

## SPECIES DIVERSITY, ABUNDANCE AND ENVIRONMENTAL ASSOCIATIONS OF LOACHES (NEMACHEILIDAE AND BALITORIDAE) IN THE CENTRAL REGION OF THAILAND

*F. William H. Beamish<sup>1</sup> and Rungthip Plongsesthee<sup>2</sup>*

### ABSTRACT

Environmental associations favorable for benthic loaches within the families Nemacheilidae and Balitoridae were the objective of this study that was conducted at 160 sites within five river systems: Southeastern, Mekong, Chao Phraya, Maeklong and Peninsula, in the central region of Thailand. Loaches in this study represented seven genera and 19 species; one each of *Tuberoschistura* and *Homalopteroides*, two *Acanthocobitis*, *Homaloptera* and *Pseudohomaloptera*, four *Nemacheilus* and seven *Schistura*. Fewest species ( $n = 3$ ) were found in the Southeastern system with four species from each of the Mekong, Chao Phraya and Peninsula systems and 13 species in the Maeklong system. Species diversity within all systems was greatest for *Schistura*. Species and relative abundance of all fishes and of loaches varied directly and inversely, respectively, with river order for the two rivers in which this was examined. Abundances varied widely among species and sites with the most abundant species being *Schistura aurantiaca*, *Schistura* cf. *sexcauda*, *Homalopteroides smithi* and *Acanthocobitis zonalternans*. Species' distributions across all five river systems examined by canonical correlation analysis (CCA) varied significantly with six environmental variables. Of greatest significance were elevation and water temperature followed by water velocity, ambient oxygen, pH and Silica. Several adaptations for co-existence in fast flowing water are identified and discussed.

Keywords: Balitoridae, Nemacheilidae, ecology, environment, environmental associations

### INTRODUCTION

Landscapes provide environmental variation that, along with biotic interactions, contribute to the distribution of freshwater fishes found in rivers. Fishes live not in random groupings but in structured associations held together by favorable environmental characteristics (ALLAN, 2004; HAYES *ET AL.*, 2006). In some cases a small number of environmental factors seem to exercise a strong influence on association structure while in others it is related to a wider range of factors (ROBINSON & TONN, 1989; EDDS, 1993). Often, it is assumed that structure and pattern in species assemblages originate from niche specialization, functional differences in the way species partition-limiting resources and respond to gradients in environmental and microclimatic conditions. Recently, this view has been challenged by neutral theory which considers that trophically similar species are functionally equivalent and patterns in community or assemblage organization can be accounted for by unusual or random processes (HUBBELL, 2001; 2005; STOKES & ARCHER, 2010). The current debate on these contrasting views suggests

---

<sup>1</sup> Environmental Science Program, Faculty of Science, Burapha University, Bangsaen, Chonburi, 20131, Thailand.  
E-mail: billbeamish@hotmail.com

<sup>2</sup> Deceased, July 16, 2014

Received 13 August 2014; accepted 9 February 2015

that neither is sufficiently broad to account for the full range of observed patterns in natural communities (MCGILL, 2003; VOLKOV *ET AL.*, 2007). Additionally, it appears that high diversity of fishes in some tropical environments may be maintained not so much by extreme specializations as by frequent occurrences of restricted environmental disturbances that, in concert with species specific vulnerabilities, prevent species from reaching equilibrium (CONNELL, 1978; MOYLE & SENANAYAKE, 1984; WATSON & BALON, 1984).

The importance of species-specific environmental factors to fish distribution has been demonstrated in temperate regions (JACKSON *ET AL.*, 2001) but by comparison these relationships have been largely ignored in species-rich tropical regions, particularly Southeast Asia (MAGURRAN *ET AL.*, 2011; KHACHONPISITSAK, 2012). The high diversity in Southeast Asia likely relates in part to the time over which specific morphologies and processes have had to evolve (BEAUFORT, 1951). On a more local scale, environmental factors such as habitat size and diversity are among the variables thought to be important (GORMAN & KARR, 1978; ANGERMEIER & SCHLOSSER, 1989; HUGUENY, 1990; BEAMISH *ET AL.*, 2005). Chemical characteristics are known also to have an important influence (FRY, 1971).

Loaches in the species-rich families Nemacheilidae and Balitoridae live mostly in close association with the substrate of small fast flowing rivers in Asia and Europe and can be abundant (KOTTELAT, 1990, 2001, 2012, 2013). The current study expands an earlier study (BEAMISH *ET AL.*, 2008) in terms of site numbers, species identity and adaptations for co-existence and was undertaken to better understand their occurrence and co-existence in rivers throughout Thailand.

## STUDY AREA

Small rivers representing first- to fourth-order tributaries (STRAHLER, 1952) of larger rivers were sampled in the central region of Thailand between latitudes 10° 30' and 15° 30' North and longitudes 98° and 102° 30' East (Figure 1). Sites ( $n = 160$ ) were sampled from rivers in five river systems following KOTTELAT (1989) except boundaries of the MaeKlong and Southeastern systems following ABELL *ET AL.*, (2008) (Figure 1), Mekong ( $n = 2$ ), Chao Phraya ( $n = 50$ ), Southeastern ( $n = 5$ ), MaeKlong ( $n = 92$ ) and Peninsula ( $n = 11$ ) between October 2000 and October 2010 (See Appendix 1 for details of each site). Number of sites was highest in the MaeKlong and Chao Phraya systems and lowest in the Mekong and Southeastern systems. Sites were selected as representative of landscapes in the central region of Thailand and provided information on environmental factors and the presence and abundance of fish species. Features of particular interest were elevation, canopy, river width, discharge and velocity in addition to water chemistry, reflecting basin geology. Length of most landscape sites was approximately 30 times the estimated average width to increase the probability of capturing all loaches and other species present (LYONS, 1992). Typically, a site was mostly riffles but also contained at least one small pool. Within landscapes, sites were chosen from road accessible locations ranging from remote, heavily forested and sparsely inhabited to lightly settled areas in which modest agriculture occurred to more heavily farmed or urban areas. Site selection presented some problems as some waterways were accessible only during a small part of the dry season, especially those at high elevations. Sites were not sampled closer than 150 m from the nearest bridge to avoid potential structure bias.

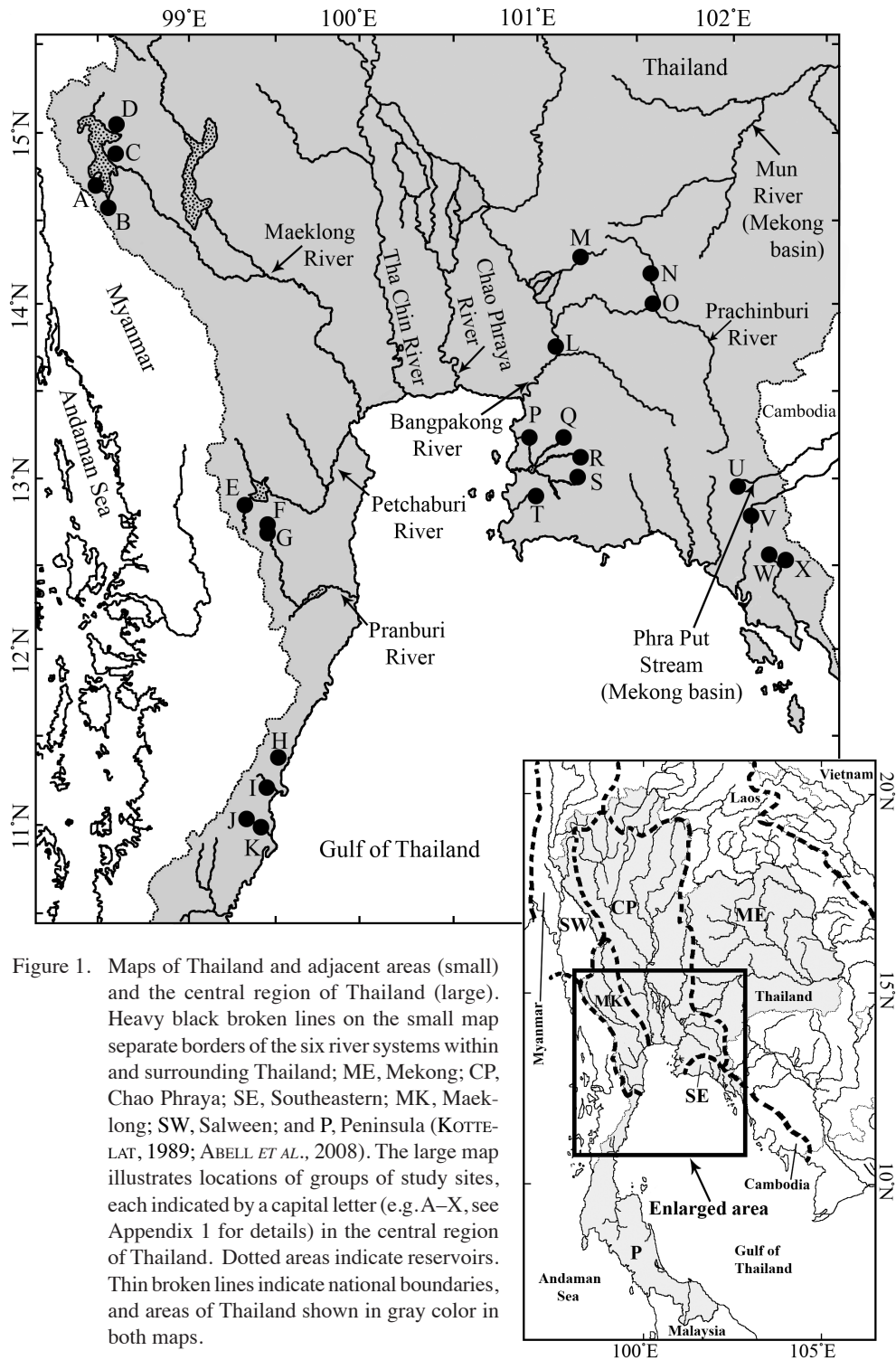


Figure 1. Maps of Thailand and adjacent areas (small) and the central region of Thailand (large). Heavy black broken lines on the small map separate borders of the six river systems within and surrounding Thailand; ME, Mekong; CP, Chao Phraya; SE, Southeastern; MK, Maeklong; SW, Salween; and P, Peninsula (KOTTELAT, 1989; ABELL *ET AL.*, 2008). The large map illustrates locations of groups of study sites, each indicated by a capital letter (e.g. A–X, see Appendix 1 for details) in the central region of Thailand. Dotted areas indicate reservoirs. Thin broken lines indicate national boundaries, and areas of Thailand shown in gray color in both maps.

## METHODS

Site measurements included temperature ( $\pm 0.3^\circ\text{C}$ ), average width ( $\pm 0.1$  m), depth ( $\pm 1$  cm) and mid depth velocity ( $\pm 1$  cm/s), the latter three being used to calculate discharge (l/s). Depth of each site was the mean of 3–5 measurements made at approximately equal intervals across the river. Velocity was measured at the surface and adjusted to represent the mean flow rate (GILLER & MALMQVIST, 1998). Turbidity (NTU), pH ( $\pm 0.1$  unit) and dissolved oxygen ( $\pm 0.1$  mg/l) were measured with regularly calibrated meters. Ammonia (mg  $\text{NH}_3\text{N/l}$ ) was measured by the salicylate method, nitrate (mg  $\text{NO}_3\text{N/l}$ ), by the cadmium reduction method, total iron (mg Fe/l) by the Ferro Ver method, alkalinity (as  $\text{CaCO}_3$  mg/l, pH 4.5) using the sulfuric acid titration method, silica (mg  $\text{SiO}_2\text{/l}$ ) using the heteropoly method and true color (platinum-cobalt color units) by the platinum-cobalt method (AMERICAN PUBLIC HEALTH ASSOCIATION, 1992). Elevation was measured by GPS ( $\pm <10\text{m}$ ). Sites were sampled throughout the year although season was not included as a variable. An earlier study by BEAMISH *ET AL.* (2005) indicated seasonal changes in fish abundances and assemblage similarity from several streams in central Thailand to vary inversely with discharge, which was included as a variable in this study.

A substrate sample was collected at each site with a hand-held acrylic corer (5 cm inner diameter) to a depth of  $10 \pm 3$  cm. Particles on the substrate surface larger than the diameter of corer were removed and included in the sample with adjustment for their size relative to total sample weight. Samples were air-dried and sieved to determine particle size distribution by weight. Six size categories were adopted from the Wentworth scale (GILLER & MALMQVIST, 1998),  $> 150$  mm (boulder to large cobble), 150–60.1 mm (large cobble to large pebble), 60–5.1 mm (large pebble to coarse gravel), 5–3.1 mm (medium to fine gravel),  $< 0.5$  mm (medium sand to silt) and the mean particle size was calculated. Substrate for each site was coded into one of six categories based on mean particle size with 1 being the smallest and 6, the largest. Substrate at a few sites was solid or almost solid bedrock and these were coded as 7.

Fishes were captured with a Smith-Root (Vancouver, WA, USA), model 15D backpack electrofisher with variable output voltage (100–1100 V), pulse width (1–120 Hz) and frequency (100 ms–8 ms). The anode was fitted with a 280 mm diameter ring. Output voltage was varied inversely with water conductivity and, for the sites in this study, was mostly between 200 and 600 V, in combination with a wave width of 60 Hz and frequencies of 1–4 ms. Settings were made, based on experience, to reduce damage to fish. Periodically small numbers of captured fishes were returned to the laboratory and held in aquaria where they exhibited no deleterious effects from electrofishing over periods of up to two years.

Seines with 3 mm mesh size were installed across the upper and lower limits of a site and their groundlines massed with rocks to reduce the probability of emigration from or immigration into the sample area. A site was electrofished by moving in a zigzag pattern from one retaining net to the other, beginning downstream or upstream based on visibility, water depth and velocity. Relative capture efficiency between upstream and downstream direction of electrofishing was compared within several larger sites and not found to differ significantly (ANCOVA,  $p < 0.05$ ). We captured few fishes of any species  $< 20$  mm in total length which was assumed to be the lower limit of vulnerability to the sampling procedure.

Fish were anaesthetized in methane tricaine sulfonate (150 mg/l) after capture. Those that could confidently be identified were enumerated and, after recovery, released downstream from the site. When fish could not be identified in the field, a few specimens were killed by

an overdose of anesthetic and preserved first in 10% formalin for 7 days and then in 70% ethanol for subsequent identification and permanent preservation. Fishes were identified from a number of sources including: SMITH, 1945; KOTTELAT, 1984, 1988, 1989, 1990, 2000, 2001; PLONGSESTHEE *ET AL.*, 2011, 2013; RAINBOTH, 1996; RANDALL & PAGE, 2012, 2015; ROBERTS, 1982; and others. One species collected in this study from the Thong Pha Phum region of Kanchanaburi Province in the Maeklong system was likely misidentified as *Homalopteroides smithi* rather than by its probable correct identity, *Homalopteroides modestus*. Confirmation was not possible as specimens were not preserved for validation. Thus, for this report any individuals of the apparently scarce *H. modestus* from rivers in Thong Pha Phum were grouped under *H. smithi*. The classification system of NELSON (2006) was followed along with names given in Catalog of Fishes (ESCHMEYER, 2015).

Total relative abundances of each and all species within a site were calculated by the maximum likelihood technique based on three to four passes at each site (CARLE & STRAUB, 1978). When species numbers were small and not amenable to this technique, a conversion factor consisting of the total abundance estimate divided by total number of fish caught was applied to adjust numbers of each species captured.

Associations among fish species, their abundance arithmetically adjusted to a common river site area of 100 m<sup>2</sup>, and physicochemical variables were considered using canonical correspondence analysis (CCA; Program CANOCO Version 4.55 October 2006 – written by Cajo J. F. Ter Braak (C) 1988–2006. Biometric-quantitative methods in the life and earth sciences. Plant Research International, Wageningen University and Research Centre Box 100, 6700 AC. Wageningen, Netherlands. CCA was employed to identify all significant environmental characteristics for species and environmental variables. These relationships were described in an ordination diagram in which species are represented by coded numbers and physicochemical variables by vectors. Statistical significance of the Monte Carlo test (1,000 permutations) on the relationship between species, their abundance and environmental factors was accepted at  $p < 0.05$ . Data were not transformed for CCA.

## RESULTS

In the Maeklong River system, 13 loach species (Nemacheilidae, 4 species; Balitoridae, 9 species) were found along with 71 other species from 92 sites. Longitudinal distribution of species in each of two rivers in this system, Khayeng (35 sites) and Pracham Mai (19 sites), showed numbers of loach species and those of all other fishes to be highest among the first order dendritic headwater streams and to decline as river order increased (Table 1). In contrast, relative abundance of loaches and of all other species, as number of fish/100 m<sup>2</sup>, increased directly with river order (Table 1). In each river, nine species of loaches were captured, with seven common to both waterways, Nemacheilidae: *Acanthocobitis zonalternans*, *Nemacheilus pallidus*, *Schistura aurantiaca*, *Schistura cf. mahnerti*, *Schistura cf. sexcauda* and *Tuberoschistura baenzigeri*; Balitoridae: *Homalopteroides smithi*, (Table 2). *Acanthocobitis botia* and *Schistura balteata* were found only in the Pracham Mai River and *Homaloptera bilineata* (Balitoridae) and *Pseudohomaloptera sexmaculata* (Balitoridae) only in the Khayeng River. Comparative relative abundances were similar for all species present in both rivers except *S. cf. sexcauda* that was considerably the more abundant in the Khayeng River. The least abundant species found in both rivers were *S. cf. mahnerti* and *T. baenzigeri*. There was a

Table 1. Mean ( $\pm$  standard deviation) number of species and relative abundance (number/100 m<sup>2</sup>) for all fish species and for loaches by river order for the Khayeng and Pracham Mai Rivers in the Maeklong system.

	Khayeng River (35 sites)		Pracham Mai River (19 sites)	
	Abundance Mean ( $\pm$ SD)		Abundance Mean ( $\pm$ SD)	
	Species	Individual fish	Species	Individual fish
All fish spp.				
Order 1	10.2 ( $\pm$ 5.0)	262 ( $\pm$ 203)	8.6 ( $\pm$ 6.8)	273 ( $\pm$ 98)
Order 2	16.5 ( $\pm$ 3.5)	257 ( $\pm$ 255)	16.0 ( $\pm$ 0)	115 ( $\pm$ 261)
Order 3	15.9 ( $\pm$ 4.9)	160 ( $\pm$ 66)	15.3 ( $\pm$ 1.2)	246 ( $\pm$ 50)
Order 4	23.5 ( $\pm$ 14.1)	117 ( $\pm$ 80)	26.0 ( $\pm$ 0)	50 ( $\pm$ 50)
Loach spp.				
Order 1	1.6 ( $\pm$ 1.5)	15 ( $\pm$ 19)	2.2 ( $\pm$ 1.5)	35 ( $\pm$ 23)
Order 2	3.0 ( $\pm$ 1.4)	16 ( $\pm$ 13)	4.5 ( $\pm$ 0.7)	29 ( $\pm$ 22)
Order 3	3.7 ( $\pm$ 1.9)	44 ( $\pm$ 36)	5.0 ( $\pm$ 1.0)	30 ( $\pm$ 3)
Order 4	5.3 ( $\pm$ 2.2)	15 ( $\pm$ 8)	5.0 ( $\pm$ 0)	6 ( $\pm$ 1)

Table 2. Range and mean relative abundance of loaches by species in the Khayeng and Pracham Mai Rivers in the Maeklong River system in western Thailand. SD indicates standard deviation of mean values.

Species	Abundance, number/100 m <sup>2</sup>			
	Khayeng (35 sites)		Pracham Mai (19 sites)	
	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD
<i>Acanthocobitis botia</i>	0	0	0–10.0	1.2 $\pm$ 2.8
<i>Acanthocobitis zonalternans</i>	0–26.5	5.0 $\pm$ 7.4	0–22.5	4.4 $\pm$ 7.7
<i>Nemacheilus pallidus</i>	0–6.0	0.5 $\pm$ 1.2	0–23.0	1.8 $\pm$ 5.3
<i>Schistura aurantiaca</i>	0–96.5	9.0 $\pm$ 19.4	0–46.6	7.6 $\pm$ 12.7
<i>Schistura balteata</i>	0	0	0–2.5	0.3 $\pm$ 0.8
<i>Schistura cf. mahnerti</i>	0–13.1	0.8 $\pm$ 2.3	0–2.9	0.2 $\pm$ 0.7
<i>Schistura cf. sexcauda</i>	0–119.0	14.8 $\pm$ 23.9	0–18.7	4.0 $\pm$ 5.6
<i>Tuberoschistura baenzigeri</i>	0–2.0	0.1 $\pm$ 0.4	0–0.9	0.1 $\pm$ 0.2
<i>Homaloptera bilineata</i>	0–1.5	< 0.1 $\pm$ 0.3	0	0
<i>Homalopteroides smithi</i>	0–28.5	5.2 $\pm$ 7.1	0–26.4	3.3 $\pm$ 6.9
<i>Pseudohomaloptera sexmaculata</i>	0–29.4	4.9 $\pm$ 8.0	0	0

suggestion that *A. zonalternans*, *S. aurantiaca* and *T. baezigneri* occurred in larger numbers at the lower order sites whereas *H. smithi*, *S. cf. sexcauda*, *P. sexmaculata* and, perhaps *N. pallidus* were the more abundant at the higher order sites. However, abundance by species varied considerably among orders, blurring patterns, if any occurred. Physical and chemical parameters were quite variable among sites but with similar mean values except for alkalinity which was the higher in the Khayeng River and turbidity and color which were higher in the Pracham Mai River (Table 3).

Environmental conditions among the five river systems varied considerably, with sites in the western region (the Maeklong system) generally a few degrees cooler and higher in pH and alkalinity than in other systems (Table 4). Water in the central region was, on average, highest in ammonia, nitrate, total iron, color and turbidity. Physical habitat characteristics including canopy, discharge, water velocity and, to a lesser extent, substrate were relatively uniform among sites. Elevation range was greatest and least in Maeklong and Peninsula systems, respectively, and similar among sites in Southeastern, the Mekong and Chao Phraya systems. Site values for elevation, width, depth, color and turbidity were unimodal in distribution, mostly favoring lower values. Temperature was also unimodal in distribution but favored relatively high values. Chemical variables also were unimodal among sites. Modal maxima for ammonia, nitrate, iron and alkalinity occurred at comparatively low values, those for silica and pH at intermediate values and those for dissolved oxygen at high concentrations, relative to air saturation.

Table 3. Range, mean and standard deviation (SD) of physicochemical factors for 35 sites in the Khayeng River and 19 sites in the Pracham Mai River, both tributaries to the Maeklong River in western Thailand.

	Khayeng		Pracham Mai	
	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD
Elevation (m)	165–308	222 $\pm$ 59	169–853	318 $\pm$ 212
Width (m)	0.7–10.3	5.8 $\pm$ 2.5	1.5–5.5	8.0 $\pm$ 6.6
Depth (cm)	5–74	27 $\pm$ 17	10–49	23 $\pm$ 13
Velocity (cm/s)	5–83	32 $\pm$ 22	8–55	36 $\pm$ 16
Canopy (%)	0–90	30 $\pm$ 27	0–90	41 $\pm$ 31
Substrate (Coded values)	2–7	5 $\pm$ 1	2–7	5 $\pm$ 2
Temperature ( $^{\circ}$ C)	17.3–28.0	24.5 $\pm$ 2.3	21.8–27.3	24.4 $\pm$ 1.6
Turbidity (NTU)	2–56	9 $\pm$ 12	2–800	89 $\pm$ 251
Color (CU)	0–99	28 $\pm$ 44	0–550	70 $\pm$ 171
pH	6.5–8.3	7.6 $\pm$ 0.5	6.3–8.2	7.6 $\pm$ 0.5
Oxygen (mg/l)	4.5–8.7	7.5 $\pm$ 0.9	5.9–8.9	7.9 $\pm$ 0.8
Ammonia (mg NH <sub>3</sub> N/l)	0–0.05	0	< 0.01–0.08	< 0.01 $\pm$ < 0.01
Nitrate (mg NO <sub>3</sub> N/l)	0–4.3	1.3 $\pm$ 1.3	0–1.7	0.6 $\pm$ 0.6
Iron (mg Fe/l)	0.1–0.8	0.3 $\pm$ 0.2	0.0–0.79	0.2 $\pm$ 0.2
Silica (mg SiO <sub>2</sub> /l)	6.5–31.8	19.9 $\pm$ 7.7	6.6–41.6	20.0 $\pm$ 10.6
Alkalinity (mg CaCO <sub>3</sub> /l)	18–381	135 $\pm$ 99	10–200	56 $\pm$ 53



Table 4. Range, mean and standard deviation (SD) of physicochemical factors for 160 sites in five river systems in the central region of Thailand.

	Southeastern (N = 5)		Mekong (N = 2)		Chao Phraya (N = 50)		Peninsula (N = 11)		Maeklong (N = 92)	
	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Mean $\pm$ SD
Elevation (m)	112-130	129 $\pm$ 17	145-156	151 $\pm$ 8	50-112	81 $\pm$ 27	50-50	50 $\pm$ 0	50-853	240 $\pm$ 145
Width (m)	3.0-10.0	5.0 $\pm$ 3.3	5.4-5.5	5.0 $\pm$ 0.1	1.0-25.5	4.0 $\pm$ 4.0	1.7-25.0	7.0 $\pm$ 6.3	0.7-18.7	6.0 $\pm$ 4.1
Depth (cm)	19-52	33 $\pm$ 12	17-39	28 $\pm$ 16	5-83	23 $\pm$ 14	11-38	27 $\pm$ 8	5-74	26 $\pm$ 15
Velocity (cm/s)	24-28	27 $\pm$ 2	50-60	55 $\pm$ 7	0-80	27 $\pm$ 18	15-67	39 $\pm$ 17	5-97	36 $\pm$ 21
Discharge (l/s)	20-740	332 $\pm$ 262	454-1254	854 $\pm$ 566	0-2777	263 $\pm$ 458	80-1174	559 $\pm$ 381	6-5491	637 $\pm$ 913
Canopy (%)	0-50	28 $\pm$ 19	10-70	40 $\pm$ 42	0-100	40 $\pm$ 26	0-80	30 $\pm$ 31	0-95	40 $\pm$ 27
Substrate (Coded)	0-7	4 $\pm$ 4	6-7	7 $\pm$ 1	0-7	4 $\pm$ 1	0-7	4 $\pm$ 2	0-7	5 $\pm$ 2
Temperature (°C)	26.5-28.5	27.1 $\pm$ 0.8	29.2-32.6	30.9 $\pm$ 2.4	22.3-31.4	26.0 $\pm$ 1.9	24.1-30.3	27.3 $\pm$ 2.1	17.3-28.8	24.5 $\pm$ 2.3
Turbidity (NTU)	1-5	2 $\pm$ 2	6-7	7 $\pm$ 1	1-439	220 $\pm$ 73	4-27	7 $\pm$ 7	0-800	26 $\pm$ 117
Colour (CU)	1-27	15 $\pm$ 10	51-53	52 $\pm$ 1	12-550	281 $\pm$ 107	27-104	57 $\pm$ 27	0-550	37 $\pm$ 86
pH	6.8-7.3	7.1 $\pm$ 0.2	7.2-8.5	7.9 $\pm$ 0.9	4.5-7.9	6.2 $\pm$ 0.6	6.1-7.4	6.9 $\pm$ 0.4	4.2-8.7	7.6 $\pm$ 0.6
Oxygen (mg/l)	7.1-8.1	7.4 $\pm$ 0.4	7.3-8.5	7.9 $\pm$ 0.8	2.3-11.5	6.9 $\pm$ 1.4	3.6-8.2	6.2 $\pm$ 1.3	3.7-9.5	7.4 $\pm$ 1.0
Ammonia (mg NH <sub>3</sub> /l)	0-0.02	0.01 $\pm$ 0	0.01-0.01	0.01 $\pm$ 0	0-0.80	0.40 $\pm$ 0.20	0.01-0.19	0.03 $\pm$ 0.10	0-0.35	0.03 $\pm$ 0.10
Nitrate (mg NO <sub>3</sub> /l)	0.2-3.8	1.5 $\pm$ 1.0	2.1-3.0	2.6 $\pm$ 1.0	0.0-33.0	16.5 $\pm$ 7.0	1.1-4.7	2.0 $\pm$ 1.0	0-17.0	1.52 $\pm$ 3
Iron (mg Fe/l)	0-0.5	0.3 $\pm$ 0	0.6-0.9	0.8 $\pm$ 0	0.2-5.7	2.9 $\pm$ 1.0	0.1-0.7	0.5 $\pm$ 0	0-1.6	0.3 $\pm$ 0
Silica (mg SiO <sub>2</sub> /l)	16.2-36.2	26.4 $\pm$ 8.0	27.4-35.8	31.6 $\pm$ 6.0	6.0-40.0	23.0 $\pm$ 8.0	13.8-30.0	18.81 $\pm$ 6	6.5-41.6	18.7 $\pm$ 8
Alkalinity (mg CaCO <sub>3</sub> /l)	22-42	28 $\pm$ 8	55-58	57 $\pm$ 2	12-380	196 $\pm$ 53	15-137	72.5 $\pm$ 51	5-576	118 $\pm$ 119



Loaches by species and relative abundances differed among sites and rivers. Of the 19 species (Nemacheilidae, 13 species; Balitoridae, 6 species) captured in the central region of Thailand, the Maeklong system provided environmental conditions suitable for the largest number of species ( $n = 13$ , Tables 5–6; Figure 2). Fewest species ( $n = 3$ ) were found in the Southeastern system. Four species were collected from each of the Mekong, Chao Phraya and Peninsula systems. Species diversity within all systems was greatest for *Schistura* with seven species, *S. aurantiaca*, *S. balteata*, *S. crocotula*, *S. kohchangensis*, *S. cf. mahnerti*, *S. cf. sexcauda* and *Schistura* sp. (an undescribed species). *Nemacheilus* contributed four species, *N. binotatus*, *N. masyae*, *N. pallidus* and *N. platiceps*. *Acanthocobitis*, *Homaloptera* and *Pseudohomaloptera* each contributed two species: *A. botia* and *A. zonalternans*; *H. bilineata* and *H. confuzina*; *P. leonardi* and *P. sexmaculata*, respectively and one each from *Homalopteroides*, *H. smithi* and *Tuberoschistura*, *T. baenzigeri*. *Schistura* diversity was highest in the Maeklong system with five species as well as eight other loaches: *Acanthocobitis botia*, *A. zonalternans*, *Homaloptera bilineata*, *Homalopteroides smithi*, *Nemacheilus binotatus*, *N. pallidus*, *N. platiceps* and *Tuberoschistura baenzigeri*. Abundances varied widely among species, sites and river systems (Table 5) with means greatest for four species, *S. aurantiaca* ( $4.5/100 \text{ m}^2$  across all 160 sites), *S. cf. sexcauda*,  $3.9/100 \text{ m}^2$ , *H. smithi*,  $3.8/100 \text{ m}^2$ , and *A. zonalternans*,  $3.1/100 \text{ m}^2$ , respectively (Table 6).



Figure 2. Photographs of selected species: A, *Schistura crocotula* (total length [TL] 41 mm, Khanan River, Prachuap Khiri Khan Province); B, *Schistura cf. mahnerti* (TL approximately 68 mm, Khanan River, Prachuap Khiri Khan Province); C, *Schistura kohchangensis* (TL approximately 70 mm, Pong Nam Ron River, Chantaburi Province); D, *Nemacheilus masyae* (TL 53 mm, Rayong River, Rayong Province); E, *Pseudohomaloptera leonardi* (TL 78 mm, Pong Nam Ron River, Chantaburi Province); F, dorsal view of *Homalopteroides smithi* (TL approximately 45 mm, Klong Paiboon; Chantaburi River, Chantaburi Province). Photographs of *H. smithi* and *P. leonardi* by R. B. Beamish; others by R. Plongsesthee.

Table 5. Range of loach abundance/100 m<sup>2</sup> by loach species within each of five river systems in the central region of Thailand. Numbers in parentheses represent number of sites sampled within each river system. ID identifies species in Figure 4.

Species	ID	Range of Abundance, numbers/100 m <sup>2</sup>				
		Southeastern (N=5)	Mekong (N=2)	Chao Phraya (N=50)	Peninsula (N=11)	Maeklong (N=92)
<i>Acanthocobitis botia</i>	1					0–10.0
<i>Acanthocobitis zonalternans</i>	2				0–16.6	0–49.3
<i>Nemacheilus binotatus</i>	3					0–11.6
<i>Nemacheilus masyae</i>	4			0–4.0		
<i>Nemacheilus pallidus</i>	5					0–23.0
<i>Nemacheilus platiceps</i>	6			0–6.2		
<i>Schistura aurantiaca</i>	7					0–96.5
<i>Schistura balteata</i>	8					0–16.3
<i>Schistura crocotula</i>	9				0–17.0	
<i>Schistura kohchangensis</i>	10	0–46.2	7.3–10.7	0–66.7		
<i>Schistura cf. mahnerti</i>	11				0–21.5	0–49.0
<i>Schistura cf. sexcauda</i>	12					0–119.0
<i>Schistura sp.</i>	13					0–1.5
<i>Tuberoschistura baenzigeri</i>	14					0–6.6
<i>Homaloptera bilineata</i>	15					0–1.5
<i>Homaloptera confuzona</i>	16	0–36.3	0–57.7			
<i>Homalopteroides smithi</i>	17	1.2–46.3	51.1–80.3	0–3.1	0–38.7	0–28.5
<i>Pseudohomaloptera leonardi</i>	18		0–62.5			
<i>Pseudohomaloptera sexmaculata</i>	19					0–46.9

Table 6. Incidence of occurrence (%) and abundance as mean numbers/100 m<sup>2</sup> (SD) for each species for all sites (160 sites) and for those sites where one or more loach species was present (101 sites). River systems are indicated by letters; ME, Mekong; CP, Chao Phraya; SE, Southeastern; MK, Maeklong; and P, Peninsula.

Species	River systems	Incidence of occurrence (%)		Abundance, Number/100 m <sup>2</sup> Mean (SD)	
		(N=160)	(N=101)	(N=160)	(N=101)
<i>Acanthocobitis botia</i>	MK	6	10	0.2(1.1)	0.3(1.3)
<i>Acanthocobitis zonalternans</i>	P, MK	29	46	3.1(7.9)	4.5(9.2)
<i>Nemacheilus binotatus</i>	MK	1	2	0.1(0.9)	0.1(1.1)
<i>Nemacheilus masyae</i>	CP	3	5	<0.1(0.3)	0.1(0.4)
<i>Nemacheilus pallidus</i>	MK	10	16	0.3(2.1)	0.6(2.4)
<i>Nemacheilus platiceps</i>	CP	1	2	0.1(0.5)	0.1(0.6)
<i>Schistura aurantiaca</i>	MK	26	41	4.5(12.8)	6.9(14.6)
<i>Schistura balteata</i>	MK	3	5	0.2(1.4)	0.2(1.6)
<i>Schistura crocotula</i>	P	2	3	0.2(1.6)	0.3(1.8)

Table 6 (continued).

Species	River systems	Incidence of occurrence (%)		Abundance, Number/100 m <sup>2</sup> Mean (SD)	
		(N=160)	(N=101)	(N=160)	(N=101)
<i>Schistura kohchangensis</i>	SE, ME, CP	6	10	1.1 (6.7)	1.7 (7.8)
<i>Schistura cf. mahnerti</i>	P, MK	14	22	1.1 (4.8)	2.2 (5.6)
<i>Schistura cf. sexcauda</i>	MK	21	33	3.9 (12.9)	5.7 (15.2)
<i>Schistura sp.</i>	MK	1	2	< 0.1 (0.1)	< 0.1 (0.1)
<i>Tuberoschistura baenzigeri</i>	MK	4	6	0.1 (0.6)	0.1 (0.7)
<i>Homaloptera bilineata</i>	MK	1	2	< 0.1 (0.1)	< 0.1 (0.1)
<i>Homaloptera confuzona</i>	SE, ME	2	3	0.6 (5.4)	0.9 (6.2)
<i>Homalopteroides smithi</i>	SE, ME, CP, P, MK	39	62	3.8 (10.0)	5.7 (11.2)
<i>Pseudohomaloptera leonardi</i>	ME	1	2	0.4 (4.9)	0.6 (5.7)
<i>Pseudohomaloptera sexmaculata</i>	MK	16	26	1.4 (5.6)	3.1 (6.7)

### Incidence of Occurrence

Species of loaches were present in 63% of the 160 sites sampled (101 sites) in the central region of Thailand. *Schistura* were present in 45% of all sites (72 of 160) and 71% of those sites where loaches were found (72 of 101). Incidence of occurrence for a single species was highest for *H. smithi* (39% and 62% of 160 and 101 sites, Table 6) followed by *A. zonalternans*, *S. aurantiaca*, *S. cf. sexcauda*, and *P. sexmaculata*. Occurrences were extremely low, < 1% for *N. binotatus*, *N. placticeps*, *Schistura sp.*, *H. bilineata* and *P. leonardi*.

Occurrence of some species was confined to a single river system. *S. aurantiaca*, *S. balteata*, *Schistura cf. sexcauda* and *Schistura sp.* were present only in the Maeklong system and *S. crocotula* only in the Peninsula system. A single species was found in two or three river systems. *S. cf. mahnerti* was present in the Peninsula and Maeklong systems and *S. kohchangensis* in three river systems, Southeastern, Mekong and Chao Phraya.

### Environmental Associations

In all river systems, distributions and abundance of loaches related significantly with six environmental variables ( $p < 0.05$  for axis 1 and 2, respectively, Monte-Carlo test with 1000 permutations; Figure 3). Each axis explains 10% of the variation and represents 55% of the species-environment relationship. The first and second axes illustrate a negative gradient of elevation (overall average,  $237 \pm 124$  m), temperature ( $24.5 \pm 3.1$  °C), velocity ( $35 \pm 16$  cm/s), pH ( $7.4 \pm 0.6$ ) and silica ( $22.0 \pm 8.3$  mg SiO<sub>2</sub>/l), respectively. Oxygen loaded positively ( $7.6 \pm 0.8$  mg/l) on the second axis. Elevation and water temperature were of greatest importance to loach distribution and abundance across all river systems with water velocity, dissolved oxygen, silica and pH significant but of lesser importance. The significance of elevation, water velocity, ambient oxygen and silica were shared across all river systems with those in the Maeklong system, although relative importance of temperature and elevation was greater across all systems than in the Maeklong alone. Further, the importance of alkalinity, iron and

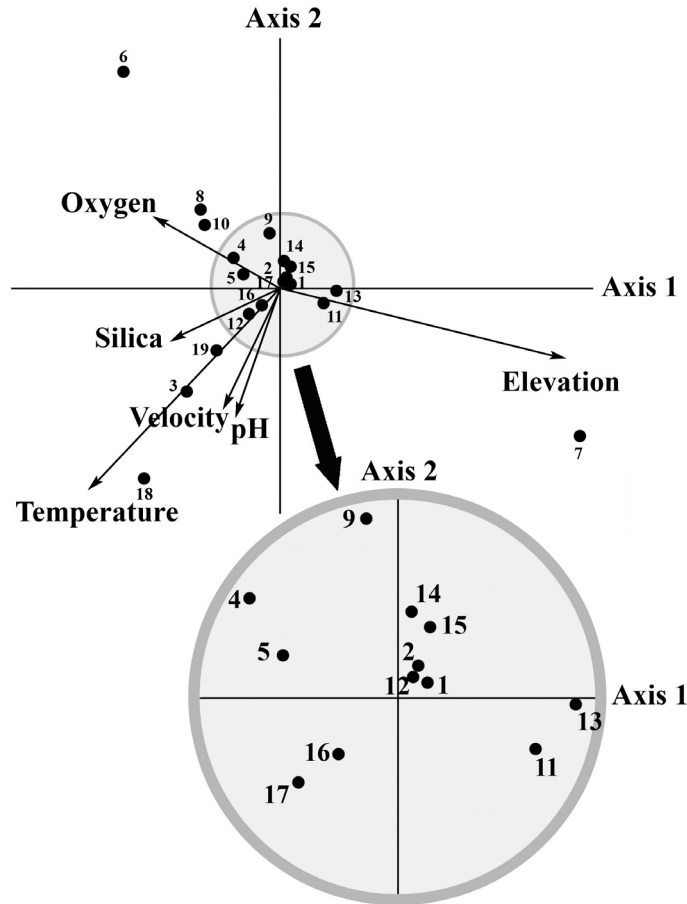


Figure 3. Distribution of loaches in this study in all five river systems in the central region of Thailand with respect to significant environmental variables, identified by canonical correspondence analysis (CCA). Numbers indicate loaches identified in Table 5. Species within the smaller and larger circles are those that associate with average values for each of the significant variables for the 160 sites. Length of each environmental vector indicates the strength of its statistical significance relative to species association.

river width to species distribution and abundance lessened across all river systems while that for pH and temperature increased relative to that in the MaeKlong system.

Over all river systems, the majority of loach species shared similar environmental conditions. This included *A. botia*, *A. zonalternans*, *N. masyae*, *N. pallidus*, *S. aurantiaca*, *S. cf. mahnerti*, *S. cf. sexcauda*, *S. sp.*, *T. baenzigeri*, *Homaloptera bilineata*, *Homalopteroides smithi* and *P. sexmaculata*. In contrast, favorable environmental conditions varied for some species. *Schistura balteata* occurred most commonly where elevations were well above the overall mean and ambient oxygen concentrations were well below. *S. balteata* was abundant and the only species found at the highest elevation site > 800 m. This was also the only site

in which aquatic vegetation was abundant. *N. platiceps* occurred most frequently where ambient oxygen was high and elevation low. *Schistura crocotula* and *Schistura kohchangensis* tended to occupy habitats of slightly lower than average elevation and elevated oxygen but otherwise average conditions. Several species, *N. binotatus*, *P. leonardi* and, to a lesser extent, *Homaloptera confuzona* were associated with sites having high temperature, pH, silica and swift water current, all above the respective overall site means of 25° C, 7.4, 22.0 mg SiO<sub>2</sub>/l and 35 cm/s. However, species' occurrences and abundances for these species were low to suggest caution in interpretation.

## DISCUSSION

Geographical location and morphological features of rivers contribute directly to their physical and chemical characteristics and these largely dictate the presence and distribution of available plants and animals (BEAUFORT, 1951). Climate and season interact to impose temporal abiotic and biotic changes (GOBAS & MCCORQUODALE, 1992). Current distributions of fish within biogeological confines are thus largely related to evolved morphological, physiological and behavioral features, processes and tolerances acting in concert with the environment.

Information on loach habitat abounds in the literature, commonly as short accounts accompanying species descriptions (RAINBOTH, 1996; OU ET AL., 2011, others). Often few descriptors are provided and impart relatively little quantitative information (e.g. 'shallow depth', 'muddy bottoms', 'fast bedrock' and 'torrential streams'). Dissolved oxygen, pH and temperature are reported sometimes. A more comprehensive approach was undertaken on Malayan balitorids by ALFRED (1969) that improved understanding of habitat associations. He assigned associations on the basis of species presence or absence into either of two categories, one based on substrate/vegetation and the other on water velocity with subcategories within each. This was supported with underwater observations. Species that occurred in several subcategories he called ubiquitous, those in or nearly in only one subcategory he called non-ubiquitous. With this Alfred assigned habitat. The study by ALFRED (1969) included one species also found in the present study, *H. smithi*, to which he assigned its habitat as ubiquitous. In the present and in an earlier study (BEAMISH ET AL., 2008), *H. smithi* was closely associated with average values for each of the significant factors and thus ubiquitous in Alfred's terminology.

A recent important and comprehensive study on habitat associations for a large number of fishes including loaches, was undertaken by SIVAMARAKSHA ET AL. (2012). The study related species richness and diversity with a large number of physicochemical and geomorphological factors for fishes in the Ping River basin in Northern Thailand. It found six physicochemical factors, dissolved oxygen, temperature, pH, conductivity, phosphorus and alkalinity and six geomorphological factors, altitude (elevation), distance from the sea, river discharge, and site depth and width to be significantly related with species richness and diversity. Although Sivamaraksha's study differed in many respects from the present study both recognized the importance of elevation, dissolved oxygen, temperature, pH, alkalinity and site depth and width. It is equally clear that while these studies have contributed importantly to fish habitat knowledge much remains to be uncovered.

The present study was in agreement with the earlier study by BEAMISH ET AL. (2008) in finding fishes in all five river systems associated with site elevation, dissolved oxygen, silica and ambient temperature but differing in identifying water velocity and pH as significant.

Most loaches occurred within a limited but similar range of environmental conditions, not far from their respective overall mean supporting their wide distribution among the sites sampled.

Single species occurrences of loaches were found for several species, most often *H. smithi*, but multiple species occurrences were also found, contrary to predictions by the competitive exclusion principle (GILPIN & JUSTICE, 1972; McGEHEE & ARMSTRONG, 1977). This assumes communities exist at competitive equilibrium and requires conditions of habitat stability and for species to be dependent on exactly the same resources. The central region of Thailand has distinct rainy and dry seasons annually with rivers that undergo annual floods and droughts typical of pulsed ecosystems, creating unstable habitats (JUNK *ET AL.*, 1989; ODUM *ET AL.*, 1995). Additionally, physicochemical conditions, predation and other factors can be expected to continually impose their influence on the nature of competitive interactions making it likely that competitive equilibrium rarely occurs, if at all (WIENS, 1977; HUSTON, 1979). Further, MCCANN *ET AL.* (1998) suggest competitive equilibrium need not occur where life history variations differ such that an advantage at one stage in a life cycle implies a disadvantage at another. The high diversity of freshwater fishes in general and loaches in particular in Southeast Asian rivers suggests that competitive exclusion may have been partially circumvented through variations in habitat stability and life histories as well as adaptations for ecological sharing, thus minimizing the potential negative effects of direct competition and less suitable habitats. In their study on resource partitioning among Sri Lankan fishes, MOYLE & SENANAYAKE (1984) found that microhabitat overlap was low among co-occurring species and that diets of fishes tended to vary when not segregated by habitat.

The importance of biotic factors in accommodating species coexistence in riffles was recently demonstrated for fish by NITHIROJPAKDEE *ET AL.* (2012, 2014). Regions of high water velocity typically accommodate relatively large benthic populations of immature insects as well as other fauna that constitute a food source for loaches. NITHIROJPAKDEE *ET AL.* (2012) found that while many coexisting fishes in riffles feed on the same functional feeding groups of macrobenthic insects (MERRITT & CUMMINS, 1996), they display temporal and spatial differences in feeding schedules that seem to foster resource sharing rather than direct competition. Moreover, morphologies of importance to spatial separation of habitat in flowing water can be inferred from shape and size of the body and fins. Loaches, particularly balitorids have to varying degrees compromised their shape so that it is partially dorsoventrally flattened lowering both drag and lift and allowing benthic refuge among rocks. Species differences in paired fin areas suggest a relationship with current speed and benthic station holding. Pectoral fin areas for *P. leonardi*, *Homalopteroides smithi*, and *S. kohchangensis* adjusted to a total length of 50 mm, were 47, 43 and 38 cm<sup>2</sup>, respectively (F.W.H. BEAMISH, unpublished). In the riffles studied by NITHIROJPAKDEE *ET AL.* (2012), *P. leonardi* occurred most frequently at micro riffle velocities of  $175 \pm 43$  cm/s followed by *H. smithi* and *S. kohchangensis* at  $39 \pm 27$  and  $34 \pm 19$  cm/s (F.W.H. BEAMISH & P. NITHIROJPAKDEE, unpublished), in broad agreement with pectoral fin areas. 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 paired and median fin area.

Improved understanding of lateral line systems of fish in concert with large pectoral fins is revealing other adaptations for specific riverine habitats. The lateral line system seems to be important to station-holding behaviors of fish that maintain their position in association with rocks (SUTTERLIN & WADDY, 1975). Fishes differ in the number and distribution of sensory neuromasts in their lateral line systems and, these, in free swimming fishes, play an important



role in monitoring water movement over their bodies and providing muscular feedback for efficient swimming in turbulent flowing water (ANDERSON *ET AL.*, 2001; COOMBS, 2001). Arrays of different types of sensory neuromasts interact to facilitate both orientation to water currents as well as to discriminate between the hydrodynamic signatures of other animals including potential prey (BLECKMANN *ET AL.*, 1991; KANTER & COOMBS, 2003; MONTGOMERY *ET AL.*, 2003; COOMBS *ET AL.*, 2007). Extending large pectoral fins laterally generates negative lift (COOMBS *ET AL.*, 2007) and contributes to station holding in flowing water. It seems likely that lateral lines and pectoral fins of some balitorids function in a similar manner and assist species such as *S. balteata* survive at high-elevation habitats where water currents are fast and food resources limited.

Loaches were associated with high dissolved oxygen despite the relatively narrow range found in this study from approximately 70 to 100% of air saturation. Several species were clearly influenced by dissolved oxygen, with *N. platiceps* associated with the highest oxygen concentrations followed by *S. kohchangensis* and *S. crocotula*, with *S. balteata* associated with lower concentrations found at high elevation sites. No information appears available on physiological adaptations in regards oxygen uptake within the balitorids but cutaneous respiration seems probable. The relationship with pH was similar to that for dissolved oxygen in that the range of values associated with most species was narrow and within that not usually considered of concern to fishes. However, blood oxygen dissociation may be impaired at low pH (FROMM, 1980; ALIBONE & FAIR, 1981) which may explain a general absence of loaches from the lowest-pH sites. Low-pH environments also have harmful effects on ion homeostasis in freshwater fish (WILSON *ET AL.*, 1999; HIRATA *ET AL.*, 2003). Silica is important to the distribution of grazing fishes such as balitorids that feed directly or indirectly on algae some of which use silica in their morphology. Most loach species were found at sites where silica was about 20 mg SiO<sub>2</sub>/l. At high elevation sites silica concentrations were generally below 10 mg SiO<sub>2</sub>/l in accord with the absence of balitorids except *S. balteata* and *N. binotatus*, to suggest their diets are comparatively free of siliceous algae. In contrast, *H. confuzona* and *P. leonardi* may be quite dependent on siliceous algae as both were found at high silica concentrations, mostly above 30 mg SiO<sub>2</sub>/l.

Argument continues on the relative importance of resource competition and sharing for species' coexistence. HUBBELL'S (2001, 2005) neutral theory suggests that trophically similar species are functionally equivalent and places less emphasis on species specific habitats. Niche theory is more favorable towards species-specific habitats that accommodate only single species, presumably through physiological, behavioral and morphological variation in regards the biotic and abiotic environment. Evidence is available in support of both theories, possibly suggesting that neither completely accounts for all assemblages or community compositions.

## CONCLUSIONS

Loaches are clearly masters of the substrate in fast flowing water in small rivers. This study examined environmental associations in sites representing diverse landscapes throughout five river systems in the central region of Thailand. Species were most common in MaeKlong system in Western Thailand, their numbers and overall abundance varying directly and inversely with river order in accord with the general pattern for fishes other than loaches. The most important of the significant environmental factors across the region were elevation and ambi-



ent temperature. Of lesser but significant importance were dissolved oxygen, water velocity, ambient silica and pH. Some variation in significant environmental factors was found in sites in the MaeKlong system. Most, but not all, loaches were associated with approximately mean levels of the significant factors. A few species showed strong associations with high levels of elevation, temperature or oxygen. The ecological importance of significant environmental factors to loaches relates to species-specific morphological adaptations for a benthic lifestyle in fast water, including body shape and fin areas and, likely, maneuverability. Potential roles of the lateral line system, especially the cephalic pores, for avoiding benthic obstructions and capturing benthic prey are considered. Although not determined directly in the current study, it is unlikely that the loaches studied here are tolerant of habitats in which ambient oxygen is much below air saturation. Rather, the charming and beautiful species within this family belong to small, relatively pristine and rapidly flowing streams and small rivers in which they are major contributors to the ecosystem.

### ACKNOWLEDGEMENTS

The first author thanks the National Science and Technology Development Agency of Thailand for their financial and logistic support, in particular Ms. R. Tantalakha and Mr. Thongchai. The Department of Fisheries provided collecting permits for which I am most appreciative. I am grateful also to Burapha University, Faculty of Science, and the Environmental Science program for their continuing support. Field assistance was provided by many including R. Beamish, P. Kangrang, C. Kongchaiya, T. Kongchaiya, R. Lagarde and P. Tookampha. I am particularly grateful for the technical assistance provided by P. Kangrang (map) and J. Ham (illustrations) and to R. Griffiths for his statistical advice. I appreciate the constructive comments and suggestions offered by two anonymous reviewers as well as those by P. Musikasinthorn and W. Brockelman. Sadly my colleague and PhD student, Rungthip Plongsesthee (Kae), succumbed to cancer before the completion of her study. She was a gifted, delightful and determined young scientist who loved aquatic ecology and taxonomy. Kae wanted to give so much more than time would allow. Thai fishery science has lost an outstanding young scientist and I, a talented young friend.

### REFERENCES

- ABELL, R., M. L. THIEME, C. REVENGA, M. BRYER, M. KOTTELAT, N. BOGUTSKAYA, B. COAD, N. MANDRAK, S. CONTRERAS BALDERAS, W. BUSSING, M. L. J. STIASSNY, P. SKELTON, G. R. ALLEN, P. UNMACK, A. NASEKA, R. NG, N. SINDORF, J. ROBERTSON, E. ARMUJO, J. V. HIGGINS, T. J. HEIBEL, E. WIKRAMANAYAKE, D. OLSON, H. L. LÓPEZ, R. E. REIS, J. G. LUNDBERG, M. H. SABAJ PÉREZ, AND P. PETRY, 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience* 58: 403–414.
- ALFRED, E. R. 1969. The Malayan Cyprinoid fishes of the family Homalopteridae. *Zoologische Mededelingen*. 43: 213–237.
- ALIBONE, M. R., AND P. FAIR. 1981. The effects of low pH on the respiration of *Daphnia magna* Straw. *Hydrobiologia* 85: 185–188.
- ALLAN, J. D. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annual Review of Ecology, Evolution and Systematics*. 35: 257–284.

- AMERICAN PUBLIC HEALTH ASSOCIATION (APHA). 1992. *Standard Methods for the Examination of water and wastewater (18<sup>th</sup> edition)*. American Public Health Association, American Water Works Association, and Water Pollution Control Federation, Washington, D.C.
- ANDERSON, E. J., W. R. MCGILLIS, AND M. A. GROSSENBAUGH. 2001. The boundary layer of swimming fish. *Journal of Experimental Biology* 204: 81–102.
- ANGERMEIER, P. L., AND I. J. SCHLOSSER. 1989. Species-area relationships for stream fishes. *Ecology* 70(5): 1450–1461.
- BEAMISH, F. W. H., R. W. GRIFFITHS, C. KONGCHAIYA, P. SA-ARDRIT, AND P. SONCHAENG. 2005. Seasonal fish abundance in three Thailand streams: Influence of discharge. *Tropical Freshwater Biology* 14: 37–60.
- BEAMISH, F. W. H., P. SA-ARDRIT, AND V. CHEEVAPORN. 2008. Habitat and abundance of Balitoridae fishes in small rivers in central Thailand. *Journal of Fish Biology* 72: 2467–2484.
- BEAUFORT, L. F. D. 1951. *Zoogeography of the land and inland waters*. Text-Books of Animal Biology. William Clowes and Sons. London. 208 pp.
- BLECKMANN, H., T. BREITYHAUPT, R. BLACKHAM, AND J. TAUTZ. 1991. The time course and frequency content of hydrodynamic events caused by moving fish, frogs, and crustaceans. *Journal of Comparative Physiology A* 168: 749–757.
- CARLE, F. L., AND M. S. STRAUB. 1978. A new method for estimating population size from removal data. *Biometrics* 34: 621–630. DOI 10.23.07/253038.
- CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
- COOMBS, S. 2001. Smart skins: Information processing by lateral line flow sensors. *Autonomous Robots* 11: 255–261.
- COOMBS, S., E. ANDERSON, C. B. BRAUN, AND M. GROSSENBAUGH. 2007. The hydrodynamic footprint of a benthic fish in unidirectional flow. *Journal of the Acoustical Society of America* 122: 1227–1237.
- EDDS, D. R. 1993. Fish assemblage structure and environmental correlates in Nepal's Gandaki River. *Copeia* 1993: 48–60.
- ESCHMEYER, W. N. 2015 *Catalog of Fishes electric version*. Available from : <http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp> (accessed 11 January 2015).
- FROMM, P. O. 1980. A review of some physiological and toxicological responses of freshwater fish to acid stress. *Environmental Biology of Fishes* 5(1): 79–93.
- FRY, F. E. J. 1971. The effects of environmental factors on the physiology of fish. Pages 1–98 in W. S. Hoar and D. J. Randall, (eds.). *Fish Physiology, Volume 6*. New York: Academic Press.
- GILLER, P. S., AND B. MALMQVIST. 1998. The biology of streams and rivers. *Biology of Habitats Series*. Oxford University Press, Oxford. 296 pp.
- GILPIN, M. E., AND K. E. JUSTICE. 1972. Reinterpretation of the invalidation of the principle of competitive exclusion. *Nature* 236: 273–274; 299–301.
- GOBAS, F. A. P. C., AND J. A. MCCORQUODALE. 1992. *Chemical dynamics in fresh water ecosystems*. Lewis Publishers, Boca Raton, FL. University of Missouri Agriculture Research Station Research Bulletin.
- GORMAN, O. T., AND J. R. KARR. 1978. Habitat structure and stream fish communities. *Ecology* 59: 507–515.
- HAYES, T. B., P. CASE, S. CHUI, D. CHUNG, C. HAEFFELE, K. HASTON, M. LEE, V.P. MAI, Y. MARJUOA, J. PARKER, AND M. TSUI. 2006. Pesticide mixtures, endocrine disruption, and amphibian declines: are we understanding the impact? *Environmental Health Perspectives* 114: 40–50.
- HIRATA, T., T. KANEKO, T. ONO, T. NAKAZATO, N. FURUKAWA, S. HASEGAWA, S. WAKABAYASHI, M. SHIGEKAWA, M. H. CHANG, M. F. ROMERO, AND S. HIROSE. 2003. Mechanism of adaptation of a fish living in a pH 3.5 lake. *American Journal of Physiology, Regulatory Integrative and Comparative Physiology* 284: R1199–R1212.
- HUBBELL, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey 448 pp.
- HUBBELL, S. P. 2005. Neutral theory and the evolution of functional equivalence. *Ecology* 19: 166–172.
- HUGUENY, B. 1990. Geographic range of West African freshwater fishes: role of biological characteristics and stochastic processes. *Acta Oecologica* 11: 351–375.
- HUSTON, M. 1979. A general hypothesis of species diversity. *The American Naturalist* 113(1): 81–101.
- JACKSON, D. A., P. R. PERES-NETO, AND J. D. OLDEN. 2001. What controls who is where in freshwater fish communities: The roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 157–170.
- JUNK, W. J., P. B. BAILEY, AND R. E. SPARK. 1989. The flood pulse concept in river-floodplain systems. in D.P. Dodge, (ed.), Proceedings of the Large River Symposium: *Canada Special Publication of Fisheries and Aquatic Science*. 106: 110–127.
- KANTER, M. J., AND S. COOMBS. 2003. Rheotaxis and prey detection in uniform currents by Lake Michigan mottled sculpin (*Cottus bairdi*). 2003. *Journal of Experimental Biology* 206: 59–70.

- KHACHONPISITSAK, S. 2012. *Biodiversity assessment of freshwater fishes: Thailand as a case study*. PhD Thesis. School of Biology, University of St. Andrews, U.K. 424 pp.
- KOTTELAT, M. 1984. Revision of the Indonesian and Malaysian Loaches of the subfamily Neomacheilinae. *Japanese Journal of Ichthyology* 31: 225–260.
- KOTTELAT, M. 1988. India and Indochinese species of *Balitora* (Osteichyes: Cypriniformes) with descriptions of two new species and comments on the family-group names Balitoridae and Homalopteridae. *Revue Suisse de Zoologie* 95: 487–504.
- KOTTELAT, M. 1989. Zoogeography of the fishes from Indochinese inland waters with an annotated check-list. *Bulletin Zoologisch Museum* 12: 1–55.
- KOTTELAT, M. 1990. Indochinese Nemacheilines, a Revision of nemacheiline Loaches (Pisces: Cypriniformes) of Thailand, Burma, Laos, Cambodia and Southern Viet Nam. Munchen: Verlag Dr. Frieddrich Pfeil.
- KOTTELAT, M. 2000. Diagnoses of a new genus and 64 new species of fishes from Laos (Teleostei: Cyprinidae, Balitoridae, Bagridae, Syngnathidae, Chaudhuriidae and Tetraodontidae). *Journal of South Asian Natural History* 5: 37–82.
- KOTTELAT, M. 2001. *Fishes of Laos*. WHT Publications, Colombo. 198 pp.
- KOTTELAT, M. 2012. Conspectus cobitidum: an inventory of the loaches of the world (Teleostei: Cypriniformes: Cobitoidea). *Raffles Bulletin of Zoology, Supplement*. 26: 1–199.
- KOTTELAT, M. 2013. The fishes of the inland waters of Southeast Asia: a catalogue and core bibliography of the fishes known to occur in freshwaters, mangroves and estuaries. *Raffles Bulletin of Zoology Supplement* 27: 1–663.
- LYONS, J. 1992. The length of stream to sample with a towed electrofishing unit when species richness is estimated. *North American Journal of Fishery Management* 12: 198–203.
- MAGURRAN, A. E., S. KHACHONPISITSAK, AND A. B. AHMAD. 2011. Biological diversity of fish communities: pattern and process. *Journal of Fish Biology* 79: 1393–1412.
- MCGILL, B. J. 2003. A test of the unified neutral theory of biodiversity. *Nature* 422: 881–885.
- MCCANN, K. S., A. HASTINGS, AND D. R. STRONG. 1998. Trophic cascades and trophic trickles in pelagic food webs. *Proceedings of the Royal Society London B* 265: 205–209.
- MCGEEHEE, R., AND R. A. ARMSTRONG. 1977. Some mathematical problems concerning the ecological principle of competitive exclusion. *Journal of Differential Equations* 23: 30–52.
- MERRIT, R. W. AND K. W. CUMMINS. 1996. An introduction to the aquatic insects of North America. Third edition, Kendall / Hunt, Iowa. 862 pp.
- MONTGOMERY, J. C., F. MCDONALD, C. F. BAKER, A. G. CARTON, AND N. LING. 2003. Sensory integration in the hydrodynamic world of rainbow trout. *Proceeding of the Royal Society*, 270 (Supplement 2) S195–S197.
- MOYLE, P. B., AND F. R. SENANAYAKE. 1984. Resource partitioning among the fishes of rainforest streams in Sri Lanka. *Journal of Zoology London* 202: 195–223.
- NELSON, J. S. 2006. *Fishes of the World* (4<sup>th</sup> ed.). John Wiley & Sons, New York. 624 pp.
- NITHIROPAKDEE, P., F. W. H. BEAMISH, AND D. L. G. NOAKES. 2012. Maintaining fish diversity in Thailand: variations in foraging behavior. *Environmental Biology of Fishes*. 95(2): 227–236.
- NITHIROPAKDEE, P., F. W. H. BEAMISH, AND T. BOONPAKDEE. 2014. Diet diversity among five co-existing fish species in a tropical river: integration of dietary and stable isotope data. *Limnology* 1599–107.
- ODUM, W. E., E. P. ODUM, AND H. T. ODUM. 1995. Nature's pulsing paradigm. *Estuaries*. 18: 547–555.
- OU, C., K. O. MONTANA, K. O. WINEMILLER, AND K. W. CONWAY. 2011. *Schistura diminuta*: a new miniature loach from the Mekong River drainage of Cambodia (Teleostei : Nemacheilidae). *Ichthyological Exploration of Freshwaters*. 22: 193–2000.
- PLONGSESTHEEL, R., L. M. PAGE, AND F. W. H. BEAMISH. 2011. *Schistura aurantiaca*, a new species from the Mae Khlong basin, Thailand (Teleostei: Nemacheilidae). *Ichthyological Exploration of Freshwaters*. 22: 169–178.
- PLONGSESTHEE, R., M. KOTTELAT, AND F. W. H. BEAMISH. 2013. *Schistura crocotula*, a new loach (Teleostei: Nemacheilidae) from Thailand. *Ichthyological Exploration of Freshwaters*. 24(2): 171–178.
- RAINBOTH, W. J. 1996. FAO species identification field guide for fishery purposes. Fishes of the Cambodian Mekong. FAO. Rome. 265 pp.
- RANDALL, Z. S., AND L. M. PAGE. 2012. Resurrection of the genus *Homalopteroides* (Teleostei: Balitoridae) with a redescription of *H. modestus* (Vinciguerra 1890). *Zootaxa*. 3586: 329–346.
- RANDALL, Z. S., AND L. M. PAGE. 2015. On the paraphyly of *Homaloptera* (Teleostei: Balitoridac) and description of a new genus of hillstream loaches from the Western Ghats of India. *Zootaxa* 3926: 57–86.
- ROBERTS, T. R. 1982. The Bornean Gastromyzontine fish genera *Gastromyzon* and *Glanioopsis* (Cypriniformes, Homalopteridae), with descriptions of new species. *Proceedings of 30 the California Academy of Science*. 42: 497–524.

- ROBERTS, T. R. 1989. The freshwater fishes of Western Borneo (Kalimantan Barat, Indonesia). *Memoirs California Academy of Science* 14: 12–210.
- ROBINSON, C. L. K., AND W. M. TONN. 1989. Influence of environmental factors and piscivory in structuring fish assemblages of small Alberta lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 81–89.
- SMITH, H. M. 1945. *The Fresh-Water Fishes of Siam, or Thailand*. Bulletin of the U.S. National Museum. 622 pp.
- STOKES, C. J., AND S.R. ARCHER. 2010. Niche differentiation and neutral theory: An integrated perspective on shrub assemblages in a parkland savanna. *Ecology* 91(4): 1152–1162.
- STRAHLER, A. N. 1952. Dynamic basis of geomorphology. *Geological Society of America Bulletin* 63: 1117–1142.
- SUTTERLIN, A. M., AND S. WADDY. 1975. Possible role of the posterior lateral line in obstacle entrainment by brook trout (*Salvelinus fontinalis*). *Journal of the Fisheries Research Board of Canada* 32: 2441–2446.
- SUVARNARAKSHA, A., S. LEK, S. LEK-AAN, AND T. JUTAGATE. 2012. Fish diversity and assemblage patterns along the longitudinal gradient of a tropical river in the Indo-Burma hotspot region (Ping-Wang River Basin). *Hydrobiologia* 694: 153–169.
- VOLKOV, A. G., T. ADESINA, AND E. JOVANOV. 2007. Closing of Venus flytrap by electrical stimulation of motor cells. *Plant Signal Behavior* 2: 139–144.
- WATSON, D. J., AND E. K. BALON. 1984. Structure and production of fish communities in tropical rain forest streams of northern Borneo. *Canadian Journal of Zoology* 62: 927–940.
- WILSON, R.W., C. M. WOOD, R.J. GONZALEZ, M.L. PATRICK, H.L. BERGMAN, A. NARAHARA, AND A.L. VAL. 1999. Ion and acid- base balance in three species of Amazonian fish during gradual acidification of extremely soft water. *Physiological and Biochemical Zoology* 72: 277– 285.
- WIENS, J. A. 1977. On competition and variable environments. *American Scientist* 65: 592–597.

Appendix 1. Distribution of study sites by rivers, provinces and river systems. River names were obtained from maps and local residents. Study sites in close proximity to each other are grouped and identified by the same letter symbol.

Site number	Symbol	Stream/River	Province	River system
1	A	E-pu	Kanchanaburi	Maeklong
2	A	Tawat	Kanchanaburi	Maeklong
3	A	Tawat	Kanchanaburi	Maeklong
4	A	Tawat	Kanchanaburi	Maeklong
5	A	Pracham Mai	Kanchanaburi	Maeklong
6	A	Pracham Mai	Kanchanaburi	Maeklong
7	A	Pracham Mai	Kanchanaburi	Maeklong
8	A	Pracham Mai	Kanchanaburi	Maeklong
9	A	Pracham Mai	Kanchanaburi	Maeklong
10	A	Pracham Mai	Kanchanaburi	Maeklong
11	A	Pracham Mai	Kanchanaburi	Maeklong
12	A	Pracham Mai	Kanchanaburi	Maeklong
13	A	Pracham Mai	Kanchanaburi	Maeklong
14	A	Pracham Mai	Kanchanaburi	Maeklong
15	A	Pracham Mai	Kanchanaburi	Maeklong
16	A	Pracham Mai	Kanchanaburi	Maeklong
17	A	Pracham Mai	Kanchanaburi	Maeklong
18	A	Pracham Mai	Kanchanaburi	Maeklong
19	A	Pracham Mai	Kanchanaburi	Maeklong
20	A	Pracham Mai	Kanchanaburi	Maeklong
21	A	Pracham Mai	Kanchanaburi	Maeklong
22	A	Pracham Mai	Kanchanaburi	Maeklong
23	A	Pracham Mai	Kanchanaburi	Maeklong
24	A	Ban Rai	Kanchanaburi	Maeklong
25	A	Ban Rai	Kanchanaburi	Maeklong
26	A	Ban Rai	Kanchanaburi	Maeklong
27	A	Ban Rai	Kanchanaburi	Maeklong
28	A	Ban Rai	Kanchanaburi	Maeklong
29	A	Ban Rai	Kanchanaburi	Maeklong
30	A	Ban Rai	Kanchanaburi	Maeklong
31	A	Ban Rai	Kanchanaburi	Maeklong
32	A	Ban Rai	Kanchanaburi	Maeklong
33	A	Ban Rai	Kanchanaburi	Maeklong
34	A	Kratenjeng	Kanchanaburi	Maeklong
35	A	Kratenjeng	Kanchanaburi	Maeklong
36	A	Satamid	Kanchanaburi	Maeklong
37	A	Pilok	Kanchanaburi	Maeklong
38	B	Khayeng	Kanchanaburi	Maeklong
39	B	Khayeng	Kanchanaburi	Maeklong
40	B	Khayeng	Kanchanaburi	Maeklong

## Appendix 1 (continued).

Site number	Symbol	Stream/River	Province	River system
41	B	Khayeng	Kanchanaburi	Maeklong
42	B	Khayeng	Kanchanaburi	Maeklong
43	B	Khayeng	Kanchanaburi	Maeklong
44	B	Khayeng	Kanchanaburi	Maeklong
45	B	Khayeng	Kanchanaburi	Maeklong
46	B	Khayeng	Kanchanaburi	Maeklong
47	B	Khayeng	Kanchanaburi	Maeklong
48	B	Khayeng	Kanchanaburi	Maeklong
49	B	Khayeng	Kanchanaburi	Maeklong
50	B	Khayeng	Kanchanaburi	Maeklong
51	B	Khayeng	Kanchanaburi	Maeklong
52	B	Khayeng	Kanchanaburi	Maeklong
53	B	Khayeng	Kanchanaburi	Maeklong
54	B	Khayeng	Kanchanaburi	Maeklong
55	B	Khayeng	Kanchanaburi	Maeklong
56	B	Khayeng	Kanchanaburi	Maeklong
57	B	Khayeng	Kanchanaburi	Maeklong
58	B	Khayeng	Kanchanaburi	Maeklong
59	B	Khayeng	Kanchanaburi	Maeklong
60	B	Khayeng	Kanchanaburi	Maeklong
61	B	Khayeng	Kanchanaburi	Maeklong
62	B	Khayeng	Kanchanaburi	Maeklong
63	B	Khayeng	Kanchanaburi	Maeklong
64	B	Khayeng	Kanchanaburi	Maeklong
65	B	Khayeng	Kanchanaburi	Maeklong
66	B	Khayeng	Kanchanaburi	Maeklong
67	B	Khayeng	Kanchanaburi	Maeklong
68	B	Khayeng	Kanchanaburi	Maeklong
69	B	Khayeng	Kanchanaburi	Maeklong
70	B	Khayeng	Kanchanaburi	Maeklong
71	B	Khayeng	Kanchanaburi	Maeklong
72	B	Khayeng	Kanchanaburi	Maeklong
73	B	Khayeng	Kanchanaburi	Maeklong
74	B	Khayeng	Kanchanaburi	Maeklong
75	B	Tuam	Kanchanaburi	Maeklong
76	B	Bang Ka Loo	Kanchanaburi	Maeklong
77	B	Bang Ka Loo	Kanchanaburi	Maeklong
78	B	Bang Ka Loo	Kanchanaburi	Maeklong
79	C	Lichia	Kanchanaburi	Maeklong
80	C	Lichia	Kanchanaburi	Maeklong
81	C	Lichia	Kanchanaburi	Maeklong

## Appendix 1 (continued).

Site number	Symbol	Stream/River	Province	River system
82	C	Lichia	Kanchanaburi	Maeklong
83	C	Lichia	Kanchanaburi	Maeklong
84	C	Lichia	Kanchanaburi	Maeklong
85	C	Thi Khrong	Kanchanaburi	Maeklong
86	D	Kreng Kravia	Kanchanaburi	Maeklong
87	E	Phetchaburi	Phetchaburi	Maeklong
88	E	Phetchaburi	Phetchaburi	Maeklong
89	F	Pranburi	Phetchaburi	Maeklong
90	F	Pranburi	Phetchaburi	Maeklong
91	F	Pranburi	Phetchaburi	Maeklong
92	G	Not known	Phetchaburi	Maeklong
93	H	Not known	Prachuap Khiri Khan	Peninsula
94	H	Not known	Prachuap Khiri Khan	Peninsula
95	H	Not known	Prachuap Khiri Khan	Peninsula
96	H	Yang Khwang	Prachuap Khiri Khan	Peninsula
97	H	Khanan	Prachuap Khiri Khan	Peninsula
98	H	Khanan	Prachuap Khiri Khan	Peninsula
99	H	Khanan	Prachuap Khiri Khan	Peninsula
100	I	Ban Hin Pit	Prachuap Khiri Khan	Peninsula
101	J	Ban Chai Thale	Prachuap Khiri Khan	Peninsula
102	J	Not known	Prachuap Khiri Khan	Peninsula
103	K	Kariam	Prachuap Khiri Khan	Peninsula
104	L	Not known	Chachoengsao	Chao Phraya
105	L	Not known	Chachoengsao	Chao Phraya
106	L	Not known	Chachoengsao	Chao Phraya
107	M	Not known	Chachoengsao	Chao Phraya
108	M	Nangrong	Nakhon Nayok	Chao Phraya
109	M	Nangrong	Nakhon Nayok	Chao Phraya
110	N	Prachangkham	Prachin Buri	Chao Phraya
111	O	Paknam	Chon Buri	Chao Phraya
112	O	Tributary of Bangpakong	Chon Buri	Chao Phraya
113	P	Kongshi	Chon Buri	Chao Phraya
114	P	Kongshi	Chon Buri	Chao Phraya
115	P	Kongshi	Chon Buri	Chao Phraya
116	Q	Ban Than Trang	Chon Buri	Chao Phraya
117	Q	Ban Than Trang	Chon Buri	Chao Phraya
118	R	Chan Ta Than	Chon Buri	Chao Phraya
119	R	Chan Ta Than	Chon Buri	Chao Phraya
120	R	Chan Ta Than	Chon Buri	Chao Phraya
121	R	Phan Sadet	Chon Buri	Chao Phraya
122	R	Not known	Chon Buri	Chao Phraya



## Appendix 1 (continued).

Site number	Symbol	Stream/River	Province	River system
123	R	Not known	Chon Buri	Chao Phraya
124	S	Khao Ha Yot	Chon Buri	Chao Phraya
125	S	Khao Ha Yot	Chon Buri	Chao Phraya
126	S	Khao Ha Yot	Chon Buri	Chao Phraya
127	S	Khao Ha Yot	Chon Buri	Chao Phraya
128	S	Khao Ha Yot	Chon Buri	Chao Phraya
129	S	Khao Ha Yot	Chon Buri	Chao Phraya
130	S	Khao Ha Yot	Chon Buri	Chao Phraya
131	S	Khao Ha Yot	Chon Buri	Chao Phraya
132	S	Khao Ha Yot	Chon Buri	Chao Phraya
133	S	Khao Ha Yot	Chon Buri	Chao Phraya
134	S	Khao Ha Yot	Chon Buri	Chao Phraya
135	S	Khao Ha Yot	Chon Buri	Chao Phraya
136	S	Khao Ha Yot	Chon Buri	Chao Phraya
137	S	Khao Ha Yot	Chon Buri	Chao Phraya
138	S	Khao Ha Yot	Chon Buri	Chao Phraya
139	T	Surasak	Chon Buri	Chao Phraya
140	T	Surasak	Chon Buri	Chao Phraya
141	T	Surasak	Chon Buri	Chao Phraya
142	T	Surasak	Chon Buri	Chao Phraya
143	T	Surasak	Chon Buri	Chao Phraya
144	T	Surasak	Chon Buri	Chao Phraya
145	T	Surasak	Chon Buri	Chao Phraya
146	T	Surasak	Chon Buri	Chao Phraya
147	T	Surasak	Chon Buri	Chao Phraya
148	T	Surasak	Chon Buri	Chao Phraya
149	T	Surasak	Chon Buri	Chao Phraya
150	T	Surasak	Chon Buri	Chao Phraya
151	T	Surasak	Chon Buri	Chao Phraya
152	T	Surasak	Chon Buri	Chao Phraya
153	T	Surasak	Chon Buri	Chao Phraya
154	U	Khlong Ta Khong	Chantaburi	Mekong
155	V	Pong Nam Ron	Chantaburi	Mekong
156	W	Sato	Trat/ Chantaburi	Southeastern
157	W	Sato	Trat/ Chantaburi	Southeastern
158	W	Sato	Trat/ Chantaburi	Southeastern
159	X	Nam Tok Khlong Kaeo	Trat	Southeastern
160	X	Khao Mapring	Trat	Southeastern

