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Original Article

Fish species, relative abundances and environmental associations in small rivers of the Mae Klong River basin in Thailand

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ABSTRACT

Fish species were collected by electrofishing from 96 sites, representing 79 species, in lightly exploited rivers in western Thailand. Significant chemical and physical environmental factors associated with species numbers and total fish abundance were identified using multiple linear regression. Total abundance correlated negatively with water depth and temperature ($r = 0.4$, $p < 0.05$), whereas species numbers correlated positively with river discharge and negatively with elevation ($r = 0.6$, $p < 0.05$). Chemical and physical factors that significantly influenced species distribution were determined using partial least squares regression analysis, ($p < 0.05$; axes 1, $r = 0.8$; axes 2, $r = 0.85$), and included elevation, river discharge, width and depth as well as ambient oxygen, alkalinity and pH. Fish were placed into four categories according to their habitat occupancy and abundance and termed; uncommon (54 species), common (16 species), even (8 species) and uneven (1 species), respectively.

Introduction

Stream fish live in habitats characterized by species-favorable abiotic and biotic conditions and in some cases a small number of environmental factors exercise a strong influence on assemblage or community structure while in others the number is considerably larger (Robinson and Tonn, 1989; Edds, 1993). The importance of species-specific environmental factors on fish distribution has long been recognized in temperate regions (Brett and Groves, 1979; Jackson et al., 2001; Yamazaki et al., 2006) but is less well understood in tropical regions, particularly Southeast Asia, where species numbers are large (Smith, 1945; Nelson, 1994; Rainboth, 1996).

Watercourses in many regions of the world including Southeast Asia have been influenced by natural and anthropomorphic events (Tongnunui and Beamish, 2009). Changes in water quality can result from direct watershed or channel modifications such as from violent storms or dam construction (Han et al., 2007). Water quality may change also as a result of indirect modifications such as the replacement of native forests with agricultural crops or by urban or industrial land uses (Dale and Beyeler, 2001) in which functional interactions between a watercourse and adjacent lands have been altered. The direct discharge of effluents from urban and industrial sources is also a well documented modifier of water quality (Leelahakriengkrai and Peerapornpisal, 2010). So extensive have been these changes that at present, it is unlikely any river in this region can be considered as pristine (Dudgeon, 2000).

Freshwater fish in Thailand are known to exceed 600 species (Smith, 1945; Vidthayanon et al., 1997) with recent predictions of as many as 1200 species (Khachonpisitsak, 2012). Some species have become extinct or have drastically declined in abundance (Vidthayanon, 2005). Habitat degradation and loss are suggested as the major causes but confirmatory studies have not been reported (Vidthayanon and Roberts, 2005; Sa-ardrit and Beamish, 2005; Beamish and Sa-ardrit, 2007).

Thailand has developed an extensive vision in support of its natural resources with a mission to preserve, conserve, develop and rehabilitate natural resources to ensure their sustainability (Thailand Office of Natural Resources and Environmental Policy and Planning, 2010; Udomsri et al., 2005; Sripen et al., 2000). This vision includes a commitment to assess the status and potential of all natural resource sectors, including biological diversity. However, the actual status of fish species and their habitats, especially in smaller river tributaries, remains mostly undetermined (Suvarnaraksha, 2013).

The present study investigated species numbers, relative abundances and habitat associations of fish in a region of western Thailand within the Tanao Sri mountain range of Kanchanaburi

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province bordering Myanmar. This region has a relatively low human population and rivers that are only lightly exploited. The objective of the study was to identify species-specific habitat characteristics that may serve as future guidelines for conservation of Thailand's diverse and, in some cases, unique fish fauna.

Materials and methods

Study area

The region investigated consisted of tributary rivers that discharge into the Kwae Noi River, some via the Vajiralongkorn Reservoir in western Thailand, mostly within about 40 km of the border with neighboring Myanmar (Fig. 1). Site selections ($n = 96$) were made from representative landscapes and land use activities in the headwater tributaries of larger rivers. All sites were accessible by road. However, some sites could be reached only during the dry season and ranged from remote, heavily forested and sparsely inhabited to lightly settled areas where some subsistence to modest commercial agriculture occurred. Sites were not sampled closer than 150 m from the nearest bridge to avoid potential structure bias.

Fish collection, identification and relative abundance

Fish were captured using a back-pack electro-fisher (model 15 D; Smith-Root; Vancouver, WA, USA), with a variable output voltage (100–1100 V), pulse width (1–120 Hz) and frequency (100–8 ms). 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 60 Hz wave width and frequencies of 1–4 ms. Settings were made, based on experience, to reduce damage to fish, particularly the initial impact (Tongnunui and Beamish, 2009). Seines with 3 mm mesh were installed across the upper and lower limits of a site and their ground-lines massed with rocks to reduce emigration from or immigration into a sampling area. Each site was electro-fished by moving in a zigzag pattern from one retaining net to the other, usually beginning downstream but sometimes upstream when visibility was high and water velocity and depth, relatively low. Usually four to six passes were made at a site. Fishing was not conducted when turbidity impaired visibility or ambient conditions threatened researcher safety. Relative capture efficiency between an upstream and downstream direction of electro-fishing have been compared within several larger sites and not found to differ appreciably (Beamish et al., 2008). Few fish of any species less than 20 mm in total length were captured which was assumed to be the lower limit of vulnerability to the sampling procedure (Beamish et al., 2008). After capture, fish that could not be identified were killed using an overdose of methane tricaine sulfonate (more than 150 mg/L) and preserved, first in 10% formalin for 7 d and then in 70% ethanol for later identification and permanent preservation. Readily identifiable fish were enumerated and released into their capture habitat. The fish were identified from a number of sources (see Kottelat, 1984, 1988, 1989, 1990, 2000, 2001; Plongsesthee et al., 2011, 2013; Rainboth, 1996; Page et al., 2012; Randall and Page, 2012, 2015; Roberts, 1982; Tongnunui and Beamish, 2009). Fish names in this report are consistent with those reported in the University of California catalog of fish (Eschmeyer and Fricke, 2016). A voucher collection was prepared and is available from S. Tongnunui, Department of Conservation Biology, Mahidol University, Kanchanaburi Campus, Lum Sum, Sai Yok, Kanchanaburi, 71150, Thailand.

Relative abundances of species within a site were calculated using the maximum likelihood technique (Carle and Straub, 1978). However, numbers for some species were small and not amenable to this technique. For these species, a conversion factor consisting of the total abundance estimate divided by the total number of fish caught was applied to adjust numbers.

Measurement of environmental parameters

At each site, stream width (±0.1 m), depth (±1 cm) and water velocity (±1 cm/s) were measured and used to estimate the water discharge (L/s) as the product of mean depth, width and velocity. The depth and velocity were the average from 3 to 5 measurements made at approximately equal intervals across a transverse transect located at about the mid length of a site. The velocity was measured with a calibrated propeller current meter (model 2C; Ott; Kempten, Germany) at approximately mid depth which was recorded as the vertical average. Canopy was estimated visually as the percentage of sky blocked by foliage directly above a sampling river site with 100% representing complete cover. Dissolved oxygen, temperature, pH and conductivity were measured with regularly calibrated probes (models HI9147, HI98127 and HI9835, respectively; Hanna; Bangkok, Thailand). Ambient ammonia, total iron, nitrite, nitrate and silica were measured as described in American Public Health Association (1992). Elevation was measured using a calibrated global positioning meter (±10 m, model 60CSx; Garmin International; Kansas City, KS, USA). Sites were sampled throughout the year; however, season was not included as a habitat variable. An earlier study on several rivers in central Thailand (Beamish et al.,

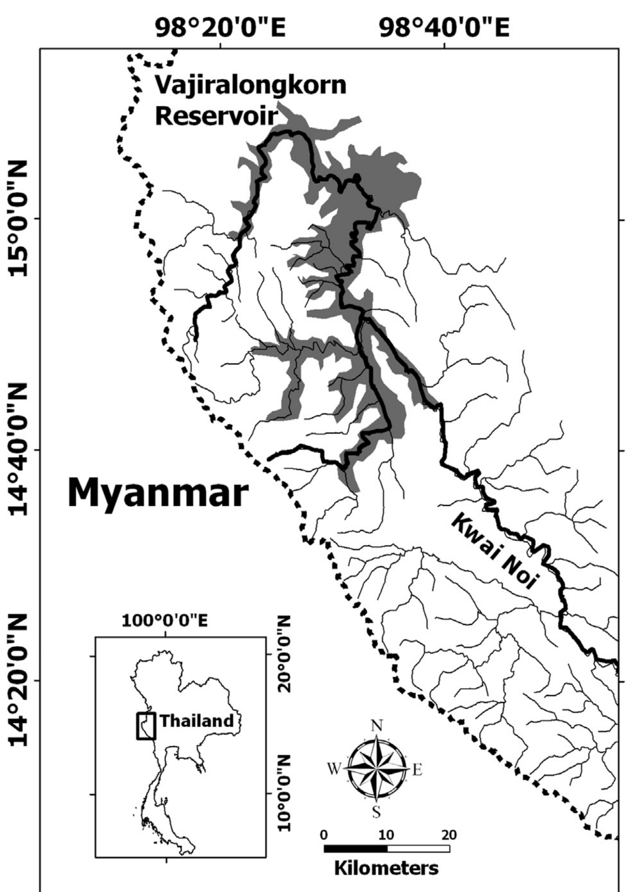

Fig. 1. Vajiralongkorn Reservoir in Thong Pha Phum district, Kanchanaburi province, Western Thailand, indicated by medium black coloration with Kwai Noi River including its pre-reservoir channel and tributaries indicated in dark black. The border between Thailand and Myanmar is indicated by a broken line.

2005) indicated seasonal changes in fish abundance and assemblage similarity varied inversely with discharge which was included in this study as a habitat variable. The substratum at each site was collected using a hand-held acrylic corer (5 cm inner diameter) to a depth of 10 ± 3 cm. Particles on the surface larger than the corer diameter were removed first but included in the sample. Samples were air dried and sieved to determine particle size distribution by weight. Six particle size categories were adopted from the Wentworth scale (Giller and Malmqvist, 1998) and coded into one of seven categories (see Tongnunui and Beamish, 2009).

Statistical analyses

The relationship between species numbers, total abundance of all fish and environmental parameters was examined using stepwise multiple linear regression analysis (MLR; version 14.5; SPSS Inc; Chicago, IL, USA) according to Steel and Torrie (1980). Species, their abundances and all environmental parameters, except for pH, were log (x+1) transformed to normalize the distribution of measured values. To avoid subjectivity, all independent variables were included in the full model with $p < 0.15$ used to assess variable inclusion and $p < 0.05$ for inclusion in the final model.

Partial least square regression (PLSR; version 2012; XLSTAT; New York, NY, USA) was used to reduce the effects of non independent or correlated environmental factors in describing their linear relationships for each of species' numbers and total fish abundance as well as species associations with environmental factors. PLSR increases the explained variance in dependent variables (Carrascal et al., 2009). The significance of environmental variables was accepted at $p < 0.05$. The importance of each significant parameter was illustrated by its vector length. A cross-validation procedure was used to assess model significance, to determine environmental factor extraction and to assign variance to independent variables (Wold, 1994; Hoffsten, 2004; Carrascal et al., 2009). Transformation [$\log_{10}(x+1)$] of species numbers and total fish abundances and all environmental variables except pH was applied to normalize the distribution of values ($p < 0.05$).

Results

The chemical and physical characteristics varied widely across sites but standard deviations of geometric means were not large for most environmental factors (Table 1). Species' site occupancies were highest for *Devario acrostomus* (76%), *Channa gachua* (72%) and *Barbodes banksi* (65%), followed by *Mastacembelus armatus* (59%), *Rasbora caudimaculata* (58%), *Paracanthocobitis zonalternans* (57%) and *Mystacoleucus chilopterus* (56%, Table 2). Most species were found at relatively few sites. Indeed, 68% of the species (54 of 79 species) were captured at fewer than 18% of the sites (17 of 96 sites).

Species numbers ranged from 1 to 30 per site with a geometric mean (±SD) of 13.7 ± 1.6 and related positively with discharge, and negatively with elevation. These relationships within the range of values measured in this study are described by Equation (1):

$$\text{Log}\,(S_r+1) = 1.727 \pm 0.277 + 0.148 \pm 0.033\,\log\,(D+1) - 0.408 \pm 0.112\,\log\,(E+1) \quad (1)$$

where S_r represents species numbers/site, D is the discharge, (measured in liters per second) and E is the elevation, (measured in meters above mean sea level). Regression coefficients are significant at $p < 0.05$ and are provided in the equation with their standard errors. The regression's F-value was 17.372 (2, 95 degrees of freedom, *df*; $p < 0.05$) and the correlation coefficient was 0.5 ($p < 0.05$). Over the range of sites, the equation predicts species numbers to increase with discharge in an asymptotic pattern for a given elevation (Fig. 2). Species numbers declined rather sharply with elevation to approximately 300 m and thereafter more gradually with few present at or above 800 m.

Total fish abundance ranged from 7 to 660 fish/100 m^2 among the 96 sites with a geometric mean of 180 ± 2.6 fish/100 m^2 and was negatively related with water depth and temperature within the range of values measured. This relationship is described by Equation (2):

$$\text{Log}\,(A_T+1) = 4.150 \pm 0.521 - 0.505 \pm 0.150\,\log\,(Dp+1) - 0.962 \pm 0.358\,\log\,(T+1) \quad (2)$$

where A_T is the total fish abundance (measured in fish/100 m^2), Dp is the depth (measured in centimeters) and T is the temperature (measured in degrees Celcius). The regression's F-value was 10.784 (2, 95 *df*, $p < 0.05$) and the correlation coefficient was 0.5 ($p < 0.05$). The regression coefficients were significant at $p < 0.05$ and are provided in the equation with their standard errors. The equation predicts total fish abundance to decline gradually from the highest values at seasonally low temperatures and to vary inversely with water depth (Fig. 3).

Fish species distribution was associated significantly with seven physicochemical variables (Fig. 4). Factors differed relatively little in importance based on vector lengths but considerably in the direction of influence. The mean relative abundance for most species (60%) was 0.1 or fewer individuals/100 m^2 (Table 2). The most abundant species (individuals/100 m^2) were *D. acrostomus* (37.2), *M. chilopterus* (24.4), *Osteochilus vittatus* (12.4), *B. banksi* (12.2) and *R. caudimaculata* (12.0). Of these, *D. acrostomus* associated with habitats of high elevation and low alkalinity (Fig. 4). In contrast, *M. chilopterus* and *O. vittatus* were captured most frequently where the elevation was low and the alkalinity was high. *B. banksi* and *R. caudimaculata* were associated with habitats of low discharge and ambient oxygen, shallow depth and narrow width. Other species displayed a broad array of associations with the significant environmental factors.

Table 1
Physical and chemical factors as geometric means (GM ± SD), and ranges for 96 studied sites in western Thailand.

Factor	Range	GM ± SD	Factor	Range	GM ± SD
Alkalinity (mg/L $CaCO_3$)	5–576	125 ± 3	Oxygen (mg/L)	1.8–9.5	7.4 ± 1.2
Ammonia (mg NH_3N/L)	0–1.0	0.03 ± 0.02	pH	6.5–8.5	7.6 ± 1
Canopy (% cover)	0–100	43 ± 3	Silica (mg SiO_2/L)	0.7–41.6	19.0 ± 2
Conductivity (μS/cm)	10–649	187 ± 3	Substratum (Code)	1–7	4.4 ± 1.5
Depth (cm)	5–74	28 ± 2	Temperature (°C)	17.3–31.2	24.5 ± 1.2
Discharge (L/s)	6–5491	509 ± 4	Total Iron (mg Fe/L)	0–5.1	0.3 ± 1.3
Elevation (m)	99–856	236 ± 2	Turbidity (NTU)	1–800	17 ± 2
Length (m)	3–130	32 ± 2	Velocity (cm/s)	3–38	32 ± 2
Nitrate (mg NO_3N/L)	0–8.6	1.5 ± 1.8	Width (m)	0.7–19	5.6 ± 1.7

Table 2
Occupancy and abundance as geometric means (GM±SD) by species across all studied sites in western Thailand rivers. Identification numbers (ID) are used in Figs. 4 and 5 to distinguish species.

Species	ID	Occupancy (% of sites)	Abundance (fish/100 m^2)
Even species (n = 8)			
Cyclocheilichthys apogon (Valenciennes, 1842)	5	24	2.2 ± 2.1
Garra fuliginosa (Fowler, 1837)	9	30	1.6 ± 2.2
Schistura vinciquerrae (Hora, 1935)	40	18	1.3 ± 2.0
Pseudomystus siamensis (Regan, 1913)	51	30	1.4 ± 2.1
Amblyceps caecutiens (Blyth, 1858)	58	48	2.0 ± 2.3
Xenentodon cancila (Hamilton, 1822)	64	45	1.0 ± 2.0
Monopterus albus (Zuiew, 1793)	65	23	1.0 ± 2.0
Pristolepis fasciata (Bleeker, 1851)	72	23	1.0 ± 2.0
Uneven species (n = 1)			
Brachydanio albolineata (Bleeker, 1850)	4	10	4.5 ± 1.5
Common species (n = 16)			
Devario acrostomus (Fang and Kottelat, 1999)	7	76	37.2 ± 7.0
Garra sp.	10	20	2.7 ± 2.6
Mystacoleucus chilopterus (Fowler, 1935)	16	56	24.4 ± 6.0
Neolissochilus stracheyi (Day, 1871)	17	22	5.0 ± 2.7
Osteochilus vittatus (Valenciennes, 1842)	21	48	12.4 ± 4.6
Rasbora caudimaculata (Volz, 1903)	28	58	12 ± 4.3
Barbodes banksi (Herre, 1940).	29	65	12.2 ± 4.2
Paracanthocobitis zonalternans (Blyth, 1860)	33	57	6.7 ± 3.5
Balitora burmanica (Hora, 1932)	34	30	2.5 ± 2.6
Homalopteroides smithi (Hora, 1932)	35	51	3.7 ± 3.0
Schistura sexcauda	39	43	7.6 ± 4.0
Schistura aurantiaca (Plongsesthee et al., 2011)	41	46	7.7 ± 4.0
Lepidocephalichthys berdmorei (Blyth, 1860)	48	43	4.3 ± 3.0
Batasio fluviatilis (Day, 1888)	52	48	2.7 ± 2.5
Mastacembelus armatus (Lacepede, 1800)	69	59	3.0 ± 1.0
Channa gachua (Hamilton, 1822).	75	72	7.6 ± 3.4
Uncommon species (n = 54)			
Cyclocheilichthys armatus (Val. in Cuv. and Val, 1842)	1	1	<0.1
Notopterus notopterus (Pallas, 1769)	2	5	0.1 ± 1.2
Barbonymus gonionotus (Bleeker, 1850)	3	2	<0.1
Cyclocheilichthys heteronema (Bleeker, 1854)	6	8	0.3 ± 1.4
Garra cambodgiensis (Tirant, 1884)	8	1	0.1 ± 1.2
Hampala macrolepidota (Kuhl and van Hasselt, 1823)	11	16	0.3 ± 1.5
Labiobarbus siamensis (Sauvage, 1881)	12	1	<0.1
Labiobarbus leptocheilus (Val in Cuv and Val, 1842)	13	2	<0.1
Lobocheilus quadrilineatus (Fowler, 1835)	14	1	<0.1
Lobocheilus rhabdoura (Fowler, 1834)	15	1	<0.1
Neolissochilus soroides (Duncker, 1904)	18	3	0.6 ± 1.6
Opsarius koratensis (Smith, 1931)	19	14	0.3 ± 1.5
Opsarius pulchellus (Smith, 1931)	20	1	<0.1
Osteochilus waandersii (Bleeker, 1852)	22	4	0.4 ± 1.5
Parachela maculicauda (Smith, 1934)	23	1	<0.1
Poropuntius deauratus (Valenciennes, 1842)	24	1	<0.1
Puntius brevis (Bleeker, 1850)	25	5	0.1 ± 1.2
Puntius masyai (Smith, 1945)	26	2	<0.1
Rasbora borapetensis (Smith, 1934)	27	1	<0.1
Systomus orphoides (Val in Cuv and Val, 1842)	30	15	2.1 ± 2.3
Pethia stoliczkana (Day, 1869)	31	15	1.0 ± 2.0
Acanthocobitis botia (Hamilton, 1822)	32	10	0.3 ± 1.5
Pseudohomaloptera leonardi (Hora, 1941)	36	1	<0.1
Homalopteroides modestus	37	1	<0.1
Nemacheilus masyae (Smith, 1983)	38	16	0.6 ± 1.7
Schistura mahnerti	42	2	<0.1
Pseudohomaloptera sexmaculata	43	4	0.3 ± 1.4
Tuberoschistura baenzigeri (Kottelat, 1983)	44	8	0.2 ± 1.3
Acanthopsis sp.	45	4	0.2 ± 1.4
Syncrossus beauforti (Smith, 1931)	46	4	<0.1
Yasuhikotakia morleti (Tirant, 1885)	47	3	<0.1
Lepidocephalichthys hasselti (Val in Cuv and Val, 1846)	49	3	0.5 ± 1.5
Pangio anguillaris (Vaillant, 1902)	50	6	0.2 ± 1.3
Mystus singaringan (Bleeker, 1864)	53	2	<0.1
Mystus cavasius (Hamilton, 1822)	54	2	<0.1
Hemibagrus nemurus (Valenciennes, 1840)	55	17	0.4 ± 1.5
Ompok cf bimaculatus (Bloch, 1794)	56	10	0.1 ± 1.3
Pterocryptis cochinchinensis (Valenciennes, 1840)	57	15	0.2 ± 1.4
Glyptothorax laonensis (Fowler, 1934)	59	2	<0.1
Glyptothorax major (Boulenger, 1894)	60	1	0.1 ± 1.2
Glyptothorax sp.	61	9	0.1 ± 1.3
Clarius batrachus (Linnaeus, 1758)	62	1	<0.1
Dermogenys pusillus (van Hasselt, 1823)	63	1	<0.1

(*continued on next page*)

Table 2 (*continued*)

Species	ID	Occupancy (% of sites)	Abundance (fish/100 m^2)
Macrognathus circumcinctus (Hora, 1924)	66	2	<0.1
Macrognathus sp.	67	2	<0.1
Macrognathus semiocellatus (Roberts, 1986)	68	1	<0.1
Parambassis siamensis (Fowler, 1937)	70	5	<0.1
Badis khwae (Kullander and Britz, 2002)	71	14	0.2 ± 1.4
Oxyeleotris marmorata (Bleeker, 1852)	73	5	0.3 ± 1.4
Trichogaster trichopterus (Pallas, 1770)	74	9	0.3 ± 1.5
Channa lucius (Cuv in Cuv and Val, 1831)	76	4	0.6 ± 1.5
Channa micropeltes (Cuv in Cuv and Val, 1831)	77	1	<0.1
Channa striata (Bloch, 1797)	78	8	0.1 ± 1.2
Tetraodon suvatti (Sontirat and Soonthornsatit, 1985)	79	8	0.1 ± 7.6

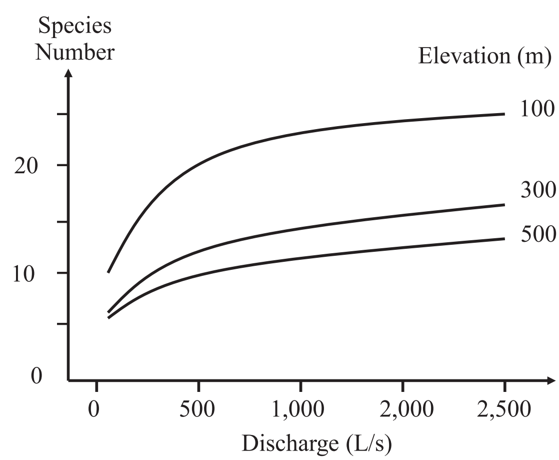

Fig. 2. Number of species/site in relation to site discharge (l/s) and elevation (m) for mean of the approximate mean width (m) and depth (cm) in the present study. Numbers were calculated from the regression (see text) for the approximate range of discharge and elevation measured at the sites.

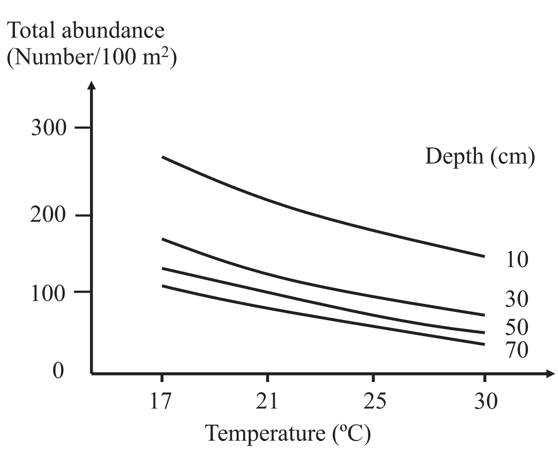

Fig. 3. Total abundance of all species in relation to water depth and temperature. Numbers were calculated from the regression (see text) for the approximate range of depth and temperature measured at the sites in this study.

Generally, abundant species were found at many sites although there were exceptions. Those that occupied more than the average number of sites (more than 17 sites) and at above average abundance (more than 2.3 fish/100 m^2) were designated 'common' species and included some shoaling species—*D. acrostomus*, *M. chilopterus*, *O. vittatus*, *B. banksi*, and *R. caudimaculata*. One shoaling species, *Brachydanio albolineata*, occupied fewer than the average number of sites (less than 17 sites) but was abundant when present (Table 2 and Fig. 5). This species was designated as 'uneven' to reflect its low site occupancy but high relative mean abundance when present (more than 2.3 fish/100 m^2). Most species were below average in abundance with some occupying many sites while others occupied only a few sites. Species that occupied many sites (more than 17 sites) but at low abundance (less than 2.3 fish/100 m^2) were grouped as 'even' and those that occupied few sites (less than 17 sites) as 'uncommon' (Fig. 5). Some uncommon species were quite abundant at a very small number of sites. Thus, abundances of two uncommon species, *Systomus orphoides* and *Pethia stoliczkana* were very low over all sites but about average based on the 14 sites where they were captured. However, the majority of uncommon species were represented by only 1 or 2 individuals among all sites.

Discussion

Distributions of freshwater fish in Southeast Asian rivers are attributed frequently to a range of factors such as climate, stream morphology and chemical and biotic factors but seldom have these variables been measured, with welcome exceptions being the studies by Beamish et al. (2008), Tongnunui and Beamish (2009) in central and eastern Thailand, and studies by Suvarnaraksha et al. (2012) in the Ping-Wang River basin. Undoubtedly, many of these habitat associations reflect evolved morphological, physiological and behavioral adaptations (for example, Alibone and Fair, 1981; Anderson et al., 2001; Coombs et al., 2007; Nithirojpakdee et al., 2012, 2014). However, linkages, particularly those with physiological and behavioral adaptations, remain poorly understood for Thai freshwater fish although they are certain to be important in providing ecological guidance in restoring or repairing damaged river ecosystems.

Fish found in the small rivers of western Thailand displayed distinctive associations with an array of habitat characteristics. Most were related to physical habitat although some chemical factors, dissolved oxygen, pH and alkalinity were also important, an observation generally consistent with the earlier findings by Beamish et al. (2008), Tongnunui and Beamish (2009) and Suvarnaraksha et al. (2012). Species numbers and total fish abundance in western Thailand each related significantly with only two physical characteristics, being water discharge and elevation for the former and depth and temperature, for the latter. High elevation sites were located on low-order tributaries where habitat diversity, discharge and productivity tended to be low and in keeping with low species numbers and abundance. At lower elevation sites habitats and species displayed greater diversity.

Many benthic species within the Cyprinidae, Balitoridae, Gobiidae and Siluriformes associate with fast flowing water and have dorso-ventrally flattened bodies that lower drag and lift,

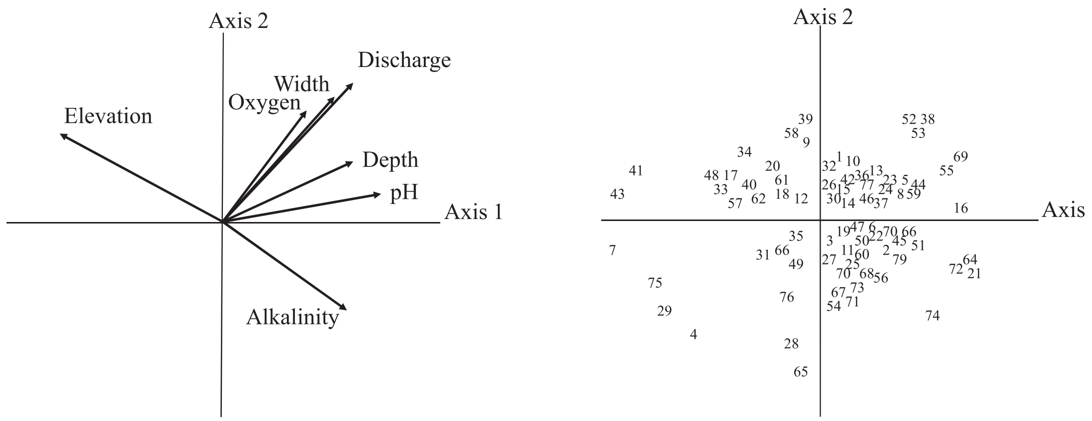

Fig. 4. Distribution of species in small western rivers with respect to significant environmental variables identified by partial least square regression. Axes 1 and 2 are correlation matrices of environmental variables and species. Vector length signifies factor importance and arrow, the direction of increasing quantities. Species are identified by numbers (Table 2).

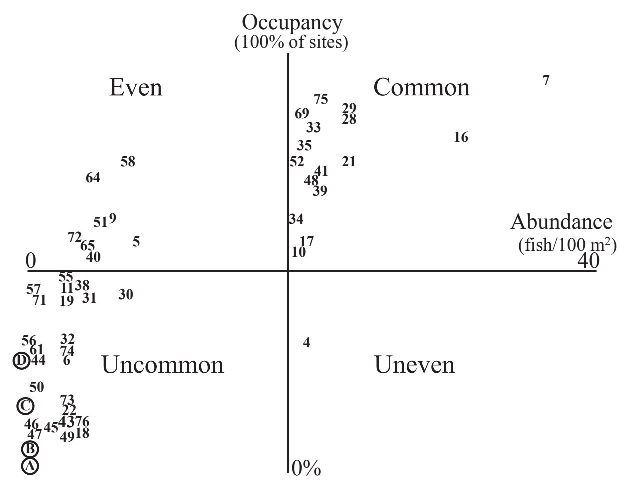

Fig. 5. Relative abundance and occupancy of fish species in small rivers of western Thailand. The x-axis indicates abundance of each species, represented by their mean number of fish/100 m^2 calculated for all sites. Species ranged in abundance from more than 0 to less than 40 fish/100 m^2. The y-axis indicates species site occupancy as number of sites at which species were found as a percentage of the all sites (0–100%). Species are grouped by relative abundance and site occupancy into common, uncommon, even and uneven (see text). Overall geometric mean abundance and occupancy were 2.3 fish/100 m^2 and 17% of sites, respectively. Numbers for species identification are listed in Table 2. Uppercase letters indicate clusters of species: A contains species 1, 8, 12, 14, 15, 20, 23, 24, 27, 36, 37, 60, 62, 63, 68, 77; B contains species 3, 13, 26, 42, 53, 54, 59, 66, 67; C contains species 2, 25, 70 and D contains species 78 and 79.

easing station holding behavior. Further, many of these benthic species have laterally extended pectoral and pelvic fins that can be partially rotated effecting lift and drag. Thoracic adhesive adaptations in the silurid, *Glyptothorax* (Ng and Hadiaty, 2008), ridges (Hora, 1930) or adhesive pads on the ventral surface of pectoral and pelvic fins (Alfred, 1969; Page et al., 2012; Biswas and Boruah, 2000; Plongsesthee et al., 2011; Beamish and Plongsesthee, 2015.) likely serve as friction devices further facilitating station holding on or near the substrate. Species differences in paired fin areas suggest a degree of habitat specialization among loaches with respect to current speed. For example, pectoral fin areas for *Pseudohomaloptera leonardi, Homalopteroides smithi* and *S. kohchangensis* adjusted to a total length of 50 mm, were 47 cm^2, 43 $cm^2$and 38 cm^2, respectively (F.W.H. Beamish, data not shown). In accord, Nithirojpakdee et al. (2012) reported *P. leonardi* occurred most frequently at micro riffle velocities of 175 ± 43 cm/s followed by *H. smithi* and *S. kohchangensis* at 39 ± 27 cm/s and 34 ± 19 cm/s, in broad agreement with pectoral fin areas.

Many river fish are morphologically adapted for sustained and prolonged swimming that can be inferred from the shape and size of their body and fins (Beamish, 1978; Daniel and Webb, 1987). Forward swimming, 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 as *O. vittatus* and *M. chilopterus* are able to swim at fast speeds and where currents are high. Species that associate with large rivers, especially where macrophytes abound, may exhibit appropriate morphological modifications such as maneuverability. Fast swimming under these conditions requires high rates of centripetal acceleration which is best achieved by fish with a short body length in which the body mass and depth are centrally concentrated as in *Puntius brevis*. Low speed maneuverability requires orienting thrust in many directions using large or long and flexible fins, capable of independent motion along their length. A deep body, as occurs in *Cyclocheilichthys apogon*, provides maneuverability but not fast speeds consistent with needs in their debris-cluttered, slow-flowing habitat. While morphologies of Thai freshwater fish are important in defining habitat, it is likely that physiological and behavioral adaptations will also be found to be important contributors (Helfman et al., 2009; Beamish et al., 2012).

Fish abundance in this study was highest during seasonally low temperatures, perhaps reflecting species recruitment patterns. Abundance declined during the following months, likely as a consequence of natural mortality, particularly among recruits (Smith and Reay, 1991; Houde, 1997) and possibly due to thermal avoidance, as ambient temperatures reached the high 20s. Thermal preferences appear not to have been measured for any freshwater species in Thailand. Interestingly, final preferential temperatures for a number of temperate fish species range between about 25 °C and 31 °C (Fry, 1971; Cooke and Philipp, 2009) in general accord with the temperatures at which abundances in the present study declined (Beamish and Sa-ardrit, 2007; Beamish et al., 2005).

The majority of common species in the present study, indeed, almost 70%, were captured at sites of below average width, depth and discharge in which oxygen and pH were also below average. In contrast, uncommon species were equally divided among habitats where significant environmental factors were above and below average values. Dissolved oxygen allows access to energy that fuels aerobic activities. Oxygen requirements vary among species under similar biological and environmental circumstances (Fry, 1971). The influence of dissolved oxygen on species occurrence in the present study is, almost certainly, a partial expression of their diverse requirements and extraction efficiencies. Habitat for some species is associated with regions of comparatively high dissolved oxygen while others are less sensitive. Often, less sensitive species have ancillary respiratory mechanisms such as the lung-like labyrinth organ present in *Trichogaster trichopterus*, the supra-branchial organ present in *Channa lucius*, *C. gachua*, and *Clarias batrachus* (Smith, 1945; Helfman et al., 2009) or the probability of cutaneous respiratory subsidy in small scaled (such as *H. smithi* and *Lepidocephalichthys hasselti*) or scale-less species (such as *Mystus* sp. and *Glyptothorax laosensis*).

Conflicts of interest

The authors declare that there are no conflicts of interest.

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