acting as a masking factor, due to the metabolic cost of osmotic regulation imposed by salinity (Farmer and Beamish, 1969). Directive factors elicit a response by an organism to a gradient of a factor. For example a change in photoperiod may cause internal physiological changes that prepare fish for a seasonal change in ambient temperature.

The non lethal environment imposes its effects on fish by the cumulative action of each factor, acting directly or indirectly within each appropriate category, on performance or metabolism. Energy generated within the non lethal range of one or more environmental factors and expressed as total metabolism is used to fuel ecological, behavioral and physiological activities. However, an individual may be denied its total potential metabolism by the action of masking and directive factors. For example when ambient oxygen is below air saturation an individual's oxygen loading capacity may be reduced. The result of one or more masking and directive factors can seriously limit the energy available to an individual to perform its various activities such as growth and reproduction.

Fry (1947) called the difference between a fish's maximum and basal metabolism the metabolic scope for activity. Scopes for activity vary widely among species in relation to specific environmental factors clearly demonstrating additional reasons why fish locate in different habitats. Despite the utility of Fry's classification system in understanding abiotic factors it does not directly consider biotic factors and their interactive effects on fish. The lack of equivalent information for any of the freshwater fishes of Thailand greatly restricts understanding their environmental needs and essentially obfuscates its potential utility for measuring environmental health, habitat restoration and conservation.

Within regions, species diversity, abundance, and distributions are related to a multitude of factors including species morphology, behavior and physiology and, of course, the environment. The occurrence of species in a habitat represents the cumulative weight and interaction of all factors, abiotic and biotic. Obviously unraveling a species' optimum habitat is wrought with

difficulties and uncertainties. Dissection of factors in the field with a view of classifying conditions seems not to be possible or at the very least, practicable. For example, what might represent an optimal chemical and physical setting for a particular species or group of species may fail to consider other factors such as the presence of competing biota or absence of a suitable habitat for reproduction. It seems that only in a laboratory setting is it practicable to measure optimum abiotic or biotic characteristics of a habitat and even there with considerable difficulty. At this point it is appropriate to distinguish between preferences and species associations. Preference is a positive and defined response by a species, with repeatable precision, within a gradient of one or more tightly regulated factors, usually determined in the laboratory. Typically the response is conditioned by prior exposure to the factor or factors under consideration, a process commonly referred to as acclimation (Prosser *et al.*, 1957; Ferguson, 1958; Beamish and Mookherjii, 1964). Association in the present context refers to statistically significant conditions where a species is likely to occur within its geographical distribution based on extensive measurements from a broad range of habitats. It is, of course, not practicable to measure all physical, chemical and biological factors any of which may influence preference or association estimates.

A large number of surveys have been conducted in small and medium rivers throughout central Thailand. These surveys have been conducted using modern electrofishing equipment that causes minimum habitat damage and is relatively unbiased with respect to species capture efficiency unlike conventional traps, seines and other nets (Beamish *et al.*, 2006; Beamish and Sa-artrit, 2006; 2007; Tongnunui and Beamish, 2009). These surveys identified and enumerated all fish and measured a number of abiotic factors at each site and have displayed distinctive associations with the chemical and physical habitat

In western Thailand, species richness varies inversely with temperature and turbidity. The relationship between richness and temperature in western Thailand clearly indicates higher richness at the lower temperatures. Not surprisingly, the small suspended particles that collectively represent turbidity also have a negative impact on species abundance. Small particles in the water column can damage gill epithelia through abrasion, hindering respiration and ionic regulation. Vision may also be restricted, reducing prey capture efficiency and predator avoidance. Adsorption of potentially toxic heavy metals on suspended particles may represent a secondary concern related with turbidity (Lloyd, 1960).

Species richness in western Thailand is related

positively with dissolved oxygen, total iron, conductivity and substrate particle size. Overall most species seek high ambient oxygen concentrations. Species differ in their extraction efficiencies and metabolic requirements although such information is not available for Thai fishes. Habitat for some species is restricted to regions of comparatively high ambient oxygen concentrations although some species are found where ambient concentrations are quite low. The positive association between species richness and the other factors likely relates to their direct and indirect influence on productivity. For example, large particles provide habitat for benthic macroinvertebrates on which so many fish species feed.

Species distributions in small and medium rivers in western Thailand related to eleven physicochemical variables through canonical correspondence analysis (CCA; Fig. 3). The first and second axes present a positive gradient of temperature and conductivity. Alkalinity, oxygen, discharge, river width, water depth and pH loaded negatively on the second axis. Elevation, silica and substratum loaded negatively on the first axis. These are mostly specific to individuals or small numbers of species and are of fundamental importance to habitat

occurrence and survival. While, there are differences among individual species associations all significant factors were of similar overall importance, based on vector length.

The most abundant species were *D. acrostomus*, *M. marginatus*, *O. vittatus*, *R. caudimaculata* and *Puntius binotatus*. Of these, *P. binotatus* occurred in greatest abundance in rivers with a substrate of relatively small particles and of narrow width, shallow depth and low discharge and ambient oxygen. *D. acrostomus* was associated with habitats of high elevation, and low temperature, conductivity and alkalinity. In contrast, *M. marginatus* and *O. vittatus* were associated with habitats of low elevation, and high temperature, conductivity and alkalinity.

Other species were associated with a further array of habitats. For example, *Oxyeleotris marmorata*, *Trichopodus trichopterus*, *Pristolepis fasciata* and *Parambassis siamensis*, while never abundant, were associated with habitats where temperature, conductivity and alkalinity were comparatively high, elevation and silica low and with substrate mostly of sand and gravel. Some species were found where one or more factors were extremely low or high. For example

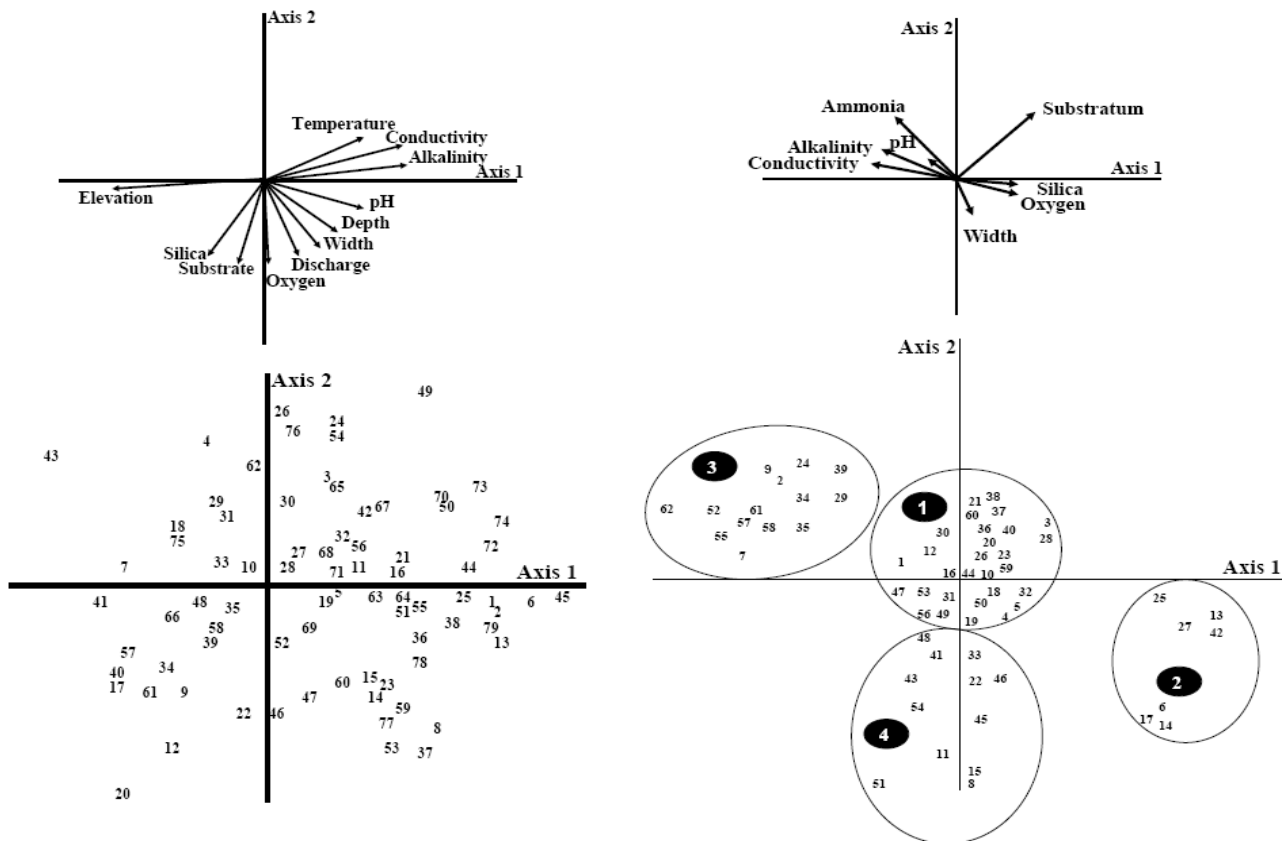


Figure 3. Distribution of species in rivers in western and southeastern Thailand with respect to significant environmental variables identified by canonical correspondence analysis. The upper panels illustrate the significant environmental variables on axes 1 and 2 and, for each, the vector length and direction. The lower panels locate species in relation to axes 1 and 2. Species are indicated by numbers (see Table 4; Tongnunui & Beamish 2009 and unpublished).

Lepidocephalichthys hasselti was associated with relatively high temperatures, low silica concentrations and a substrate of small particle sizes. *Garra cambodgiensis*, *Glyptothorax laosensis*, *Mystus singaringan* and *Hemimyzon* sp. occurred in relatively wide rivers where depth and discharge were well above average.

An association with silica was also important for some species, particularly for the relatively abundant *Neolissochilus stracheyi*, *G. fuliginosa*, *Balitora* sp. and *Schistura vinciguerrae* and may relate to its importance in diatom ontogeny and this organism's importance as a food source for benthic macroinvertebrates on which many fishes feed (Ward-Campbell et al., 2005; Winkelmann et al., 2011). Diatoms are probably also of direct dietary importance for some species (Schriver et al., 1995).

Elevation was an important factor with few species occurring at high elevations. *D. acrostomus* was associated with elevations to approximately 700 m and, again, relatively high discharge. This laterally compressed species is not adapted for station holding but is considered morphologically adapted for fast swimming (Rainboth, 1996). *Schistura aurantiaca* (Plongsesthee et al., 2011) and *Schistura balteata* are also associated with high elevations with both morphologically well adapted for station holding in swift water currents.

In a companion study, conducted at 95 sites on small rivers in southeastern Thailand, Tongnunui and Beamish (2009) found species richness to be lower than in the west with the percentage similarity of fishes at only 23%. Not surprisingly the significant environmental factors also differed between the two regions Ammonia was a significant factor in the southeast but not west in accord with the greater agricultural and urban activity in the former region. Discharge, elevation and temperature did not relate significantly with species distribution and abundance in the southeast, in contrast to their greater importance in the west. Species in the southeast were distributed clearly within four groups with respect to the significant habitat characteristics (Fig. 3). The most speciose group contained 29 species that were associated with average values for the significant environmental factors and consisted of five of the most abundant species, *Danio albolineatus*, *P. binotatus*, *Rasbora paviana*, *D. pusilla* and *M. marginatus*. The 12 species in group 4 occurred in low abundance and were associated with rather wide river sites but otherwise the environmental conditions were not unlike those in group 1. Group 2 contained only seven species all in low abundance and intolerant of poor water quality, being sensitive to low dissolved oxygen and high ammonia, alkalinity and pH. These characteristics provide a mechanism from which to assess habitat health in accord with a number of indices that are currently in

use elsewhere Sites in the fourth group had the highest concentrations of ammonia, alkalinity, conductivity, and pH along with the lowest concentrations of dissolved oxygen and silica. This group contained fourteen species with five, *Channa striata*, *Esomus metallicus*, *O. niloticus*, *Trichopsis vittata* and *T. trichopterus*, being moderate to quite abundant and widespread.

The apparent tolerance of some fish species to ammonia is of particular interest. Ammonia is usually regarded as highly toxic to fish, particularly the undissociated form at high pH and low dissolved oxygen. Tolerance to ammonia is thought to vary among species and to increase with exposure to sublethal concentrations (Wang and Walsh, 2000) but supportive evidence is scarce. Ammonia tolerance is facilitated in some species including *Clarias batrachus* and *Anabas testudineus* through branchial and cutaneous chloride excretory cells, conversion of ammonia to urea or to non-essential free amino acids and muscle storage (Jow et al., 1999; Lim et al., 2001; Saha et al., 2002; Tay et al., 2006).

Oxygen's low solubility in water especially at high temperatures causes it to be in short supply even at air saturation and to impose a metabolic hardship. The metabolic need for oxygen and the adaptations associated with its extraction varies widely among those species that have been examined. Gill surface area across which respiratory gases are exchanged has been reported by some to be relatively larger among active than sedentary species (Hughes, 1966) but more recently this appears to be equivocal, particularly in freshwater fishes. Other adaptations include accessory respiratory organs or suprabranchial chambers and cutaneous respiration (Lim et al., 2001; Munshi et al., 2005). Of the oxygen-tolerant species in the southeast Thailand study, the anabantids, *T. trichopterus* and *T. vittatus*, were the most abundant species. Presumably they have gained considerable independence from low oxygen concentrations through their lung-like labyrinth organs. *C. striata* and *A. testudineus*, both with respiratory assistance from suprabranchial organs were also in this group although not in high abundance. It is interesting that two of the three non-indigenous species in this study, *O. niloticus* and *Poecilia reticulata*, are in this group, indicating their capacity to tolerate unfavorable conditions that undoubtedly has contributed to their success as invader species.

In summary, distributions of Thailand's freshwater fish species can be expected to relate directly to their sustainable environmental needs with those for each species being distinctive, even unique. Understanding the environmental and biological needs of the rich freshwater fish fauna will be a formidable task. For many, probably most, species these requirements are

Table 4. Species identity of numbers (ID) used in Fig. 3. Western and southeastern regions are indicated by W and SE, respectively.

Species	ID		Species	ID	
	W	SE		W	SE
<i>Acanthocobitis botia</i>	32		<i>Mystus mysticetus</i>		34
<i>Acanthocobitis zonalternan</i>	33	24	<i>Mystus singaringan</i>	53	
<i>Acanthopsis</i> sp.1	45	29	<i>Nandus nebulosus</i>		49
<i>Acanthopsis</i> sp.2		30	<i>Nemacheilus masyae</i>	38	26
<i>Amblyceps mangois</i>		38	<i>Nemacheilus platiceps</i>		27
<i>Amblyceps mucronatum</i>	58		<i>Neolissochilus blanci</i>		11
<i>Anabas testudineus</i>		55	<i>Neolissochilus soroides</i>	18	
<i>Badis siamensis</i>	71		<i>Neolissochilus stracheyi</i>	17	
<i>Balitora</i> sp.	34		<i>Notopterus notopterus</i>	2	1
<i>Barbonymus gonionotus</i>	3	2	<i>Ompok bimaculatus</i>	56	36
<i>Batasio fluviatilis</i>	52		<i>Opsarius koratensis</i>	19	
<i>Betta prima</i>		56	<i>Opsarius pulchellus</i>	20	
<i>Channa gachua</i>	75	59	<i>Oreochromis mossambicus</i>		51
<i>Channa lucius</i>	76	60	<i>Oreochromis niloticus</i>		52
<i>Channa micropeltes</i>	77		<i>Osteochilus lini</i>		13
<i>Channa striata</i>	78	61	<i>Osteochilus vittatus</i>	21	12
<i>Chitala ornata</i>	1		<i>Osteochilus waandersii</i>	22	
<i>Clarias batrachus</i>	64	39	<i>Oxyeleotris marmorata</i>	73	53
<i>Cyclocheilichthys apogon</i>	5	4	<i>Pangio anguillaris</i>	50	
<i>Cyclocheilichthys armatus</i>	6	5	<i>Parachela maculicauda</i>	23	14
<i>Cyclocheilichthys heteronema</i>		6	<i>Parambassis siamensis</i>	70	48
<i>Danio acrostomus</i>	7		<i>Poecilia reticulata</i>		62
<i>Danio albolineatus</i>	4	3	<i>Poropuntius deauratus</i>	24	15
<i>Dermogenys pusillus</i>	63	40	<i>Pristolepis fasciata</i>	72	50
<i>Doryichthys boaja</i>		42	<i>Pseudomystus siamensis</i>	51	33
<i>Doryichthys martensii</i>		43	<i>Pterocryptis cochinchinensis</i>	57	37
<i>Esomus metallicus</i>		7	<i>Puntius binotatus</i>	29	20
<i>Garra cambodgiensis</i>	8		<i>Puntius brevis</i>	25	
<i>Garra fuliginosa</i>	9		<i>Puntius lateristriga</i>		21
<i>Garra</i> sp.	10		<i>Puntius masyai</i>	26	
<i>Glyptothorax laosensis</i>	59		<i>Puntius orphoides</i>	30	22
<i>Glyptothorax major</i>	60		<i>Puntius partipentozona</i>		23
<i>Glyptothorax</i> sp.	61		<i>Puntius stoliczkanus</i>	31	
<i>Hampala macrolepidota</i>	11	8	<i>Rasbora borapetensis</i>	27	16
<i>Hemibagrus nemurus</i>	55	35	<i>Rasbora caudimaculata</i>	28	
<i>Hemimyzon</i> sp.	37		<i>Rasbora dusonensis</i>		17
<i>Homaloptera smithi</i>	35	25	<i>Rasbora paviana</i>		18
<i>Homaloptera</i> sp.	36		<i>Rasbora trilineata</i>		19
<i>Labiobarbus leptocheilus</i>	13	9	<i>Rhinogobius</i> sp.		54
<i>Labiobarbus siamensis</i>	12		<i>Schistura aurantiaca</i>	41	
<i>Lepidocephalichthys berdmorei</i>	48	31	<i>Schistura desmotes</i>	39	
<i>Lepidocephalichthys hasselti</i>	49	32	<i>Schistura kohchangensis</i>	28	
<i>Lobocheilos quadrilineatus</i>	14		<i>Schistura</i> sp.2	42	
<i>Lobocheilos rhabdoura</i>	15		<i>Schistura</i> sp.3	43	
<i>Macrognaathus circumcinctus</i>	66	45	<i>Schistura vinciguerrae</i>	40	
<i>Macrognaathus semiocellatus</i>	68		<i>Syncrossus beauforti</i>	46	
<i>Macrognaathus siamensis</i>		46	<i>Tetraodon suvattii</i>	79	
<i>Macrognaathus</i> sp.	67		<i>Trichopodus trichopterus</i>	74	57
<i>Mastacembelus armatus</i>	69	47	<i>Trichopsis vittata</i>		58
<i>Monopterus albus</i>	65	44	<i>Tuberoschistura baenzigeri</i>	44	
<i>Mystacoleucus marginatus</i>	16	10	<i>Xenentodon cancila</i>	62	41
<i>Mystus cavasius</i>	54		<i>Yasuhikotakia morleti</i>	47	

likely also to be temporally dynamic. However, few geographic regions of the world are blessed with such a taxonomically and esthetically rich and valuable resource, certainly worthy of conservation. However, without improved ecological understanding of Thai rivers and their inhabitants it is unlikely that any amount of rhetoric or conservation patronage will stem species extinctions. The conduct of life sustaining activities in rivers is shaped by favorable environmental conditions. Conditions important to individual species, their abundance and distribution need to be understood and maintained if Thailand's rich fish fauna is to persist but the investment is worthwhile and the dividends likely to be generous.

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