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Size-dependent Foraging on Aquatic and Terrestrial Prey by the Endangered Taiwan Salmon *Oncorhynchus masou formosanus*

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Lin-Yan Liao, Ming-Chih Chiu, Yii-Shing Huang, and Mei-Hwa Kuo (2012) Size-dependent foraging on aquatic and terrestrial prey by the endangered Taiwan salmon *Oncorhynchus masou formosanus*. *Zoological Studies* **51**(5): 671-678. Terrestrial subsidies are important resources for drift-feeding fishes. The contribution of these subsidies to fish diets increases with predator size or age because larger fish can feed on a wider range of prey. We assessed how the relative abundance of aquatic and terrestrial insects in the diet of the endangered Taiwan salmon *Oncorhynchus masou formosanus* (Jordan and Oshima) changed with salmon body size. We found that aquatic invertebrates were the most important prey in the diet of Taiwan salmon. However, the diet of small (8.0-14.8 cm) Taiwan salmon significantly differed from that of large salmon (19.1-25.2 cm). The proportion of the diet comprised of terrestrial prey and its trophic diversity increased with salmon body size. We did not identify the specific reasons, such as foraging limitations, for the size-dependent dietary shift. However, it is clear that the endangered, drift-feeding, Taiwan salmon relies on terrestrial resources for an important part of its diet. For conservation and management purposes, we urge that the restoration of forest vegetation, especially in riparian zones, be one of top priorities. http://zoolstud.sinica.edu.tw/Journals/51.5/671.pdf

Key words: Drift, Invertebrates, *Oncorhynchus masou formosanus*, Stream, Taiwan salmon.

Regulation of food-web structure and dynamics has frequently been studied within an ecosystem, but seldom among multiple, interacting ecosystems (Romero and Srivastava 2010). Regulatory processes are important in trans-ecosystem linkages between aquatic and terrestrial food webs (Polis et al. 1997, Nakano and Murakami 2001, Baxter et al. 2005). Awareness of these processes is especially important for low-latitude stream ecosystems, such as ones in tropical-subtropical Taiwan, which have rather different trophic relationships than those at mid-latitudes (Coat et al. 2009, Dudgeon et al. 2010). Bottom-up and top-down processes act through predator-prey interactions that cross the boundaries between riparian and freshwater ecosystems (Chiu et al. 2008). Trophic linkages can provide subsidies, such as when riparian birds feed on emerging aquatic insects (Epanchin et al. 2010). Resource inputs from donor habitats are important to the persistence of biological assemblages in recipient habitats (Kawaguchi et al. 2003). In addition, inputs from adjacent ecosystems to the foraging selection of predators can be consumer size- or age-dependent (Montori et al. 2006, Dineen et al. 2007, Gustafsson et al. 2010).

In fish, dietary shifts during development and growth are common, and are largely attributed to morphological and developmental changes that occur with age (Barbini et al. 2010, Kreitzer et al. 2010). As body size and energy requirements increase, and morphological constraints, especially the gape, decrease, fish change their foraging to find optimal prey (Barriga and Battini 2009).

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In drift-feeding fish, such as the Taiwan salmon *Oncorhynchus masou formosanus* (Jordan and Oshima), the proportion of the diet comprised of terrestrial invertebrate prey is greater for large than for small conspecifics (Montori et al. 2006, Dineen et al. 2007, Gustafsson et al. 2010). Smaller conspecific fish probably do not consume as much terrestrial prey due to their limited gape, and because foraging on surface-drifting terrestrial prey increases their risk of predation (Gustafsson et al. 2010). In addition, small conspecifics tend not to occupy focal positions with priority access to large, surface-drifting prey (Nakano 1995a b). As a result, resource inputs from terrestrial systems decrease competition among conspecifics for aquatic prey, increasing the efficiency of resource partitioning in fish populations (Nakano 1994, Dineen et al. 2007).

In forest streams, allochthonous prey from productive, terrestrial ecosystems help maintain fish populations (Kawaguchi et al. 2003). Thus, anthropogenic activities that reduce riparian vegetation decrease inputs of terrestrial invertebrates into lotic ecosystems, which could negatively impact fish populations. Understanding these interactions and relationships is critical to the conservation of the Taiwan salmon *O. masou formosanus* and other endangered fish (Yan 2000). Taiwan salmon are land-locked and are endemic to tributaries of the Dajia River in central Taiwan. Due to habitat degradation caused by logging, agriculture, and the destruction of riparian vegetation by other causes, Taiwan salmon are restricted to a few streams. Currently, there is scant information about the trophic ecology of Taiwan salmon (Yan 2000). Knowing more about prey availability and the importance of terrestrial invertebrates in their diet would facilitate their conservation and management, and aid habitat restoration. Therefore, we quantified and compared the composition of the diets of large and small Taiwan salmon and looked for evidence of dietary shifting. Because larger fish have greater foraging abilities and fewer morphological constraints, the general hypothesis for drift-feeding fish states that a greater proportion of the diet of large individuals will be comprised of surface-drifting prey than for smaller conspecifics. Thus, we specifically predicted that terrestrial invertebrates would comprise a larger fraction of the diet of large than small Taiwan salmon.

MATERIALS AND METHODS

Study stream

This study was conducted in Yousheng Stream, a tributary of the Dajia River in the mountains of central Taiwan (Fig. 1). The watershed area is 31 km^2. Annual rainfall is about 1500 mm (weather station D2F23, 1985-1998), and spring monsoons and summer typhoons frequently lead to discharge rates of > 10 m^3/s at the confluence of Cijiawan and Yousheng Streams (Chiu et al. 2008). The study area runs for 500 m along a natural section of Yousheng Stream between 24°23.673'N, 121°21.069'E (downstream end) and 24°23.788'N, 121°20.494'E (upstream end), and is at about 2000 m in elevation. Woody riparian vegetation forms a closed canopy over the stream. The stream substrate is composed largely of cobble and rubble (6.4-25.6 cm), and the stream habitat is mostly composed of runs and riffles with only a few deep pools. The study section is far upstream of agricultural areas. We used a multi-parameter water quality meter (model WQC-24, TOA-DKK, Tokyo, Japan) to measure the water quality once a month in 2010. Water temperature

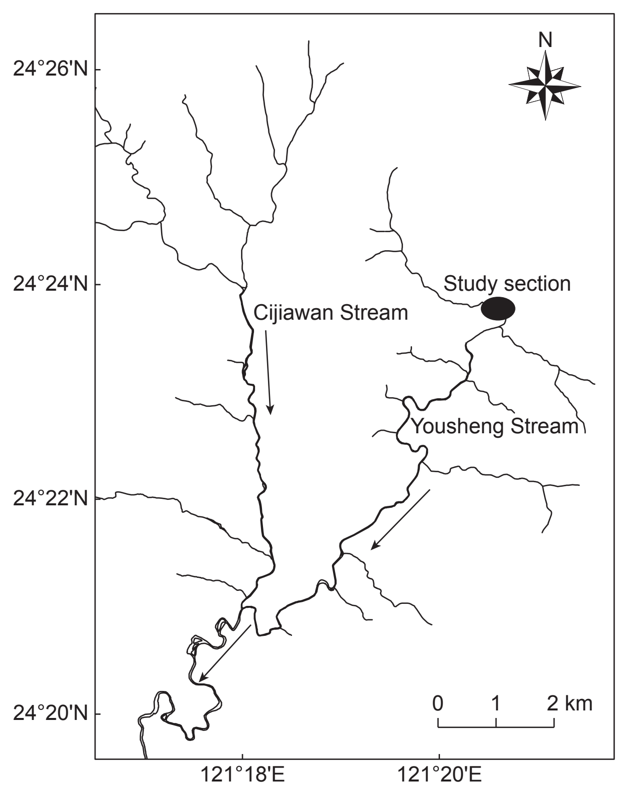

Fig. 1. Map of the upstream drainage of the Dajia River, central Taiwan. Arrows indicate the direction of stream flow.

in this stream section was 8.2-15.0°C, pH was 7.52-8.20, conductivity was 13.0-17.1 μS/cm, and dissolved oxygen was 7.78-9.53 mg/L. Cijiawan Stream, a neighboring tributary in Shei-Pa National Park, has the largest population of Taiwan salmon. However, Taiwan salmon had not lived in Yousheng Stream for 30 yr until Shei-Pa National Park released 75 wild salmon and 75 hatchery-reared salmon in June 2009, and 350 hatchery-reared salmon in May 2010.

Taiwan salmon sampling and prey identification

On 23 Aug. 2010, 48 salmon were caught by electrofishing at randomly selected habitats, including pools, runs, and riffles. To avoid severely disturbing this rare, endangered fish species, yet still obtain a sufficiently large sample, only 48 of the roughly 500 salmon in this stream (about 10% of the population) were collected. The stomach contents of each salmon were obtained by flushing the gut with water using a Seaburg's pump (Seaburg 1957). After flushing, we measured their total lengths with a ruler, and then the salmon were released at the location where they were captured. The 48 salmon formed 2 distinct groups: 11 large fish in their 3rd year of life, 19.1-25.2 cm long (total length), and 37 small salmon in their 1st year of life, 8.0-14.8 cm long (total length). The large fish (7 wild salmon and 4 hatchery-reared salmon) were a subset of the 150 salmon released in their 2nd year of life in 2009. The small fish (34 wild salmon and 3 hatchery-reared salmon) were from the 350 salmon released in their 1st year of life in 2010 and offspring of the large fish. To identify the large fish and the 2 cohorts of small fish, we marked the hatchery-reared and wild fish when they were released, and newborn wild salmon in early 2010 by clipping different fins (adipose, left pelvic, and/or right pelvic fins) for each cohort.

Each prey item in the stomach contents was identified to the lowest taxonomic level possible with taxonomic keys, and its life stage was recorded to determine whether the prey came from terrestrial or aquatic habitats (Kang 1993, Merritt and Cummins 1996, Kawai and Tanida 2005). Adults and nymphs/larvae of all insect orders and non-insect taxa were placed into habitat use categories.

Data analyses

All 48 salmon had prey in their stomachs, but 1 salmon had only 1 prey item in its stomach. Because a fish with only 1 prey item did not satisfy the criteria for calculation of the Shannon diversity index and we wanted to maintain the same sample size for all analyses, we excluded this fish from all subsequent analyses.

The focus of this study was size-dependent food preferences of salmon. A previous study in the same stream showed that hatchery-reared and wild fish coexisted in the same habitats (Huang 2010), and hatchery-reared salmon had the same habitat preferences as wild salmon. In this study, 41 salmon were wild and 7 were hatchery-reared. We used 2-way crossed analysis of similarities (ANOSIM, Clarke and Warwick 2001) based on a Bray-Curtis dissimilarity matrix on the fraction of prey from each prey category in the diet of Taiwan salmon, and found that no significant difference existed between diets of hatchery-reared and wild salmon (Global R = -0.314, p = 0.790). However, diets of large and small salmon significantly differed (Global R = 0.511, p = 0.001). Therefore, we combined data for hatchery-reared and wild salmon in our study and all subsequent analyses.

The relationship between diet composition and body size was examined using a multivariate analysis. To ordinate the 47 salmon in the sample, we used non-metric multidimensional scaling (MDS, Clarke and Warwick 2001) based on a Bray-Curtis dissimilarity matrix on the fraction of prey from each prey category in the diet of Taiwan salmon. A stress value of < 0.2 indicated that the plot contained convincing information (Clarke and Warwick 2001). Based on the same Bray-Curtis dissimilarity matrix, ANOSIM (Clarke and Warwick 2001) was used to determine whether the diet compositions of large and small Taiwan salmon significantly differed. The significance level of the analysis was set to 0.05. The 2 analyses (MDS and ANOSIM) were performed with PRIMER software (Clarke and Warwick 2001). We also used Schoener's overlap index (Schoener 1970) to estimate diet overlap between the 2 size-groups.

We used the Spearman rank-order correlation test to determine whether the dietary contribution of terrestrial prey increased with the body size of Taiwan salmon (PROC CORR, SAS Institute 1999). In addition, a correlation analysis was used to determine if there was a positive relationship between niche width and body size in Taiwan salmon. The niche width of each salmon was estimated using the Shannon diversity index on prey categories in its diet (Sánchez-Hernández et al. 2011), and was calculated using PRIMER software (Clarke and Warwick 2001). The significance level of both correlation analyses was set to 0.05.

RESULTS

Altogether, 2097 identified prey items were collected from the gut contents of 48 Taiwan salmon (Table 1). All prey were invertebrates, and 85.74% were larvae/nymphs or pupae of aquatic insects in the orders Diptera, Ephemeroptera, Plecoptera, Trichoptera, and Coleoptera. For large Taiwan salmon, the most abundant prey were aquatic Plecoptera (18.63%) and Trichoptera (18.32%). For small salmon, aquatic Ephemeroptera (27.04%) and Plecoptera (26.99%) were the most abundant. Overall, terrestrial invertebrates accounted for 14.26% of all prey items. However, they comprised 39.13% of the diet of large Taiwan salmon, but only 9.75% of the diet of small salmon.

The MDS plot (Fig. 2, 2D stress = 0.18) indicates that the diet composition differed between small and large fish, and this dietary shift seemed to correspond to a gradient along MDS axis 1. In addition, ANOSIM results showed that the composition of the diets of the 2 size groups significantly differed (Global $R = 0.505$, $p = 0.001$). Schoener's index indicated that the diet composition of small and large fish overlapped by 67.99%. Therefore, the significant difference in

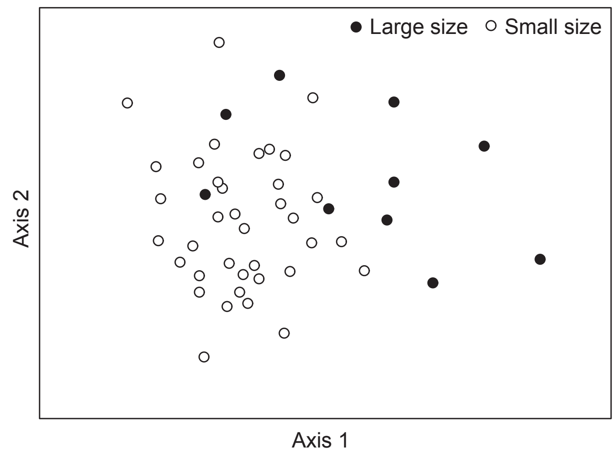

Fig. 2. MDS ordination of the diets of 10 large (19.1-25.2 cm) and 37 small (8.0-14.8 cm) Taiwan salmon *O. masou formosanus*, based on a Bray-Curtis dissimilarity matrix on the proportion of prey items in each prey category. Diet compositions of small to large fish changed along axis 1. One large salmon with only 1 prey item in its stomach was excluded from this analysis.

Table 1. Taxonomy and relative abundances (%) of the 2097 prey items found in the guts of 11 large (19.1-25.2 cm) and 37 small (8.0-14.8 cm) Taiwan salmon *O. masou formosanus*

Prey taxon	Large salmon (%)	Small salmon (%)	Total (%)
Aquatic	**60.87**	**90.25**	**85.74**
Coleoptera larvae	2.80	0.28	0.67
Diptera larvae and pupae	9.94	17.13	16.02
Ephemeroptera nymphs	11.18	27.04	24.61
Plecoptera nymphs	18.63	26.99	25.70
Trichoptera larvae and pupae	18.32	18.82	18.74
Terrestrial	**39.13**	**9.75**	**14.26**
Coleoptera larvae and adults	4.35	1.41	1.86
Collembola	0.31	0.17	0.19
Diptera larvae and adults	8.07	3.04	3.81
Ephemeroptera subimagoes and imagoes	2.17	0.96	1.14
Hemiptera	8.70	1.86	2.91
Hymenoptera	6.52	0.85	1.72
Lepidoptera larvae and adults	2.17	0.17	0.48
Orthoptera		0.06	0.05
Plecoptera adults	1.86	0.11	0.38
Psocoptera	3.11	0.11	0.57
Thysanoptera		0.06	0.05
Trichoptera adults	0.62	0.51	0.52
Non-Insecta	1.24	0.45	0.57

diet composition resulted from the 32.01% that did not overlap.

The fraction of terrestrial prey and the body size of Taiwan salmon were significantly positively correlated (Fig. 3, $r = 0.50$, $p = 0.0003$). Terrestrial insects comprised < 20% of the diet of most small fish and 0%-80% of the diet of large salmon (Fig. 3). Dietary niche breadth and the body size of Taiwan salmon were significantly positively correlated (Fig. 4, $r = 0.43$, $p = 0.0026$), indicating that the diet of large Taiwan salmon varied more than that of small salmon. The trophic diversity in the diets of small and large fish had a similarly wide range (Fig. 4).

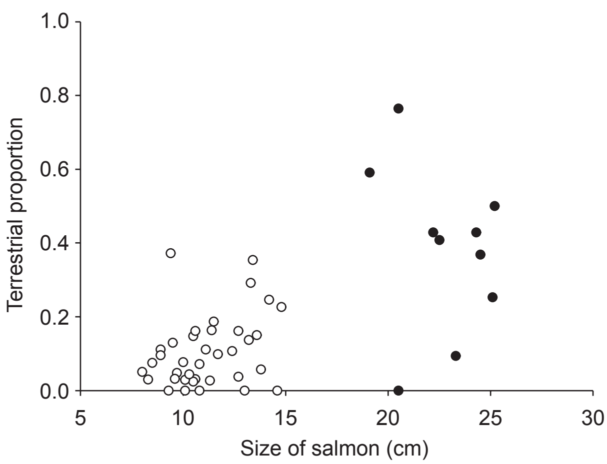

Fig. 3. Spearman correlation between body size and the proportion of prey items comprised of terrestrial prey in the diets of 47 Taiwan salmon *O. masou formosanus* ($r = 0.50$, $p = 0.0003$). One salmon with only 1 prey item in its stomach was excluded from this analysis.

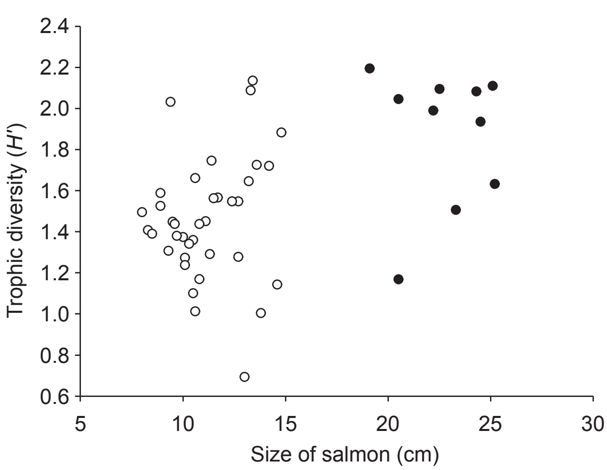

Fig. 4. Spearman correlation between the body size and trophic diversity in the diets of 47 Taiwan salmon *O. masou formosanus* ($r = 0.43$, $p = 0.0026$). One salmon with only 1 prey item in its stomach was excluded from this analysis.

DISCUSSION

In this study, aquatic invertebrates were the most important prey in the diet of Taiwan salmon. This agrees with the results of a previous study on this species (Yan 2000) and results of studies on other drift-feeding fishes (Bridcut 2000, Dineen et al. 2007, Sánchez-Hernández et al. 2011). However, terrestrial prey were also important, constituting roughly 14% of the diet of Taiwan salmon and about 16%-33% of the diets of other drift-feeding fishes (Montori et al. 2006, Dineen et al. 2007). In addition, we found that as with other drift-feeding fishes (Nagoshi et al. 1988, Morita and Suzuki 1999, Montori et al. 2006, Dineen et al. 2007), terrestrial prey constituted a larger proportion of the diet of large, than small, Taiwan salmon, clearly indicating a size-dependent change in the diet of this drift-feeding fish.

Size-related shifts in the diet composition are well documented among fish species, and several hypotheses for this shift were proposed. For example, shifts in diet composition can result from changes in morphological and physiological traits, in that the foraging opportunities of small fish are more limited than those of larger conspecifics (Barbini et al. 2010, Kreitzer et al. 2010). These same hypotheses for dietary shifts can also explain the higher fraction of terrestrial prey in stomachs of large individuals of drift-feeding fish, including the Taiwan salmon. We found that aquatic invertebrates were the most important prey for both small and large Taiwan salmon. In addition, subsidies of terrestrial invertebrates from riparian habitats with native vegetation were important for large salmon and should be included in conservation plans for this endangered fish (Kuo 2008).

Body size is a key factor affecting prey acquisition by predators. Because terrestrial invertebrate prey tend to be larger than aquatic invertebrate prey, larger drift-feeding fish can better exploit this resource than smaller conspecifics (Nakano et al. 1999b, Montori et al. 2006). However, other studies found that small juvenile salmon rely heavily on terrestrial invertebrates (Kato 1991, Nakano and Kaeriyama 1995), possibly due to the small size of the terrestrial prey. Thus, morphological and/or physiological limitations are not the only potential hypotheses to explain size-related shifts in diet compositions.

In stream fishes, predation risks tend to decrease with body size (Schlosser 1987). Larger conspecifics forage more and experience lower predation risk in pools (Heggenes et al. 1999), which are calmer habitats where surface-drifting terrestrial prey tend to collect. Even in less-foraged riffles, we suppose that the greater swimming abilities of larger fish allow them to better deal with the faster currents and turbulence than smaller conspecifics and thereby encounter more terrestrial prey. For drift foragers of sympatric species, large fish species have higher dominances than small ones for favorable drift-foraging positions (Nakano and Furukawatanaka 1994, Nakano et al. 1999a). Based on a size-structured dominance hierarchy, large conspecific fish outcompete small fish to occupy focal points (nearer the pool inlet) that provide access to large, surface-drifting prey (Nakano 1995a b). Ultimately, these foraging abilities and thus habitat use could be factors determining the increasing contribution of terrestrial invertebrates to the diet of large fish predators, as found in this and previous studies (Montori et al. 2006, Dineen et al. 2007, Gustafsson et al. 2010).

Prey size is a commonly used key quantitative measure to compare diets and foraging behaviors. In streams, terrestrial prey is often larger than aquatic prey (Nakano et al. 1999b, Meissner and Muotka 2006, Montori et al. 2006), and fish would presumably prefer terrestrial prey to aquatic invertebrates for this reason alone. Large prey is easier to detect, which reduces search times (Naef-Daenzer and Keller 1999). However, prey abundance can strongly affect predator-prey encounter rates. Usually, larger prey are less abundant than smaller prey, presenting predators with a tradeoff between search time and prey quality (Chiu et al. 2009). Prey profitability is a function of prey quality and handling time. Among invertebrate prey, a large body size, high exoskeleton hardness, and high distastefulness are associated with high handling costs (Sherry and McDade 1982). For prey of a given size, softer prey, such as free-living trichopteran larvae, are less costly than chitinous prey. Brown trout preferentially forage for large aquatic prey, and for prey of a given size, the consumption of terrestrial prey is more dependent on the relative abundance of the prey than on their size (Rincón and Lobón-Cerviá 1999). Therefore, drift-feeding fish might prefer to forage for prey with optimal traits under existing conditions, irrespective of their being terrestrial or aquatic. As shown in previous studies (Montori et al. 2006, Sánchez-Hernández et al. 2011), the dietary niche breadth and trophic diversity of larger Taiwan salmon are greater than those of smaller conspecifics. In addition, we found that the proportion of terrestrial prey in the diet of several large salmon was low, but the trophic diversity in their diet was high, indicating that these large fish foraged on more taxa of aquatic prey, possibly including large species.

Our results support the hypothesis that a shift in the dietary niche breadth exists with an increasing body size of Taiwan salmon. Trans-ecosystem subsidies could improve the population persistence by increasing the dietary niche breadth, facilitating size-dependent foraging behaviors and decreasing competition for common trophic resources. In addition, energy flows across an ecosystem could stabilize the food web dynamics of recipient habitats (Takimoto et al. 2002), especially if the seasonal peak in external subsidies occurs when local resources are most diminished (Nakano and Murakami 2001). In our study, changes in the composition of the diet of Taiwan salmon occurred during a relative decline in local resources during the flooding season (Chiu et al. 2008).

Habitats with different riparian vegetation types provide terrestrial subsidies that affect size-class interactions among drift-feeding fish (Dineen et al. 2007). This reliance on allochthonous resources must be considered when designing conservation programs for endangered, drift-feeding fish, such as the Taiwan salmon. An increase in terrestrial subsidies is closely associated with more-efficient resource partitioning and better population maintenance, especially when the supply of autochthonous prey is temporally reduced. To successfully restore Taiwan salmon in their native habitats, several factors must be considered. In addition to the effects of typhoons and agricultural activities on the fish and their major aquatic prey (Kuo et al. 2004, Chiu et al. 2008, Makiguchi et al. 2009), we urge that the restoration of forest vegetation, especially in riparian zones, be a top priority.

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