การปรับตัวของปลาในแม่น้ำก่อให้เกิดความสมบูรณ์ของชนิดของปลา
Adaptations in River Fishes Facilitate Species Richness

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บทคัดย่อ

แนวความคิดของสิ่งแวดล้อม (The cooncept of environmental) การปรับตัวทางด้านการกินอาหาร เป็นแนวคิดที่มีความสัมพันธ์เกี่ยวเนื่องกันกับลักษณะทางฟีโนไทป์ หรือ จีโนไทป์ ซึ่งถือเป็นสิ่งสำคัญที่ช่วยให้สิ่งมีชีวิตต่างๆ สามารถดำรงชีวิตและรับมือกับลักษณะอันจำเพาะของแต่ละแหล่งที่อยู่อาศัยได้ดีขึ้น รวมทั้งสิ่งมีชีวิตอื่นๆ ด้วย ซึ่งจะมีประโยชน์ในวงกว้างสำหรับการทำความเข้าใจเกี่ยวกับความชุกชุมของสิ่งมีชีวิตกับการอยู่ร่วมกันของสิ่งมีชีวิต ในสภาวะแวดล้อมที่มีการเปลี่ยนแปลงไปมาอยู่ตลอดเวลาของแหล่งน้ำในประเทศไทย อันเป็นแหล่งที่อยู่อาศัยของปลา ทำให้ปลาต้องปรับตัวเพื่อให้เข้ากับคุณลักษณะทางเคมีกายภาพ อาจก่อให้เกิดความหลากหลายของสิ่งมีชีวิตมากขึ้นการศึกษาในครั้งนี้จึงมีวัตถุประสงค์เพื่อศึกษาลักษณะทางเคมีกายภาพในแหล่งน้ำต่างๆ ในภาคกลางของประเทศไทย ที่มีผลต่อปลาสองวงศ์ ซึ่งอาศัยร่วมกันในแหล่งน้ำเดียวกัน คือ วงศ์ปลาตะเพียน (Cyprinidae) และ วงศ์ปลาจิ้งจก (Balitoridae) และ ปลาอันดับ Siluriformes การปรับตัว เกิดขึ้นทั้งในรูปแบบของการกินอาหาร รูปแบบของการกินอาหารเป็นการปรับตัวอย่างหนึ่งโดยปลาที่อยู่อาศัยอยู่บริเวณเดียวกันสามารถอยู่ร่วมกัน ด้วยการแบ่งสรรทรัพยากรอาหารและมีความหลากหลายของสิ่งมีชีวิต และค้านกับหลักการเบื้องต้นของการกำจัดสิ่งมีชีวิตจากการแข่งขัน (Theory of competitive exclusion) ความแตกต่างของชนิดอาหารของปลาเพียงเล็กน้อย แต่มีความสำคัญซึ่งเป็นการลดการแข่งขันในและเป็นการเพิ่มโอกาสที่ส่งเสริมให้มีความหลากหลายของชนิดปลา นอกจากนี้การปรับตัวทางด้านการสืบพันธุ์ทั้งทางด้านความดกไข่และขนาดของไข่ของวงศ์ปลาจิ้งจก (Balitoridae) ซึ่งจะมีลักษณะใกล้เคียงกันเป็นสิ่งสำคัญที่นำมาซึ่งความคงอยู่ของขนาดประชากรปลาทั้งหมด

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Abstract

The concept of environmental, feeding and reproductive adaptations refers to phenotypic-or genotypic related characteristics that enable an organism to better cope with specific habitats including other biota and has wide application in understanding species richness and co-existence. Conditions vary within rivers in Thailand providing habitats for those fishes adapted for the physico-chemical conditions and may facilitate high species diversity. The present study describes the physico-chemical qualities in a large number of rivers in central Thailand as well as those characteristics associated with the habitat occurrences of species within two families, Cyprinidae and Balitoridae and one Order, Siluriformes. Adaptations occur also in feeding patterns by fishes occupying similar habitats allowing for resource sharing and species diversity and counter the theory of competitive exclusion. Small but perhaps important dietary differences among species further lessen competition and enhance opportunities for species diversity. Reproduction adaptations in fecundity and oocyte diameter among closely related species within the Familiy Balitoridae are suggestive of further adaptations for stability in overall fish population size.

Keywords : adaptations, environment quality, feeding, reproduction, species diversity.

INTRODUCTION

The diversity of freshwater fishes in Thailand and other countries in Southeast Asia is among the greatest in the world, especially on the basis of geographic area. The species richness in Southeast Asian rivers is in contrast to what might be predicted from the view that competition and predation are the most important factors controlling both species and numbers of fish. The concept of competitive exclusion held by some (Gilpin & Justice, 1972; McGehee & Armstrong, 1977), assumes communities exist at competitive equilibrium. This concept applies under conditions of habitat stability and uniformity and for species dependent on exactly the same resources. In contrast, physical and chemical conditions, predation and other factor are continually imposing their influence on population sizes and the nature of competitive interactions, making it likely that competitive equilibrium rarely occurs, if at all (Wiens, 1977; Huston, 1979).

Even if competitive equilibrium is never achieved, the expected outcome of competition might be an eventual predominance of only a few competitors. Recent theoretical evidence suggests this need not occur where life history variations differ such that an advantage at one stage implies a disadvantage at another stage of the life cycle (McCann et al., 1998). Where life history strategies or tactics do not imply advantages, increasing intensity of competition should result in a decrease in species evenness and eventually species number. Intense competition should result in low diversity among competing species and high diversity might be expected where competition is weak. This suggests that in Southeast Asia, species success may relate in part to acquired physiological advantages including those associated with environmental quality that allow them to occupy habitats unsuitable for other species. Advantages may occur in relation to diet and feeding schedules that allow species to share rather than compete for resources. Variation in modes of reproduction may also contribute to species coexistence success. Adaptive responses have been described as a tactic if phenotypic or strategy if genotypic in origin (Muller et al., 2007). However, for this report, adaptation will be used to represent both phenotypic- and genotypic- derived responses as sufficient information to categorize responses is unavailable.

The present study examines variations in species occurrences in relation to environmental quality for some fishes commonly found in the headwaters of Thai rivers. Documentation is provided also on diet, feeding schedules and fecundity for some commonly occurring fishes in headwater rivers. These variations are considered in relation to the rich diversity of fishes found in the rivers of Thailand.

MATERIAL AND METHODS

Thailand's aquatic ecosystems are supported by six major watersheds (Vidthayanon et al., 1997). Of these, sites on five watersheds or river systems were sampled in this study. Mekong, Chao Phraya, Maeklong, Peninsular and Southeast (Figure 1). The study area lies between latitudes of approximately 11° and 15° N and longitudes of approximately 97° 30° and 102° 60°E representing an area of about 23,000 km^2.

Sites were road-accessible. Some of the sites on which environmental associations were determined 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 to more heavily farmed or urban areas. Most of the 159 sites sampled for the environmental association study were located in Maeklong (n= 91) and Chao Phraya (n= 50) river systems. In Maeklong river systems, most sites (n=81) were located on streams that either discharge directly to Kwae Noi River or indirectly via the Khao Laem reservoir in Kanchanaburi province. Kwae Noi River flows into River Kwae and then Maeklong River before discharging into the Gulf of Thailand. The remaining eight sites were located in Petchaburi province.
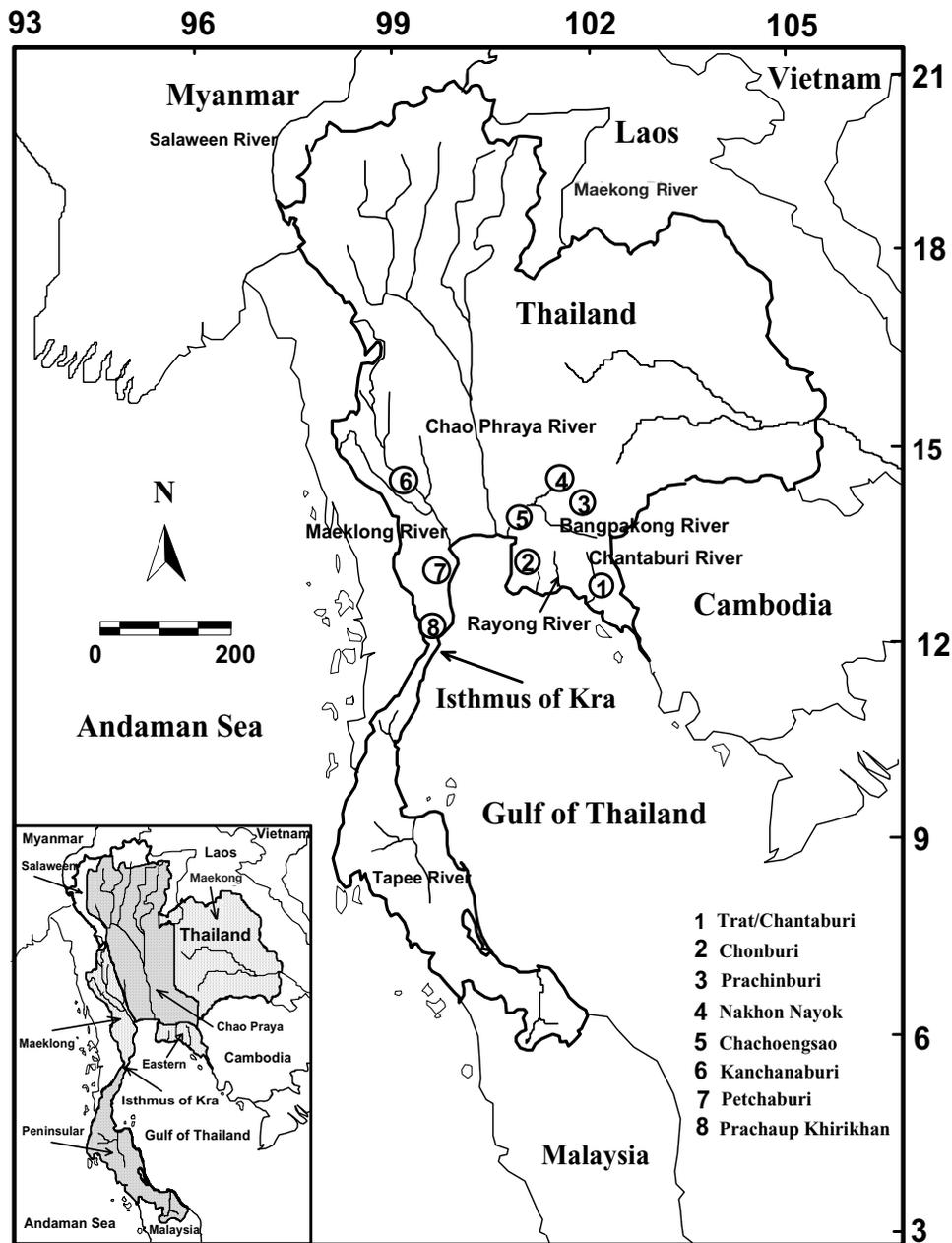
Figure 1. Map of Thailand. The larger map indicates the major rivers, provinces and neighboring countries. The study area was bounded to the north between approximately 13° 15¹ latitude and 102° 15¹ longitude to the east and 15° latitude and 98° 40¹ longitude to the west. In the west, the southern boundary extended across the Peninsula at approximately 11° latitude. The inset map indicates the location of the six river systems of Thailand.

Sites in Chao Phraya watershed were on small rivers within Chonburi, Chachoengsao, Nakhon Nayok and Prachinburi provinces. The 11 sites sampled from the Peninsular river system were in Prachuap Khirikhan province while the seven sites in the Eastern river system were located on streams in the eastern portions of Chantaburi and Trat provinces.

Studies on fish feeding schedules were conducted at sites on headwater tributaries of Chantaburi River in Eastern watershed. Studies on fish reproduction were conducted at sites on Rayong and Khong rivers in Chantaburi; several headwater tributaries of Kwae Noi River in Kanchanaburi province and one site on Shikoo River in Prachuap Khirikham province.

Sites for the environmental study were chosen where channel width, water depth, canopy and substratum composition did not vary substantially within the study reach. An effort was made also to select sites where the distribution of substratum particle size was similar throughout site length. The imposition of these habitat constraints restricted the length of most sites to under 50 m.

Fish were captured for the environmental and feeding studies by non lethal electrofishing with a Smith-Root, model 15 D backpack electro-fisher. Output voltage was varied mostly between 200 and 600 volts in combination with a wave width of 60 Hz and frequencies of 1-4 ms. Fish were captured for the fecundity study with an Abp2 Electrofisher (University of Wisconsin, USA) set at 250 V with an frequency rate of 60-70 pps and duty cycle of 10- 20%. In all cases seine nets with mesh of about 3 mm were installed across the upper and lower limits of a site to reduce the probability of emigration from or immigration to the study site. Usually four or five passes were made at a site to estimate fish abundance (Carle & Strub,1978).

After each pass, fish captured for the environmental study were anaesthetized in methaine tricaine sulfonate (approximately 150 mg•l^{-1}), and those fishes that could confidently be identified were enumerated and, after recovery, released downstream from the site. Fish to be used for the feeding and fecundity studies were killed by an overdose of methaine tricaine sulfonate after capture and preserved. When fishes could not be identified in the field they were killed by an overdose of anesthetic and preserved in 10% formalin for subsequent identification in the laboratory. Fish were identified from a number of sources (Beamish et al., 2008). We used the names of fishes given in the University of California catalogue of fishes (Eschmeyer, 2008).

On each sampling occasion in the environmental study, width (±0.1 m), depth (±1 cm) and velocity (±1 cm•s^{-1}) were measured, each at least three times, and the mean used to estimate discharge (l•s^{-1}). Canopy was estimated visually with 100% representing complete cover. Regularly calibrated meters were used to measure temperature (±0.1°C), conductivity (±5 μS•cm^{-1}), turbidity (NTU), pH (±0.1 unit) and dissolved oxygen (±0.1 mg•l^{-1}). Measurements of other chemicals were made using methods in APHA (1992). Elevation was measured with a Global Positioning Systems meter (±10 m). Sites were sampled through the year, however, season was not included as a habitat variable. An earlier study by Beamish et al., (2005) indicated seasonal changes in fish relative abundance and assemblage structure from several streams in Central Thailand to vary inversely with discharge which was included in this study as a habitat variable.

Substratum at each site was collected with a hand-held acrylic corer (5 cm inner diameter) to a depth of 10±3 cm. Particles on the surface larger than the diameter of the corer were removed before a sample was taken and included in the estimate. Six particle size categories were adopted from the Wentworth scale (Gillner & Malmqvist, 1998), and coded 1 to 6 with 1 being the smallest: <0.5 mm (medium sand to silt), 0.51-3 mm (fine gravel to coarse sand), 3.1-5 mm (medium to fine gravel), 5.1-60 mm (large pebble to coarse gravel), 60.1-150 mm (large cobble to large pebble), >150 mm (boulder to large cobble). The substratum at a few sites was solid or almost solid bedrock and coded as 7.

Feeding periodicity was based on the weight of stomach contents from fish collected at 6 h intervals over 24 h periods. After capture fish were killed in an overdose of anesthetic and preserved, first in 10% formalin for one week, then in 80% ethanol for permanent storage. An incision was made in the abdomen of fish to expedite preservation of the stomach contents. Prior to stomach removal and after preservation in formalin and ethanol, fish were weighed ($\pm$0.1 mg) and standard length ($\pm$1.0 mm) measured. Stomach contents were represented by the material retrieved from that portion of the digestive tract between the cardiac and pyloric sphincters. After placing stomach contents of fish on a tissue to remove excessive water, stomach contents were weighed ($\pm$0.1 mg).

Fecundity was measured on fish species within the family Balitoridae. Fish were captured at approximately monthly intervals, measured for total length ($\pm$1.0 mm), given a diagnostic mark and preserved as in the feeding study. Gonads (ovary or testes) were removed, weighed ($\pm$0.1 mg) and preserved in Gilson's fluid. Gonadosomatic index, (GSI) was determined as gonad weight relative to total (Brewer *et al.,* 2008). Total counts of oocytes or eggs were made when under 1000 or, when over 1000, as duplicate subsamples each approximately 10% of the total volume (Bagenal & Braum, 1968). Maximum diameters of 10 oocytes from each female were measured under a microscope with a micrometer.

Canonical correspondence analysis (CCA, PC-ORD 3.2) was employed to identify important species-related environmental characteristics. Species richness, species abundances and environmental variables were centered and normalized within the program. In the canonical correspondence analysis, statistical significance of the relationship between a set of environmental factors and fish species was taken using a Monte Carlo permutation test with 1000 permutations. Statistical significance of all tests was accepted at P<0.05.

Total relative abundance of all fishes as well as individual species within a site were calculated by the maximum likelihood technique (Carle & Straub, 1978). Numbers for many species were small and not amenable to this technique. When this occurred a conversion factor consisting of the estimated total abundance of all fish captured at a site divided by total number of all fish actually caught at the same site was applied to adjust the numbers of each species captured. Fish relative abundance was arithmetically adjusted to an area of 100 m^2.

Weights of stomach contents for individuals of each species were transformed by log (x+1) to normalize their distributions at each sampling time and expressed as linear regressions against corresponding standard lengths. Regressions for the four sampling times were compared for each species by ANCOVA (P<0.05). Adjusted mean values were compared among sampling times with ANOVA (P <0.05)

RESULTS

Water quality varied greatly among sites within and among river systems. At sites within Maeklong river system, water was, on average, a few degrees cooler and higher in pH and alkalinity than in the other river systems. Water at the Chao Phraya sites was, on average, highest in ammonia, nitrate, total iron, color and turbidity. Physical habitat characteristics such as water depth and velocity, substrate composition and canopy while diverse within river systems, were broadly similar among river systems. Substrate composition varied from sand to bedrock among sites but gravel was the average particle size within each river system. Canopy ranged from full cover to total exposure but was mostly in the range of 15-30% cover. The two exceptions were river width and discharge that were, on average, least in the Chao Phraya river system. Elevation was mostly between 100 and 300 m, with an overall mean of 176$\pm$ 1.3 m.

Table 1. Geometric means, standard deviations (SD) and approximate ranges for the important physico-chemical characteristics of all sample sites for species associations within the Families Cyprinidae andBalitoridae and the Order, Siluriformes. Physico-chemical characteristics not found to be statistically significant are not given.

	Mean	SD	Range
Elevation, m	176	1.3	92-853
Width, m	4.8	1.8	0.7-18.7
Depth, cm	23	2	7-<100
Velocity, cm s-1	25	2	<2- 86
Discharge, I s-1	211	5	<50->1000
Substrate*	4.2	1.4	0-7
Temperature, C	24.6	1.1	16.9->30
Conductivity, μS cm-1	121	2	20->350
Turbidity, NTU	7	2	<1->50
Color, CU	20	3	9->100
pH	7.3	0.6	4.0-8.5
Oxygen, mg l-1	7.3	1.2	4.7->9.0
Ammonia, μg l-1	40	108	0->500
Nitrate, mg l-1	1.3	1.7	0.4->5
Total iron, mg l-1	0.4	1.3	<0.3->2.0
Silica, mg l-1	16.5	1.6	<4->40

Table 2. Incidences of occurrence, %, and geometric mean abundance of cyprinid species adjusted to an river area of 100 m^2. Means were calculated from values at sites where the species was present. ID represents the identification number assigned each species (Figure 2).

	ID	Incidence of Occurrence, (%)	Mean Abundance (N 100m^2)
Cypriniformes			
Cyprinidae			
Amblyrhynchichthys truncatus (Bleeker 1851)	17	<1	1.1
Barbodes gonionotus (Bleeker 1850)	22	<1	1.3
Danio albolineatus (Blyth 1860)	7	25	19.0
Crossocheilus reticulatus (Fowler 1834)	36	2	37.0
Cyclocheilichthys apogon (Valenciennes. 1842)	18	16	2.5
Cyclocheilichthys armatus (Valenciennes 1842)	19	6	2.5
Cyclocheilichthys heteronema (Bleeker 1850)	20	<1	1.8

	ID	Incidence of Occurrence, (%)	Mean Abundance (N 100m^2)
Devario acrostomus (Fang & Kottelat 1999)	8	39	20.1
Esomus metallicus Ahl 1924	9	3	7.1
Garra cambodgiensis (Tirant 1884)	37	2	4.1
Garra fuliginosa (Fowler 1837)	38	13	4.3
Garra sp.	39	12	7.0
Poropuntius hampaloides (Vinciguerra 1890)	24	12	1.5
Labiobarbus siamensis (Sauvage 1881)	31	<1	0.3
Labiobarbus leptocheilus (Valenciennes 1842)	32	2	2.5
Lobocheilus quadrilineatus (Fowler 1835)	33	<1	0.4
Lobocheilus rhabdoura (Fowler 1834)	123	<1	0.4
Mystacoleucus marginatus (Valenciennes 1842)	21	43	12.8
Neolissochilus blanci (Pellegrin & Fang 1940)	15	3	5.2
Neolissochilus stracheyi (Day 1871)	16	19	8.0
Neolissochilus soroides (Duncker 1904)	119	2	15.7
Onychostoma gerlachi (Peters 1880)	114	<1	0.6
Opsarius koratensis (Smith 1931)	4	6	4.6
Barilius pulchellus (Smith 1931)	5	<1	5.1
Osteochilus hasselti (Valenciennes 1842)	34	35	7.7
Osteochilus lini Fowler 1935	35	1	2.9
Osteochilus waandersii (Bleeker 1852)	122	2	3.9
Parachela maculicauda (Smith 1934)	6	<1	0.4
Paralaubuca rivero (Fowler 1935)	3	<1	0.4
Poropuntius deauratus (Valenciennes 1842)	23	9	18.6
Puntius brevis (Bleeker 1850)	25	4	2.3
Puntius masyai Smith 1945	26	1	1.6
Rasbora borapetensis Smith 1934	10	11	6.8
Rasbora caudimaculata Volz 1903	11	33	7.2
Rasbora myersi Brittan 1954	12	<1	0.6
Rasbora paviana (Trant 1885)	13	33	14.6
Rasbora trilineata Steindachner 1870	14	1	3.4
Puntius binotatus (Valenciennes 1842)	27	70	11.4
Puntius lateristriga (Valenciennes 1842)	28	<1	1
Puntius orphoides (Valenciennes 1842)	29	17	5.8
Puntius partipentozona (Fowler 1934)	30	4	1.6
Puntius stolitezkae (Day 1869)	117	7	3.6
Puntius sp.	121	<1	0.6

Cyprinids dominated the fish populations at most of the sites and all river systems, both in terms of species richness and numerical abundance. Overall, cyprinids represented approximately 35% of all species captured. Cyprinids were absent at only two of the sites across all river systems with a maximum of 10 and 11 species occurring at each of seven and one site, respectively. Cyprinid richness varied among river systems from 11 to 32 species, with the largest and fewest being found in Maeklong and in Eastern and Peninsula river systems, respectively (Beamish *et al.,* 2006).

Incidence of occurrence was high for about seven cyprinids, *Puntius binotatus*, *Mystacoleucus marginatus*, *Devario acrostomus*, *Osteochilus hasselti*, *Rasbora caudimaculata*, *Rasbora paviana*, and *Danio albolineatus* (Table 3). Indeed, approximately 70% of the species were found at <10% of the sites. Numerical abundance of cyprinids was also well above that for any of the other 27 families of fishes represented in the catches. Indeed, across all sites only five species were both widely distributed and abundant; *D. acrostomus, R. paviana, M. marginatus, P. binotatus* and *D. albolineatus.*

Table 3. Incidences of occurrences and geometric means for Balitoridae species along with species identification numbers (ID) used in Figure 3. Species without identification numbers were not used in the CCA analysis

	ID	Incidence of Occurrence, (%)	Mean Abundance (N $100m^2$)
Cypriniformes			
Balitoridae			
Acanthocobitis botia (Hamilton 1822)	1	8	0.11
Acanthocobitis zonalternans (Blyth 1860)	2	38	0.87
Balitora sp.	3	13	0.27
Homaloptera bilineata Blyth 1860	3	1	0.01
Homaloptera confuzona Kottelat 2000	4	4	0.01
Homaloptera smithi Hora 1932	5	46	1.24
Homaloptera sp. 1		1	0.05
Nemacheilus binotatus Smith 1933	6	4	0.01
Nemacheilus masyae Smith 1933	7	17	0.17
Nemacheilus platiceps Kottelat 1990	8	4	0.03
Schistura desmotes (Fowler 1834)	9	23	0.63
Schistura kohchangensis Smith 1933	10	4	0.09
Schistura vinciguerrae (Hora 1935)	11	16	0.26
Schistura sp. 1	12	31	0.90
Schistura sp. 2		2	0.02
Schistura sp. 3	13	7	0.09
Schistura sp. 4	14	2	0.06
Tuberoschistura baenzigeri (Kottelat 1983)	15	6	0.10

All cyprinid species were included in the ordination analysis. The potential for useful information on habitat characteristics for rare or uncommon species was felt to be of greater ecological value than the negative impact of their limited occurrence on the analysis. Species and their distribution and abundance were significantly correlated with five habitat characteristics (p=0.012, 0.001 and 0.001 for axes 1, 2 and 3, Monte Carlo test with 1000 permutations). The first and second axes of the CCA were both highly significant explaining 55 and 48% of the variability, respectively (Figure 2). Undoubtedly the variability explained by each axis would have been higher had it not been for the large number of species absent from many of the sites. Each axis explains a statistically significant proportion of the species-environment relationship. The first axis illustrates a positive gradient of habitat width ($r^2 = 0.26$), discharge ($r^2 = 0.34$), dissolved oxygen ($r^2 = 0.23$) and alkalinity ($r^2 = 0.23$). Temperature ($r^2 = 0.57$) loaded positively on the second axis. Habitat correlations were 0.88, 0.84 and 0.74 for axis 1, 2 and 3, respectively. The other habitat variables did not correlate significantly with cyprinid species and their abundance. Each of the five significant habitat characteristics increases along a vector in Figure 2, away from the origin with its length being a measure of the rate of change. Species of high occurrence and abundance had the highest correlation with the significant habitat variables.
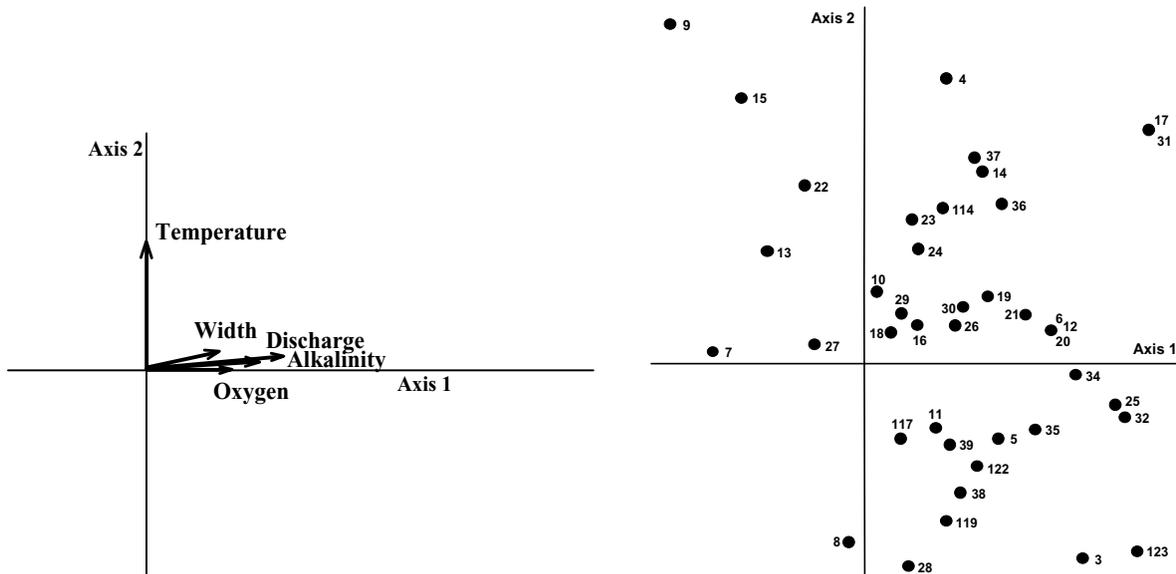
Figure 2. Distribution of cyprinid species with respect to significant habitat variables identified by canonical correspondence analysis for axis 1 and 2. Numbers represent species identified in Table 2. Re drawn from Beamish et al., (2006)

Cyprinids reacted to a wide range of the significant habitat characteristics (Figure 2). Generally, the more abundant and commonly occurring species were comparatively conservative in their habitat preferences. Of all the species, 17 were captured at 10 or more sites across all watersheds. Most of the common species favored only modestly greater than the overall averages for habitat width, discharge, alkalinity and dissolved oxygen. This was particularly the case for *Cyclocheilichthys apogon, M. marginatus, Neolissochilus stracheyi, R. caudimaculata, P. binotatus* and *Puntius. orphoides*. While there were differences in the position of the common species with

respect to the significant habitat characteristics, they tended to be comparatively small. Only a few of the common species were found at the comparative extremes of one or more habitat characteristics. Thus, *D. albolineatus* was found at sites of narrow width, low discharge, alkalinity and oxygen but moderate temperature. In contrast, *D. acrostomus* were captured in water of low temperature while *Opsarius koratensis* were found where temperature was high. Among the species captured at fewer than 10 sites, extremes in low and high temperature were demonstrated by *Esomus metallicus* and *Neolissochilus blanci* and L*obocheilus rhaboura, Paralaubuca riveroi* and *Puntius lateristriga*, repectively, although the latter three were captured at only a single site. Wider rivers and high discharge, alkalinity and dissolved oxygen characterized the sites where *Amblyrhynchichthys truncatus, Labiobarbus leptocheilus,* L*abiobarbus siamensis* and *Puntius brevis* were found, although, again site number was low. Relative variation among the significant habitat characteristics did not differ between the frequently and infrequently captured species.

Balitorids were present in 75% of the sites and were represented by a total of 18 species or 13.3% of all species in the study. Species number were adjusted to an area of 100 m^2 as described in Beamish *et al.* (2008). The highest number of species recorded at a site was seven, which occurred at moderate elevations in the mountainous Maeklong watershed where the geometric mean was 1.9 ± 1.8 species 100 m^2, virtually identical to that for the mountainous Eastern watershed, 1.8 ± 1.8 species 100 m^2. Species numbers were intermediate at 0.9 ± 1.9 species 100 m^2 in the Peninsula River system and least in Chao Phraya river system at 0.4 ± 1.7 species 100 m^2. In both the Peninsula and Chao Praya river systems, the terrain is less mountainous.

Balitorid incidences of occurrence and numerical abundances were high for only a few species (Table 3). Highest occurrences were for *Homaloptera smithi*, the only species found in all river systems, and *Acanthocobitis zonalternans* and *Schistura* sp.1 both found in the Peninsula and Maeklong river systems. Numerical abundance of all balitorids combined was not high with most sites having fewer than 19 individuals 100 m^2 (Figure 3) and an overall geometric mean. of 4.9 ± 3.6 fish 100 m^2 representing 3.8% of all fishes captured across all sites.
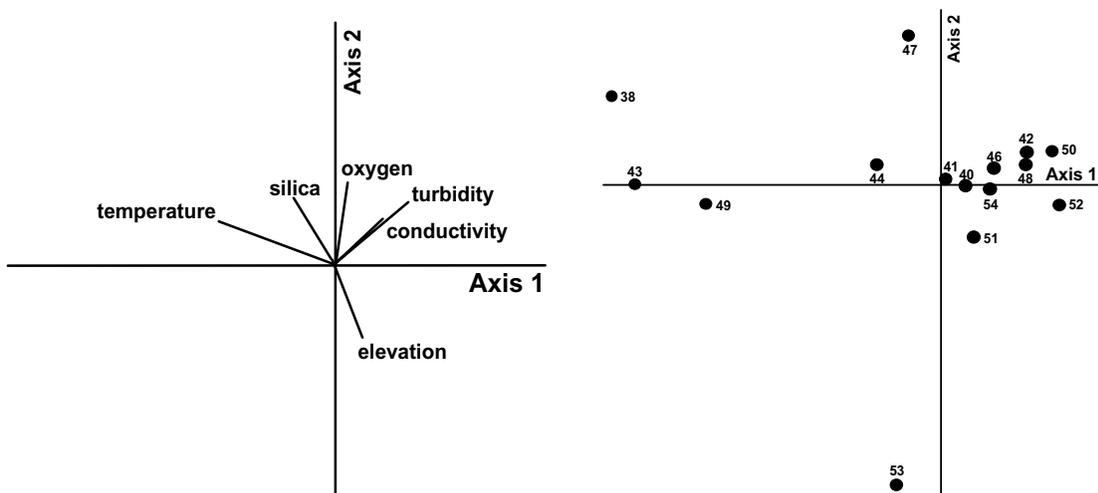
Figure 3. Distribution of Balitoridae species with respect to significant habitat variables identified by canonical correspondence analysis on axis 1 and 2. Numbers indicate species identified in Table 3. Redrawn from Beamish *et al.* (2008).

In preparation for ordination analysis, some adjustments were made to the data. No balitorids were captured at 21 sites. The capture efficiency of the electrofisher over four passes was high but, at an estimated 95–97% (Carle, & Strub, 1978), the possibility of not capturing all species could not be excluded. Hence it was not absolutely certain that balitorids were absent at these sites. Further, the statistical package available for CCA analysis would not accept information from sites where no balitorids were captured. To allow the inclusion of information for analysis, a small number of the most abundant and widespread species, *H. smithi*, 0.001 fish 100 m^2, was added where no balitorids were captured. Additionally, the four species whose incidences of occurrences were <3%, *Homaloptera bilineata*, *Homaloptera* sp.1, *Schistura* sp.2 and *Schistura* sp.4, were deleted out of concern for the reliability of their habitat information.

The CCA analysis indicated individual species to be correlated with five habitat characteristics, temperature, oxygen, turbidity, silica and elevation (P < 0.05 and < 0.01 for axes 1 and 2, respectively, Monte-Carlo test with 1000 permutations) in addition to the importance of elevation, substratum and silica to balitorid species numbers and abundance identified in Beamish et *al.* (2008). Each axis explains a statistically significant proportion of the species–environment relationship, the first, 87% and the second,79% of the variability, respectively. The first and second axes illustrate a positive gradient of turbidity (r^2 = 0.29), temperature (r^2 = 0.23), oxygen (r^2 = 0.22) and silica (r^2 = 0.21), respectively (Figure 3). Elevation loaded negatively (r^2 = 0.27) on the second axis. Habitat correlations were 0.89 and 0.83 for axis1 and 2, respectively.

The eight most abundant species (Table 3) were associated by the CCA analysis with habitats of near average values for most of the significant variables (Figure 3). Among these species, *Schistura desmotes*, *Balitora* sp. and *Schistura vinciguerrae* were associated with above average turbidities, while above average temperatures and elevations were indicated for *H. smithi* and *Schistura* sp. 1, respectively.

One or more of the significant habitat factors differed substantially from average among some of the less abundant species. *Schistura kohchangensis* and *Homaloptera confuzona* were affiliated with comparatively high temperatures within the narrow range recorded, and *Schistura* sp. 3 was associated with high elevations and low ambient concentrations of oxygen and silica. *Nemacheilus platiceps* was most common in habitats high in dissolved oxygen and silica and at low elevations. The most notable habitat characteristic associated with *Nemacheilus binotatus* was a higher than average temperature. The remaining four species, *Acanthocobitis botia*, *Acanthocobitis zonalternans*, *Nemacheilus masyae* and *Tuberoschistura baenzigeri*, were closely associated with average values for the significant habitat characteristics.

Silurids or catfishes were present in 67% of the 159 sites in all river systems with a maximum of five species occurring at four sites. Richness varied among river systems from 4 to 13 species with the largest number being found in Maeklong. The fewest species, four, were captured in Eastern and Peninsula river systems. The highest elevation at which silurids were captured was 450 m with *Amblyceps maccronatum* and *Glyptothorax* sp. being present at the single site.

Incidence of occurrence was not high for any catfish species within any river system and no species was captured in all watersheds (Beamish & Sa-ardrit, 2006; Table 4). Over all sites, incidences of occurrences were highest at 69, 29 and 28% for *A. maccronatum*, *Mystus havmolleri* and and *Pseudomystus siamensis.* Incidences while low for all other species were generally highest in Maeklong river system. Numerical abundance of silurids was not high relative to the total numbers of fish captured. The geometric mean (GM) for all species of silurids was 2.53.1 fish/100 m across all 159 sites, representing only approximately 2% of the total mean abundance for all fish (1272.7 fish/100m). Abundance was highest for *P. siamensis, M. havmolleri* and *Amblyceps. foratum* with only *P. siamensis* averaging over 1 fish/100m^2 (Table 4).

Table 4. Incidences of occurrences and geometric means for silurid species along with species identification numbers (ID) used in Figure 4. Species without identification numbers were not used in the CCA analysis.

	ID	Incidence of Occurrence, (%)	Mean Abundance (N 100m^2)
Siluriformes			
Bagridae			
Hemibagrus nemurus (Valenciennes 1840)	69	18	0.21
Pseudomystus siamensis (Regan 1913)	64	28	1.02
Mystus gulio (Hamilton 1822)	65	<1	0.05
Mystus havmolleri Smith 1931	66	29	0.46
Mystus micracanthus Bleeker 1846	67	2	0.06
Mystus mysticetus Roberts 1992	68	1	0.03
Mystus singaringan (Bleeker 1846)	118	1	0.05
Siluridae			
Ompok bimaculatus (Bloch 1797)	70	14	0.15
Pterocryptis cochinchinensis (Valenciennes 1840)	71	9	0.09
Silago maculata Quero & Gauthier 1824	124	<1	<0.01
Amblycipitae			
Amblyceps maconatum Ng & Kottelat 2000	72	25	0.08
Amblyceps foratum Ng & Kottelat 2000	73	69	0.29
Sisoridae			
Glyptothorax laoensis Fowler 1934	74	2	0.05
Glyptothorax major (Boulenger 1894)	75	1	0.03
Glyptothorax platypgonoides (Bleeker 1855)	76	7	0.50
Glyptothorax sp.	120	4	<0.01
Clariidae			
Clarias batrachus (Linnaeus 1758)	77	5	0.09

All silurid species were included in the ordination analysis as, again, the potential for useful information on habitat characteristics for rare or uncommon species was felt to be of greater ecological value than the negative impact of their limited occurrence on the analysis. In addition to the importance of velocity, turbidity, oxygen, iron and pH to silurids' species richness and abundance described in Beamish & Sa-ardrit (2006), individual species' abundance was significantly correlated with three habitat characteristics, temperature, conductivity and dissolved oxygen (p=0.004, 0.001 and 0.001 for axes 1, 2 and 3, Monte Carlo test with 1000 permutations). The first and second axes of the CCA were both highly significant explaining 80 and 67% of the variability, respectively (Figure 4). Each axis explains a statistically significant proportion of the species-environment relationship. The first axis illustrates a positive gradient of dissolved oxygen (r^2 = 0.81) and a negative gradient of temperature (r^2 = 0.19), and conductivity (r^2 = 0.09).

Temperature ($r^2 = 0.1$) and oxygen ($r^2 = 0.17$) loaded negatively on the second axis and conductivity, positively ($r^2 = 0.29$). Habitat correlations were 0.91 and 0.89 for axis 1 and 2, respectively. Other habitat variables did not correlate significantly with silurid species and their abundances and were not included in the CCA analysis. Each of the significant habitat characteristics increases along a vector, away from the origin with its length being a measure of the rate of change.
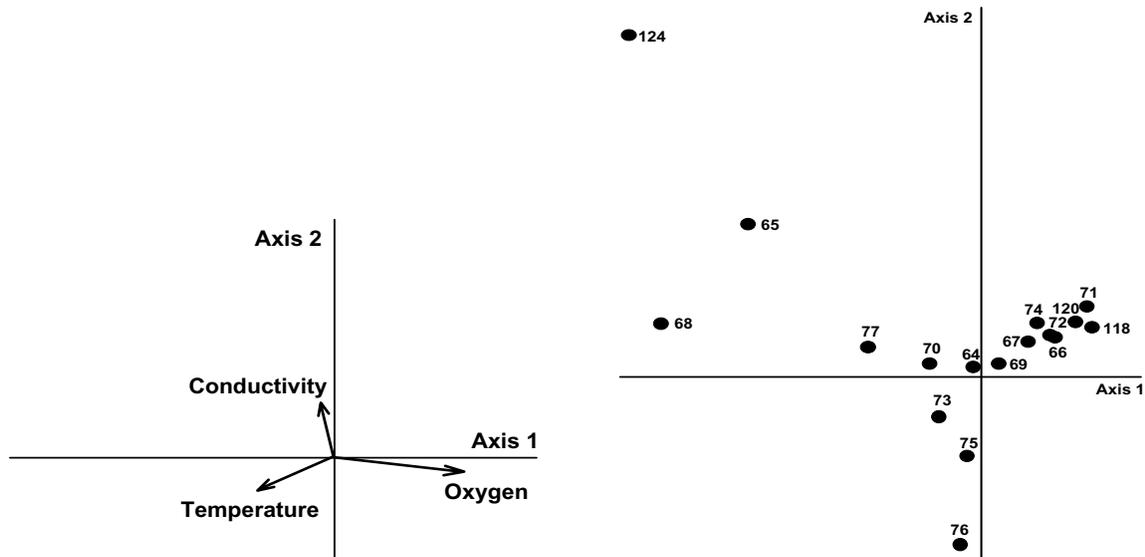
Figure 4. Distribution of silurid species with respect to significant variables identified by canonical correspondence analysis for axix 1 and 2. Numbers represent species identified in Table 4. Redrawn from Beamish & Sa-ardrit (2006).

Silurids reacted to a broad range of the significant habitat characteristics. Again, the more abundant and commonly occurring species were comparatively conservative in their habitat preferences. Of the 17 species, 7 were captured at 20 or more sites across all river systems. Many of the common species were clustered near the overall habitat averages where silurids were captured; temperature (24.6±1.4 C), conductivity (121±2 μS/cm) and dissolved oxygen (7.3±1.2 mg/L). This was particularly the case for *P. siamensis, Hemibagrus. nemurus, Ompok bimaculatus* and *A. foratum*. Differences in the positions of the common species with respect to the significant habitat characteristics tended to be comparatively small. Thus, *Pterocryptis cochinchinensis, A. foratum* and *M. havmolleri* are predicted to prefer slightly higher than average oxygen and conductivity concentrations and lower temperatures.

Glyptothorax sp. is positioned at lower than average temperature and above average oxygen. *Glyptothorax platypgonoides* favors water of low conductivity while *Clarias batrachus* were captured in water of low oxygen and high temperatures. Two species, *Mystus mysticetus* and *Mystus gulio* occurred in water of low oxygen and high conductivity and temperature.

Temporal changes in stomach contents were examined for four species, *S. kohchangensis, N. masyae, H. smithi* and *Glyptothorax major* at intervals of 6 h over a 24 h period to determinate feeding schedules. For each species and within each of the four sampling times, weight of stomach contents increased with standard length of fish. This relationship was expressed as a series of linear regressions between stomach contents (mg) and standard length (mm). For each species, regression slopes did not

differ significantly (P> 0.05) among the four sampling times, providing for the calculation of a mean slope (Table 5). However, regression coefficients or elevations differed significantly among some species' regressions (P <0.05). These slopes were used to adjust species' stomach contents for each sampling time to correspond to that for a fish of 40 mm (Figure 5).

Table 5. Regression coefficients for the relationship between standard length (mm) and stomach contents (mg) for four species at each of four sampling times. Slopes did not differ significantly within each species for the four sample times and are represented by a mean value (see text). Cumulative number of individuals examined for each species is given under N.

Species	Cumulative N	Standard length range (mm)	Mean slope	Regression coefficients			
				6 hrs	12 hrs	18 hrs	24 hrs
H. smithi	22	20.1 – 33.7	0.007	0.070	0.182	0.044	-0.192
G. major	45	39.0 - 57.9	0.003	0.517	0.113	0.326	0.487
N. masyae	33	44.7 - 57.5	0.022	-0.526	-0.349	0.100	-0.677
S. kohchangensis	67	37.9 - 59.6	0.002	0.441	0.862	1.235	0.567
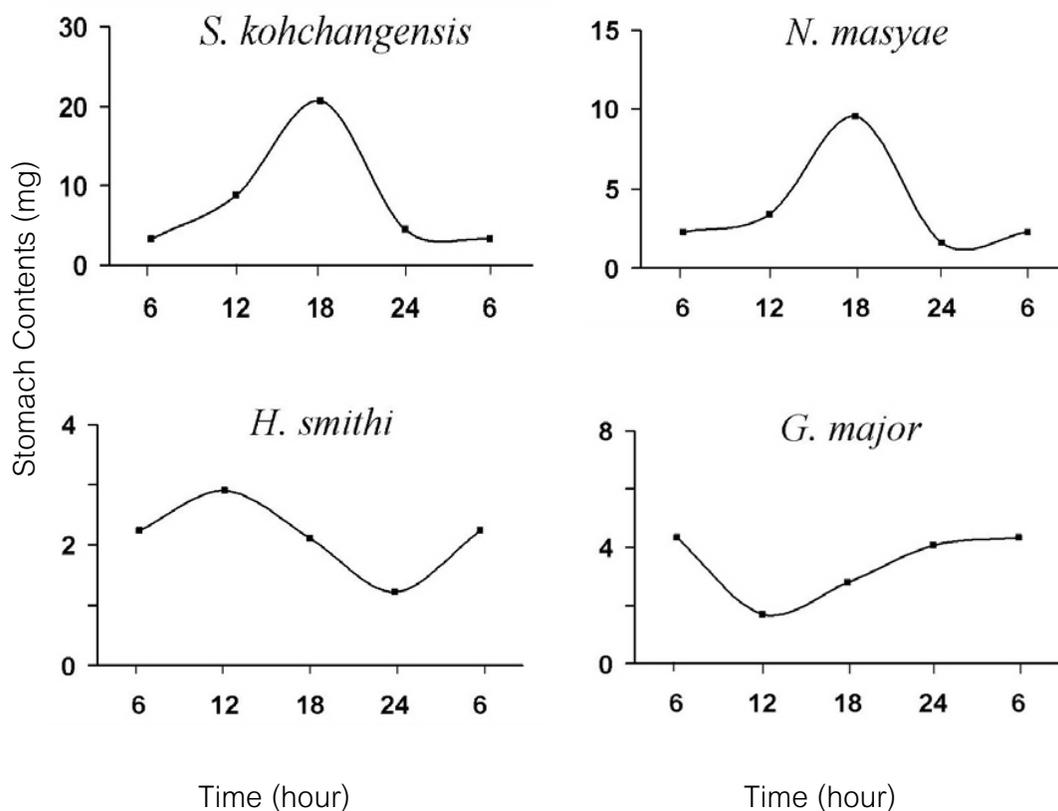
Figure 5. Temporal feeding patterns for four fishes sampled from headwater tributaries of Chantaburi River at 6-hour intervals in February 2009. Each value has been adjusted from linear regressions to correspond to that for a fish of 40 cm standard length (see text).

Food consumption followed a clear temporal pattern for most species with variations in maximum and minimum values (Figure 5). Differences were particularly pronounced for *S. kohchangensis* and *N. masyae*. Further, time of maximum feeding also varied among species. Both *S. kohchangensis* and *N. masyae* fed most actively during the transition from daylight to darkness. In contrast, *H. smithi* fed most actively during the transition from darkness to daylight, 6 hours. *G. major* fed most actively between midnight and daybreak.

Preliminary examination of fecundity among fishes within the Family Balitoridae indicated large variation among closely related species (Figure 6). Thus, mature *Schistura* sp. produced small numbers of oocytes but of large individual size (Table 6) whereas fecundity of *Balitora* sp.

was higher but variable with oocytes of small size. Fecundity of one *Balitora* sp. individual was over 11,000 whereas that for a second individual was only slightly above 1000. While the species identity of *Balitora* was not determined the two individuals are believed to be the same species. Oocytes were of similar size for both individuals with large differences in ovary size or GSI. On the other hand fecundity, oocyte diameter and GSI for individuals of *Schistura* sp. from two different rivers were quite similar. GSI was measured over each species' period of reproduction. Maximum values differed considerably among species (Table 6). Interestingly, maximum GSI for *Schistura* sp. was similar between two rivers and dissimilar for two individuals of *Balitora* sp. from the same river and location.

Table 6. Fecundity of Balitoridae species captured from several rivers. Fecundity and oocyte values are mean values and their standard deviations. Number of fish is given under N. TL refers to total fish length. Oocyte diameters are based on 10 oocyte measurements for each fish. GSI, gonadosomatic ratio, refers to ovary weight relative to fish weight, with reported values in the table being maximum values over the species' period of reproduction.

Species	River	N	TL(mm)	Fecundity	Oocyte diameter (mm)	GSI (%)
S. desmotes	Khayeng	1	69	125	1.43±0.06	5.8
S. vinciguerrae	Khayeng	2	68	1,575±427	0.42±0.01	7.0±2.0
Schistura sp.	Pakkok	8	45	33±12	1.66±0.17	10.1±2.6
Schistura sp.	Shikoo	3	48	51±13	1.67±0.18	10.6±3.3
S. kohchangenensis	Pongnamron	3	59	1,563±306	0.67±0.01	15.9±2.5
Balitora sp. 1A	Pongnamron	1	60	11,279	0.45±0.01	38.9
Balitora sp. 1B	Pongnamron	1	43	1,123	0.41±0.06	11.4

DISCUSSION

The concept of environmental, feeding and reproductive adaptations refers to phenotypic- or genotypic related characteristics that enable an organism to cope with its habitat including other biota thereby facilitating survival and has wide application to understanding species richness and co-existence. Adaptations differ widely among

species (Fry, 1947; Brett, 1979). The present study clearly demonstrates differences among species in terms of environmental and feeding associations that are suggestive of preferences. Only recently have the environmental requirements of many of the indigenous freshwater fishes in Thailand's rivers been investigated (Beamish *et al.,* 2005; 2006; 2008; Beamish & Sa-ardrit 2007; Tongnunui & Beamish

2009) and no published information could be found on temporal feeding schedules or modes of reproduction for any of Thailand's freshwater fishes. Differences in fecundity and egg size found in this study for closely related balitorid species represent differences in parental energy investment with population implications..

The diverse array and high abundance of cyprinids relative to other species in small rivers in central Thailand is, not surprisingly, consistent with their prominence throughout their distribution (Howes, 1991). In Thailand, >35% of the described freshwater fishes are cyprinids (Smith, 1945; Vidthayanon et al., 1997) with similar proportions reported elsewhere in Southeast Asia (Inger & Chin,1962; Roberts, 1989 and Zakaria-Ismail & Sabariah, 1994).

Broad genetic and phenotypic adaptations, described mostly for temperate cyprinid species, have allowed cyprinids to occupy physically, chemically and biologically diverse habitats. Thus, some cyprinids such as *Carassius carassius* display a tolerance for low ambient oxygen, unavailable to many other species, through efficient extraction mechanisms or relying, at least in part, on anaerobic metabolism particularly when temperature is low (Blazka, 1958). Most of the cyprinids for which information is available are eurythermal with a large capacity for thermal resistance adaptation (Wieser, 1991). Further, there is evidence among temperate and tropical cyprinids of genetic adaptations and phenotypic plasticity in growth rate as well as in their ultimate size, the former accommodating to cohabiting species, the latter, a range of habitats (Mann, 1991). Some species display adaptive modifications in their digestive tract such as a reduction of stomach size and increased intestine length allowing them to survive on the typically more abundant plant material when animal material is scarce (Persson, 1991). The success of cyprinids may also be linked with their wide range of familial life histories and reproductive styles (Balon, 1975; Mills, 1991). Many cyprinids, particularly the smaller species, have high reproductive efforts (Gale & Buynak, 1982; Mills, 1991)

contributing to their high abundance and, perhaps easing colonization of unstable environments (Cambray & Bruton, 1985).

In an earlier related study, diet and feeding adaptations among seven co-habiting cyprinid species was examined (Ward-Campbell & Beamish, 2005). Dietary overlap was low. Morphological characters, in particular, mouth height and position, body weight and depth and digestive tract length accounted for differences in diet among the species. Other studies have also suggested a strong relationship between a fish's morphology and diet (Wikramanayake 1990, Hugueny & Pouilly, 1999). The present study adds, for the first time, evidence of different feeding schedules among co-existing fishes, thereby reducing trophic conflicts.

Other morphological features can also contribute to species diversity within rivers. While regions of high water velocity are generally hostile for fish, some, including *O. hasselti* and *Garra fuliginosa* are ideally suited due to their lower hydrodynamic drag, a consequence of their more rounded cross-sectional body shape. In contrast, a deep body as occurs in *C. apogon* provides maneuverability in their debris-cluttered habitat with slow flowing water. Upturned mouths are indicative of surface feeding, a characteristic of *D. acrostomus* and *R.caudimaculata*. Both species are commonly found in areas of slow flow where their common prey, taxa of the order Hymenoptera, are vulnerable when they fall to the surface. Interestingly, these cyprinids also possess a caudal peduncle that is both deep and wide, a characteristic associated with fast-start swimming and, for these species, is likely associated with predator avoidance.

Other morphologies of distributional and co-existence importance to cyprinids can be inferred from the shape and size of their body and fins (Webb, 1998). Thus, species with a short body length such as *Puntius partipentozona* may be expected to exhibit swimming agility which is consistent with the dense vegetation and debris where they were captured. Species with long based dorsal fins,

capable of independent motion along their length and moderately rounded bodies such as *P. siamensis* and *L. leptocheilus* can be expected to be strong swimmers with good maneuverability. Both species were found in habitats of high discharge. Cyprinids with a wide and deep caudal peduncle and an apparently flexible body such *P. brevis, O. hasseltii* and *M. marginatus* are adapted for swimming in areas of high flow. Other species live in regions of high discharge by taking refuge from the high velocities through specific morphologies. *Garra* live in regions of high discharge by maintaining a close association with the substrate aided by large pectoral fins which, in flowing water, almost certainly serve as depressors.

Temperature has long been recognized to limit the range of species directly and indirectly (Cravens, 1982, Taylor *et al.*, 1993). In central Thai rivers, water temperatures fluctuate little compared to changes in temperate regions. Nevertheless, it was a significant factor to species distribution in this study. Despite the importance of temperature to fish distribution through its effect on their physiology and behavior, no specific published information was found for Thai freshwater fishes. Of the commonly captured species in this study, O. *koratensis* was associated with sites where temperatures were in the region of $30^{\circ}C$ as was also the case for the less frequently captured *E. metallicus* and *N. blanci*. This contrasts with those cyprinids associated with comparatively low temperatures, which in this study were just under $20^{\circ}C$, including the commonly captured *D. acrostomus* and the relatively uncommon *P. lateristriga, P. riveroi* and *L. rhaboura*. In this study the strength of interpretation of temperature and other significant environmental factors on species distribution is, of course, expected to be greater for the common than the uncommon species. The majority of cyprinid species were clustered not far from the overall mean of approximately 25C. With most sites between 20 and 30C, temperature is unlikely to pose a threat as a lethal factor. However, it can be expected to exercise an impact on a species' overall level of performance, particularly among species with a limited range of thermal tolerance.

Worldwide there are large knowledge gaps in the habitat characteristics of silurid fishes. These gaps are even larger in terms of our understanding on how alterations in habitat effect fish populations, although there is a perception that the insidious degradation in habitat that has occurred in most, if not all, countries is the major cause of fish population declines (Beamish *et al.,* 1986).

Generally the catfishes in this study exhibited greatest species richness and numbers in clear, flowing water, high in dissolved oxygen, iron and pH. Characteristics such as a hard substrate of cobble or boulders not found to be significant in the present study have been identified as important in other studies (Simonson & Neves, 1992; Tan & Ng, 2000). However, substrate composition is clearly correlated with water velocity that was found significant in the present study.

Few measurements appear to have been made of silurid metabolic requirements, however, Burgess (1989) assumed them to be low. To the extent this is correct, the positive association between both species richness and abundance and ambient dissolved oxygen is a little surprising. This is especially so for species with branchial adaptations or that may subsidize their metabolism through cutaneous respiration. Equally surprising is the inverse relationship between abundance or species richness and turbidity described in Beamish & Sa-ardrit (2006). Many, if not most silurids are nocturnally active and thought to rely more on the sensory function of cells located in their barbels than eyesight in locating food. However, silurid occurrence in water low in turbidity and high in both dissolved oxygen and total iron may not relate directly to their environmental preferences but to those of organisms high in their dietary agenda, algae and benthic invertebrates. Thus, iron is important in plant metabolism and oxygen production, a consequence of primary production. Insects and some other benthic macroinvertebrates better perform some physiological functions such as cuticle or shell secretion when pH and alkalinity are high (Gillner & Malmqvist, 1998).

The diet of many silurids including species of *Mystus, Glyptothorax* and *Amblyceps*, includes a high proportion

of plant material and insects (Rainboth, 1996) so that their occurrence at sites with average to above average dissolved oxygen and conductivity, with temperatures slightly below average may relate as much to the environmental preferences of their food sources as there own. Other silurids, were associated with habitats of relatively low oxygen particularly *M. gulio* and *M. mycetus* and to a lesser extent, *C. batrachus* and *O. bimaculatus*. The latter two species are commonly found in standing water where oxygen is likely to be low with *C.batrachus* possessing an arborescent-like organ within the branchial chamber enabling them to access atmospheric air (Smith, 1945). The occurrence of *M.gulio* along with *S. maculata* in water of relatively high conductivity is in accord with their common occurrence in brackish water. In contrast, *Glyptothorax major* and *G. platypgonoides* frequented water of lower relative conductivity that presumably is related to their ion regulatory physiology.

River loaches in this study exhibited greatest species diversity and abundance, in rivers at relatively elevated locations with water high in silica, reflective of regional solute dynamics and a rocky substratum indicating fast flows. Earlier recognition of the importance of these physical habitat characteristics provided the basis for their other common names, hillside or torrent loaches (Alfred, 1969; Freyhof & Serov, 2001). Distributions by river systems in this study were often, but not always, the same as those described earlier by Vidthayanon *et al.* (1997) for the same river systems. For example, both studies reported the presence of *H. smithi* in all river systems and *A. botia* only in the Maeklong River. In contrast, *H. bilineata* was found in the Maeklong River system in the present study, whereas Vidthayanon *et al.* (1997) reported it only from the Salween River system, north of Maeklong and the limits of this study. *Balitora* sp. was captured in the Maeklong River in this study, a river system in which Vidthayanon *et al.* (1997) reported no *Balitora* species to be present. More recently, Kottelat (2000) reported *H. confuzona* to occur in the Mekong River system and coastal basins in south-eastern

Thailand but not the Maeklong where it was found in this study. Similarly, new distributions were found also for *N. masyae* and *Nemacheilus platiceps*, although not the objective of the present study, clearly indicating information gaps.

Despite uncertainties in distributions, some balitorid species are geographically separated, while others share similar distributions. Species in each group may have similar or distinctive habitat associations. Thus, *S. kohchangensis* is separated from other balitorid species by its association with relatively high ambient temperatures in addition to its apparent geographic restriction to eastern Thailand. *N. platiceps* also appears restricted to eastern Thailand and is unique among the balitorids in this study in its association with low elevations and high ambient oxygen and silica concentrations. Similar patterns were found in other river systems. For example, *Schistura* sp.3 was found only in the Maeklong where it is associated with streams at high elevations in contrast to *H. confuzona*, for example, with the same distribution but with an apparent penchant for high temperatures and low elevations. Where habitat separation clearly occurs, the significant factors can be expected to influence boundaries directly, indirectly, or through some combination of both. Some factors operate on fishes by restricting metabolic capacity and hence performance through species-specific interactions and tolerances (Fry, 1971; Brett, 1979). Habitat factors may also act indirectly on fishes, for example, by altering the composition of the food resource base or through their effect on competitors or predators.

Resource sharing was found for the more common balitorid species suggesting the importance of additional factors. Partitioning of food resources is certainly among these (Ross, 1986). Earlier (Giller, 1984; Schoener, 1974) and in the present study, temporal feeding patterns within the same habitat or space are suggestive of a resource-sharing adaptation that almost certainly eases their co-existence through reduced competition (Bjornsson, 2001). A similar resource sharing behavior has been reported in

lakes where some fish species move into deep water at night where they feed and, possibly avoid predation (Gliwicz & Jachner, 1992; Link *et al.*,1993; Baumgartner *et al.*, 2008).

Species sharing similar habitats may or may not differentially exploit the food resource base. In an ongoing dietary study, P. Nithirojpakdee (unpublished data) found *S. kohchangensis*, *N. masyae*, *H. smithi* and *G. major* feed mostly on insects within the Orders Trichoptera, Ephemeroptera and Diptera (chironomids), but in slightly different proportions. In an earlier study on Thai fishes that share the same habitat Ward-Campbell *et al.* (2005) found dissimilarities in diet that were related to different mouth and digestive tract morphologies. Herder & Freyhof (2006) examined the gut contents of a large number of fishes in small habitats in a Vietnam river and concluded that coexistence was by partitioning food resources for which species were morphologically adapted as well as by habitat choice.

McIntosh (1995) suggested that where uncertain and severe abiotic conditions occur, species composition may be shaped by interactions with species-specific biological characteristics. Conceivably, species might exhibit overlap in resource use where environmental variation is sufficient to reduce species abundance to levels below which resource limitation occurs or shifts competitive advantages from one species to another. Other variations in habitat and feeding specializations have also been suggested to explain the structure of river fish assemblages (Gorman & Karr, 1978; Fausch, 1984).

Rostral and maxillary barbels on the head of balitorids probably serve a sensory function in foraging and may explain the positive association with turbid water. That temperature was of particular significance to *H. confuzona* and *S. kohchangensis* even within the narrow range found among the stations suggests them to be tropical stenotherms. *N. platiceps* was found where ambient oxygen and silica were high and elevation low. These different responses may relate directly or indirectly to the habitat conditions where a species can best perform its various

activities. Attribution of environmental preference in the absence of supportive physiological and behavioural information, however, merits interpretive caution. This is further complicated by limnological autocorrelations.

The occurrence of some species such as *N. platiceps, H. smithi* and *Schistura* sp.4 where water was comparatively high in silica may relate particularly to its importance in diatom ontogeny and their importance as a food source for benthic macroinvertebrates on which balitorids feed (Ward-Campbell *et al.,* 2005; Herder & Freyhof, 2006). Diatoms are probably also of dietary importance to balitorids but have not been specifically distinguished from the broader dietary category of algae on which loaches do feed (Dundgeon, 1987; Ward-Campbell *et al.,* 2005; Herder & Freyhof, 2006).

Failure to find velocity a significant factor is probably a manifestation of temporal and dynamic changes that are commonplace in low-order rivers. Thus, low flows recorded at stations sampled during the dry season may have interacted with those recorded at other stations during the wet season in concert with other habitat factors to mask the importance of velocity. No balitorids were found at low-flow locations, and they are well adapted for life in moving water. In particular, their depressed body with a flat ventral surface, large and laterally expanded paired fins and a sub-terminal to inferior mouth are all adaptations that allow station holding on a hard substratum in rapidly flowing water (Webb *et al.,* 1996). Some species contain ridges on their ventral surface (Hora, 1930), while some species of *Balitora* have adhesive pads on the rays of their paired fins (Roberts, 1982) that undoubtedly serve as friction devices further facilitating station holding in flowing water.

Balitorid coexistence appears strengthened by variation in reproductive modes, in this study by differences in fecundity and egg size. Fish use reproductive tactics (fecundity and egg size) to share food resources (Timi *et at.*, 2005). Oocyte size relates directly to larval size and likely also acceptable dietary food items. Large eggs produce large larvae that are capable of ingesting relatively large

food items while larvae emerging from small eggs are more likely to feed on small dietary items. For those species reproducing at similar times this will assist in reducing competition for food. Equally likely but not part of the present study is the probability that larvae of similar size but from different species differ to varying degrees in dietary preferences thereby evening predation pressure on food resources. Large variation in fecundity within a species and habitat as suggested in this study is particularly interesting and certainly requires further study with larger samples. It is, of course, possible the low fecundity found for one individual could indicate oocyte atresia perhaps resulting from inadequate food resources. This is supported by a lower GSI.

In summary, the present study has identified a number of adaptations associated with environmental quality, reproduction and the sharing of food resources by fishes that assist in reducing competition in similar habitats and allow for high species diversity. Should conservation become an issue of importance in Thailand, attention to these adaptations and others will be important to the development and preservation of fish community structure and abundance in the rivers of Thailand.

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