

Effects of Typhoon Disturbance on the Abundances of Two Mid-Water Fish Species in a Mountain Stream of Northern Taiwan

Ling-Chuan Chuang¹, Bao-Sen Shieh², Chi-Chang Liu^{1,2,3}, Yao-Sung Lin^{1,2,3}, and Shih-Hsiung Liang^{4,*}

¹Department of Life Science, National Taiwan University, No. 1, Sec. 4, Roosevelt Road, Taipei 106, Taiwan

²Department of Biomedical Science and Environmental Biology, Kaohsiung Medical University, No. 100, Shihchuan 1st Road, Kaohsiung 807, Taiwan

³Institute of Ecology and Evolutionary Biology, National Taiwan University, No. 1, Sec. 4, Roosevelt Road, Taipei 106, Taiwan

⁴Department of Biotechnology, National Kaohsiung Normal University, 62 Sanchung Rd., Yanchao, Kaohsiung 824, Taiwan

(Accepted February 1, 2008)

Ling-Chuan Chuang, Bao-Sen Shieh, Chi-Chang Liu, Yao-Sung Lin, and Shih-Hsiung Liang (2008) Effects of typhoon disturbance on the abundances of two mid-water fish species in a mountain stream of northern Taiwan. *Zoological Studies* 47(5): 564-573. The objective of this study was to use a 9 yr dataset to evaluate the responses of *Onychostoma barbatula* and *Candidia barbata* abundances to 3 typhoon events in a mountain stream of northern Taiwan. The association of habitat variables with fish abundances was also explored. Bimonthly electrofishing was conducted at 4 sampling sites, and habitat variables of water depth and stream length were measured after each fish sampling. Few or no significant differences in fish abundances for each site were identified among bimonthly sampling periods and years. Abundance variations did not significantly differ before and after typhoon periods in the 9 yr dataset, in typhoon years, or in non-typhoon years. These results indicated that typhoon impacts on the abundances of these 2 mid-water fishes are minor despite the potential for habitat alteration in mountain streams of Taiwan. Mid-water fish in Taiwan may adapt to flow fluctuations in mountain stream by their good swimming performance, and by staying in or quickly dispersing to deeper regions as refuges. Based on the results of this study, typhoons invading Taiwan during the wet season should be cautiously regarded as a natural disturbance. However, floods caused by typhoons which occur in the dry season may still cause reproductive threats to aquatic organisms in Taiwan. Given that global warming may become more serious in the future, greater emphasis should be placed on determining drought impacts on stream organisms in Taiwan as there is currently a lack of academic information and *in situ* experience.

<http://zoolstud.sincica.edu.tw/Journals/47.5/564.pdf>

Key words: Typhoon disturbance, *Onychostoma barbatula*, *Candidia barbata*, Taiwan.

Storms and floods in mountain watersheds and headwater streams can generate drastic effects on land forms, riparian vegetation, channel morphology, and aquatic communities (Swanson et al. 1998). Debris flows and landslides caused by floods can alter stream habitats and cause high mortality in fish species. As a result, a major flood can modify behaviors (Fitzsimon and Nishimoto 1995) and community structures of fishes (Power et al. 1985), and can significantly reduce, or

sometimes extirpate, fish from their habitats (Collins et al. 1981). Previous research has documented fish responses to flood impacts, with those of some extreme events persisting for years (Murphy and Meehan 1991, Grossman et al. 1998), and also those fish communities with high resistance or resilience to major floods (Pusey et al. 1993, Dolloff et al. 1994).

Typhoons are a natural disturbance that commonly appear, with an average of 3.7 per yr, in

*To whom correspondence and reprint requests should be addressed. Tel: 886-7-7172930 ext. 7310. Fax: 886-7-6051365.
E-mail:shliang@nknuc.nknu.edu.tw

Taiwan from July to early Oct. (Wu and Kuo 1999). Streams in Taiwan are characterized by short lengths, steep gradients, and fast currents. When a typhoon hits the island, heavy rainfall frequently results in severe flooding, and often causes landslides and debris flows in mountain streams. Although a previous study which was confined to a mountain stream and examined the effects of a single typhoon in Taiwan, suggested that severe typhoon-generated floods may significantly transform habitat structures, the impacts on fish populations could be relatively small (Tew et al. 2002). The long-term effects of typhoons on fish communities in mountain streams have been little investigated because of a lack of pre-typhoon data. In this study, we used a 9 yr database to examine the effects of typhoon disturbances on the abundances of 2 mid-water fish, *Onchostoma barbatula* and *Candidia barbata*, in a small mountain stream of northern Taiwan.

MATERIALS AND METHODS

Sampling area and sampling sites

Hapen Creek is a headwater tributary of the Nanshih River at elevations of 500-1200 m (Fig. 1). It is a natural, well-protected mountain stream which rises in the Fushan Experimental Forest of northern Taiwan. The riparian zone of Hapen Creek is dominated by natural broadleaf forests. The average gradient of the stream in the study area is 17.5 m/km (Chang et al. 1998). Monthly air temperature ranged from 11.5 to 23.7°C over the sampling period. Six fish species have been found in this stream, which is dominated by 2 mid-water species, *O. barbatula* and *C. barbata* (Chang et al. 1998).

Four sampling sites, S1, S2, S3, and S4, were established from upstream to downstream (Fig. 1, Table 1). The distances of these 4 sampling sites on Hapen Creek from the main branch of the Nanshih River were 4.2, 2.6, 1.6, and 0.7 km, respectively.

Precipitation and typhoon periods

The wet season in the Hapen Creek watershed lasts approximately from June to Nov., with the remaining time considered the dry season (Shaw et al. 2001) (Fig. 2). Stream discharge is closely correlated with rainfall and is highly variable in the Hapen Creek drainage (Shaw et al. 2001).

The typhoon period and wet season overlap in the study region (Fig. 2). During 1970-2005, 21 of 26 officially documented typhoons appeared in July and Aug. in northern Taiwan (Central Weather Bureau 2006). Three typhoons, Herb in 1996, Prapiroon in 2000, and Sinlaku in 2002, occurred in northern Taiwan during the study period. These 3 typhoons passed near the sampling area in either Aug. or early Sept.

Fish sampling

Fish sampling was conducted on 4 stream sections from 1995 to 2003. At least 2 riffle-pool cycles of each section were sampled, and sampling length generally exceeded 50 m. Bimonthly samples were generally made in each year, except for only 2 samples taken in 1999 and 5 samples in 2003. A battery-powered backpack-mounted electrofisher (150-300 V, 1 A pulsed DC) was used. Fish sampling on each pool/riffle lasted 15 min, with a total of at least 60 min. In each collection, at least 2 field assistants collected stunned fish with dip nets. Collected fish were

Table 1. Mean values and coefficient of variation (CV) for morphometric variables at 4 sampling sites along Hapen Creek

Site	Mean				CV (%)			
	Velocity (m/s)	Width (m)	Depth (cm)	Maximum depth (cm)	Velocity (m/s)	Width (m)	Depth (cm)	Maximum depth (cm)
S1	1.0	4.9	86.4	17.0	179.6	24.1	21.3	17.4
S2	0.8	6.7	37.7	14.0	83.3	11.1	27.8	38.8
S3	0.8	7.2	89.1	23.6	110.2	13.0	20.9	14.3
S4	0.7	6.6	84.7	24.7	89.3	14.5	29.5	17.3

identified to species, their total length measured, and total individuals counted for each species in the field, and then they were released back to the sampled sections.

Habitat variables

Habitat variables were measured immediately after fish sampling was conducted. In each pool/riffle area, 3 permanent transects perpendicular to the stream were delineated. Measured parameters included flow velocity, stream width, water depth, and maximum water depth within each sampling site. The stream width was determined by the transect length above the water surface. Water

depth and flow velocity were measured at 1 m intervals along each transect. Water depth was measured with a wood stick (in cm), and flow velocity was evaluated at 60% depth from the bottom with a digital current meter (Model 2100, Swoffer).

Data analysis

Data analyses were conducted using SAS (vers. 8.0, SAS Institute Inc.). In this study, individuals with a total length of > 3.1 mm were used to ensure sampling efficiency. The total number of collected individuals for each species was divided by the sampling time to calculate the

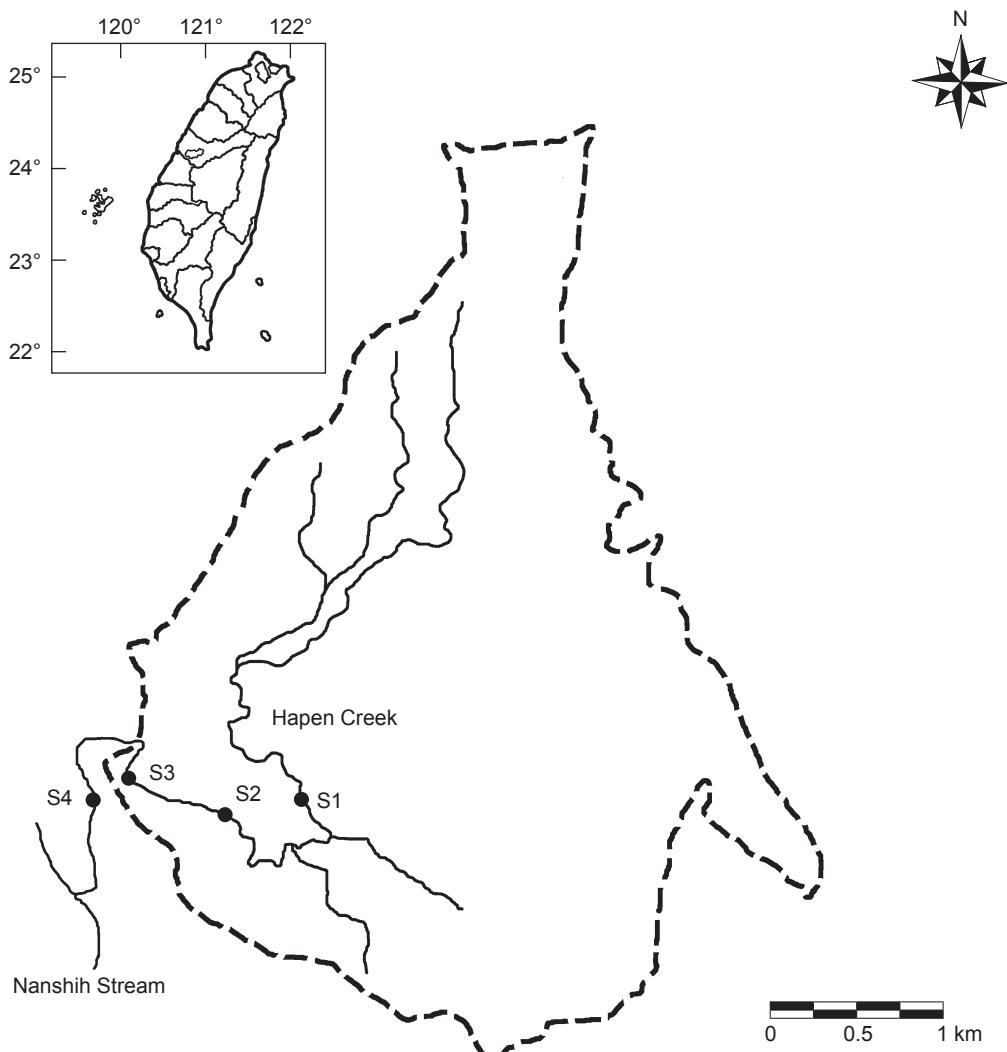


Fig. 1. Fish sampling sites (S1-S4) in Hapen Creek, northern Taiwan. The dotted line denotes the boundary of the Fushan Experimental Forest.

fish abundance (no. captured/15 min).

Intra- and inter-annual variations in fish abundances at the 4 sampling sites over 9 yr were first examined. At each site, analysis of variance (ANOVA) was used to evaluate among-year variations in mean fish abundances and within-year variations of the 6 bimonthly sampling periods. If a significant difference was found, a Ryan-Einot-Gabriel-Welsh Quotient (REGWQ) post hoc comparison was used to identify differences among years and among periods.

Because typhoons passed through Taiwan in Aug. and early Sept. during 1970-2005, pre- (Jan.-June) and post-typhoon periods (July-Dec.) were classified for each year. For each fish species, Student's *t*-test was used to compare abundance variations at each site between pre- and post-typhoon periods for the entire sampling period, for typhoon years (1996, 2000, and 2002), and for non-typhoon years. In addition, paired *t*-test was used to compare differences in fish abundances for each site in the July/Aug. and Sept./Oct. periods between typhoon and non-typhoon years.

In Hapen Creek, a previous study indicated that abundances of mid-water fish were more strongly associated with hydrological variables than other environmental variables like substrate and instream cover (Chuang et al. 2006); thus stepwise multiple regressions were used to model the correlations between fish abundances and

habitat characteristics including flow velocity, water depth, and stream width. Two levels of habitat characteristics were selected for the analysis. First, the average and coefficient of variation (CV) of habitat parameters within each site were used to represent the microhabitat complexity of each site for each sampling event. Second, to construct a temporal variability model, annual CVs of morphometric and velocity variables were calculated to provide an estimate of habitat stability over time. Abundances of *O. barbatula* and *C. barbata* were used as response variables.

RESULTS

Intra-annual variations in fish abundances

Differences in bimonthly fish abundances at each site were not statistically significant for either fish species during 1995-2003 (ANOVA, $p > 0.05$) (Figs. 3, 4). At each site, neither fish species showed a lower abundance in July/Aug., when typhoons were frequently recorded, compared to the other sampling months.

Inter-annual variations in fish abundances

Abundances of *O. barbatula* at sites 2 ($F_{8,40} = 2.8, p < 0.05$) and 4 ($F_{8,40} = 2.4, p < 0.05$)

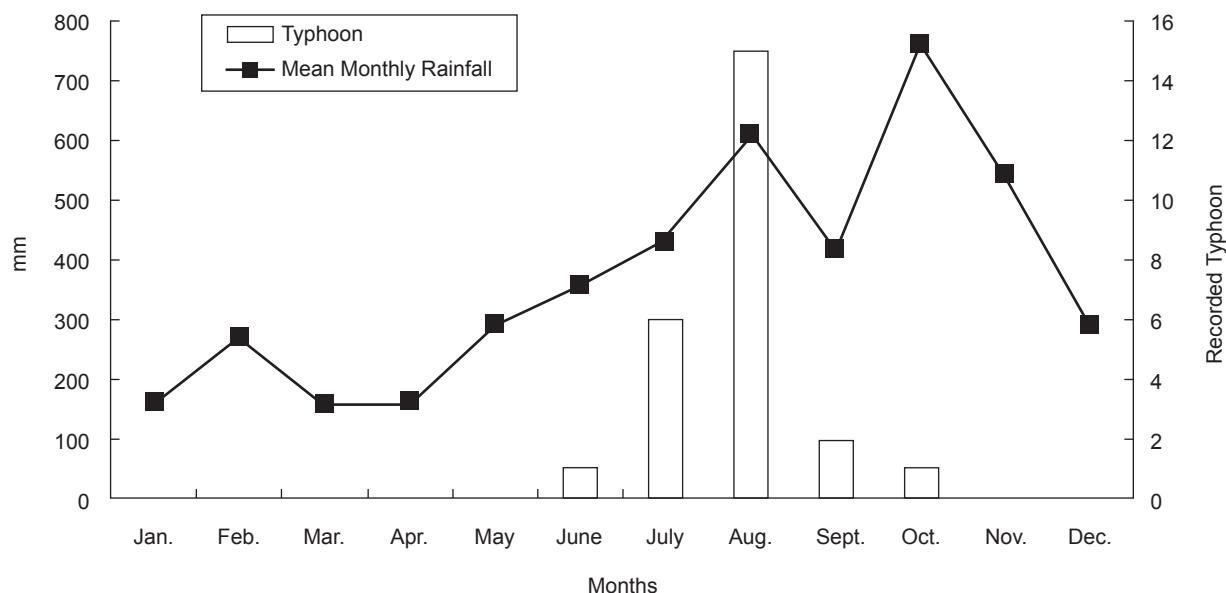


Fig. 2. Monthly mean rainfall (mm) from 1994 to 2000 in the Fushan watershed. Monthly totals of registered typhoons from 1970 to 2005 were also calculated.

significantly varied among years (Fig. 5). Abundances of *C. barbata* did not significantly differ among years except at site 1 ($F_{8,37} = 3.4$, $p < 0.01$) (Fig. 6). However, except for the abundance of *O. barbatula* at site 4 in 1996, neither fish species displayed significantly lower abundances in typhoon years compared to non-typhoon years.

Pre- and post-typhoon variations

Abundance variations of *O. barbatula* did not statistically differ between pre- and post-typhoon periods over the 9 yr period or between non-typhoon and typhoon years (Table 2). Comparisons of abundances between pre- and post-typhoon periods of *C. barbata* showed

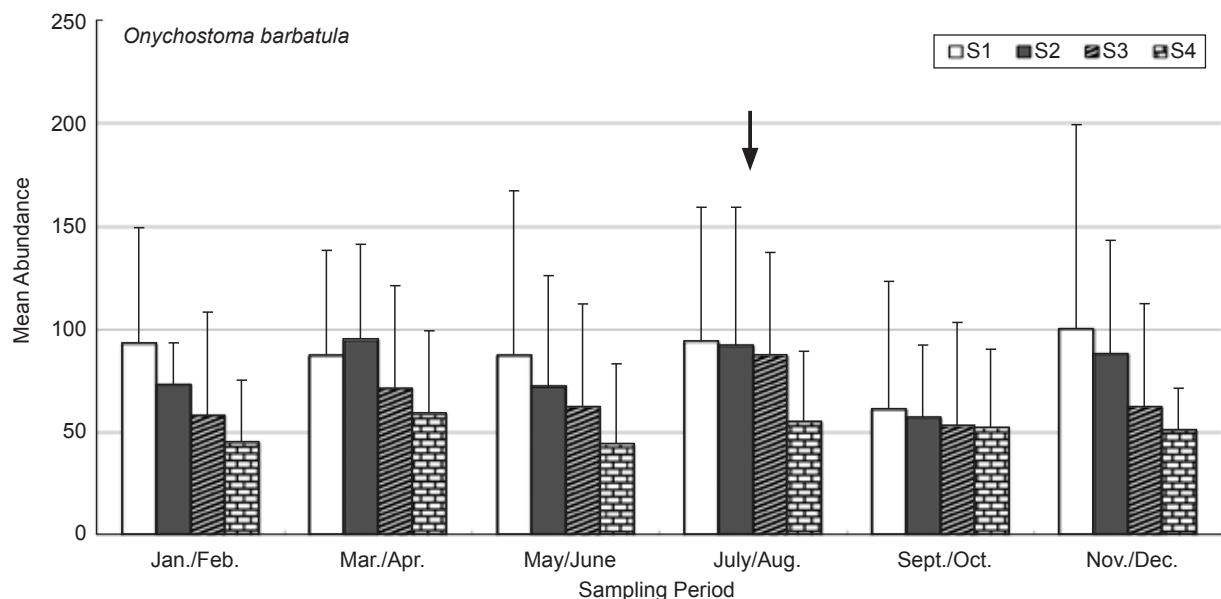


Fig. 3. Mean (± 1 S.E.) bimonthly total abundances of *Onychostoma barbatula* at 4 sampling sites in Hapen Creek from 1995 to 2002. The arrow indicates the most frequent time that typhoon events occurred.

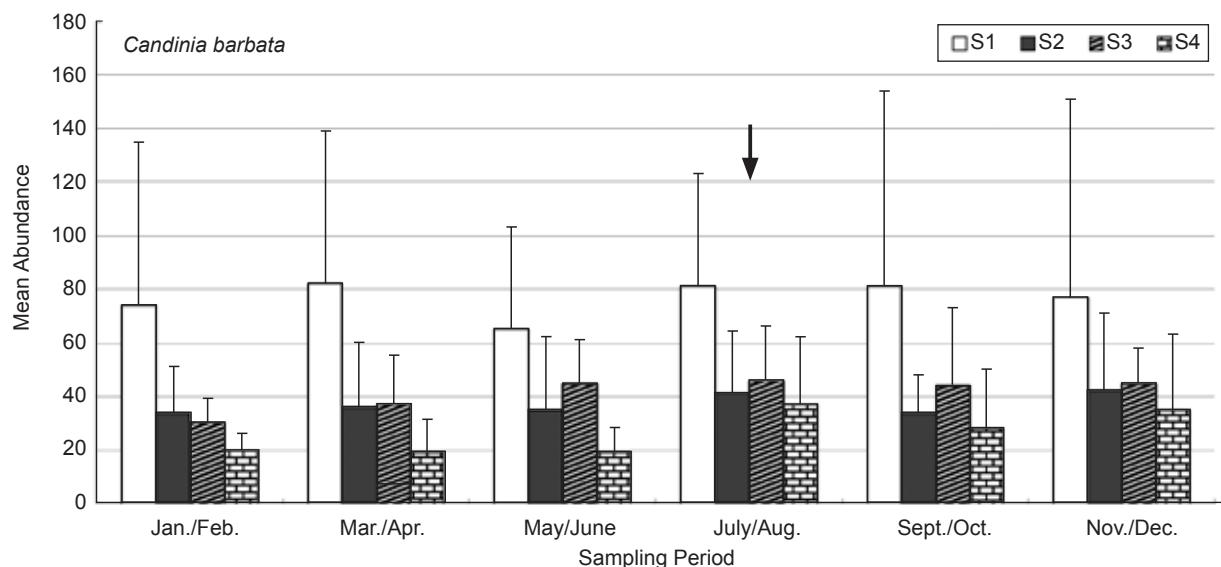


Fig. 4. Mean (± 1 S.E.) bimonthly total abundances of *Candinia barbata* at 4 sampling sites in Hapen Creek from 1995 to 2002. The arrow indicates the most frequent time that typhoon events occurred.

that they did not significantly differ in typhoon years (Table 2). Additionally, despite significant differences being found at site 4 over the 9 yr period and in non-typhoon years, abundances of *C. barbata* in the post-typhoon period were greater than those in the pre-typhoon period.

Fish abundances of neither species showed significant differences between typhoon and non-typhoon years in the July/Aug. and Sept./Oct.

periods at each site ($p > 0.05$).

Habitat Associations

Within-habitat variability model

Onychostoma barbatula was correlated with shallow and narrow waters that showed

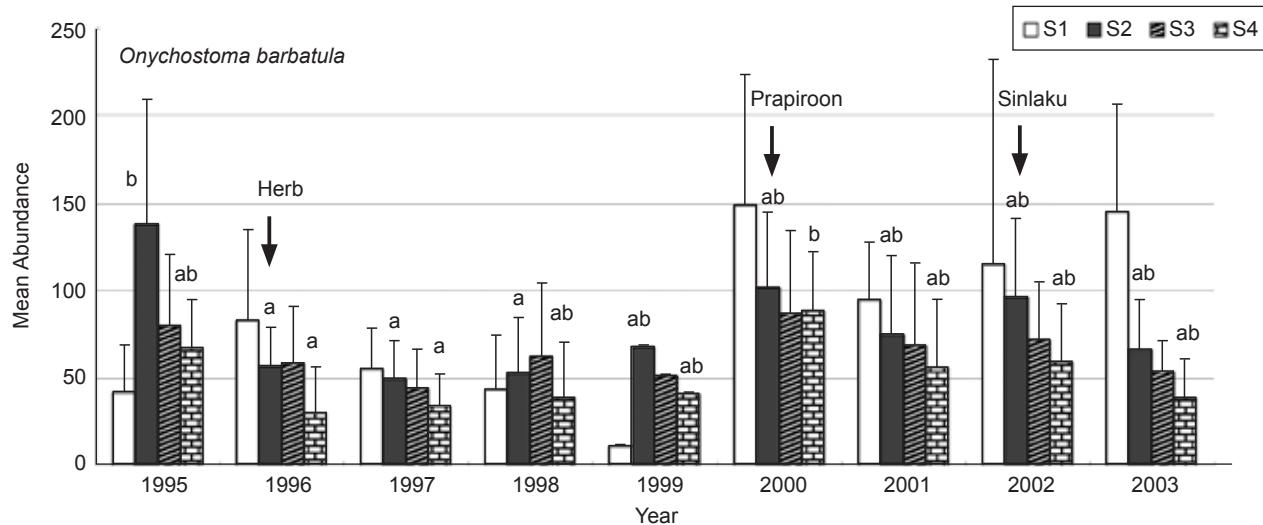


Fig. 5. Mean (± 1 S.E.) annual total abundances of *Onychostoma barbatula* at 4 sampling sites in Hapen Creek from 1995 to 2002. Years with the same letters do not significantly differ. The arrows indicate typhoon events which are labeled with the name of the storm.

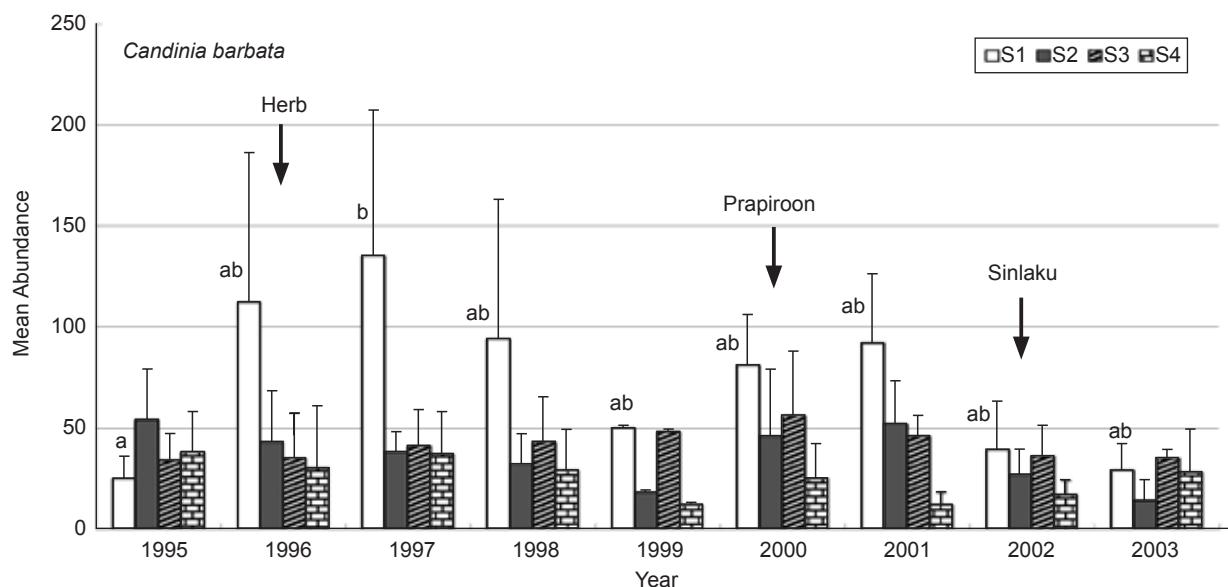


Fig. 6. Mean (± 1 S.E.) annual total abundances of *Candidia barbata* at 4 sampling sites in Hapen Creek from 1995 to 2002. Years with the same letters do not significantly differ. The arrows indicate typhoon events which are labeled with the name of the storm.

little morphometric variation (Table 3). A multiple regression model indicated that abundances of *O. barbatula* were negatively associated with average width and average depth of the stream, and the CVs of width and depth. None of the other variables was significantly associated with

abundances of *O. barbatula* ($p > 0.15$). The suggested model explained 25.5% of the spatial variations in abundances of *O. barbatula* in Hapen Creek.

Candidia barbata not only preferred shallow and narrow waters, but also deeper regions with

Table 2. Mean (± 1 S.E.) abundances of pre- and post-typhoon periods of *Onychostoma barbatula* and *Candidia barbata* at 4 sites in Hapen Creek for the entire sampling period, typhoon years, and non-typhoon years. *t*-test results of species abundances between pre- and post-typhoon periods are also given

Sampled years	Site (<i>n</i>)	<i>Onychostoma barbatula</i>			<i>Candidia barbata</i>				
		Pre-typhoon	Post-typhoon	<i>t</i>	<i>p</i>	Pre-typhoon	Post-typhoon	<i>t</i>	<i>p</i>
1995-2002	S1 (46)	58.6 \pm 12.5	77.2 \pm 15.7	0.19	> 0.05	51.8 \pm 11.1	63.1 \pm 12.9	0.27	> 0.05
	S2 (49)	76.6 \pm 42.1	79.2 \pm 53.9	0.31	> 0.05	35.1 \pm 21.9	39.1 \pm 22.6	0.62	> 0.05
	S3 (49)	63.4 \pm 30.9	67.0 \pm 40.7	0.35	> 0.05	37.4 \pm 15.5	44.9 \pm 20.5	1.43	> 0.05
	S4 (49)	49.4 \pm 35.7	52.9 \pm 30.2	0.37	> 0.05	19.1 \pm 8.9	33.2 \pm 24.2	2.70	< 0.01
Non-typhoon years	S1 (30)	85.8 \pm 53.4	53.5 \pm 47.3	1.74	> 0.05	81.3 \pm 57.7	71.4 \pm 65.9	0.44	> 0.05
	S2 (31)	80.2 \pm 43.8	71.9 \pm 60.6	0.43	> 0.05	39.4 \pm 23.6	32.6 \pm 17.5	0.90	> 0.05
	S3 (31)	60.2 \pm 31.7	62.5 \pm 38.8	0.17	> 0.05	39.2 \pm 15.4	42.0 \pm 12.9	0.54	> 0.05
	S4 (31)	40.8 \pm 32.0	52.9 \pm 24.3	1.17	> 0.05	19.7 \pm 9.8	36.3 \pm 23.3	2.61	< 0.05
Typhoon years	S1 (16)	101.0 \pm 73.0	139.8 \pm 98.3	0.90	> 0.05	59.9 \pm 33.2	101.2 \pm 65.2	1.66	> 0.05
	S2 (18)	80.1 \pm 40.1	92.4 \pm 45.2	0.61	> 0.05	29.9 \pm 15.1	52.7 \pm 31.7	2.06	> 0.05
	S3 (18)	70.3 \pm 39.5	74.6 \pm 38.3	0.23	> 0.05	37.7 \pm 20.9	49.7 \pm 29.7	1.00	> 0.05
	S4 (18)	59.7 \pm 38.2	57.9 \pm 41.4	0.09	> 0.05	16.9 \pm 8.7	34.7 \pm 28.7	1.95	> 0.05

Table 3. Results of stepwise multiple regressions relating *Onychostoma barbatula* and *Candidia barbata* abundances and morphometric variables of 4 sites along Hapen Creek. The microhabitat model was based on the mean and coefficient of variation (CV) of morphometric variables within each site. The temporal variability model was based on the annual means and CVs of morphometric variables. Only those variables that were statistically significant ($p < 0.15$) in the models are shown. No variable met the 0.15 significance level for entry into the temporal variability model of *Candidia barbata*

<i>Onychostoma barbatula</i>	Parameter	Partial R^2	<i>F</i>	<i>p</i>
Microhabitat model				
Mean width (m)	-7.27	0.1463	21.37	< 0.01
Mean depth (cm)	-1.11	0.0377	5.09	< 0.01
Width CV	-120.68	0.0229	12.06	0.02
Depth CV	-41.92	0.0479	3.55	< 0.01
Temporal variability model				
Depth CV	1.16	0.11	3.72	0.06
<i>Candidia barbata</i>	Parameter	Partial R^2	<i>F</i>	<i>p</i>
Microhabitat model				
Mean width	-7.74	0.1508	29.84	< 0.01
Maximum depth (cm)	0.65	0.0289	6.04	0.01
Mean depth	-2.58	0.0125	2.54	0.11
Depth CV	10.32	0.0174	3.5	0.06

high variations in water depth. Abundances of *C. barbata* were best predicted by a multiple regression model that included positive associations with maximum water depth of the stream and the CV of water depth and negative associations with average width and average depth of the stream. The suggested model explained 21.0% of the spatial variations in abundances of *C. barbata* in Hapen Creek.

Temporal variability model

The results of the multiple regression analysis revealed that no variables of temporal variation were significantly correlated with *C. barbata* abundances (Table 3). Abundances of *O. barbatula* were most often correlated with waters demonstrating high variability in depth (Table 3). The suggested model explained approximately 11.0% of the variations in the spatial abundances of *O. barbatula* among years.

DISCUSSION

Impacts of typhoons on mid-water fish abundances

In Taiwan, strong water currents in mountain streams create series of deep pools connected by riffles and runs. Although high oxygen concentrations and diverse feeding, resting, and breeding habitats exist in mountain streams of Taiwan (Han et al. 2000), fish have to adapt to a wide range of dynamic flow conditions during floods and muddy waters caused by downpours in the rainy season and typhoon periods.

Typhoons commonly occur in summer in subtropical and tropical regions of Asia (Wu and Kuo 1999). Commonly appearing from July to early Oct. in Taiwan, floods caused by typhoons have long been considered a major disturbance of habitat structure and animal communities in streams, especially in mountainous regions. As documented by Tew et al. (2002), pools were significantly smaller, riffles were larger, debris and mud filled the stream channels, and water turbidity was greatly elevated in Qishan Stream of southern Taiwan after typhoon Herb. Headwaters, upper stream habitats, and mountain streams are more susceptible to structural modifications caused by typhoons.

Although previous studies documented

how typhoons greatly modify habitat structures, the results of this study indicated that typhoons' impacts on mid-water fish abundances in Hapen Creek, a subtropical mountain stream, might be relatively minor. Intra- and inter-annual abundances of *O. barbatula* and *C. barbata* in Hapen Creek displayed almost no significant variations. Comparisons between pre- and post-typhoon abundances within typhoon and non-typhoon years also displayed almost no significant variations for either fish species.

Fish communities commonly recover after a flood, but the required time for the recovery varies. Pre-flood assemblages were reestablished within 8 mo in an Ozark stream (Arkansas, USA) following a catastrophic flood (Matthews 1988). In Kings Creek of Kansas, USA, a tall-grass prairie stream, recovery of the headwater fish population was also rapid, within 3 mo (Fritz et al. 2002). Compositional changes in the fish community in Qishan Stream of southern Taiwan were not detectable 14 mo after typhoon Herb, the most severe typhoon to occur since 1970 in Taiwan (Wu and Kuo 1999, Tew et al. 2002). The 14 mo recovery time may be overestimated because it was impossible to sample immediately after Herb due to destruction of roads. The results of this study suggest that typhoon impacts on mid-water fish abundances are minor based on the comparison of fish abundances 6 mo before and after typhoons. Additionally, no significant difference was found in either the July/Aug. or Sept./Oct. periods between typhoon and non-typhoon years. Based on those 2 observations, the recovery time of mid-water fish abundances after a flooding disturbance, at least in mountain streams of northern Taiwan, could be shorter than 14 mo, possibly only 2–6 mo.

Adaptive mechanisms of mid-water fish in mountain streams

Abundances of both fish species being negatively correlated with stream width and depth indicate that both are adapted to mountain streams with habitats of fluctuating flow regimes and morphometry. However, *O. barbatula* had greater abundances than *C. barbata* in Hapen Creek (Figs. 3, 4). *Candidia barbata*, with a laterally compressed body and larger pectoral fin, is more specialized and prefers slow-moving pools compared to *O. barbatula*, with its cylindrical body and smaller pectoral fins (Chuang et al. 2006). Based on ecomorphological characteristics,

Chuang et al. (2006) postulated that *C. barbata* was mainly distributed in mid-stream sections because of its weaker swimming performance, while *O. barbatula* is able to dominate in creeks at higher elevations because of its better swimming ability. This postulation was supported by the observation that *O. barbatula* had greater abundances than *C. barbata* within and among years in Hapen Creek in this study.

The findings that *O. barbatula* abundances were negatively associated with variations in stream width and water depth suggest that this fish species might not adapt well to systems with fluctuating morphometry. This might explain the decline of *O. barbatula* abundances after typhoons, as we observed after typhoon Herb.

In contrast to *O. barbatula*, *C. barbata* abundances were positively correlated with maximum depth and water depth CV. In addition to fast currents, montane drainage basins typically experience rapid rises and falls during floods in the rainy season, localized rainstorms, and typhoons (Gupta 1988). Given its weaker swimming ability compared to *O. barbatula*, *C. barbata* may adapt to hydrological dynamics in mountain streams by staying in deeper habitats as refuges or quickly dispersing to refuges through flooded corridors. In Quebrada Prieta of the Luquillo Experimental Forest, Puerto Rico, Covich et al. (1991) reported that atyid shrimp resisted storm flows best when in wide, deep pools. In Taiwan, Tew et al. (2002) observed that seasonal floods in mountain streams usually provide deepened waterways between pools. *Candidia barbata* may migrate and move from shallow to deeper habitats through such waterways to reduce flooding impacts. Using a different adaptation mechanism from *O. barbatula*, *C. barbata* may be able to maintain its population abundances in mountain streams despite its weaker swimming performance.

Based on the results of this study, we posit 2 mechanisms which might be adopted by mid-water fish species to adapt to hydrologic dynamics in mountain streams of Taiwan. First, benefiting from its morphological advantages, *O. barbatula* uses its better swimming performance to endure the fast and variable currents; however, this species is limited in tolerating hydrologic fluctuations. Compared to *O. barbatula*, *C. barbata*, despite its weaker swimming ability, has greater flexibility in enduring hydrologic and morphometric variability by staying in deeper water and/or quickly dispersing to refuges during flooding disturbances.

Management implications

The rainy season in northern Taiwan occurs from June to Nov. The typhoon period in this region is also concentrated in July and Aug., with an average of 400-600 mm rainfall falling monthly. Based on the overlap of the wet season and typhoon period and the results from this study, researchers should be cautious in defining typhoons as a natural disturbance to aquatic organisms in mountain streams during wet season of Taiwan.

We generally expect that storm-generated flooding in mountain streams of subtropical areas will change biotic abundances and community compositions by altering food supplies and habitat structure (Covich et al. 1991 2006). With constricted stream widths and shallow water depths, heavy rainfall events could have frequent and long-lasting effects on high-gradient streams. Gupta (1988) indicated that rainfall events in the tropics are characterized by very large pulses, and these intense rains are often associated with hurricanes (typhoons). Predictions differ regarding the effects of global warming and El Niño periods on the frequency and intensity of future typhoons and the spatial distribution of rainfall events (Gray 1990). If typhoons do become more frequent and possibly of greater intensity, their effects on aquatic organisms of mountain streams are likely to become more important, and may differ from what we report in this study. Another possibility is that the spatial rearrangement of rainfall amounts may generate drought events and other negative impacts like greatly reduced habitat quality and availability by decreasing pool volumes and hydrologic connectivity of flowing waters (Bencala 1993, Covich et al. 2000, Pringle 2003). Due to a shortage of available information and experience, more emphasis should be placed on conducting related research and evaluating drought impacts on aquatic organisms in montane streams of Taiwan.

Acknowledgments: We thank the Taiwan Forestry Research Institute, Taipei, Taiwan for providing facilities and accommodations at the Fushan Research Center, Ilan County. We also thank the anonymous reviewers who provided valuable comments on this manuscript. We are grateful to the research assistants and students of the Biodiversity Research Lab of the Department of Life Science, National Taiwan University, Taipei, Taiwan for help with fieldwork. This study was

supported by the National Science Council of Taiwan (NSC86-2621-B-002-012-A07, NSC87-2621-B-002-013-A07, NSC88-2621-B-002-011-A10, and NSC95-2313-B-017-002-MY3).

REFERENCES

- Bencala KE. 1993. A perspective on stream-catchment connections. *J. North Am. Benthol. Soc.* **12**: 44-47.
- Central Weather Bureau. 2006. Typhoon database. Available at <http://rdc28.cwb.gov.tw/>. Accessed 12/29/2007.
- Chang SH, PF Lee, YS Lin. 1998. Reproductive biology of *Varicorhinus barbatulus* in Hapen Creek, Fushan, Taipei County, Taiwan. *Ann. Taiwan Mus.* **41**: 53-69. (in Chinese)
- Chuang LC, YS Lin, SH Liang. 2006. Ecomorphological comparison and habitat preference of 2 cyprinid fishes, *Varicorhinus barbatulus*, and *Candidia barbatus*, in Hapen Creek of northern Taiwan. *Zool. Stud.* **45**: 114-123.
- Collins JP, C Young, J Howell, WL Minckley. 1981. Impact of flooding in a Sonoran stream, including elimination of an endangered fish population (*Poeciliopsis o. occidentalis*, Poeciliidae). *Southwest Nat.* **26**: 415-423.
- Covich AP, TA Crowl, T Heartsill-Scalley. 2006. Effects of drought and hurricane disturbance on headwater distribution of palaemonid river shrimp (*Macrobrachium* spp.) in the Luquillo Mountains, Puerto Rico. *J. North Am. Benthol. Soc.* **25**: 99-107.
- Covich AP, TA Crowl, SL Johnson, D Varza, DL Certain. 1991. Post-hurricane Hugo increases in atyid shrimp abundance in a Puerto Rican montane stream. *Biotropica* **23**: 448-454.
- Dolloff CA, PA Flebbe, MD Owen. 1994. Fish habitat and fish populations in a southern Appalachian watershed before and after Hurricane Hugo. *Trans. Am. Fish. Soc.* **123**: 668-678.
- Fitzsimons MJ, RT Nishimoto. 1995. Use of fish behavior in assessing the effects of hurricane Iniki on the Hawaiian island of Kaua'i. *Environ. Biol. Fish.* **43**: 39-50.
- Fritz KM, JA Tripe, CS Guy. 2002. Recovery of three fish species to flood and seasonal drying in a tall grass prairie stream. *Trans. Kan. Acad. Sci.* **105**: 209-218.
- Gray WM. 1990. Strong association between West African rainfall and U.S. landfall of intense hurricanes. *Science* **249**: 1251-1256.
- Grossman GD, RE Ratajczak, M Crawford, MC Freeman. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecol. Monogr.* **68**: 395-420.
- Gupta A. 1988. Large floods as geomorphic events in the humid tropics. In VR Baker, RC Kochel, PC Patton, eds. *Flood geomorphology*. New York: J Wiley, pp. 301-305.
- Han CC, KS Tew, IS Chen, LY Su, LS Fang. 2000. Environmental biology of an endemic cyprinid, *Varicorhinus alticorpus*, in a subtropical mountain stream of Taiwan. *Environ. Biol. Fish.* **59**: 153-161.
- Matthews WJ. 1988. Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. *Copeia* **1986**: 388-397.
- Murphy ML, WR Meehan. 1991. Stream ecosystems. Bethesda, MD: American Fisheries Society Special Publication 19.
- Power ME, WJ Matthews, AJ Stewart. 1985. Grazing minnows, piscivorous bass and stream algae: dynamics of a strong interaction. *Ecology* **66**: 1448-1456.
- Pringle CM. 2003. What is hydrologic connectivity and why is it ecologically important? *Hydrol. Process.* **17**: 2685-2689.
- Pusey BJ, AH Arthington, MG Read. 1993. Spatial and temporal variation in fish assemblage structure in the Mary River: the influence of habitat structure. *Environ. Biol. Fish.* **37**: 355-380.
- Swanson FJ, SL Johnson, SV Gregory, SA Acker. 1998. Flood disturbance in a forested mountain landscape. *BioScience* **48**: 681-689.
- Tew KS, CC Han, WR Chou, LS Fang. 2002. Habitat and fish fauna structure in a subtropical mountain stream in Taiwan before and after a catastrophic typhoon. *Environ. Biol. Fish.* **65**: 457-462.
- Wu CC, YH Kuo. 1999. Typhoons affecting Taiwan – current understanding and future challenges. *Bull. Am. Meteorol. Soc.* **80**: 67-80.