Habitat characteristics of the cyprinidae in small rivers in Central Thailand

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Abstract Cyprinids were sampled, by electrofishing, from 159 sites on small rivers in four major watersheds across central Thailand. Total abundance, estimated by the depletion method, varied directly with water velocity and, inversely with discharge while species richness varied inversely with habitat width and, directly with ambient oxygen and alkalinity. Numerical abundance of cyprinids was well above that for any of the other 27 families of fishes represented in the catches. Incidence of occurrence was high only for a few cyprinid species in each watershed with most species present in ≤10% of the sites. Across all sites, cyprinids represented approximately 35% of all species captured and were absent from only two sites. Species richness was highest in the Maeklong watershed. Canonical correspondence analysis identified five significant habitat variables, temperature, habitat width, discharge, ambient oxygen and alkalinity, and the extent to which each influenced the distribution of the 41 cyprinid species. The results are discussed in relation to environmental factors and ecological adaptations.

Keywords Abiotic factors · Conservation · Abundance · Occurrence · Habitat characteristics · Species richness

Introduction

Habitat provides the medium in which fish may fluorish or perish, as well as for the company they keep. The importance of habitat has long been recognized through studies on environmental influences on individual species (Beamish 1964a, b; Brett 1964, 1979; Albaugh 1972) and assemblages (Felley and Hill 1983; Lobb and Orth 1988; Meffe and Sheldon 1988). These and other studies have identified important environmental variables for riverine and lake-dwelling fishes, particularly in temperate regions of the world (Gee and Northcote 1963; Fava and Tsai 1974; Jackson et al. 2001). By comparison these relationships have been largely neglected in tropical regions, although see Rodriquez and Lewis (1977) and Tejeriro-Garro et al. (1998) in South America and Martin-Smith (1998), Lee (2001) and Beamish et al. (2003) in Southeast Asia.

How well a fish does within a habitat is largely governed by the extent to which the collective environmental factors restrict metabolism in

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concert with the cost of performing routine activities such as swimming, feeding and breeding. The energy available for these activities, termed scope for activity by Fry (1947), represents the difference between the maximum aerobic and basal or standard metabolic rates (Fry 1947, 1971; Brett and Groves 1979). At environmental extremes this value approaches zero, so restricting activities as to ultimately cause death. Within this general framework, tolerance ranges and performance optima in relation to the environment can be expected to vary both in range and magnitude among species (Wohlschlag 1964; Holeton 1974; Brett and Groves 1979) and, may at least partially account for distributional differences among fishes within a watershed. This becomes particularly important where ranges of environmental factors, particularly those related to temperature such as dissolved oxygen differ widely as in tropical and temperate waterways. Within a watershed, species that overlap in environmental tolerances and preferences may coexist through other differences such as morphology and behavior (Gatz 1979; Labropoulou and Eleftheriou 1997; Hugueny and Pouilly 1999; Ward-Campbell and Beamish 2005).

The hugely speciose and ecologically diverse Cyprinidae, the largest family of all freshwater fishes (Nelson 1994) with more than 1500 species have evolved partially through highly adapted body forms and mouth structures (Ward-Campbell et al. 2005) so that they occupy virtually all habitats throughout their distribution (Howes 1991). Indeed, in Southeast Asia, the distributional summit of cyprinids (Rainboth 1991), they may contribute 40% or more of the species in a watershed (Taki 1978; Watson and Balon 1984) or an entire country (Smith 1945). Despite their importance, quantitative measurements of specific environmental characteristics have been made for relatively few species even in temperate regions of the world. This information is important not only to understanding their environmental ecology but, where populations or species are declining, in assisting with conservation measures. Perhaps as important is the usefulness of this information in constructing bioassessment models to monitor water quality. The present study examined cyprinid distributions and abundance in relation to habitat characteristics in central Thailand.

Study area

Thailand's aquatic ecosystems are supported by six major watersheds (Vidthayanon et al. 1997). Of these, sites on four watersheds were sampled in this study, Chao Phraya, Maeklong, Peninsular and Southeast (Fig. 1). The study area lies between latitudes of approximately 11° and 15° N and longitudes of approximately 97°30′ and 102°

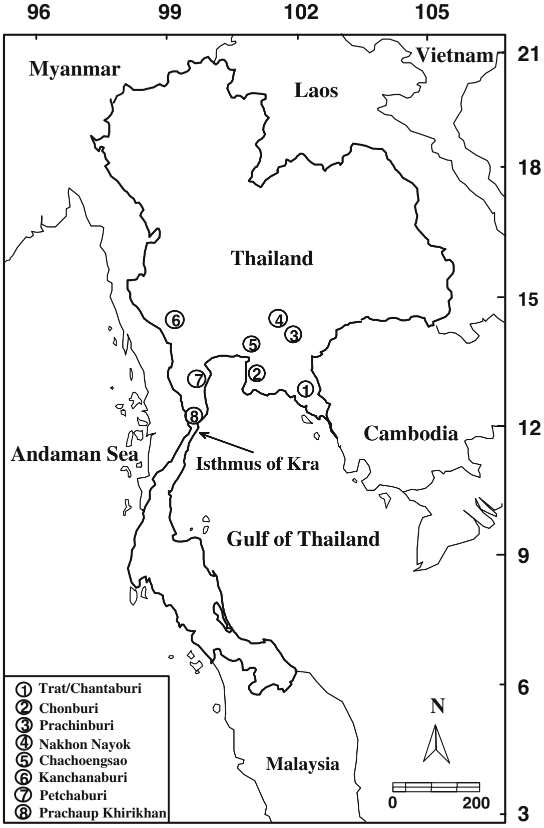

Fig. 1 Map of Thailand and neighboring countries. The study area was bounded to the north between approximately 13°15′ latitude and 102°15′ longitude to the east and 15° latitude and 98°40′ longitude to the west. The Gulf of Thailand represented the southern boundary to the east. In the west, the southern boundary extended across the Peninsula at approximately 11° latitude. The provinces in which sites were sampled are identified in the inset and by numbers. See also Table 1 for river names and number of sites on each river

60′ E, representing an area of approximately 23,000 km^2.

Northern Thailand lies between the Salween and Mekong rivers and most of the area drains to the headwaters of the Chao Phraya River. The northeast area drains mostly into the Mekong River while central Thailand is drained by the main channel of the Maeklong and Chao Phraya rivers. The Peninsular watershed refers to the area south from the Isthmus of Kra and includes six short river systems, four that discharge into the Gulf of Thailand and, in the southern portion of the watershed, two discharge into the Andaman Sea. The Southeast watershed is bounded by a mountain range that divides Thailand and Cambodia and to the west, by the Gulf of Thailand and includes three comparatively short river systems. Chao Phraya is the main river of northern and central Thailand and is of great importance to commerce. It originates from streams from two northern mountain ranges and discharges into the Gulf of Thailand after passing through Bangkok, a city of over eight million people. The Maeklong River system includes several major rivers, Kwae Noi, Kwae Kae and Petchaburi as well as other smaller rivers north of the Isthmus of Kra. These systems are probably among the least disturbed lotic ecosystems in Thailand, although some have not been spared the effects of dam construction and other forms of human activity.

Fish were sampled from 159 sites on small rivers, ≤25 m in width in the four watersheds (Table 1). Most sites were located in Maeklong ($n = 91$) and Chao Phraya ($n = 50$) watersheds. In Maeklong watershed, most sites ($n = 85$) 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 Meaklong River before discharging into the Gulf of Thailand. The remaining six sites were located in Petchaburi province. Sites in Chao Phraya watershed were on small rivers within Chonburi, Chachoengsao, Nakon Nayok and Prachinburi provinces. The 11 sites sampled from the Peninsular watershed were in Prachuap Khirikhan province while the seven sites in the Eastern watershed were located on streams in the eastern portions of Chantaburi and Trat provinces.

Materials and methods

Sample stations were selected from locations ranging from heavily forested and sparsely inhabited to lightly settled areas where some subsistence to modest commercial agriculture occurred to more heavily farmed or urban areas. A station might consist of several or, more frequently, a single site. A site consisted of a length of stream, usually not more than 50 m, of similar habitat. Most sites were sampled only once but some, several times. Sites were sampled throughout the year except when high discharges restricted visibility and personal safety. Stream order was assigned from topographical maps when available.

In preparation for sampling a site, seine nets of about 3 mm mesh, were installed across the upper and lower limits of the site to reduce emigration from or immigration into the enclosed area. Seine groundlines were weighted with rocks to further reduce fish escapement under the nets. The decision on the length of stream to electrofish was based in part on the total length of similar habitat available as well as by physical constraints imposed by water velocity in concert with discharge. When velocity and discharge were high it was difficult to fix retaining nets for long periods because of accumulating leaves and other debris. Prior to electrofishing, conductivity was measured and used to set the voltage (100–1100 V) and electrical wave configuration to enhance fish capture efficiency and minimize harm to fish. A site was electrofished either by moving systematically from the downstream retaining net upstream to the second net or in the reverse direction. The choice to begin upstream was made when light conditions and water velocity were such as to increase the visibility of stunned fish.

Electrofishing involved two people, one to operate the shocker unit and one to capture the temporarily stunned fish. Usually four or five passes were made at each site. Relative capture efficiency did not change significantly among sites at a station where comparisons could be made. Rates at which the logarithm of number of fish captured declined with the logarithm of number of electrofishing passes did not change significantly among sites within stations (ANCOVA, $P > 0.05$), regardless of the direction of fishing.

Table 1 Location and numbers of sampling sites by watershed, province and river name, where known

Watershed	Province	River	Sites
Eastern	Trat	Khao Mapring	1
Eastern	Trat	Nam Tok Khlong Kaeo	1
Eastern	Trat/ Chantaburi	Khlong Sato	3
Eastern	Chantaburi	Khlong Pong Nam Ron	1
Eastern	Chantaburi	Khlong Klang	1
Chao Phraya	Chonburi	Kongshi	3
Chao Phraya	Chonburi	Ban Than Trang	2
Chao Phraya	Chonburi	Chan Ta Than	3
Chao Phraya	Chonburi	Phan Sadet	1
Chao Phraya	Chonburi	Unknown	2
Chao Phraya	Chonburi	Surasak	17
Chao Phraya	Chonburi	Unknown	1
Chao Phraya	Chonburi	Khao Ha Yot	15
Chao Phraya	Chonburi	Paknam	1
Chao Phraya	Chonburi	Tributary of Bangpakong	1
Chao Phraya	Prachinburi	Prachangakham	1
Chao Phraya	Chachoengsao	Unknown	1
Chao Phraya	Nakhon Nayok	Nangrong	2
Peninsula	Prachuap Khirikhan	Unknown	3
Peninsula	Prachuap Khirikhan	Klong Yang Khwang	1
Peninsula	Prachuap Khirikhan	Shikoo	3
Peninsula	Prachuap Khirikhan	Ban Hin Pit	1
Peninsula	Prachuap Khirikhan	Ban Chai Thale	1
Peninsula	Prachuap Khirikhan	Unknown	1
Peninsula	Prachuap Khirikhan	Khlong Kariam	1
Maeklong	Petchaburi	Petchaburi	2
Maeklong	Petchaburi	Pranburi	4
Maeklong	Kanchanaburi	Pak Kok	2
Maeklong	Kanchanaburi	Khayeng	37
Maeklong	Kanchanaburi	Phacham Mai	15
Maeklong	Kanchanaburi	Ban Rai	6
Maeklong	Kanchanaburi	Kapok	5
Maeklong	Kanchanaburi	Kratenjeng	2
Maeklong	Kanchanaburi	Lichia	5
Maeklong	Kanchanaburi	Unknown	1
Maeklong	Kanchanaburi	Kreng Kravia	1
Maeklong	Kanchanaburi	Thi Khrong	1
Maeklong	Kanchanaburi	Satamid	1
Maeklong	Kanchanaburi	Pilok	1
Maeklong	Kanchanaburi	E-pu	1
Maeklong	Kanchanaburi	Tawat	3
Maeklong	Kanchanaburi	Tuam	1
Maeklong	Kanchanaburi	Bang Ka Loo	3

After each pass, fish were anaesthetized in a dilute solution of methaine tricaine sulfonate (approximately 150 mg l^{-1}) and, in most cases, immediately identified to species. Afterwards fish were released generally downstream from the sample site. When unable to assign species status in the field, a small number of the unidentified species were killed by an overdose of anaesthetic and preserved in 10% formalin for subsequent identification in the laboratory.

Current systematics of Thai freshwater fishes is equivocal. For this report the classification system of Nelson (1994) was followed along with most of the names given in the check list of Vidthayanon et al. (1997). Names for a few species were updated from recent taxonomic revisions. Fish were identified from a number of sources including: Smith (1945), Brittan (1954), Banarescu (1971), Sontirat (1976), Rainboth (1985, 1996), Lumlertdacha (1986), Kottelat (1998), Karnasuta (1993), Fang and Kottelat (1999). A voucher collection was prepared and is maintained in the Institute of Marine Sciences at Burapha University, Bangsaen, Chonburi (Catalogue number—BIMS: FF. 0001-002). Fish were preserved in 10% formalin for 10 days and then transferred to 70% ethanol for permanent storage.

Total abundance of fish within a site was calculated by the maximum likelihood technique (Carle and Strub 1978). Numbers for many species were small and not amenable to this technique. Hence a conversion factor consisting of the total abundance estimate divided by total number of fish caught was applied to adjust the numbers of each species captured. Fish abundance was arithmetically adjusted to an area of 100 m^2. Earlier (Beamish et al. unpublished data), it was demonstrated that within sampling stations in central Thailand, fish abundance reflected an aggregated distribution as between site variance increased linearly with mean population density. A log-transformation removed this correlation on the mean and suggested an overall standard deviation (SD) of 1.3 about the abundance estimate that is assumed for all species estimates in this study.

Habitat characteristics measured at each site included temperature (°C), width (±0.1 m), depth (±1 cm) and velocity (±1 cm s^{-1}), the latter three being used to calculate discharge (l s^{-1}). Depth was the mean of three to five measurements made at approximately equal intervals across the river. Velocity was measured at the surface and adjusted to represent the mean flow rate (Gillner and Malmqvist 1998). Conductivity (μS cm^{-1}), turbidity (NTU), pH (±0.1 unit) and dissolved oxygen (±0.1 mg l^{-1}) were measured with regularly calibrated meters. Ammonia (mgNH_3N l^{-1}) was measured by the salicylate method, nitrate (mgNO_3N l^{-1}), the cadmium reduction method, total iron (mg Fe l^{-1}) by the FerroVer method, alkalinity (as $CaCO_3$ mg l^{-1}, pH 4.5) using the sulfuric acid titration method, silica (mg SiO_2 l^{-1}) using the heteropoly method and true color (platinum–cobalt color units) by the platinum–cobalt method (APHA 1992). Elevation was measured by GPS for many but not all sites.

A substrate sample was collected at each site 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 and included in the sample with adjustment for their size relative to the 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 and Malqvist 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), 3–0.51 mm (fine gravel to coarse sand), < 0.5 mm (medium sand to silt) and the mean particle size calculated. The 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. The substrate at a few sites was solid or almost solid bedrock and these were coded as 7.

Multiple linear regression (MLR, SPSS11.5) was applied to examine the relationships between each of species richness and abundance and the significant habitat variables. Canonical correspondence analysis (CCA, PC-ORD) was employed to identify the importance of environmental characteristics to cyprinid species. Species richness and abundance and environmental variables, except for pH, were log $(x + 1)$ transformed to normalize the distribution of values and, in the case of environmental factors, to accommodate differences in scale and thus provide balance to their correlation with species distribution. 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 999 permutations. Statistical significance of all tests was accepted at $P < 0.05$.

Results

Water quality varied greatly among sites within and among watersheds. At sites within Maeklong watershed, water was on average a few degrees cooler and higher in pH and alkalinity than in the other watersheds (Table 2). Water at the Chao Phraya sites was on average highest in ammonia, nitrate, total iron, color and turbidity. Physical

Table 2 Chemical and physical characteristics of the sites in the watersheds

	Eastern watershed			Chao Phraya		
	Mean	SD	Range	Mean	SD	Range
Elevation, m	133	1	112–156	90	2	92–112
Width, m	4.6	1.7	2.0–10.0	3.2	0.6	1–25.5
Depth, cm	29	2	17–52	21	2	<5–83
Velocity, cm s^{-1}	33	1	24–60	20	2	1–80
Discharge, l s^{-1}	443	2	291–1264	95	5	1–2777
Canopy, %	18	4	0–70	28	2	0–100
Substrate*	3.3	1.7	0–7	3.7	0.4	0–7
Temperature, C	28.1	1.1	26.6–32.6	27	0.1	22.3–31.4
Conductivity, μS cm^{-1}	52	1	39–74	122	1	34–671
Turbidity, NTU	3	2	1–	13	2	1–439
Color, CU	16	4	0–53	78	1	12–550
PH	7.3	0.6	6.8–8.5	6.8	0.1	5.8–7.9
Oxygen, mg l^{-1}	7.5	1.1	7.1–8.5	6.4	0.2	2.3–11.5
Ammonia, mg l^{-1}	0.01	<0.01	0–0.02	0.08	0.13	0–0.67
Nitrate, mg l^{-1}	1.6	0.6	0.2–3.8	3.1	1.1	0–33
Total iron, mg l^{-1}	0.4	0.2	0.04–0.87	0.8	0.4	0.18–5.70
Silica, mg l^{-1}	26.9	0.3	16.2–36.2	21.0	1.0	<6–40.0
Alkalinity, mg l^{-1}	32	1.0	22–58	40	1	12–380
	Peninsular Watershed			Maeklong Watershed		
Elevation, m				228	1	157–853
Width, m	5.5	0.8	1.7–25	5.0	0.7	0.7–18.7
Depth, cm	26	0.4	13–38	23	1	<4–74
Velocity, cm s^{-1}	36	1	15–67	27	2	0–88
Discharge, l s^{-1}	500	2	81–1165	260	3	<10–5491
Canopy, %	16	3	0–80	30	2	0–95
Substrate*	3.9	0.8	0–7	4.1	0.5	0–7
Temperature, C	27.2	0.1	24.2–30.3	24.3	0.1	17.3–28.8
Conductivity, μS cm^{-1}	159	4	32–6500	117	2	10–1467
Turbidity, NTU	7	1	0–24	6	2	0–800
Color, CU	52	1	27–104	13	3	0–550
PH	6.9	0.1	6.1–7.4	7.5	0.1	4.2–8.7
Oxygen, mg l^{-1}	6.2	0.2	5.4–8.2	7.3	0.2	4.5–9.5
Ammonia, mg l^{-1}	0.03	0.05	0.01–0.19	0.02	0.05	0–1.00
Nitrate, mg l^{-1}	1.8	0.3	1.1–4.7	1.1	0.9	0–17.0
Total iron, mg l^{-1}	0.48	0.25	0.12–1.44	0.28	0.30	0–5.10
Silica, mg l^{-1}	17.8	0.3	13.8–30.0	16.7	0.5	6.5–41.6
Alkalinity, mg l^{-1}	51	2	15–137	74	2	5–576

Sample sizes for all but elevation were 7, 50, 11 and 89 for Eastern, Chao Phraya, Peninsula and Maeklong watersheds, respectively. Elevation was measured at 7, 30, 0, and 83 sites in Eastern, Chao Phraya, Peninsula and Maeklon watersheds. Means ± SD were calculated on log $(x + 1)$ values except for pH which was not transformed. *Substrate particle sizes in the table are for the coded values described in the text

habitat characteristics such as water depth and velocity, substrate composition and canopy while diverse within watersheds, were broadly similar among watersheds (Table 2). Substrate composition varied from sand to bedrock among sites but gravel was the average particle size within each watershed. Canopy ranged from full cover to total exposure but was mostly in the range of 15–30% cover. The two exceptions in similarity of physical characteristics among watersheds were river width and discharge that were, on average, least in the Chao Phraya watershed. Elevation was mostly between 100 and 300 m, with an overall mean of 180 ± 2 m ($n = 119$). Elevation of the unmeasured sites was estimated to be less than 200 m. Four sites had elevations above 700 m.

Cyprinids dominated the fish populations at most of the sites and all watersheds, 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 159 sites across all watersheds with a maximum of 10 and 11 species occurring at each of seven and one site, respectively. Cyprinid richness varied among watersheds from 11 to 32 species, with the largest number being found in Maeklong where the number of sample sites was also highest (Table 3). The fewest species were captured in Eastern and Peninsula watersheds where the number of sample sites was lowest.

Species richness was influenced by several habitat characteristics across all watersheds and is described by the equation:

Table 3 Incidence of occurrence, %, by species for each of the watersheds

	ID	Eastern	Chao Phraya	Peninsular	Maeklong
Cypriniformes					
Cyprinidae					
Amblyrhynchichthys truncatus (Bleeker 1851)	17				1
Barbodes gonionotus (Bleeker 1850)	22		4		2
Brachydanio albolineatus (Blyth 1860)	7	14	52	36	10
Crossocheilus reticulatus (Fowler 1834)	36	29			1
Cyclocheilichthys apogon (Val. in Cuv. & Val. 1842)	18		2	18	25
Cyclocheilichthys armatus (Val. in Cuv. & Val. 1842)	19		6		8
Cyclocheilichthys heteronema (Bleeker 1850)	20		2		
Danio acrostomus Fang & Kottelat 1999	8			45	63
Esomus metallicus Ahl 1924	9		8	9	
Garra cambodgiensis (Tirant 1884)	37	29	2		
Garra fuliginosa (Fowler 1837)	38	14			22
Garra sp.	39				21
Hampala macrolepidota Kuhl & van Hasselt in van Hasselt 1823	24	29	8		14
Labiobarbus siamensis (Sauvage 1881)	31				1
Labiobarbus leptocheilus (Val. in Cuv. & Val. 1842)	32				3
Lobocheilus quadrilineatus (Fowler 1835)	33				1
Lobocheilus rhabdoura (Fowler 1834)	123				1
Mystacoleucus marginatus (Val. in Cuv. & Val. 1842)	21	14	32		56
Neolissochilus blanci (Pellegrin & Fang 1940)	15		10		
Neolissochilus stracheyi (Day 1871)	16	57		27	23
Neolissochilus soroides (Duncker 1904)	119				3
Onychostoma gerlachi (Peters 1880)	114			9	
Opsarius koratensis (Smith 1931)	4				11
Opsarius pulchellus (Smith 1931)	5				1
Osteochilus hasselti (Val. in Cuv. & Val. 1842)	34		14	27	51
Osteochilus lini Fowler 1935	35		4		
Osteochilus waandersii (Bleeker 1852)	122				3
Parachela maculicauda (Smith 1934)	6		2		
Paralaubuca riveroi (Fowler 1935)	3				1
Poropuntius deauratus (Valenciennes 1842)	23	100	6		4
Puntius brevis (Bleeker 1850)	25				7
Puntius masyai Smith 1945	26				2
Rasbora borapetensis Smith 1934	10	14	10		2
Rasbora caudimaculata Volz 1903	11				57
Rasbora myersi Brittan 1954	12		2		
Rasbora paviei (Trant 1885)	13	43	74	82	3
Rasbora trilineata Steindachner 1870	14		2	9	
Systomus binotatus (Val. in Cuv. & Val. 1842)	27	57	84	72	63
Systomus lateristriga (Val. in Cuv. & Val. 1842)	28			9	
Systomus orphoides (Val. in Cuv. & Val. 1842)	29		26	9	14
Systomus partipentozona (Fowler 1934)	30		14		
Systomus stolitezkae (Day 1869)	117				12
Systomus sp.	121				1

Number of sites from the Eastern, Chao Phraya, Peninsula and Maeklong watersheds was 7, 50, 11 and 91, respectively. ID represents the identification number assigned each species

$$\log(S+1) = -0.180 - 0.141\log(W+1) + 0.813\log(\mathrm{O}+1) + 0.139\log(A+1)$$

Variable	Regression coefficient	SE	t
Intercept	−0.180	0.174	−1.037
Width	−0.141	0.062	−2.262
Oxygen	0.813	0.193	4.216
Alkalinity	0.139	0.034	4.109

where S is richness of cyprinid (species/ 100 m^2), W, habitat width (m), O, dissolved oxygen (mg l^{-1}), and A, alkalinity, (mg l^{-1}). Species richness at each site was adjusted to an area of 100 m^2 from the overall geometric mean of 97 m^2 ($n = 159$) using a calculated slope of 0.168 and log ($x + 1$) transformation of both variables. Habitat characteristics retained in the equation had significant t-values at $P < 0.05$.

The regression's F-value is 11.908 (3, 155 df, $P < 0.05$) and correlation coefficient, 0.433 ($P < 0.05$). Neither skewness nor kurtosis was significant. The equation predicts species richness to vary inversely with habitat width. Thus, species richness is expected to decrease from 5.2 to 3.3 100 m^{-2} with an increase in width from 1 to 25 m when oxygen and alkalinity are 8 and 50 mg l^{-1}, respectively. It is worth noting that this comparison is based on equal areas not river lengths. Species richness increased also with alkalinity and dissolved oxygen. With an increase in oxygen from 4 to 8 mg l^{-1}, a habitat width of 5 m and an alkalinity of 50 mg l^{-1}, richness is predicted to increase from 2.3 to 4.3 species 100 m^{-2}. For an increase in alkalinity from 25 to 200 mg l^{-1}, forecasted richness would be expected to increase from 3.8 to 5.4 when width is 5 m and oxygen, 8 mg l^{-1}. Elevation was not included in the regression analysis because of the large number of missing values. However, at the four highest sites, with elevations of approximately 700–850 m, cyprinid richness ranged only from 0 to 2 species.

Incidence of occurrence was high only for a few cyprinids in each of the watersheds and only three species were captured in all watersheds, *Brachydanio albolineatus*, *Rasbora paviei*, and *Systomus binotatus* (Table 3). Incidences of occurrence were ≥50% for only three and five species in Chao Phraya and Maeklong, respectively. Indeed, most species were found at ≤10% of the sites in both watersheds. In the more lightly sampled Peninsular and Eastern watersheds, occurrences were again comparatively high for only two and three cyprinids, *R. paviei* and *S. binotatus* and *Poropuntius deauratus, S. binotatus* and *Neolissochilus stracheyi*, respectively. Only one of the commonly captured species, *N. stracheyi*, was absent from Chao Phraya watershed with two, *R. paviei* and *P. deauratus*, absent from the catches in Maeklong, *Garra cambodgiensis* was confined mostly to Eastern watershed and *Rasbora caudimaculata* and *Systomus stolitezkae* confined mostly to Maeklong.

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 as well as within watersheds, cyprinids accounted for almost 57% of all fish captured with a geometric mean (±SD) of 55 ± 6 fish 100 m^{-2} for all sites. Numerical abundance of cyprinids was highest with a geometric mean of 71 ± 3 fish 100 m^{-2} in Chao Phraya and lowest in Peninsula and Maeklong at 41 ± 4 and 49 ± 8 fish 100 m^{-2}, respectively. Only a few species were particularly abundant in each watershed (Tables 4 and 5). In Chao Phraya, the three species that had high occurrences, *B. albolineatus, R. paviei* and *S. binotatus* were also abundant along with *Mystacoleucus marginatus*, which was, however, captured at fewer sites. Of the species captured most frequently in Maeklong, *Danio acrostomus* was most abundant. When present, *B. albolineatus* was abundant. In Eastern watershed, *P. deauratus, B. albolineatus* and *N. stracheyi* were abundant when present but only *P. deauratus* was common to all sites. In Peninsular watershed, the most abundant species when present were *Systomus orphoides, S. binotatus* and *N. stracheyi* with only *S. binotatus* being present at most sites.

Cyprinid numerical abundance varied inversely with river order. For those sites in Maeklong watershed where order could be assigned, geometric mean (±SD) abundance was 139 (±6) cyprinids 100 m^{-2} in first order streams (23 sites) and decreased to 72 (±0.4), 35 (±4) and 31 (±8)

Table 4 Abundance by species and watershed

Species	Eastern watershed			Chao Phraya watershed			
	Abundance (N 100 m^{-2})			Species	Abundance (N 100 m^{-2})		
	Mean	SD	Range		Mean	SD	Range
B. albolineatus	100			*B. gonionatus*	1.3	1.2	1.2–1.5
C. reticulatus	5.3	1.3	4.4–6.4	*B. albolineatus*	16.5	7.2	0.4–1330
G. cambodgiensis	7.9	1.4	6.3–9.9	*C. apogon*	2.6		
G. fuliginosa	0.7			*C. armatus*	2	2.6	0.7–4.4
H. macrolepidota	1.3	2.4	0.7–2.4	*C. heteronema*	1.8		
N. stracheyi	16.3	10	2.6–402.6	*E. metallicus*	8.5	3	2.6–29.5
M. marginatus	0.7			*G. cambodgiensis*	0.2		
P. deauratus	24.4	3.1	12.1–297.0	*H. macrolepidota*	1.7	5.2	0.6–20
R. borapetensis	42			*M. marginatus*	19.8	6.8	0.3–208
R. paviei	9.1	4.6	1.6–27.8	*N. blanci*	5.2	6.2	1.2–60
S. binotatus	7.3	6.6	0.7–69.3	*O. hasselti*	4	3.1	0.9–25.6
				O. lini	2.9	1.2	2.5–3.3
				P. maculicauda	0.4		
				P. deauratus	10.9	6.2	1.8–70
				R. borapetensis	1.2	5.9	0.2–19
				R. myersi	0.6		
				R. paviei	16.6	4.1	0.7–229
				R. trilineata	5.2		
				S. binotatus	16.1	3.5	0.7–152
				S. orphoides	4.2	2.8	1.1–26.7
				S. partipentozona	1.6	1.7	0.9–3.8

Means (SD) are geometric values and were calculated from values at sites where the species was present. Some species were captured at only one site

fish 100 m^{-2} in second (13 sites), third (23 sites) and fourth (23 sites) order rivers. Order could not be confidently assigned to enough sites in the other watersheds for similar comparisons.

The most important habitat characteristics to cyprinid abundance were velocity and discharge, a relationship described by the equation:

$$\log(N+1) = 2.168 + 0.510\log(V+1) - 0.469\log(D+1)$$

Variable	Regression coefficient	SE	*t*
Intercept	2.168	0.172	12.585
Velocity	0.510	0.159	3.205
Discharge	−0.469	0.088	−5.346

where N is abundance of cyprinids 100 m^{-2}, V, water velocity, cm s^{-1} and D, discharge, l s^{-1}. Velocity and discharge were the only significant habitat characteristics.

The regression's *F*-value is 14.571 (3, 155 df, $P < 0.05$) and the correlation coefficient, 0.397, significant at $P < 0.05$. Neither skewness nor kurtosis was significant. Thus, for a given discharge, cyprinid abundance increased with velocity and for a given velocity, abundance varied inversely with discharge.

In preparation for ordination analysis two sites were deleted due to the absence of cyprinids. All species were included in the 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 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 999 permutations). The first and second axes of the CCA were both highly significant explaining 55% and 48% of the variability, respectively, with the third axis explaining 38%. 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

Table 5 Abundance by species and watershed

Peninsular watershed				Maeklong watershed			
Species	Abundance (N 100 m^{-2})			Species	Abundance (N 100 m^{-2})		
	Mean	SD	Range		Mean	SD	Range
B. albolineatus	3.5	4	0.5–13.3	*A. truncatus*	1.1		
C. apogon	5.3	2.4	2.8–9.9	*B. gonionotus*	1.1	1.3	0.9–1.3
D. acrostomus	4.3	8.1	0.2–16.6	*B. albolineatus*	23.9	3.9	6.8–107.2
E. metallicus	1.4			*C. apogon*	2.3	4.5	0.1–138.6
N. stracheyi	15.5	1.4	12–22.5	*C. armatus*	2.7	2.2	0.9–6.7
O. gerlachi	0.6			*C. reticulatus*	101		
O. hasselti	7.9	2.8	2.9–22.8	*D. acrostomus*	20.3	6.5	0.5–328.3
R. paviei	12.4	5.4	1–222	*G. fuliginosa*	4.5	2.4	1.1–46.9
R. trilineata	1.6			*Garra* sp.	7	4	0.4–61.2
S. binotatus	16.5	4.8	1.5–263	*L. leptocheilus*	2.5	12.3	0.3–43.5
S. lateristriga	1			*L. quadrilineatus*	0.4		
S. orphoides	22			*L. rhaboura*	0.4		
				L. siamensis	0.3		
				M. marginatus	10.9	6.3	0.1–278.3
				N. soroides	15.7	2.6	5.6–37.4
				N. stracheyi	4.6	4.6	0.3–71.7
				O. koratensis	4.6	10.2	0.3–120.0
				O. pulchellus	5.1		
				O. hasselti	8.3	5.2	0.5–183.6
				O. waandersii	3.7	5.4	0.9–31.3
				P. riveroi	0.4		
				P. deauratus	8.8	2	3.1–15.4
				P. brevis	2.3	3.2	0.4–7.0
				P. masyai	1.6	2.2	0.9–2.8
				P. riveroi	0.4		
				R. borapetensis	3.2	2.2	1.8–5.6
				R. caudimaculata	7.2	4.3	0.3–150.0
				R. paviei	4.3	1.5	2.7–5.9
				S. binotatus	8	4	0.4–164.3
				S. orphoides	6.1	4.9	0.4–84.9
				S. stolitezkae	3.6	3.8	0.6–12.9
				Systomus sp.	0.6		

Means (SD) are geometric values and were calculated from values at sites where the species was present. Some species were captured at only one site

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 and were not included in the CCA analysis. Each of the five significant habitat characteristics increases along a vector in Fig. 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. Mean r-values (±SD) for the most common six species (captured at >40 sites) was 0.3 ± 0.1 and for the least frequently captured species (captured at 3 or fewer sites, $n = 18$), 0.1 ± 0.04.

Cyprinids reacted to a wide range of the significant habitat characteristics (Fig. 2). Generally, the more abundant and commonly occurring species were comparatively conservative in their habitat preferences. Of the 41 species, 17 were captured at 10 or more sites across all watersheds. Most of the common species favored only modestly

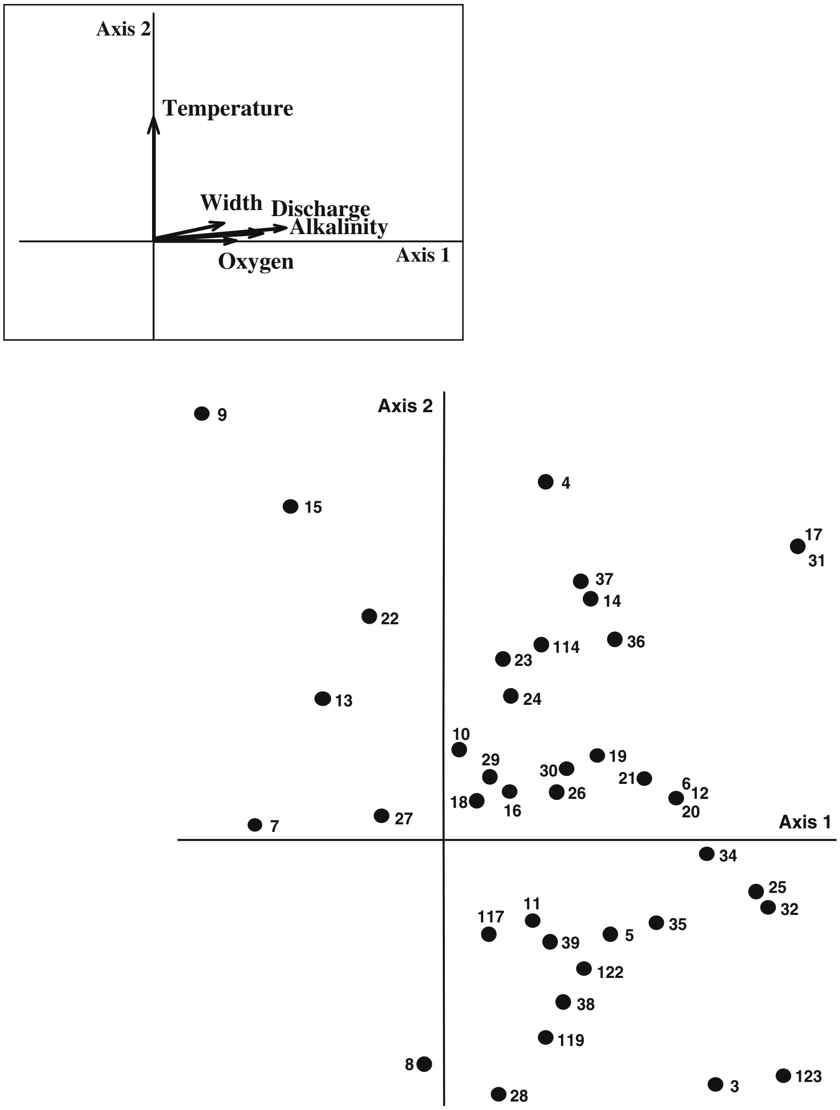

Fig. 2 Distribution of cyprinid species with respect to significant habitat variables identified by canonical correspondence analysis for axis 1 and 2. Numbers represent species identified fully in Table 2

greater than the overall averages for habitat width (4.2 ± 2.0 m), discharge ($199 \pm 5\ \mathrm{l\ s^{-1}}$), alkalinity ($57 \pm 3\ \mathrm{mg\ l^{-1}}$) and dissolved oxygen ($6.9 \pm 1.2\ \mathrm{mg\ l^{-1}}$). This was particularly the case for *Cyclocheilichthys apogon, M. marginatus, N. stracheyi, R. caudimaculata, S. binotatus* and *S. 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, *B. 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 *Lobocheilus rhaboura, Paralaubuca riveroi* and *Systomus lateristriga*, respectively, 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

Discussion

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 elsewhere in Thailand and, indeed throughout their distribution (Howes 1991). In all of Thailand, approximately 39% of the 549 freshwater fishes described in Smith (1945) are cyprinids, similar to the 36% in the more recent list by Vidthayanon et al. (1997). In a single river in northern Thailand, Champasri (2003) found over 40% of the 37 species to be cyprinids while a similar relation was found in Mekong River by Taki (1978). Cyprinids have been found at similar proportions elsewhere in Southeast Asia, for example, in Borneo by Inger and Chin (1962), Watson and Balon (1984) and Roberts (1989) and in Peninsular Malaysia by Johnson (1967), Bishop (1973), Mohsin and Ambak (1983) and Zakaria-Ismail and Sabariah (1994).

In this study only a few environmental factors were found to exercise a significant effect on species richness and total abundance. That relative fish abundance was higher in first order streams is reflected in its positive relationship with water velocity and negative with discharge. Velocity was identified also as important in a study by Schlosser (1985), Martin-Smith (1998) and Lamouroux et al. (1999). In a concurrent study in Maeklong watershed, Cooper (2003) found, in a habitat constrained ordination analysis, that fish assemblages were structured by similar habitat characteristics as invertebrate assemblages. However, the extent to which this was food-related was not clear. Relative abundance of benthic macroinvertebrates was not related directly to velocity. The trophic status of many of the cyprinid species in this study has either not been determined or is not readily available. However, for the few species for which trophic status is reported, it is about equally divided among herbivores (algivores and detritivores), terrestrial insectivores and benthic insectivores (Ward-Campbell and Beamish unpublished data). This suggests that the benthic invertebrate community, while important may not be the only major food source for the cyprinid population. A similar observation was made earlier in North Borneo by Inger (1955). Further, cyprinids are exploited for human consumption, often heavily, throughout Thailand. A casual impression was that exploitation was less on first order streams, many of which were in pristine areas, than on higher order streams.

The finding that species richness was the higher in narrow stream habitats is at odds with some observations (Smith and Miller 1986; Beecher et al. 1988) but not all (Mathews and Gelwick 1990). Harrel et al. (1967) found an increase in species richness with temperate stream order that they related to available habitat and smaller environmental fluctuations. Angermeier and Karr (1983) found species richness in small central Panama streams to increase with width (1–6 m) that was partially associated with food availability. Not infrequently it is suggested that as a river widens more discrete habitat units are created. However, seldom are these units or their fauna quantitatively described. In the present study, dissolved oxygen and alkalinity were also important to species richness, the former almost certainly reflecting the imposition of physiological constraints on metabolism and, the latter, its positive influence on plant productivity and, regulation of acid–base homeostasis in animals (Claiborne 1998). At most sites alkalinity was not high, further reinforcing its biological importance. Dissolved oxygen was an important environmental factor to species richness also in studies by Zalewski and Naiman (1984) and Beamish et al. (2003).

Relative fish abundance was large also at the few sites examined at high elevations and in contrast to low species richness. These sites, all first order streams were located above steep waterfalls that would be expected to serve as a barrier to any upstream migration. In accord, fewer cyprinid species were found at high altitude stream sites in Malaysia (Rahim et al. 2002) and in Nepal where Edds (1993) found the number of cyprinid and other species to vary inversely with altitude.

In addition to the important factors in this study, other studies have identified factors not found to be significant in this study, for example, water depth (Mendelson 1975; Baker and Ross 1981; Meffe and Sheldon 1988), water clarity and substrate composition (Gorman and Karr 1978; Rose and Echelle 1981; Martin-Smith 1998). There seems little doubt that a few habitat characteristics play an important role in the distribution of stream fishes, yet, among rivers, there is little consistency in the specific factors. This may be a consequence of the resident species' trophic preferences, behavioral patterns and physiological optima but, perhaps also may reflect biases generated as a consequence of frequent movements to and from habitats by at least some species

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 through efficient extraction mechanisms or relying, at least in part, on anaerobic metabolism (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 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), again within and between species. Many cyprinids, particularly the smaller species, have high reproductive efforts (Gale and Buynak 1982; Mills 1991) contributing to their high abundance and, perhaps facilitating colonization of unstable environments (Cambray and Bruton 1985).

The cyprinid species in this study differed considerably in their morphologies. In a concurrent study, diet and feeding adaptations among seven co-habiting cyprinid species was examined (Ward-Campbell and Beamish unpublished data). 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 (Gatz 1979; Wikramanayake 1990; Piet 1998; Hugueny and Pouilly 1999) while others found this relationship to be weak (Douglas and Matthews 1992; Motta et al. 1995). Other morphological features can also contribute to habitat ecology. Thus, occupation of regions of high discharge and flow by species such as *Osteochilus hasselti* and *Garra fuliginosa* is facilitated by lower hydrodynamic drag, a consequence of their more rounded cross-sectional body shape. In contrast, a deep body as occurs in *C. apogon* allows for increased maneuverability during turns, due to a reduction of the moment of inertia around the turning axis accounting, in part for its propensity for regions of lower discharge and abundant debris. 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, likely associated with predator avoidance.

Other morphologies of distributional 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 *Systomus 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 *L. 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. Thus, *Garra* live in regions of high discharge by maintaining a close association with the substrate though their sucker shaped mouth and large pectoral fins which, in flowing water, almost certainly serve as depressors.

Climatic conditions related to precipitation and temperature also provide constraints on a species' potential range. Site occupation, within the potential range, is due to a combination of biogeographic factors and contemporary factors at a smaller scale (Smith and Powell 1971). Precipitation can influence species composition and abundance through any of the activities it creates such as water velocity (Grossman et al. 1998), ground and surface water supply and composition as well as basin morphology, the latter being manifested in habitat diversity (Flebbe and Dolloff 1995).

Temperature has long been recognized to limit the range of species directly and indirectly (Brown 1974; 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, although not to diversity or abundance. 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°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°C, including the commonly captured *D. acrostomus* and the relatively uncommon *S. lateristriga, P. riveroi* and *Lobocheilus 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 25.5 ± 1.1°C. With most sites between 20 and 30°C, 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 and behavior, particularly among species with a limited range of thermal tolerance.

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