

# Trophic model of the subtropical headwater stream habitat of Formosan landlocked salmon *Oncorhynchus formosanus*

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**ABSTRACT:** Using the Ecopath approach and a network analysis, a mass-balance trophic model was constructed to analyze the structure and energy flows of a high-altitude subtropical headwater stream, Chichiawan Stream, the only habitat of the Critically Endangered Formosan landlocked salmon *Oncorhynchus formosanus*. Natural abundances of carbon and nitrogen isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were used as a complementary method to stomach content analysis to trace food sources of consumers in the stream. Riparian  $\text{C}_3$  plants were the major food source of dominant gatherer and filterer aquatic insects, while diatoms were the major food source of scraper aquatic insects. Lindeman trophic analysis indicated that the flows of detritivory and herbivory were quantitatively equally important as food sources for consumers in the stream, suggesting a close terrestrial–aquatic linkage. The trophic model of Chichiawan Stream comprised 13 compartments and 4 integer trophic levels with the highest trophic level of 3.12 for birds. The pedigree index for the trophic model was 0.71, indicating a high-quality model. The mixed trophic impacts indicated that the biomass of Formosan salmon was unlikely constrained by food sources or predation pressure by birds. In a comparative analysis with other trophic models of temperate mountain streams, the total consumer biomass and mean trophic transfer efficiency were relatively low in this subtropical mountain stream, which is characterized by high precipitation, steep channels, rapid current velocity, and changing flow regime. To conserve the Formosan salmon, the first priorities are agricultural runoff control and maintaining a well-vegetated riparian zone.

**KEY WORDS:**  $\delta^{13}\text{C}$  ·  $\delta^{15}\text{N}$  · Chichiawan Stream · Riparian  $\text{C}_3$  plants · Diatoms · Ecopath · Network analysis

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## INTRODUCTION

Our understanding of tropical/subtropical streams is rather limited because studies of these systems have been restricted to only a few geographic re-

gions (Boyero et al. 2009). Further studies on trophic structure and dynamics from all tropical streams are particularly needed (Boyero et al. 2009), as the prevailing notions of trophic structure and energy flow in streams are primarily based on research under-

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taken in temperate regions. Dudgeon et al. (2010) indicated that trophic models for northern temperate streams are inadequate for describing tropical systems. High-altitude tropical streams might be functionally more similar to temperate streams than to their lowland counterparts; however, they might differ from temperate streams because of the more constant conditions of light and temperature in the tropics than in temperate regions.

Chichiawan Stream ( $24^{\circ} 23' N$ ,  $121^{\circ} 18' E$ ) is a subtropical headwater stream of Tachia River in central Taiwan at an elevation between 1770 and 1900 m (Fig. 1). This stream is the last refuge of the Taiwanese landlocked salmon *Oncorhynchus formosanus*, one of the southernmost natural salmon populations in the world (Oshima 1955). Overexploitation and habitat degradation due to agricultural development and dam establishment are thought to have

resulted in severe decreases in the abundance and distributional area of Formosan salmon after the 1960s (Tsao et al. 1998), and its population size was recently estimated to be only 1000 to 3000 individuals (Chung et al. 2008). This species was listed as Critically Endangered by the IUCN in 1996 (Kottelat 1996). Due to its Critically Endangered status, the abundance of Formosan salmon has been extensively monitored since 1984. Substratum composition, grain size (Chung et al. 2008), and hydrological conditions (e.g. current velocity and water depth, Tsao et al. 1998) were emphasized as important factors in the distribution of this fish. Up to 50% of the variation in the abundance of Formosan salmon can be explained by physicochemical parameters and substratum composition (Hsu et al. 2010), but the importance of trophic relationships on the abundance of Formosan salmon has received much less attention.

Efforts to conserve and restore stream ecosystems are often hindered by a limited understanding of the dynamics of trophic structure and energy flows (DeLong & Thorp 2006, Hoeninghaus et al. 2007). Stomach content analyses of Formosan salmon have shown that aquatic insects are its main food source (Ueno 1937, Lin et al. 2006), and a potential predator of salmon in Chichiawan Stream is the striated heron *Butorides striatus amurensis* (Sun 2004). However, it is not known whether food resources and/or predation pressure are limiting factors for the fish population in Chichiawan Stream.

Although stomach contents of Formosan salmon provide a taxonomic resolution of food sources with regard to aquatic insects (Ueno 1937, Lin et al. 2006), different food items consumed may have different digestion rates, which may underestimate the contribution of labile food sources and overestimate the importance of recalcitrant food sources (Hershey & Peterson 1996). Moreover, stomach contents may only represent the feeding conditions immediately prior to capture rather than being an indicator of long-term average food consumption. Lau et al. (2009) indicated the importance of distinguishing between assimilated and consumed food to obtain a reliable picture of a stream food web. Using stable isotope analysis (SIA) as a complementary method to stomach content analysis, the aims of this study were (1) to determine the food sources fueling Chichiawan Stream, (2) to construct the food web and organic matter flows of this high-altitude subtropical stream, and (3) to use network analysis (Field et al. 1989) to characterize the interconnected flows of organic matter from food sources to top predators in the food web.

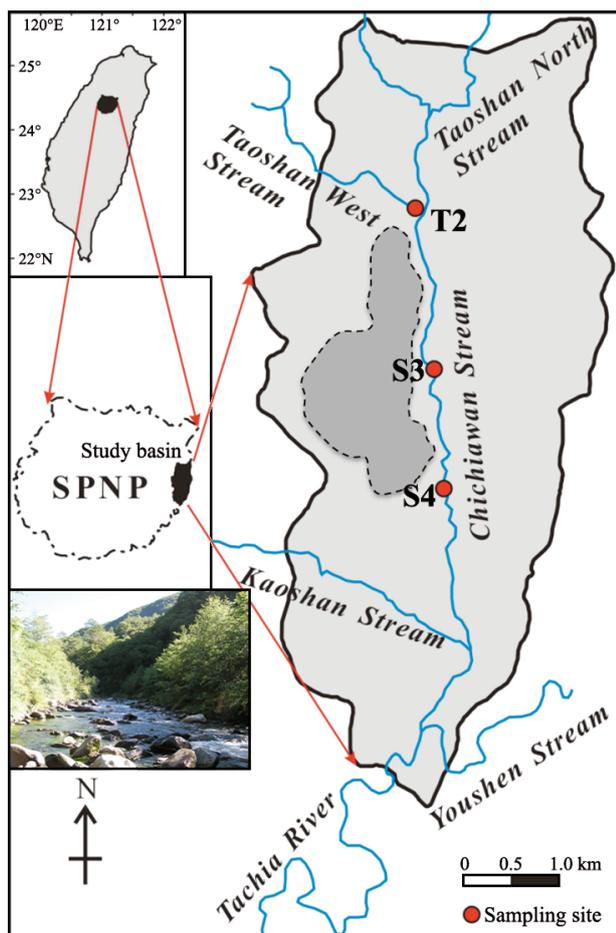


Fig. 1. Locations of the long-term ecological monitoring sites (T2, S3, and S4) and an agricultural area (dark grey) along Chichiawan Stream, Taiwan, and a photograph taken at site S4. SPNP: Shei-Pa National Park

## MATERIALS AND METHODS

### Study area

Chichiawan Stream is a third-order stream located in the Wuling basin of Shei-Pa National Park in subtropical Taiwan (Fig. 1). The stream is 15.3 km long and 7.1 to 12.3 m wide, with a high gradient of 13% and a catchment area of 76 km<sup>2</sup> (Lin et al. 1990). The mean forest canopy cover in Chichiawan Stream is 37.3% (Tsai et al. 2010). The mean water temperature is 12°C, ranging from 18°C in summer to 10°C in winter, and mean annual precipitation is 1642 mm, with mean monthly rainfall being generally <40 mm in the dry season (October to February), and frequently exceeding 300 mm during the wet season (May to September; 1981–2010 data from Taichung station, Climatological data annual reports, Taiwan Central Weather Bureau). On average, 3.4 typhoons directly affect this basin every year.

Riffles are the major habitat in Chichiawan Stream and comprise >80% of the stream area (Lin et al. 2006). The streambed was primarily created by deposition of weathered sandstone and slate. The mean discharge is 1.84 to 2.30 m<sup>3</sup> s<sup>-1</sup> during the dry season and 2.58 to 2.96 m<sup>3</sup> s<sup>-1</sup> in the wet season (Chung et al. 2008). Current velocity remains fast year round, averaging 0.33 m s<sup>-1</sup> in the dry season and 0.49 m s<sup>-1</sup> in the wet season (Hsu et al. 2010). Consequently, the streambed consists of a high proportion of pebbles (42%) in the dry season (winter), but is dominated by rubble (26%) and boulders (21%) in the wet season (summer) (Lin et al. 2006).

Three long-term monitoring sites have been established along Chichiawan Stream since 2004 (Fig. 1) which cover the main distribution area of the Formosan salmon. Site T2 is located in the upstream reach at an elevation of 1900 m, Site S3 is in the midstream reach at 1790 m, and Site S4 is in the downstream reach at 1742 m. The upper reach of Chichiawan Stream is bordered by riparian forest, but the midstream reach has been developed for agriculture by removing some natural riparian vegetation, including an area of 104 ha of cultivated vegetables and fruit (apples, peaches, pears). The impact of agricultural fertilizer (NO<sub>2</sub><sup>-</sup> + NO<sub>3</sub><sup>-</sup>)

inputs on downstream water quality and epilithic algae is significant (Yu & Lin 2009).

### Field sampling and parameter determination

Samples were collected from all 3 sites from December 2006 to February 2007 (dry season) and during July and August 2007 (wet season) to take account of seasonal changes. All samples and parameters used to construct the model were assembled as much as possible from our own studies (Tables 1 & 2). Phytoplankton biomass in terms of chlorophyll *a* (chl *a*) was determined spectrophotometrically by immediately filtering triplicate water samples through Whatman GF/F filters in the field and then extracting the filters in 90% acetone for 24 h at 4°C in the dark following the methods of Su et al. (2004). Periphyton biomass was estimated by randomly scraping epilithic biofilm off a surface area of 50 cm<sup>2</sup> of rocks (n = 9) with a toothbrush and then extracting the chl *a* in 90% acetone (Yu & Lin 2009). Diatoms were the most dominant taxa of the periphyton communities in the stream and contributed 85% of the total cell numbers, followed by cyanobacteria and filamentous green algae (Yu & Lin 2009). Only the C:N molar ratios of periphyton samples which were <16 were used for SIA, as these were indicative of diatom-rich

Table 1. Compartments and input parameters for the trophic model of Chichiawan Stream. P/B: production:biomass ratio; Q/B: consumption:biomass ratio; P/Q: production:consumption ratio; UN: unassimilated part of the food; WW: wet weight

Group	Biomass (g WW m <sup>-2</sup> )	P/B (yr <sup>-1</sup> )	Q/B (yr <sup>-1</sup> )	P/Q	UN
1. Phytoplankton	0.054	85.0			
2. Periphyton	45.94	48.0			
3. Shredders	0.026	2.9 <sup>a,b</sup>		0.14 <sup>a,b</sup>	0.70 <sup>c</sup>
4. Scrapers	0.852	6.0 <sup>d,e</sup>		0.06 <sup>f</sup>	0.50 <sup>c</sup>
5. Filterers	0.089	8.4 <sup>e</sup>		0.12 <sup>h</sup>	0.50 <sup>c</sup>
6. Gatherers	0.212	12.7 <sup>f,i</sup>		0.08 <sup>i</sup>	0.65 <sup>c</sup>
7. Predators	0.254	6.0 <sup>g</sup>		0.25 <sup>h</sup>	0.20 <sup>b</sup>
8. Non-insect grazers	0.693	6.0 <sup>k</sup>		0.12 <sup>k</sup>	0.40 <sup>l,m</sup>
9. Flatworms	0.467	8.1 <sup>h</sup>		0.20 <sup>h</sup>	0.24 <sup>h</sup>
10. Minnows	0.118	0.7 <sup>n</sup>	5.6 <sup>n</sup>		0.20 <sup>j</sup>
11. Formosan salmon	1.270	1.1 <sup>n,o</sup>	4.3 <sup>n</sup>		0.20 <sup>j</sup>
12. Birds	0.015	1.3 <sup>p</sup>	46.0 <sup>p</sup>		0.20 <sup>j</sup>
13. Detritus	8.839				

<sup>a</sup>Grafius & Anderson (1980), <sup>b</sup>Iversen (1988), <sup>c</sup>Welch (1968),  
<sup>d</sup>Benke et al. (1984), <sup>e</sup>Carlisle & Clements (2003), <sup>f</sup>Benke & Jacobi (1994),  
<sup>g</sup>Benke et al. (2001), <sup>h</sup>Meyer & Poepperl (2004), <sup>i</sup>Dermott (1981),  
<sup>j</sup>Christensen et al. (2004), <sup>k</sup>Poepperl (2003), <sup>l</sup>Altig & McDearman (1975),  
<sup>m</sup>Hunter (1975), <sup>n</sup>Froese & Pauly (2007), <sup>o</sup>Chung et al. (2007),  
<sup>p</sup>Wiens & Nussbaum (1975)

Table 2. Diet composition matrix assembled from research data and the literature for the construction of the trophic model of Chichiawan Stream. Values represent the proportion by weight of each prey item in the diet

Prey group	Predator group											
	3	4	5	6	7	8 <sup>a</sup>	9 <sup>b</sup>	10	11 <sup>c</sup>	12		
1. Phytoplankton			0.05	0.05								
2. Periphyton	0.26	0.70	0.15	0.20	0.10	0.50	0.3	0.50		0.05		
3. Shredders					0.005			0.01	0.005	0.01		
4. Scrapers			0.05		0.28			0.14	0.34	0.26		
5. Filterers			0.01		0.03			0.02	0.05	0.08		
6. Gatherers			0.01		0.14			0.04	0.10	0.06		
7. Predators			0.02		0.08			0.04	0.05	0.20		
8. Non-insect grazers							0.05	0.05	0.04	0.15		
9. Two-headed flatworm							0.01					
10. Shovelmouth minnow											0.01	
11. Formosan salmon									0.01	0.02		
12. Birds												
13. Detritus	0.74	0.30	0.71	0.75	0.365	0.50	0.64	0.20	0.05			
Imported detritus										0.355	0.16	

<sup>a</sup>Madsen (1992); <sup>b</sup>Reynoldson (1975); <sup>c</sup>Ueno (1937), Lin et al. (2006), and the stable isotope analyses of this study

samples (cf. Frost et al. 2007). Filamentous green algae (*Cladophora* spp.) for SIA were sampled by hand.

Net production rates of periphyton and phytoplankton were concurrently determined from changes in dissolved oxygen (DO) concentrations in chambers (10 cm wide × 25 cm long × 15 cm deep) using stream water only and periphyton+stream water in outdoor flowing water tanks placed in Chichiawan Stream to maintain the temperature at ambient levels following the methods of Lin et al. (2005) at each site in each season. The stream water chamber was used to both determine the production rates of phytoplankton and correct the DO measurements in the periphyton+stream water chamber. To determine periphyton production, randomly selected cobbles (n = 15, ca. 65 mm) with periphyton on them were collected from riffles, and one cobble was put in each chamber. Incubation was conducted around noon (10:00–14:00 h) when irradiance was saturated, and each tank was exposed to different irradiances (0, 30, 50, 70, and 100% shading) by interposing screens with different mesh sizes. Three replicate chambers were incubated for each irradiance level. The relationship between net production rates and irradiances (the P-I curve) at each site in each season was described by the equation of Jassby & Platt (1976) using a nonlinear curve-fitting procedure in the program SigmaPlot 8.0 (SPSS). Annual net production rates of periphyton and phytoplankton were respectively calculated by integrating interpolated net production rates under various irradiances by referring

to the P-I curve and surface light data in each season (2006–2007 data from Taichung station, Climatological data annual reports, Taiwan Central Weather Bureau). DO concentrations were monitored with a DO meter (Model 52, YSI). Oxygen production rates were converted to carbon fixation rates using a photosynthetic quotient of 1.2 (Meyercordt & Meyer-Reil 1999).

Biomasses of aquatic invertebrates were quantified using a Surber sampler (with an area of 30.48 × 30.48 cm and a mesh size of 250 μm). Six random samples in riffles were taken at

each site in each season. These were carried back to the laboratory to determine the biomass and identify organisms to the lowest possible taxonomic level using available keys (Merritt & Cummins 1996, Kawai & Tanida 2005) except for the Chironomidae, which were only classified into Tanypodinae and non-Tanypodinae. Samples for SIA were placed in clean water for 1 d to allow for gut evacuation.

Fish populations were counted by snorkeling during the daytime between ca. 10:00 and 17:00 h. Counting began at the downstream end at each site (about 300 m long) and was completed in a single upstream pass. Two trained snorkelers slowly swam upstream parallel to the main channel and counted fish outwards and towards the bank nearest to them to avoid double-counting. Prior to the actual counting, estimating fish lengths was practiced on objects of known length lying on the stream bottom with the help of a ruler for size estimation. Three life stages were classified according to the fish total length (Chung et al. 2007): 5–15 cm for juvenile salmon, 15–25 cm for subadults, and >25 cm for adults. There has been little study on the biology of the other dominant fish species in the stream, the shovelmouth minnow *Varicorhinus barbatulu*, so classification of minnow size classes was based on the total lengths of Formosan salmon. The total abundance of each size class for both fishes was recorded at each site. Biomass was estimated by the length–weight relationship using an empirical equation of Lan (2005). Samples of Formosan salmon for SIA were collected using a cast net (area 10 m<sup>2</sup>, mesh size 1 cm).

Point-count observations were conducted to estimate the species and abundance of birds along the stream. Trained observers stood at a fixed point on the shores of the stream at each site for 8 min and recorded everything they heard and saw with the aid of binoculars during the first 3 h of daylight. In each season, 3 counts were conducted at each site to overcome varying detectability over time and among species. Biomass was calculated by multiplying the average live weight of a given species taken from Sun (2004) by bird abundance values for that species.

Few studies have been carried out on small aquatic invertebrates in Taiwan, so the production:biomass ratio (P/B), consumption:biomass ratio (Q/B), production:consumption ratio (P/Q), and unused consumption (UN) were derived from the literature (Table 1). Estimates of Q/B for fish were computed using an empirical model developed by Palomares & Pauly (1989). Estimates of P/B for fish were obtained by searching FishBase (Froese & Pauly 2007). P/B and Q/B values for birds were computed using the empirical model developed by Wiens & Nussbaum (1975) and Crocker et al. (2002), respectively. UN values of fish and birds were assumed to be 20% (Christensen et al. 2004).

Senesced or microbe-conditioned leaves from dominant riparian C<sub>3</sub> and C<sub>4</sub> plants best represent terrestrial detritus in streams (Finlay 2001), and these were picked off the ground by hand for SIA. Dominant C<sub>4</sub> plants were *Arundo formosana* and *Miscanthus floridulus*. Dominant C<sub>3</sub> plants were *Alnus formosana*, *Pinus taiwanensis*, *Polygonum multiflorum* var. *hypoleucum*, *Quercus variabilis*, *Tetrapanax papyriferus*, and *Vaccinium bracteatum*.

In each season at each site, 3 hoop-nets (1 mm mesh, 50 cm long, with a 25 × 25 cm front opening) were firmly placed in the water with the opening completely submerged at 1/4, 1/2, and 3/4 of the distance from the left bank to collect upstream inputs of coarse particulate organic matter (CPOM). Five aerial or vertical-input traps were hung over the water surface of the stream from nearby trees at each site to collect vertical inputs of CPOM. Three lateral-input traps held by 2 stakes were each installed on the right and left banks at each site to collect inputs of CPOM from the lateral directions. On each sampling occasion, these traps stayed for a 48 h period. Benthic organic matter (BOM) was also collected from the streambed in triplicate using a square-sided benthic sampler with an area of 0.1 m<sup>2</sup> fitted with a 1 mm mesh hoop-net. Transported organic particles in the stream of 0.45 μm to 1 mm were treated as fine particulate organic matter

(FPOM). To collect FPOM, 2 l of water were collected and filtered in triplicate through pre-weighed 0.45 μm Millipore filters. All samples were brought back to the laboratory where they were sorted and weighed after drying in an oven at 60°C for 24 h. FPOM was determined by subtracting the mass of the inorganic seston from the dry mass after burning in a 450°C muffle furnace for 4 h.

Factors used for conversion between chl *a*, carbon, dry weight, and wet weight were based on a table summarized by Opitz (1996). Biomass data were then recorded as the wet weight (WW) m<sup>-2</sup>, and flow data were recorded as WW m<sup>-2</sup> yr<sup>-1</sup>.

Diet composition of Formosan salmon was primarily derived from previous stomach content analyses (Ueno 1937, Lin et al. 2006). Stomach or gut contents of shovelmouth minnows, aquatic insects, and tadpoles were sorted taxonomically and counted. Diet composition analysis followed the methods described by Hyslop (1980). SIA was used as a complementary method to stomach content analysis. Few published data are available on the diets of gastropods and flatworms in Taiwan, so this information was obtained by searching the literature (Reynoldson 1975, Madsen 1992). Bird diets were determined by observing the types of prey and examining regurgitated pellets which consist of the indigestible parts of food.

## SIA

For small-sized aquatic insects, multiple individuals from the same taxon were pooled and treated as a single replicate, and the entire body was used for SIA. For large fish, individual specimens were treated as replicates, and only muscle tissues were used for SIA. All samples were rinsed with deionized water. Plant tissues were dried in an oven at 60°C for 48 h and then ground up. Animal tissues were freeze-dried and then ground up. Subsamples (of around 1.0 mg) of dried tissue were enclosed in tin capsules and analyzed on a continuous-flow isotope ratio mass spectrometer (Thermo Finnigan Delta<sup>plus</sup> Advantage) coupled with an elemental analyzer (Carlo-Erba EA 2100). Stable isotope data were reported in standard notation as:  $\delta X (\text{‰}) = 1000[(R_{\text{sample}}/R_{\text{standard}}) - 1]$ , where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ .  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  is the ‰ deviation of the sample from the international standard, i.e. Pee Dee Belemnite for the  $\delta^{13}\text{C}$  analysis and air N<sub>2</sub> for the  $\delta^{15}\text{N}$  analysis (Gonfiantini et al. 1995). The precisions of the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  analyses were <0.15 and 0.20‰, respectively.

### Estimates of food source contributions

In order to identify the major food sources of a given consumer, we used the dual-isotope, multiple-source mixing model IsoSource (Phillips & Gregg 2003) in both the dry and wet seasons. Tolerance of IsoSource was set to 0.05‰, which is an indication of a feasible solution (Phillips & Gregg 2003). The tolerance increased to higher values when the isotope values of dominant consumers were outside the polygons enclosing all possible food sources.

Fractionation values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between a consumer and its food sources were carefully assessed before employing IsoSource. DeNiro & Epstein (1978) found that an animal is about 1‰ enriched in  $\delta^{13}\text{C}$  relative to its diet. Minagawa & Wada (1984) showed that the mean enrichment in  $\delta^{15}\text{N}$  with a single feeding process is 3.4‰. McCutchan et al. (2003) reported that the enrichment of  $\delta^{13}\text{C}$  is  $1.3 \pm 0.30\%$  (mean  $\pm$  SE) and that of  $\delta^{15}\text{N}$  is  $2.9 \pm 0.32\%$  for muscle samples, but the enrichment for samples of whole organisms is  $0.3 \pm 0.14\%$  for  $\delta^{13}\text{C}$  and  $2.1 \pm 0.21\%$  for  $\delta^{15}\text{N}$ . Based on the literature and our own observations, we applied trophic enrichment values of 1.0‰  $\delta^{13}\text{C}$  and 3.4‰  $\delta^{15}\text{N}$  for each trophic transfer in Formosan salmon for which muscle tissues were analyzed. However, trophic enrichment values of 0.5‰  $\delta^{13}\text{C}$  and 2.3‰  $\delta^{15}\text{N}$  were applied to correct for isotopic shifts of small-sized aquatic insects for which the entire body was analyzed (McCutchan et al. 2003). A *t*-test was used to determine whether  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of plants, algae, aquatic insects, and Formosan salmon significantly differed between the dry and wet seasons in Chichiawan Stream.

### Modeling approach

A trophic model of Chichiawan Stream was constructed using the Ecopath routine in the Ecopath with Ecosim software system (Christensen et al. 2004) to quantify organic matter flows in the food web. For each compartment *i*, a mass-balance budget can be expressed as:

$$P_i - B_i M2_i - P_i \times (1 - EE_i) - EX_i - AC_i = 0 \quad (1)$$

where M2 is predation mortality, EE is ecotrophic efficiency (i.e. the part of the production that is either passed up the trophic level or exported),  $1 - EE$  is 'other mortality,'  $EX_i$  is the portion of *i* exported to other systems, and  $AC_i$  is the accumulation of *i* during the study period.

A predator group *j* is connected to its prey groups by its consumption. Thus, Eq. (1) can be re-expressed as:

$$B_i \times P/B_i \times EE_i - \sum_j B_j - Q/B_j \times DC_{ji} - EX_i - AC_i = 0 \quad (2)$$

where  $DC_{ji}$  is the fraction of prey *i* in the average diet of predator *j*. It was assumed that the food matrix remained stable during the study period.

Consumption of *j* is then connected to its production, which can be re-expressed as:

$$\sum_j B_j \times Q/B_j = P_j + R_j + UN_j \quad (3)$$

where R is respiration. For further details and algorithms of the Ecopath model structure, see Christensen et al. (2004).

### Model compartments

Major species of aquatic insects with similar sizes and diets in Chichiawan Stream were grouped within the same compartment. Bacterial biomass was included in the compartment of organic detritus as recommended by Christensen et al. (2004). A 13-compartment model for the stream was developed consisting of the following groups: (1) phytoplankton, (2) periphyton (mainly diatoms), (3) shredder aquatic insects (including Nemouridae, Lepidostomatidae, and Sericostomatidae), (4) scraper aquatic insects (Heptageniidae), (5) filterer aquatic insects (including Simuliidae, Hydropsychidae, and Stenopsychidae), (6) gatherer aquatic insects (including Chironomidae, Ephemeridae, and Ephemerellidae), (7) predator aquatic insects (including Perlidae, Rhyacophiliidae, and Tipulidae), (8) non-insect grazers (including tadpoles of *Bufo bankorensis* and *Pseudoamolops sauteri* and the gastropods *Hipppeutis* sp. and *Lymnaea* sp.), (9) two-headed flatworm *Dugesia japonica*, (10) shovelmouth minnow, (11) Formosan salmon, (12) birds (including the Asian dipper *Cinclus pallasii* and Mandarin duck *Aix galericulata*), and (13) detritus. Exports of fish and invertebrates due to consumption by forest animals were assumed to be small compared to those within the stream and therefore were not included in the model. The pedigree routine (Funtowicz & Ravetz 1990) was used to determine an overall index of model 'quality,' based on the origin and quality of each input datum of the model.

### Model balancing and verification

Because Ecopath uses linkages of production of 1 compartment with consumption of other compart-

ments to calculate 1 missing parameter for each group, the most questionable parameter of each compartment can be treated as an unknown and calculated by Ecopath. In this study, the biomass of each compartment and primary productivity were the most reliable data. EE was treated as an unknown and calculated by Ecopath. Some P/B, Q/B, and DC values of invertebrates were assembled from the literature (Tables 1 & 2) and were considered to be less reliable in the stream model. Therefore, they were gradually modified during the balancing exercise. Most of the changes were rather small and remained within 20% of the input value. Verifying the realism of the Ecopath model followed the general methodology described by Christensen et al. (2004).

### Network analysis

Transfer details of organic matter from primary producers and detritus to top predators in the food web can be revealed using network analysis (Field et al. 1989). The mixed trophic impacts (Ulanowicz & Puccia 1990) were calculated to assess the direct and indirect impacts of a change in the biomass of each compartment on the other compartments. The sum of consumption, exports, respiratory flows, and flows into detritus or the total system throughput (TST) is indexed in terms of how much matter the system processes. The Finn cycling index (FCI) of the cycle analysis (Kay et al. 1989) was used to measure how

retentive the stream was. The Lindeman trophic analysis (Kay et al. 1989) summarizes the complicated food web in terms of a single linear food chain. The trophic efficiency of the transfer from one aggregated trophic level to the next can be calculated as the fraction of the input of organic matter to a given level that is transferred to the next higher level.

## RESULTS

### Isotopic signatures of basal sources

$\delta^{13}\text{C}$  values of the 4 major basal sources in Chichiawan Stream showed distinct differences, regardless of season (dry or wet; Table 3). The increasing order of enrichment in  $\delta^{13}\text{C}$  values was riparian  $\text{C}_3$  plants, FPOM, diatoms, filamentous green algae, and riparian  $\text{C}_4$  plants. No significant seasonal variations in  $\delta^{13}\text{C}$  values were found for riparian  $\text{C}_3$  and  $\text{C}_4$  plants, diatoms, or filamentous green algae.

$\delta^{15}\text{N}$  values of diatoms and filamentous green algae were relatively enriched over those of riparian  $\text{C}_3$  and  $\text{C}_4$  plants (Table 3). No significant seasonal variations in  $\delta^{15}\text{N}$  values were found for riparian  $\text{C}_3$  or  $\text{C}_4$  plants. However,  $\delta^{15}\text{N}$  values of diatoms were significantly more enriched in the dry than in the wet season.  $\delta^{15}\text{N}$  values of filamentous green algae tended to be more enriched in the dry season, although the statistical significance could not be determined because there was only a single measurement.

Table 3.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (mean  $\pm$  1 SE) of basal food resources and dominant consumers and C:N molar ratios (mean  $\pm$  1 SE) of basal food resources collected from Chichiawan Stream during the dry and wet seasons. The number of replicates (if any) is in parentheses. FPOM: fine particulate organic matter, na: samples unavailable. Asterisks indicate a significant difference between the wet and dry seasons: \* $p < 0.05$ , \*\* $p < 0.05$ , \*\*\* $p < 0.001$

	Dry season			Wet season		
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N ratio	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N ratio
<b>Basal food resources</b>						
$\text{C}_3$ riparian plants	$-29.6 \pm 0.2$ (27)	$-1.8 \pm 0.4$ (27)	$22.6 \pm 2.0$ (27)	$-30.1 \pm 0.4$ (27)	$-1.9 \pm 0.5$ (27)	$25.1 \pm 2.1$ (27)
$\text{C}_4$ riparian plants	$-13.3 \pm 0.5$ (3)	$-2.1 \pm 0.2$ (3)	$35.2 \pm 4.9$ (3)	$-13.4 \pm 0.5$ (4)	$-2.0 \pm 0.7$ (4)	$40.0 \pm 4.2$ (4)
Diatoms	$-21.5 \pm 3.5$ (4)	$2.2 \pm 0.3$ (4)	$12.1 \pm 1.5$ (4)	$-25.3 \pm 1.2$ (6)	$-0.3 \pm 0.6$ (6)**	$8.2 \pm 0.2$ (6)
Filamentous green algae	-20.1	1.1	9.0	$-17.6 \pm 1.4$ (3)	$-0.9 \pm 1.2$ (3)	$11.4 \pm 0.6$ (3)
FPOM	$-24.9 \pm 0.2$ (3)	$-0.2 \pm 1.4$ (3)	$8.1 \pm 0.3$ (3)	$-24.4 \pm 0.7$ (2)	$2.1 \pm 1.1$ (2)	$12.4 \pm 2.3$ (2)
<b>Consumers</b>						
Predators	$-24.7 \pm 0.7$ (4)	$3.5 \pm 0.7$ (4)		$-24.8 \pm 0.9$ (2)	$3.0 \pm 0.2$ (2)	
Gatherers	$-25.0 \pm 0.5$ (8)	$2.0 \pm 0.3$ (8)		$-28.9 \pm 0.2$ (3)***	$1.1 \pm 0.1$ (3)	
Filterers	$-26.0 \pm 0.3$ (5)	$2.4 \pm 0.1$ (5)		$-23.2 \pm 0.2$ (3)***	$1.9 \pm 0.1$ (3)*	
Scrapers	$-26.4 \pm 0.4$ (8)	$2.1 \pm 0.2$ (8)		$-28.8 \pm 0.1$ (4)***	$0.4 \pm 0.1$ (4)***	
Shredders	na	na		-27.6	0.1	
Formosan salmon	$-24.0 \pm 0.9$ (2)	$6.1 \pm 0.1$ (2)		$-23.8 \pm 0.3$ (11)	$6.0 \pm 0.3$ (11)	

In the dry season, mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of FPOM indicated that it was comprised of organic matter derived mainly from riparian  $\text{C}_3$  plants and diatoms (Fig. 2). However,  $\delta^{15}\text{N}$  values of FPOM tended to be more enriched in the wet season than in the dry season ( $p = 0.10$ ) and were relatively enriched over those of riparian plants and algae (Table 3).

### Isotopic signatures of consumers

In Chichiawan Stream, shredder aquatic insects were caught only in the wet season. Despite different diets,  $\delta^{13}\text{C}$  values of the 5 major feeding guilds of aquatic insects were similar, with mean values ranging from  $-23.2$  to  $-28.9\text{‰}$  (Table 3).  $\delta^{13}\text{C}$  values of gatherers and scrapers were significantly more enriched in the dry season compared to the wet season. Conversely,  $\delta^{13}\text{C}$  values of filterers were significantly more enriched in the wet season.

In the dry season, variations in  $\delta^{15}\text{N}$  values of gatherers, filterers, and scrapers were relatively small, and the mean values ranged from 2.0 to 2.4‰ (Table 3).  $\delta^{15}\text{N}$  values of aquatic insects were significantly more enriched or tended to be so in the dry season.  $\delta^{15}\text{N}$  values of predators were more enriched than those of other aquatic insects by 1.5 to 1.9‰.

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of Formosan salmon in Chichiawan Stream averaged  $-23.9$  and 6.1‰, respectively (Table 3). Seasonal variations in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of the salmon were not significant. The results of SIA indicated that the trophic position of salmon is about 2 relative to the basal sources in both the dry and wet seasons (Fig. 2).

### Food sources of consumers

Riparian  $\text{C}_3$  plants were the major food source for gatherers in the dry season and for filterers in the wet season (Table 4). The mean contributions of riparian  $\text{C}_3$  plants to gatherers and filterers reached 56 and 92%, respectively. Diatoms were the major food source of scrapers in the wet season. The mean contribution of diatoms to scrapers reached 79%. Riparian  $\text{C}_4$  plants contributed little to the food of the dominant consumers. FPOM was not found to contribute to any of the dominant consumers in Chichiawan Stream.

In the dry season, the food sources of predators were primarily scrapers and secondarily filterers (Table 5). Major food sources for Formosan salmon differed in the dry and wet seasons. In the dry season, the major food source for salmon was predators, but this shifted to filterers in the wet season.

### Food web structure

The pedigree index was 0.71 for the trophic model of Chichiawan Stream, indicating a high-quality model, given that most inputs came from local, well-sampled, high-precision data. Trophic levels esti-

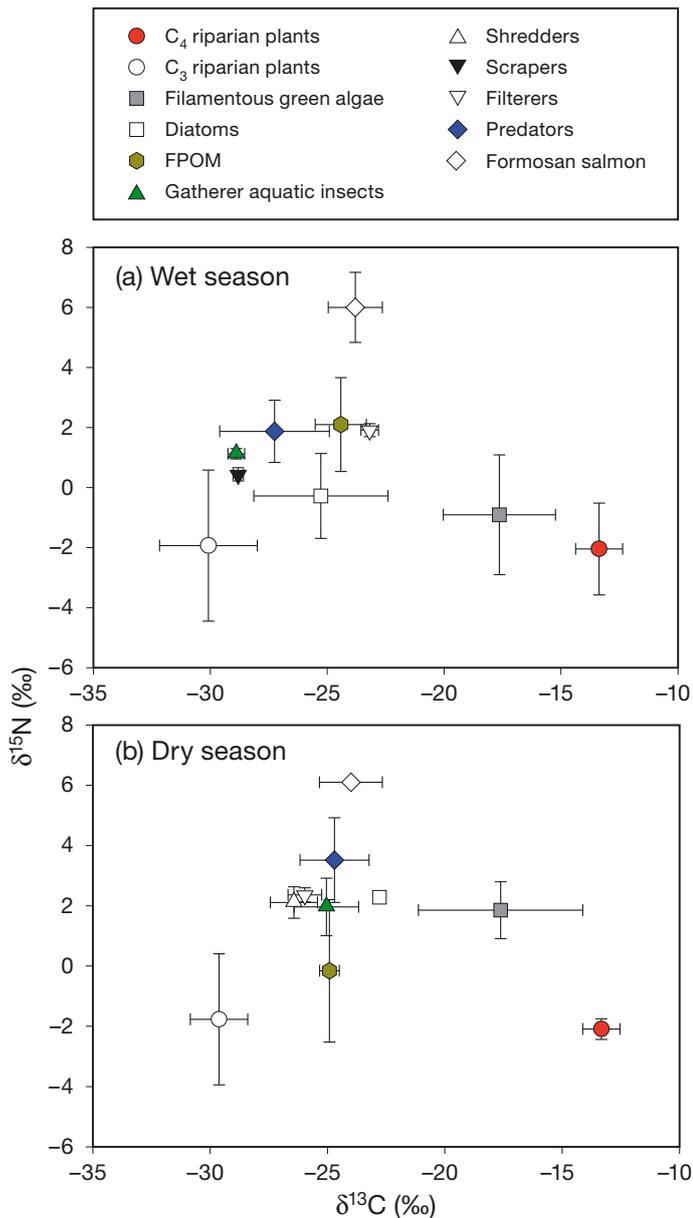


Fig. 2.  $\delta^{15}\text{N}$  vs.  $\delta^{13}\text{C}$  (mean  $\pm$  1 SE,  $n = 1-27$ ) of basal food resources and dominant consumers collected from Chichiawan Stream during the wet and dry seasons. FPOM: fine particulate organic matter

Table 4. Percentage contribution (mean with the 1–99th percentile range in parentheses) of basal food sources to consumers calculated by IsoSource models for Chichiawan Stream during the dry and wet seasons

	C <sub>3</sub> riparian plants	C <sub>4</sub> riparian plants	Diatoms	<i>Cladophora</i> sp.
Dry season				
Gatherers ( <i>Baetis</i> spp.)	56 (55–57)	3 (0–7)	24 (9–36)	17 (0–34)
Wet season				
Filterers ( <i>Hydropsyche</i> spp.)	92 (90–94)	2 (0–4)	3 (0–8)	3 (0–6)
Scrapers ( <i>Rhithrogena ampla</i> )	0 (0–1)	1 (0–2)	79 (77–80)	20 (18–22)

Table 5. Percentage contributions (mean with 1–99th percentile range in parentheses) of dominant primary consumers to secondary consumers calculated by IsoSource models for Chichiawan Stream during the dry and wet seasons

	Collectors	Filterers	Scrapers	Shredders	Predators
Dry season					
Predators ( <i>Neoperla</i> spp.)	12 (5–19)	34 (0–71)	54 (24–80)		
Formosan salmon	20 (0–56)	14 (0–36)	12 (0–34)		54 (41–63)
Wet season					
Formosan salmon	2 (0–7)	73 (65–78)	4 (0–14)	16 (7–23)	4 (0–15)

mated by Ecopath from the weighted average of prey trophic levels varied from 1.00 for primary producers and detritus to 3.12 for birds (Fig. 3). The most prominent compartment in the stream was periphyton, comprising 92% of the system's total living biomass. Consumers accounted for only about 8% of the remaining total living biomass. The EE of periphyton was low (0.04), indicating that 96% of the production of periphyton was not immediately used and entered the detrital pool (Table 6). The trophic level of Formosan salmon was 2.97, and its biomass accounted for about 2.5% of the total living biomass. An omnivory index of only 0.40 indicated that the Formosan salmon mainly feeds on aquatic insects with a narrow range of trophic levels of 2.00 to 2.58 (Table 6). The EEs of these aquatic insects were generally far smaller than 0.95, indicating that aquatic insects were not consumed in excess of their production in the stream. Birds were the only predators of Formosan salmon in the stream except for the salmon itself. The EE of Formosan salmon was only 0.05, which indicated that only 5% of its biomass was predated upon by birds or cannibalistically.

### Mixed trophic impacts

The mixed trophic impacts analysis indicated that periphyton and detritus were the most influential compartments in the stream model (Fig. 4). An increase in periphyton biomass or detritus mass would have a great positive effect on aquatic insects, other invertebrates, fish, and birds, implying the significance of periphyton and detritus as food sources for consumers.

The mixed trophic impact analysis also demonstrated that increasing the biomass of scrapers would have a minor positive impact on predators and Formosan salmon. Conversely, increasing the biomass of salmon would have minor negative impacts on scrapers and filterers. The minor interactions can be attributed to the relatively small biomasses of salmon and aquatic insects in the stream (Table 1). Increasing the biomasses of birds and the shovelmouth minnow would have little impact on Formosan salmon. However, increasing the biomass of salmon would have a moderate negative impact on its biomass.

### Trophic flows

The Lindeman trophic analysis aggregated compartmental throughputs of the 13 compartments in a simple food chain with 4 integer trophic levels (Fig. 5). The detritivory:herbivory (D:H) ratio of 0.94 indicated that the herbivory flow slightly exceeded detritivory flow in the stream. This suggests that primary production and detritus input are equally important as food sources for consumers in the stream. The contribution of net primary production to the stream by periphyton was 2205 g WW m<sup>-2</sup> yr<sup>-1</sup> or 117 g C m<sup>-2</sup> yr<sup>-1</sup>, which far exceeded the 4.6 g WW m<sup>-2</sup> yr<sup>-1</sup> (0.24 g C m<sup>-2</sup> yr<sup>-1</sup>) from phytoplankton. The trophic efficiency was 4.2% for the combined flows from primary production and detritus for trophic level II (Fig. 5). Efficiency decreased at higher levels and was 0.3% for trophic level IV. The geometric mean of trophic efficiencies for the aggregated food chain from levels II to IV was calculated to be 1.5%.

The TST of Chichiawan Stream was 4620 g WW m<sup>-2</sup> yr<sup>-1</sup> (Table 7). The difference between net prim-

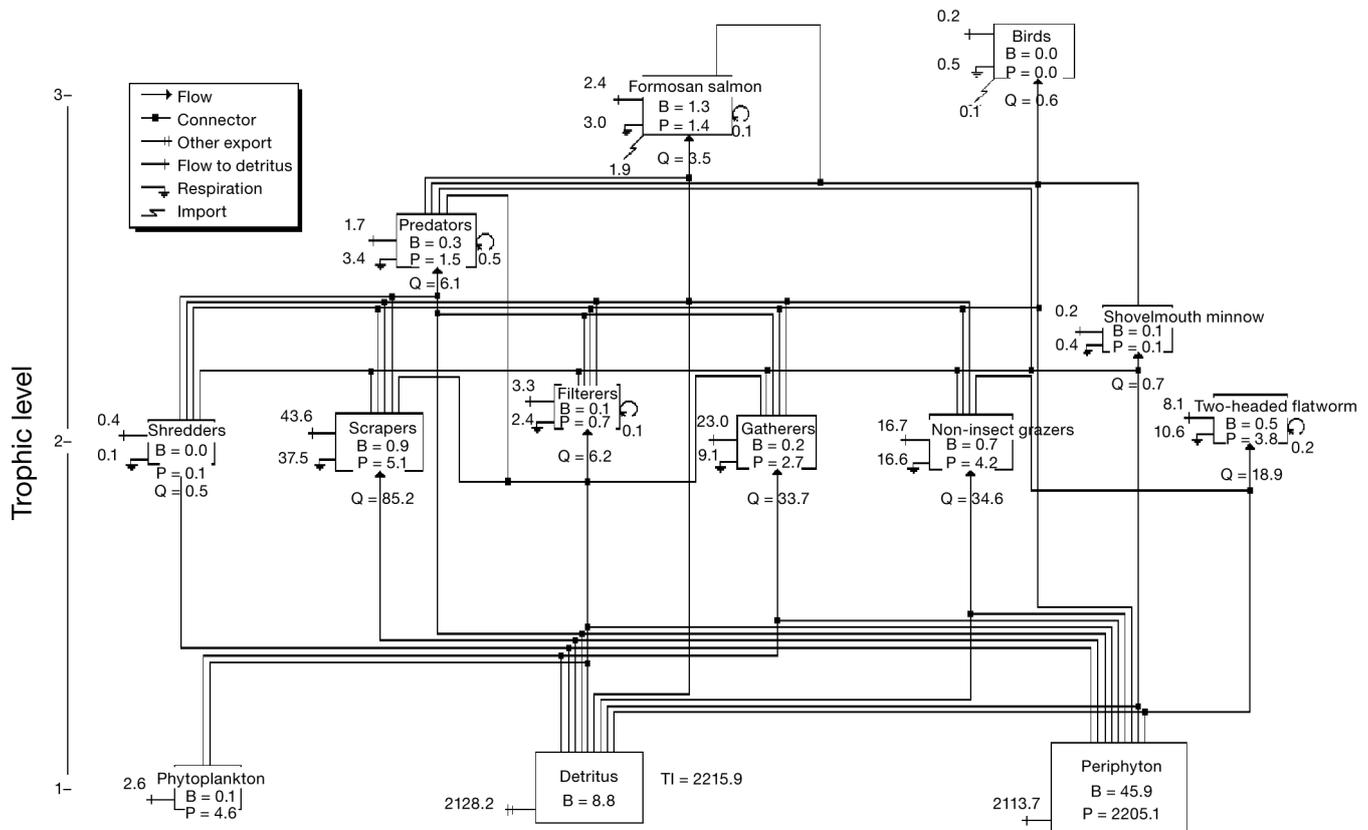


Fig. 3. Trophic model of Chichiawan Stream. Box size is proportional to the square root of the compartmental biomass (B) in g wet weight (WW) m<sup>-2</sup>. Production (P), consumption (Q), sum of all flows into detritus (TI), and other flows are in g WW m<sup>-2</sup> yr<sup>-1</sup>. Circular arrows to the right of some boxes indicate flow back to the compartment itself

ary production (NPP) and total R (i.e. net system production) in the stream was 2126 g WW m<sup>-2</sup> yr<sup>-1</sup> (113 g C m<sup>-2</sup> yr<sup>-1</sup>). The NPP:R ratio of 26.4 indicated that the stream was highly autotrophic, which implies that much more organic matter was being produced than was being consumed in the stream. The cycle analysis showed that all cycled flows accounted for only 1.10% of the TST (i.e. FCI).

## DISCUSSION

Stream food webs generally rely on 2 major food sources: autochthonous primary production originating from the stream itself, and allochthonous organic matter from the surrounding landscape transferred to the stream as leaf litter, woody debris, and dissolved organic carbon. Finlay (2001) found that algal production was a major diet of scrapers at all headwater sites where scrapers were present, and of gatherers and filterers at some sites. He indicated that in streams with a watershed area of  $\geq 10$  km<sup>2</sup>,  $\delta^{13}\text{C}$  values of consumers were more related to algal than ter-

restrial carbon sources for all groups except shredders, even though most organic matter in the streams was terrestrially derived. In tropical headwater streams in Hong Kong, Lau et al. (2009) also found that autochthonous sources are possibly more important than terrestrial detritus inputs to secondary production. However, Hoeninghaus et al. (2007) indicated that direct riparian inputs were more important than algal production for higher-gradient stream food webs. In the high-altitude subtropical Chichiawan Stream, with a watershed area of 76 km<sup>2</sup> and a high gradient of 13%, we found that algal production contributed most to the food sources of scrapers. However, the present study also demonstrated that allochthonous sources derived from the riparian forest contributed most to the food sources of gatherers and filterers in the stream. Lindeman trophic analysis of the stream model showed that herbivory and detritivory flows were quantitatively equally important as food sources for consumers in the stream. In an adjacent headwater, the food web was also fuelled by both autochthonous and allochthonous resources (Huang et al. 2007).

Table 6. Ecopath parameter estimation for the trophic model of Chichiawan Stream. Values in parentheses refer to original inputs. TL: trophic level; EE: ecotrophic efficiency; GE: gross efficiency; WW: wet weight

Group	TL	EE	GE	Consumption (g WW m <sup>-2</sup> yr <sup>-1</sup> )	Respiration (g WW m <sup>-2</sup> yr <sup>-1</sup> )	Flow to detritus (g WW m <sup>-2</sup> yr <sup>-1</sup> )	Predation mortality (g WW m <sup>-2</sup> yr <sup>-1</sup> )	Net efficiency	Omnivory index
1. Phytoplankton	1.00	0.43	-	-	-	2.60	1.99	-	-
2. Periphyton	1.00	0.04	-	-	-	2113	91.4	-	-
3. Shredders	2.00	0.95	(0.14)	0.54	0.09	0.38	0.07	0.47	0.00
4. Scrapers	2.00	0.81	(0.06)	85.2	37.5	43.6	4.15	0.12	0.00
5. Filterers	2.10	0.79	(0.12)	6.23	2.37	3.28	0.59	0.24	0.11
6. Gatherers	2.00	0.57	(0.08)	33.7	9.09	23.0	1.53	0.23	0.00
7. Predators	2.58	0.69	(0.25)	6.10	3.35	1.69	1.05	0.31	0.32
8. Non-insect grazers	2.00	0.31	(0.12)	34.7	16.6	16.7	1.30	0.20	0.00
9. Two-headed flatworm	2.06	0.05	(0.20)	18.9	10.6	8.13	0.19	0.26	0.06
10. Shovelmouth minnow	2.33	0.08	0.13	0.66	0.45	0.21	0.01	0.16	0.26
11. Formosan salmon	2.97	0.05	0.26	5.46	2.97	2.42	0.07	0.32	0.40
12. Birds	3.12	0.00	0.03	0.69	0.53	0.16	0.00	0.04	0.22
13. Detritus	1.00	0.04	-	-	-	-	-	-	0.05

Our results further demonstrated that the food sources of filterers and gatherers in Chichiawan Stream were primarily riparian C<sub>3</sub> plants in both the dry and wet seasons. These feeding guilds of aquatic insects combined with predators were the major food sources of Formosan salmon in this stream. Our results suggest a close terrestrial-aquatic linkage that highlights the function of riparian plants in transferring energy through trophic cascades of this subtropical headwater stream. It is clear that the riparian zone along Chichiawan Stream should be well-vegetated in order to provide food sources for aquatic insects on which the Formosan salmon feeds.

This study also demonstrated that riparian C<sub>3</sub> plants were much more important than C<sub>4</sub> plants in contributing to the food sources of dominant consumers in the stream. The contribution of riparian C<sub>4</sub> plants was negligible. One possibility is that the C:N molar ratios of C<sub>3</sub> plant samples were lower than those of C<sub>4</sub> plant samples (Table 3), as these were indicative of more labile samples. The other possibility is that C<sub>4</sub> plants are the source of only a small fraction of the terrestrial detritus reaching the stream. Tsai et al. (2010) surveyed land uses along Chichiawan Stream by digitizing aerial photographs in a geographic information system and found that the percentage cover of riparian C<sub>4</sub> plants in the Wuling basin was small (about 0.1%).

The lower reach of Chichiawan Stream is moderately influenced by agriculture (Yu & Lin 2009). In the dry season, NO<sub>3</sub><sup>-</sup> concentrations of the stream water were higher and δ<sup>15</sup>N values of NO<sub>3</sub><sup>-</sup> were more enriched (Peng et al. 2012). Therefore, δ<sup>15</sup>N values of both green algae and diatoms, but not terrestrial plants, were more enriched in the dry than in the wet season. The relatively depleted δ<sup>15</sup>N values in the wet season can be attributed to the fact that a high proportion of NO<sub>3</sub><sup>-</sup> flowing into the stream water was derived from the large amount of rainfall, the δ<sup>15</sup>N values of which were about 0‰ (Kendall & Caldwell 1998). Conversely, in the dry season, instead of rainfall, NO<sub>3</sub><sup>-</sup> flowing into the stream was leached mainly from nearby soils, the δ<sup>15</sup>N values of which were about 2 to 5‰ (Kendall & Caldwell 1998).

Filamentous green algae were observed more frequently in open-canopy sections of the Chichiawan Stream that are subject to high NO<sub>3</sub><sup>-</sup> concentrations (Yu & Lin 2009). Despite this, SIA demonstrated that filamentous green algae were not the major food source of the dominant aquatic insects in the stream, indicating that a relatively low proportion of the macroalgae was being consumed. If agricultural

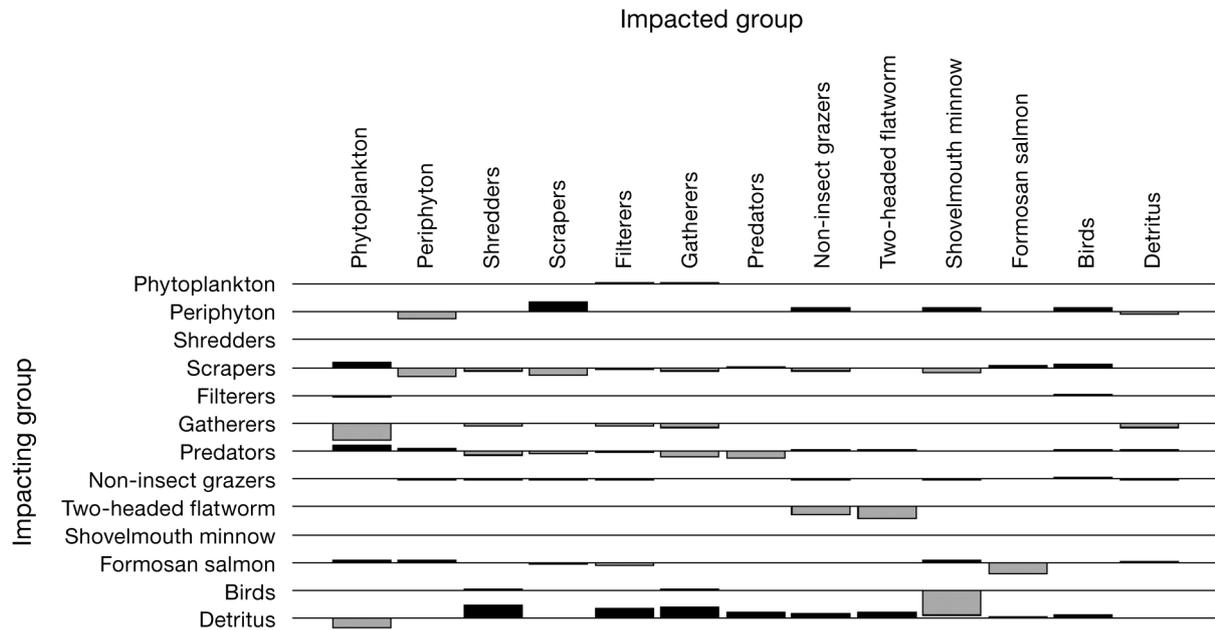


Fig. 4. Mixed trophic impacts of the trophic model of Chichiawan Stream, showing direct and indirect impacts that an increase in the biomass of a compartment on the left of the histograms would have on compartments positioned above it. Black (grey) bars pointing upwards (downwards) indicate positive (negative) impacts. Impacts are relative, not absolute, but are comparable between histograms

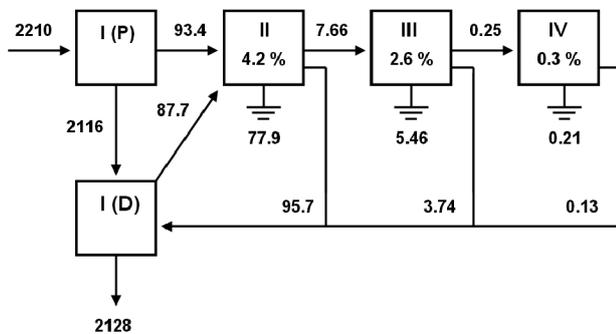


Fig. 5. Lindeman trophic analysis of the trophic model of Chichiawan Stream. The compartmental throughputs ( $\text{g wet weight m}^{-2} \text{ yr}^{-1}$ ) of the 13 compartments were aggregated into a concatenated chain of transfers through 4 integer trophic levels. Flows from primary producers (P) and from detritus (D) and flows out of the bottoms represent respiration. Trophic efficiencies (%) of the transfer from 1 aggregated trophic level to the next were calculated as the fraction of the input of organic matter to a given level that was transferred to the next higher level. Trophic level I: producers; II: herbivores or primary consumers; III: carnivores or secondary consumers; IV: top carnivores or tertiary consumers

activity continues as usual in the stream, more filamentous green algae will likely accumulate on the sediments and cause the water quality to deteriorate.

Using SIA, we discovered a seasonal shift in the diet of Formosan salmon in Chichiawan Stream. Predators were the major food sources during the dry

season, but this shifted to filterers in the wet season, when these insects comprised 73% of the food sources. Lin et al. (2006) found that in the wet season, scrapers had the highest relative abundance among feeding guilds of aquatic insects, followed by filterers. In the dry season, however, the highest relative abundance of feeding guilds of aquatic insects was of scrapers, followed by gatherers and predators. Although small-sized scrapers were the most abundant feeding guild of aquatic insects in both seasons in Chichiawan Stream, they were not the primary food sources for Formosan salmon. The seasonal diet shift of salmon from predators in the dry season to filterers in the wet season may be due to the large rainfall amounts which often remove a high proportion of large-sized predators in the wet season (Chiu et al. 2008).

The trophic model of Chichiawan Stream showed that the biomass of aquatic insects available for the Formosan salmon was much greater than the amount it consumed, which suggests that the fish are generally not constrained by food sources. This can be reflected by the mixed trophic impacts analysis, which demonstrated that increasing the biomass of aquatic insects would have a minor impact on Formosan salmon. Fishing for Formosan salmon is prohibited by the Taiwanese government, and the mixed trophic impacts analysis demonstrated low

Table 7. Comparisons of ecosystem attributes between Chichiawan Stream and mountain streams in temperate regions. NPP: total net primary production; NSP: net system production; R: total respiration; B: total biomass; TST: total system throughput; TE: trophic transfer efficiency; WW: wet weight; na: data not available

Study site	Chichiawan Stream, Taiwan	Steina Stream, Germany <sup>a</sup>	Alte Schwentine River, Germany <sup>b</sup>
Sum of consumption (g WW m <sup>-2</sup> yr <sup>-1</sup> )	192	6489	13239
Sum of exports (g WW m <sup>-2</sup> yr <sup>-1</sup> )	2128	9.1	14.7
Sum of respiration (g WW m <sup>-2</sup> yr <sup>-1</sup> )	84	3441	3455
Sum of all flows into detritus (g WW m <sup>-2</sup> yr <sup>-1</sup> )	2216	9764	12013
TST (g WW m <sup>-2</sup> yr <sup>-1</sup> )	4620	19703	28722
NPP (g WW m <sup>-2</sup> yr <sup>-1</sup> )	2210	857	2896
NSP (g WW m <sup>-2</sup> yr <sup>-1</sup> )	2126	2430	560
NPP:R	26.4	0.25	0.84
NPP:B	44	5.48	0.91
B:TST	0.01	0.01	0.11
Total biomass (B, no detritus) (g WW m <sup>-2</sup> yr <sup>-1</sup> )	50	156	168
TE (%)	1.5	2.6–7.1	0.2–6.0
Finn's cycling index (%)	1.1	25.1	na

<sup>a</sup>Meyer & Poepperl (2004); <sup>b</sup>Poepperl (2003)

predation pressure by birds on the fish. Habitat uses by salmon and the sympatric shovelmouth minnow were distinct. Hsu et al. (2010) discovered that Formosan salmon used habitats which were subject to lower temperatures and were distributed in reaches at higher elevations than those of shovelmouth minnow. The diet composition matrix also demonstrated that the Formosan salmon is insectivorous, whereas the shovelmouth minnow relies heavily on algae. Our results indicate that hydrological conditions and substratum composition might be more important than predation and competition in influencing the abundance of Formosan salmon in Chichiawan Stream.

Trophic modelling is a tool for comparative analyses of ecosystems (Christian et al. 2005) that may be helpful in characterizing the structure and functioning of Chichiawan Stream. However, few researchers have attempted to construct trophic models for streams using the Ecopath approach, with the exception of 2 mountain streams in Germany (Poepperl 2003, Meyer & Poepperl 2004). The TST of Chichiawan Stream was remarkably low in terms of the flow per unit area compared to the 2 temperate streams (Table 7), due to the low consumption and respiration of consumers in the stream. However, the NPP of Chichiawan Stream

was comparable to the reported values of the 2 temperate streams. This indicates that consumer biomass is relatively low in Chichiawan Stream, which is reflected in the extremely high NPP:R and NPP:B ratios and low B compared to reported values from the 2 temperate streams. Although Lindeman trophic analysis showed that herbivory and detritivory flows were quantitatively equally important as food sources for consumers in Chichiawan Stream, the relatively lower FCI value indicated that a lower proportion of organic matter is recycled through detrital pathways by consumers (Table 7). Therefore, the geometric mean transfer efficiency of Chichiawan Stream is lower than those of the 2 temperate streams.

Continental islands in the tropics/subtropics of the western Pacific are characterized by mountainous watersheds, high precipitation, and high water runoff (Smith et al. 2003). Chichiawan Stream fits these characteristics, as it has relatively short, straight, steep channels in a comparatively small, narrow basin. The rapid current velocity and changing flow regime in the stream have likely depressed consumer biomass and influenced the trophic transfer of organic matter in the food web (Chang et al. 2012). Our model reveals that the relatively low biomass of consumers was insufficient to consume excess growth of macroalgae that resulted from nutrient loading. Thus, agricultural activity in particular makes Chichiawan Stream even more vulnerable. To conserve the Formosan salmon, the first priority is agricultural runoff control and maintaining a well-vegetated riparian zone. Riparian vegetation may not only provide food sources for salmon in the stream, but may also protect stream water quality by trapping debris and sediments and filtering pollutants through physical and biological processes (Seavy et al. 2009). Moreover, riparian vegetation may lower water temperature, promote water infiltration, and reduce runoff to the stream as more precipitation falls as rain (Brauman et al. 2007). These would make Chichiawan Stream more resistant against rising temperature, extreme floods, and altered surface flows anticipated from climate change.

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