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Longitudinal variation in energy flow networks along a large subtropical river, China

Sai Wang[a], Lin Wang[a], Hao-Yen Chang[b], Feng Li[a], Jin-Peng Tang[a], Xing-An Zhou[a], Xing Li[a], Shi-Mi Tian[a], Hsing-Juh Lin[b,**], Yang Yang[a,c,*]

[a] Research Center of Hydrobiology, Jinan University, Guangzhou, China
[b] Department of Life Sciences, National Chung Hsing University, Taichung, Taiwan
[c] Research Center of Tropical and Subtropical Aquatic Ecological Engineering, Ministry of Education Engineering, Jinan University, Guangzhou, China

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ABSTRACT

To understand the longitudinal variation in the structure and functioning of large river ecosystems, six Ecopath models were constructed to exhibit the energy flows of aquatic food webs along the subtropical East River in China. Input parameters were primarily obtained from field data collected in 2012–2016; model outputs were estimated by network analysis. Longitudinally, ecosystem characteristics of the East River had high spatial heterogeneity. The biomass, production, and consumption, of which > 75.8% of each was distributed at trophic level (TL) II, were determined by aquatic insects upstream, molluscs midstream, and zooplankton downstream. Carnivorous fish occupied the maximal TL of 2.95–3.50. Due to the different trophic interactions of regional food webs, the keystone groups shifted from odonate larvae in headwaters to piscivorous fish upstream/midstream, to zooplankton downstream, and to phytoplankton near the estuary. Aquatic insects, insectivorous fish, epiphytes, and hydrophytes, all of which had ecotrophic efficiencies > 0.99, were critical groups that influenced mass balance through short prey supply. The mean transfer efficiencies (TEs) through TLs II–IV had the lowest values of 1.8–4.1% upstream and increased to the highest levels of 8.0–8.4% midstream before they decreased to 6.4–7.0% downstream. The low TEs along the river were limited mainly by the lack of carnivorous fish upstream and the low predation on mollus and plankton midstream/downstream. A series of theory and information indices showed that the pristine upstream system was mature but underdeveloped in organisation; in contrast, the downstream systems in the urban and industrial reaches were immature and stressed in terms of excessive phytoplankton production and short cycling.

1. Introduction

River ecosystems are influenced by regional climate, geography, and hydrology, which in turn influence the distribution of organisms through reciprocal feedbacks (Humphries et al., 2014). Following *The Ecology of Running Waters* (Hynes, 1970), the river continuum concept (Vannote et al., 1980), flood pulse concept (Junk et al., 1989), and riverine productivity model (Thorp and Delong, 1994) have summarised how rivers change biologically (e.g., in species composition, the distribution of functional groups, autochthonous vs. allochthonous organic matter) from source to mouth. Accordingly, downstream shifts in these living/non-living components of food webs and their internal predator-prey links might determine region-specific material supply and demand (Power and Dietrich, 2002; Thorp et al., 2006), which influences the energy flows throughout fluvial ecosystems.

However, because of the geographic partitioning of biozonations in running waters, it is difficult to integrate the ecological attributes of species or functional groups in discrete habitats (Allan and Castillo, 2007). Additionally, compared with closed and semi-closed systems (e.g., lake, reservoir, pond, lagoon, bay), open rivers receive organic matter input from upper stream and riparian zones (Dudgeon, 2000), leading to complex trophic interactions. Thus, there are challenges in quantifying food-web structures and in synthesising overall material/energetic pathways, and the trophic processes and dynamics of riverine ecosystems are less understood known than their lacustrine and marine counterparts (Power and Dietrich, 2002). In particular, absent from the

* Corresponding author at: Research Center of Hydrobiology, Jinan University, No. 601, Huangpu Road West, Guangzhou, Guangdong, 510632, China.
** Corresponding author at: Department of Life Sciences and Innovation and Development Center of Sustainable Agriculture, National Chung Hsing University, 145 Xingda Rd., Taichung, 402, Taiwan.
E-mail addresses: hjlin@dragon.nchu.edu.tw (H.-J. Lin), yangyang@scies.org (Y. Yang).

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Fig. 1. Location of the six sampling sites along the main channel of the East River.

literature are spatial comparisons of energy flow patterns and ecosystem properties from headwaters to estuaries.

To advance our understanding of river ecosystems, it is essential to precisely sketch the trophic networks and use common indicators to evaluate system functioning (Christensen, 1995). Over the last three decades, this gap has been reduced with the application of ecological modelling and a large body of standardised food web models (Colléter et al., 2015). Based on an approach proposed by Polovina (1984) and further developed by Christensen and Pauly (1992), Ecopath software, which relies on straightforward mass-balance constraints and non-linear trophic interactions, was originally used to assess marine fisheries. Currently, although Ecopath has been generalised to freshwater systems (e.g., lakes, reservoirs; see Villanueva et al., 2008; Darwall et al., 2010), its use in large rivers, which differ greatly in downstream hydrologic and topographical units, has been less reported (but see models built on headwater streams, Meyer and Poepperl, 2004; Lin et al., 2012; Warren et al., 2014).

Through network analysis of Ecopath, production, consumption, predation, trophic impacts, and ecotrophic/transfer efficiency can be estimated to describe how energy flows in systems and the roles that groups play therein (Monaco and Ulanowicz, 1997). Moreover, a series of theory and information indices (e.g., cycle, connectance, omnivory, ascendency) allow researchers to compare the properties of ecosystems with different sizes, geographic locations, and trophic statuses (Baird and Ulanowicz, 1993). Therefore, Ecopath, which provides multiple systematic indicators, is suitable for studying the longitudinal heterogeneity of fluvial trophic networks. With model outputs, policymakers can recognise the developmental stage, maturity, stability, and diversity of any aquatic system, which satisfies the needs of stream/river conservation and management (Pauly et al., 2000).

Furthermore, compared with studies of food web structures and energy flow networks undertaken in temperate zones, exploration of aquatic ecosystems in the tropics/subtropics is still limited because of the restricted geographic distribution of these ecosystems (Boyero et al., 2009). Dudgeon et al. (2010) suggested that ecological notions (e.g., faunal distribution, trophic dynamics) for northern temperate streams are inadequate for describing tropical streams; for example, due to the constant illumination and high water temperature, lowland tropical streams are functionally more different from temperate streams than from their high-altitude counterparts. However, except for Duan et al. (2009) and Lin et al. (2012), who simulated the energy flows in the Pearl River Estuary and Chichiawan Stream, few Ecopath models have been constructed for subtropical streams/rivers; thus, further evidence of ecosystem properties and associated comparative analyses are needed.

Located in a subtropical monsoon climate, the East River is of great importance for power generation, irrigation, navigation, and water supply in Guangdong Province. The biotic and abiotic parameters of the East River, including habitats, water quality, and species composition, have been studied since 2012. To gain insight into the structure and functioning of large river ecosystems, the specific objectives of this study were to 1) quantify the energy flows of food webs in six sections of the East River, 2) estimate the major production and consumption flows in regional food webs, 3) analyse the trophic interactions among functional groups and find the keystone groups, 4) characterise the spatial differentiation of trophic efficiencies and ecosystem properties, and 5) identify the potential anthropogenic disturbances that influence the energy transfer and maturity of the ecosystem.

2. Materials and methods

2.1. Study area and sampling sites

The East River is 562 km long and has a drainage area of 35,340 km^2, with an annual average precipitation of 1750 mm and discharge of 32.4 billion m^3. As the main source of potable water for Hong Kong (> 80%), Shenzhen, Dongguan, and Guangzhou, the ecology and environment of the East River ecosystem are of the upmost importance to the sustainable development of the Pearl River Delta (Lee et al., 2007). Due to economic development over the past several