•研究报告•

低头坝驱动山区溪流局域栖息地和
鱼类群落的同质化

卜倩婷[#]　李　献[#]　朱　仁　储　玲　严云志[*]

(安徽师范大学生命科学学院, 安徽省高校生物环境与生态安全省级重点实验室, 安徽芜湖 241000)

摘要: 确定溪流鱼类多样性对环境变化和人类干扰的响应, 可为溪流生态系统及鱼类多样性的保护和管理提供科学基础。本文基于对安徽省青弋江流域上游的4条一级河源溪流中39个低头坝、78个调查样点(针对每个低头坝所处河段, 分别设置坝上蓄水区(impounding area)和坝下非蓄水区(free-flowing area)各1个调查样点)的调查数据, 研究了低头坝对局域栖息地和鱼类群落同质化的驱动作用。共采集鱼类27种, 隶属5目10科, 其中蓄水区和非蓄水区的物种分别为23种和27种。主坐标分析和主坐标典范分析结果显示, 蓄水区与非蓄水区间的局域栖息地存在显著差异, 同非蓄水区相比, 蓄水区的底质粗糙度和异质性较小但水深和水宽较大; 置换多元分散分析结果显示, 蓄水区局域栖息地特征的空间变异显著低于非蓄水区, 呈现出明显的同质化现象。以非蓄水区为对照, 蓄水区鱼类群落的相似性在研究的4条溪流、2个不同季度呈现出相似的变化趋势, 即: 一些鱼类群落间的相似性上升但另外一些群落间的相似性下降, 且其相似性变化大小(ΔCS_J)与初始相似性显著负相关; 当初始相似性较低时, $\Delta CS_J > 0$; 当初始相似性较高时, $\Delta CS_J < 0$。本研究表明, 低头坝导致了坝上蓄水区局域栖息地特征空间变异的下降, 呈现出明显的栖息地同质化; 但蓄水区鱼类群落同时存在同质化和异质化2个过程, 群落间初始相似性大小决定了其同质化或异质化: 初始相似性较低呈同质化、较高则异质化。

关键词: 栖息地同质化; 生物同质化/异质化; 溪流鱼类; 低头坝

Low-head dams driving the homogenization of local habitat and fish assemblages in upland streams of the Qingyi River

Qianting Bu[#], Xian Li[#], Ren Zhu, Ling Chu, Yunzhi Yan[*]

Provincial Key Laboratory of Biotic Environmental and Ecological Safety, College of Life Sciences, Anhui Normal University, Wuhu, Anhui 241000

Abstract: Identifying how fish assemblages in upland streams respond to environmental changes and anthropogenic activities is the basis for the conservation and management of upland stream systems and fish diversity. Based on data collected from 78 sampling sites (including 39 impounding areas and 39 free-flowing segments, respectively) associated with 39 low-head dams in four 1st-order streams of the Qingyi basin in Anhui Province, we investigated the effect of low-head dam on the habitat homogenization and the biotic homogenization of fish assemblages in upland streams. A total of 27 species representing 10 families and 5 orders were collected, among which 23 and 27 species were collected from the impounding and free-flowing areas, respectively. Principal coordinate analysis (PCoA) and canonical analysis of principal coordinates (CAP) results showed that the local habitat differed significantly between impounding and free-flowing areas, the former characterized by relatively low substrate coarseness and heterogeneity and the latter showing shallower water depth and width. Permutational analysis of multivariate dispersions (PERMDISP) result indicated that the heterogeneity in spatial variability of the local habitat was significantly lower in the impounding areas than the free-flowing areas, suggesting habitat homogeneity in the impoundments of

low-head dams. The variations in the coefficient of similarity of fish assemblages in the impoundments relative to that found in the free-flowing segments were consistent across the four study streams and the two sampling seasons. Compared with that in the free-flowing segments, the between-assemblage similarities for fishes in the impoundments either increased or decreased, of which ΔCS_J was negatively related to the initial similarity of fish assemblages. ΔCS_J was positive when the initial similarity was lower than 50%, while ΔCS_J was negative when the initial similarity was more than 50%. Our results suggest that low-head dams may decrease the spatial variability in local habitat within the impounding areas of dams and result in the homogeneity of the local habitat. However, the variations in fish assemblages within these impoundments include two ecological processes, i.e., biotic homogeneity and heterogeneity. The biotic homogeneity/heterogeneity depends on the size of the initial similarity between different assemblages. The assemblages showing relatively low initial similarity will be homogenized and those of high initial similarity will be heterogenized.

Key words: habitat homogenization; biotic homogenization/heterogeneity; stream fishes; low-head dam

受人类活动的影响, 全球生物多样性正以前所未有的速度发生变化: 广布种不断扩散和引种、土著种日益濒危和灭绝; 广布种对土著种的取代过程降低了生物群落的特质并提高了群落间的相似性, 进而导致"生物同质化"(biotic homogenization) (Mckinney & Lockwood, 1999; Olden, 2006; 王光美等, 2009; Magurran et al, 2014)。生物同质化包括遗传同质化、分类同质化和功能同质化(Dar & Reshi, 2014)。生物同质化的生态后果非常严重: 遗传同质化将降低种群遗传变异, 影响种群的进化潜力及其适应环境变化的能力(Stockwell et al, 1996; Storfer, 1999; Petsch, 2016); 分类同质化和功能同质化将使得食物链/食物网结构趋于单一, 影响生物群落和生态系统的抗干扰能力(Beisner et al, 2003; Olden et al, 2004; Petsch, 2016)。

河源溪流(headwater stream)是淡水生态系统类型之一, 是河流网络体的重要组成部分, 常位于海拔较高的山地; 同湖泊等静水系统及大型河流相比, 河源溪流具有水文动荡、栖息地简单、营养外源性等特点(Vannote et al, 1980; Meyer et al, 2007; 王文剑等, 2013)。因溪流系统的栖息地简单且环境容纳量小, 溪流鱼类局域群落的物种多样性(即α多样性)较低; 但是, 作为对河源溪流独特环境的高度适应, 溪流鱼类具有极高的特有性, 且河源溪流的底质、水文等环境条件多样, 其鱼类群落的空间异质性非常高, 因而群落间的物种组成变化幅度(即β多样性)较大(Scott & Helfman, 2001; Jaramillo-Villa et al, 2010)。河源溪流鱼类的高度特化性、较窄的地理分布、较低的生殖力等特点, 导致它们对环境变化和人为干扰异常敏感(Scott & Helfman, 2001; Meyer et

al, 2007; Buisson & Grenouillet, 2009)。然而, 当前溪流鱼类及其多样性正面临着森林砍伐、水坝建设、土地利用等多重威胁(March et al, 2003; Meyer et al, 2007; Rasmussen et al, 2013)。

低头坝(low-head dam)是山区河源溪流中的一类极具普遍性的人类活动形式, 主要用于满足农业灌溉、居民用水、休闲娱乐等人类需要(Yan et al, 2013; Chu et al, 2015)。因坝头较低, 河水可直接漫过低头坝而进行表层泄流, 这与中下层泄流的高头坝明显不同(McCully, 1996; Poff & Hart, 2002)。小型低头坝的蓄水能力及其对水文情势的调节能力都远低于大型高头坝, 对溪流生态系统及其鱼类多样性的影响作用程度和辐射范围都明显较小(Gillette et al, 2005; Yan et al, 2013)。但是, 低头坝的数量远大于大型水坝, 其累积蓄水面积甚至可能超过后者(Rosenberg et al, 2000), 因而对鱼类多样性的影响可能也不容小视(March et al, 2003)。目前, 有关大型水坝对鱼类群落同质化的驱动作用已有不少报道(Pool & Olden, 2012; Vitule et al, 2012; Kornis et al, 2015), 研究表明, 大型水库导致多样的水文情势和栖息地条件被较为单一的静水系统所取代, 促进静水性外来鱼类对亲流性土著鱼类的取代, 进而降低了鱼类群落原有的特质并呈现出同质化现象(Rahel, 2003; Moyle & Mount, 2007; Vitule et al, 2012)。尽管低头坝改变水文情势和栖息地特征的能力远低于大型水坝, 但两者对局部河段环境条件和鱼类群落的影响却具有共性之处, 如抬高水位、降低流速、增大沉积作用并减小底质等; 栖息条件变化进而导致广布性静水或缓流鱼类对亲流性土著鱼类的取代(Gillette et al, 2005; Poulet, 2007;

Yan et al, 2013)。从这点出发, 低头坝可能具有与大型水坝类似的作用, 也能够驱动河源溪流鱼类群落的同质化过程。然而, 目前有关低头坝对溪流鱼类群落同质化的影响少见报道。

本文以青弋江流域上游的4条一级河源溪流为研究区域, 针对其中的39个低头坝分别设置2类调查样点(坝上蓄水区和坝下非蓄水区)共78个, 通过现场调查和取样, 比较研究了蓄水区和非蓄水区之间局域栖息地特征和鱼类群落相似性的异同, 探讨了低头坝对河源溪流局域栖息地和鱼类群落同质化的驱动作用, 为研究区域内河源溪流鱼类多样性的保护提供科学依据。

1 材料与方法

1.1 研究区域

青弋江位于安徽省黄山北部, 东北流向, 属长江下游南岸的一条支流。干流全长309 km, 流域面积7,195 km²。属我国亚热带季风气候, 年气温范围 –2.1 (1月)至27.5℃ (7月) (平均为17.8℃); 年降水量近2,000 mm, 但约79%的降水集中在春季和夏季, 而冬季降水仅约5%。因水力发电、农业灌溉、居民用水和休闲娱乐等需要, 自20世纪中后期以来, 青弋江干流及各级支流上修建了大量的水坝, 其中大小不等的水电站约200座、低头坝近1,000座(Chu et al, 2015; Li et al, 2016)。

1.2 样点设置与野外调查

本研究调查的低头坝共39个, 位于青弋江上游的4条一级河源溪流中, 各溪流的低头坝分别为5个、8个、16个和10个(图1)。每个低头坝的坝体高度都小于4 m, 且坝上蓄水区的水深 < 1 m, 以满足涉水采集鱼类。每个低头坝各设置2个调查样点, 即坝上蓄水区和坝下非蓄水区; 视蓄水区为受低头坝影响的受试样点, 非蓄水区为对照样点。其中, 坝上蓄水区直接位于低头坝上游的蓄水水域, 其调查河道长度视蓄水区大小而定: 若蓄水区长不足50 m, 调查全部蓄水区; 若超过50 m, 则从水坝位置往上游调查50 m。坝下非蓄水区位于低头坝下游的流水河段, 距离其上游的低头坝300–500 m, 具体调查河段位置根据可抵达性和可操作性来确定, 调查河段长度为50 m。

2014年7月(丰水期)和11月(枯水期), 使用背式电鱼器(CWB-2,000P, 输入12 V, 输出250 V)对上述调查样点进行鱼类标本采集, 1人电鱼, 2人捕捞, 按"之"字型路线进行取样。依据Nelson (2006)和陈小勇(2013)的目科级分类系统, 在新鲜状态下对鱼类的分类地位进行现场鉴定(吻虾虎鱼(*Rhinogobius*)仅鉴定至属的水平)。统计并记录各样次渔获物的物种组成和数量, 处理后的标本固定于甲醛溶液, 带回实验室备用。
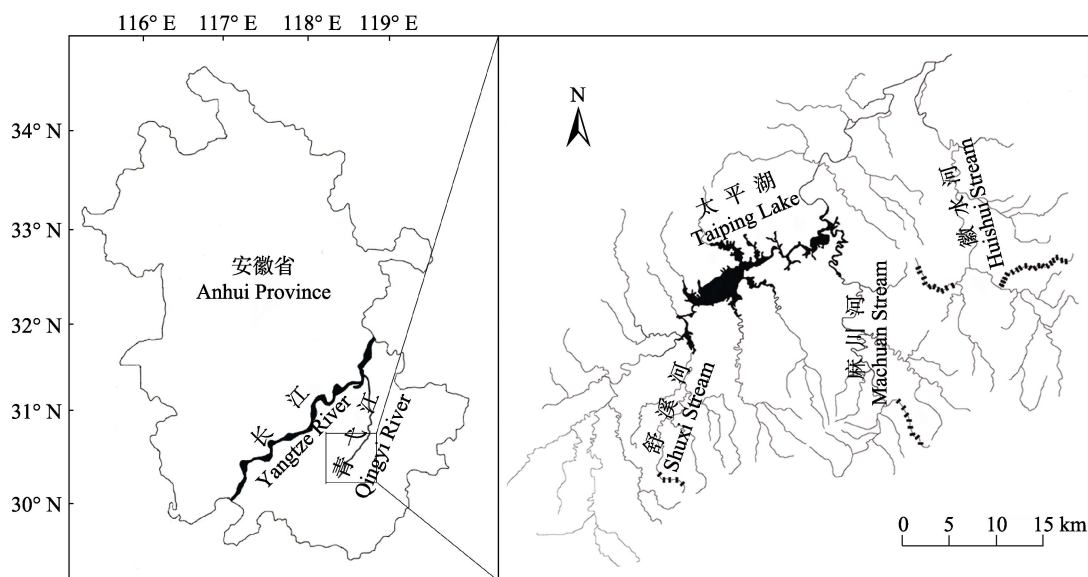
现场调查并测度10个局域栖息地因子: 水宽

图1 青弋江河源溪流所调查的低头坝位点示意图。黑色长柱形代表调查的低头坝。
Fig. 1 Locations of low-head dams surveyed in the headwater streams of the Qingyi River. Black pillars represent the low-head dams surveyed in this study.

(m)、水深(m)、流速(m/s)、水温(℃)、溶氧(ppm)、pH值、电导率(mS/cm)、植被覆盖率(%)、底质粗糙度和底质异质性。首先, 将每个调查河段分为5个等距的横断面, 在每个横断面上测量水宽; 其次, 将每断面分为5个等距的截点, 在每个截点处测量水深, 并在每个截点的60%水深处使用便携式流速仪(FB 111, 美国)测量水流流速。使用便携式水质测试仪(YSI Professional Plus)测度水温、溶氧量、pH值和电导率。植被覆盖率是根据岸边植被成荫覆盖水面比例来目测。此外, 参照Bain (1999)的方法对每个调查河段的底质大小进行打分: 每研究样点的河床分为10个断面, 根据底质颗粒直径来评估每个断面的主要底质类型及其得分: 0, < 0.059 mm; 1, 0.06–1 mm; 2, 2–15 mm; 3, 16–63 mm; 4, 64–256 mm; 5, > 256 mm。视这10组数据的平均值和标准差分别为底质粗糙度和异质度。

1.3　数据分析与统计

计算每个物种的出现频次和相对多度, 其中, 出现频次(frequency of occurrence, FO)为某物种出现的样点数占全部调查样点数的百分比, 而相对多度(relative abundance, RA)为某物种的个体数占全部样点渔获物个体总数的百分比。

基于局域栖息地数据(log转化)的Euclidean距离矩阵, 运用3种多元统计方法解析蓄水区和非蓄水区之间局域栖息地特征的异同。首先, 运用主坐标分析(principal coordinates analysis, PCoA)对各调查样点的栖息地特征进行排序, 该方法可根据样点间栖息地特征的不相似性大小将各样点进行散点分布。其次, 运用主坐标典型性分析(canonical analysis of principal coordinates, CAP)检验蓄水区和非蓄水区之间局域栖息地的平均差异, 该方法可通过置换检验来解析不同组别间矩阵数据的差异, 并对上述PCoA所显示的信息进行补充。再次, 运用置换多元分散分析(permutational analysis of multivariate dispersions, PERMDISP)检验蓄水区和非蓄水区之间栖息地特征空间变异的差异, 该方法可结合ANOVA F-统计来比较预先定义的各组别间同质性/异质性程度的差异显著性。上述统计分析在PRIMER 7.0软件中进行。

运用Jaccard's指数来计算各样点间鱼类群落(二元数据, 0和1分别代表某物种的无和有)的相似性系数(coefficient of similarity, CS): $CS_J = c/(a + b - c)$, 式中a、b分别代表两群落的物种数, c代表两群落共有的物种数, 该计算过程分蓄水区和非蓄水区2类生境独立进行, 分别获得蓄水区的$CS_{J蓄}$指数和非蓄水区的$CS_{J非}$指数。因每坝上蓄水区在建坝前的历史数据缺乏, 本文采用"空间替代时间"的方法, 以坝下非蓄水区为对照来解析建坝后蓄水区鱼类群落的相似性变化。因此, 计算上述$CS_{J蓄}$与$CS_{J非}$的差值(ΔCS_J): $\Delta CS_J = CS_{J蓄} - CS_{J非}$, 并根据$\Delta CS_J$值的大小来确定蓄水区鱼类群落的相似性变化: 若$\Delta CS_J > 0$, 蓄水区的鱼类群落相似性上升, 呈同质化现象; 若$\Delta CS_J < 0$, 则相似性下降, 为异质化。进一步, 视非蓄水区鱼类群落的相似性系数为初始相似性, 运用Pearson相关分析来检验ΔCS_J与初始相似性的关系, 以确定蓄水区鱼类群落的同质化/异质化过程是否受到初始相似性大小的影响。Pearson相关分析在SPSS 22.0软件中进行, 视$P < 0.05$为显著相关。

2　结果

2.1　鱼类物种组成概况

共采集鱼类11,671尾, 共27种, 隶属5目10科, 其中鲤科15种, 占物种总数的55.6%。蓄水区和非蓄水区的鱼类物种分别为23种和27种, 小鳈(*Sarcocheilichthys parvus*)、胡鮈(*Huigobio chenhsienensis*)、似鮈(*Belligobio nummifer*)、黄鳝(*Monopterus albus*)仅出现于非蓄水区。蓄水区的常见种有3种(出现频率大于40%), 分别为宽鳍鱲(*Zacco platypus*)、吻虾虎鱼一种(*Rhinogobius* sp.)和河川沙塘鳢(*Odontobutis potamophila*), 而非蓄水区的常见种有6种, 除上述3种外, 还包括高体鰟鲏(*Rhodeus ocellatus*)、麦穗鱼(*Pseudorasbora parva*)和棒花鱼(*Abbottina rivularis*)。河川沙塘鳢、鲫(*Carassius auratus*)、泥鳅(*Misgurnus anguillicaudatus*)、马口鱼(*Opsarrichthys bidens*)、棒花鱼、中华青鳉(*Oryzias sinensis*)、小黄黝鱼(*Micropercops swinhonis*)在蓄水区的相对多度高于非蓄水区, 吻虾虎鱼、高体鰟鲏、银鮈(*Squalidus argentatus*)、切尾拟鲿(*Pseudobagrus truncatus*)、短须鱊(*Acheilognathus barbatulus*)和福建小鳔鮈(*Microphysogobio fukiensis*)在非蓄水区具有较高的相对多度, 宽鳍鱲、麦穗鱼、光唇鱼(*Acrossocheilus fasciatus*)、原缨口鳅(*Vanmanenia stenosoma*)、稀有花鳅(*Cobitis rarus*)、中华细鲫(*Aphyocypris chinensis*)等在2类生境中的相对多度较为接近(表1)。

表1 蓄水区和非蓄水区的鱼类物种组成、出现频次和相对多度

Table 1 Species composition, frequency of occurrence and relative abundance of fishes collected in the impounding and free-flowing segments

种 Species	出现频次 Frequency of occurrence		相对多度 Relative abundance	
	蓄水区 Impounding	非蓄水区 Free-flowing	蓄水区 Impounding	非蓄水区 Free-flowing
鲤形目 Cypriniformes				
鳅科 Cobitidae				
中华花鳅 *Cobitis sinensis*	8.97	15.38	0.94	0.64
稀有花鳅 *C. rarus*	7.69	12.82	1.06	1.07
泥鳅 *Misgurnus anguillicaudatus*	38.45	29.49	1.71	0.80
爬鳅科 Balitoridae				
原缨口鳅 *Vanmanenia stenosoma*	11.54	26.92	0.67	0.60
鲤科 Cyprinidae				
宽鳍鱲 *Zacco platypus*	91.03	97.44	49.78	50.41
中华细鲫 *Aphyocypris chinensis*	3.85	3.85	0.12	0.07
马口鱼 *Opsarrichthys bidens*	23.08	19.23	1.11	0.80
尖头鱥 *Phoxinus oxycephalus*	5.12	3.85	1.19	0.12
光唇鱼 *Acrossocheilus fasciatus*	16.67	28.21	1.41	1.19
鲫 *Carassius auratus*	38.46	37.18	3.86	1.53
高体鳑鲏 *Rhodeus ocellatus*	35.90	66.67	5.05	9.63
短须鱊 *Acheilognathus barbatulus*	3.84	11.54	0.07	0.62
麦穗鱼 *Pseudorasbora parva*	34.62	53.85	2.11	2.00
小鰾 *Sarcocheilichthys parvus*	0.00	6.41	0.00	0.18
银鮈 *Squalidus argentatus*	11.54	21.79	0.52	0.81
棒花鱼 *Abbottina rivularis*	21.79	43.59	3.54	2.49
福建小鳔鮈 *Microphysogobio fukiensis*	1.28	7.69	0.02	0.81
胡鮈 *Huigobio chenhsienensis*	0.00	2.56	0.00	0.76
似鳍 *Belligobio nummifer*	0.00	2.56	0.00	0.04
鲇形目 Siuriformes				
钝头鮠科 Amblycipitidae				
司氏鮡 *Liobagrus styani*	3.85	10.26	0.15	0.16
鲿科 Bagridae				
切尾拟鲿 *Pseudobagrus truncatus*	3.85	23.08	0.07	0.29
颌针鱼目 Beloniformes				
怪颌鳉科 Adrianichthyidae				
中华青鳉 *Oryzias sinensis*	15.38	11.54	1.29	0.38
合鳃鱼目 Synbranchiformes				
合鳃鱼科 Synbranchidae				
黄鳝 *Monopterus albus*	0.00	3.85	0.00	0.04
刺鳅科 Mastacembelidae				
中华刺鳅 *Sinobdella sinensis*	1.28	7.69	0.02	0.09
鲈形目 Perciformes				
沙塘鳢科 Odontobutidae				
河川沙塘鳢 *Odontobutis potamophila*	53.85	60.26	7.50	4.07
小黄黝鱼 *Micropercops swinhonis*	6.41	1.28	0.20	0.01
虾虎鱼科 Gobiidae				
吻虾虎鱼一种 *Rhinogobius* sp.	60.26	92.31	17.58	20.37

2.2 栖息地同质化

局域栖息地的PCoA第1轴和第2轴分别解释了栖息地变异的41.6%和22.2% (7月)、50.4%和19.2% (11月)。水宽和水深主要与第一轴负相关,而底质粗糙度和异质性则主要与第二轴负相关(表2)。根据PCoA双标图,无论7月还是11月,蓄水区样点主要

表2 栖息地因子和PCoA轴的Spearman相关系数
Table 2 Spearman correlations of habitat variables with the two axes of PCoA

栖息地变量 Habitat variables	7月 July		11月 November	
	PCoA1	PCoA2	PCoA1	PCoA2
水宽 Water width	**−0.66**	−0.34	**−0.51**	0.12
水深 Water depth	**−0.58**	−0.23	**−0.80**	−0.32
底质粗糙度 Substrate coarseness	**0.41**	**−0.70**	0.22	**−0.90**
底质异质性 Substrate heterogeneity	0.14	**−0.56**	0.09	**−0.36**
流速 Current velocity	0.09	−0.13	0.03	−0.09
植被盖度 Canopy	0.01	0.09	0.01	0.01
溶氧 Dissolved oxygen	−0.08	0.03	0.01	−0.02
水温 Water temperature	−0.02	−0.03	0.02	0.01
电导率 Conductivity	−0.16	−0.22	−0.19	−0.05
pH值 pH	−0.03	0.02	−0.12	0.01

粗体数字显示相关性> 0.35或< –0.35。
Bold data show the correlation > 0.35 or < –0.35.

分布于双标图的左上角, 分布较为集中; 非蓄水区样点则主要位于右下角, 分布较为松散(图2)。同非蓄水区相比, 蓄水区的底质粗糙度和异质性较小, 但水深和水宽相对较大(图2)。CAP结果显示, 蓄水区和非蓄水区之间的栖息地条件存在显著差异(7月: trace = 0.91, P < 0.01; 11月: trace = 0.78, P < 0.01)。PERMDISP分析结果显示, 蓄水区和非蓄水区之间的栖息地同质性也存在显著差异(7月: F = 46.80, P < 0.01; 11月: F = 11.12, P < 0.01), 其中, 蓄水区各样点的局域栖息地同质性较高, 平均Euclidean距离为0.45 ± 0.02 (7月)和0.62 ± 0.04 (11月); 非蓄水区各样点的栖息地异质性较高, 其平均Euclidean距离为

0.81 ± 0.05 (7月)和0.91 ± 0.08 (11月)。

2.3 鱼类群落同质化/异质化

4条溪流、2个季节的ΔCS_J呈现出相似的分布及变化趋势(图3)。首先, 部分ΔCS_J > 0, 部分ΔCS_J < 0, 分别表示鱼类群落同质化和异质化两个不同的生态过程。其次, ΔCS_J与初始相似性呈显著负相关(P < 0.05), 随初始相似性上升, ΔCS_J下降。研究区域内的鱼类群落同质化/异质化过程取决于两个群落的初始相似性大小: 初始相似性较低(< 50%左右)时, 大多数ΔCS_J > 0, 鱼类群落同质化明显; 当初始相似性较高(> 50%左右)时, 大多数ΔCS_J < 0, 鱼类群落呈现为异质化(图3)。

3 讨论

本研究发现, 同非蓄水区相比, 低头坝坝上蓄水区的局域栖息地特征显著变化, 其底质粗糙度和异质性显著下降; 不同蓄水区之间栖息地空间异质性显著下降, 表现出明显的栖息地同质化现象。但蓄水区鱼类群落相似性变化取决于初始相似性大小: 当初始相似性较低时, 同质化现象明显; 当初始相似性较高时, 则异质化明显。

溪流系统的环境异质性极高, 在较小的空间尺度上, 受地势起伏、河流蜿蜒等的影响, 溪流河道的水流流态多样, 具有不同的水文形态单元, 即栖息地斑块(habitat patch), 不同栖息地斑块的水流流速、底质条件等差异显著, 因而引起溪流鱼类的物种组成、习性及数量呈现出较小尺度上的空间分布变化(Schlosser, 1982; Erös & Grossman, 2005; 朱仁
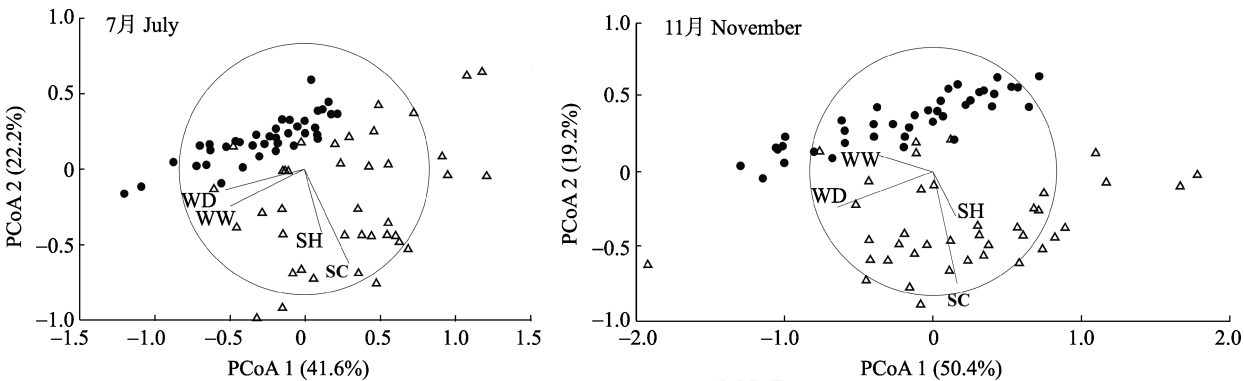

图2 蓄水区和非蓄水区局域栖息地的主坐标分析双标图。 实心圆圈和空心三角形分别代表蓄水区和非蓄水区; **WW、WD、SH和SC**分别代表水宽、水深、底质异质性和粗糙度。
Fig. 2 Scatter of sites in habitat PCoA bioplots between impounding and free-flowing segments. Solid circles and open triangles represented impounding and free-flowing segments, respectively. WW, WD, SH and SC represented water width, water depth, substrate heterogeneity and coarseness, respectively.
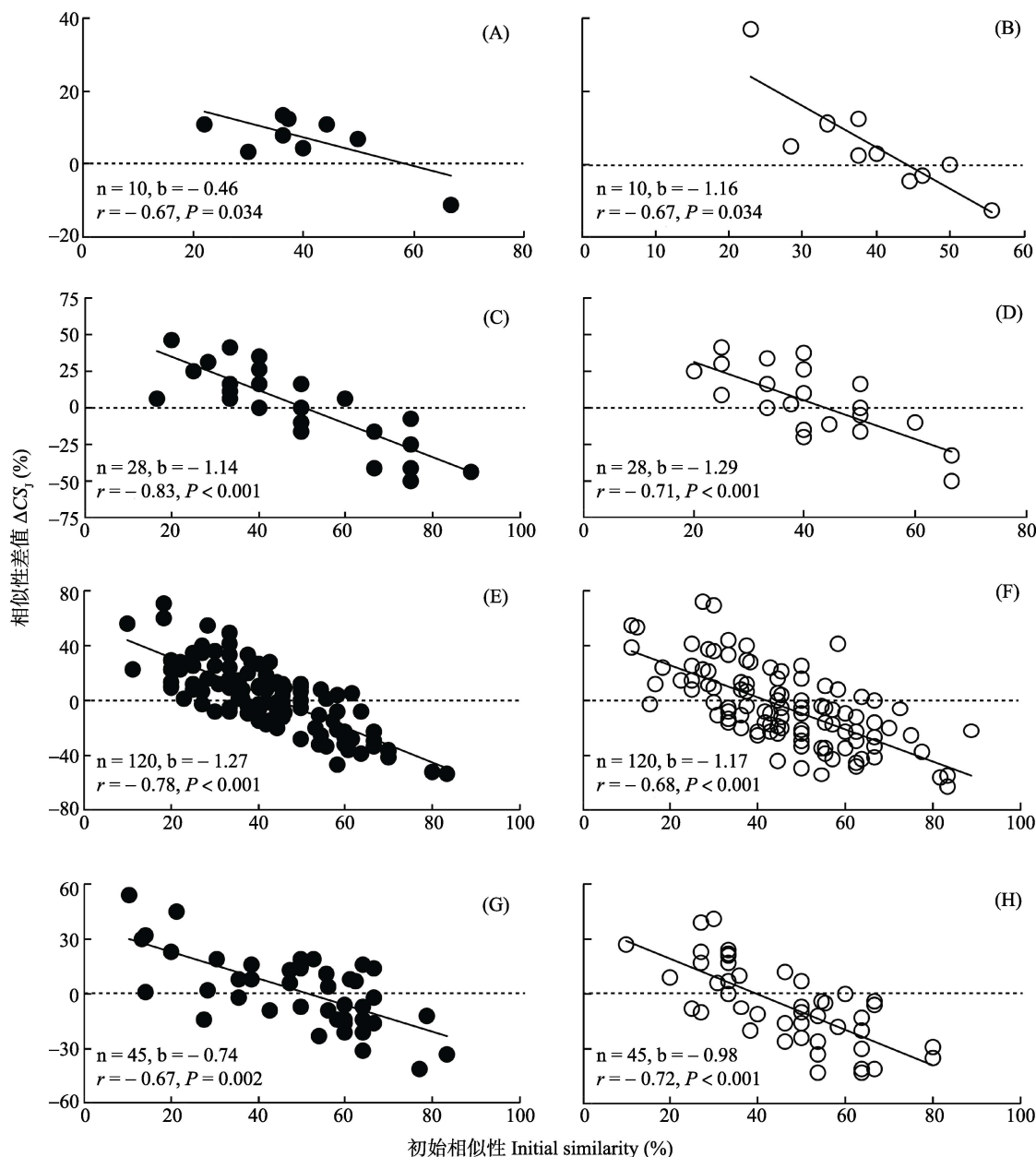
图3 蓄水区与非蓄水区的鱼类群落相似性变化(Δ*CS*J)及其同初始相似性的关系。A和B、C和D、E和F、G和H分别代表4条1级河源溪流; 左图和右图分别代表7月份和11月份。

Fig. 3 Variations in the coefficient of similarity between the fish assemblages in the impounding areas and the free-flowing segments (Δ*CS*J) and the relationship between Δ*CS*J and the initial similarity. A and B, C and D, E and F, G and H represent the four study streams, respectively; the left and right figures represented that in July and November, respectively.

等, 2015)。在较大的空间尺度上, 如沿着"上游–下游"纵向梯度, 溪流系统的栖息地复杂性、多样性及稳定性都显著变化, 因而导致溪流鱼类等水生生物群落的相应变化(Vannote et al, 1980; Sui et al, 2014; 储玲等, 2015)。然而, 受河道治理、水坝建设、土地利用等人类活动的影响, 溪流栖息地多样性和异质性严重下降, 溪流生态系统及其鱼类多样性受到

严重威胁(Allan, 2004; Torgersen & Close, 2004; Moyle & Mount, 2007; Li et al, 2017)。就水坝而言, 已有大量研究表明, 大型水坝的蓄水作用严重降低了不同河道间原有的水文情势、水流流态等的变化, 进而导致溪流系统的栖息地同质化(Torgersen & Close, 2004; Marchetti et al, 2006; Moyle & Mount, 2007; Petesse & Petrere, 2012)。本研究发现, 与大型

水坝类似, 低头坝也能够降低其坝上蓄水区栖息地特征的空间异质性, 并导致栖息地同质化过程。尽管小型的低头坝影响溪流系统的非生物环境与水生生物的作用程度和范围都比大型水坝小得多, 但低头坝和大型水坝对蓄水区的栖息地特征的影响具有一定的相似性, 即两者都能抬高蓄水区的水位、降低流速并减小底质(Poff & Hart, 2002; Graf, 2006; Poulet, 2007; Yan et al, 2013)。

低头坝对局域栖息地的改变进一步导致了局域鱼类群落的变化(Tiemann et al, 2004; Gillette et al, 2005; Poulet, 2007; Yan et al, 2013)。就坝上蓄水区而言, 其鱼类多样性下降且物种组成发生变化: 同对照样点相比, 蓄水区的亲流性鱼类物种减少而缓流或静水性物种增多(Yan et al, 2013), 促进了本地入侵种(native invader)对河源溪流的生态入侵(Scott & Helfman, 2001)。在本研究区域内, 诸如麦穗鱼等本地入侵种又可通过潜在的种间作用关系进一步胁迫土著亲流鱼类(Chu et al, 2015)。上述因低头坝所引起的土著种减少而入侵种增多的现象, 缩影出当前全球生物多样性危机——生物同质化(Marchetti et al, 2006; Moyle & Mount, 2007; Casatti et al, 2009; Rahel, 2010)。已有研究表明, 大型水坝的蓄水作用导致了入侵物种对土著物种的取代, 降低了各地鱼类区系原有的特质, 促进了鱼类区系的同质化进程(Marchetti & Moyle, 2001; Petesse & Petrere, 2012; Głowacki & Penczak, 2013; Daga et al, 2015)。然而, 本研究表明, 同对照点相比, 尽管低头坝坝上蓄水区发生了明显的栖息地同质化现象, 但其局域鱼类群落的相似性变化却包括同质化和异质化2个过程, 且其相似性变化趋势依赖于群落间的初始相似性大小。已有研究表明, 在大尺度下的生物同质化过程中可能存在很多小尺度下的生物异质化现象; 生物同质化/异质化与很多因素相关联, 如时间和空间尺度大小、物种/类群属性等(Rahel, 2010)。从时间尺度来看, 尽管长时间尺度上入侵种取代土著种并致使生物同质化, 但入侵种取代土著种需要一个时间过程, 因而同一区域不同时间节点的同质化进程不同(McKinney, 2008)。类似地, 在小空间尺度上, 入侵种对各个小空间单元的扩散存在一定的偶然性, 这种偶然性将导致小空间单元间鱼类群落不相似性上升; 但在大空间尺度上, 入侵种扩散与土著种绝灭必然造成其生物群落

特质下降(Olden & Poff, 2003; Qian & Mcglone, 2009)。

在本研究区域(青弋江流域), Yan等(2013)发现低头坝坝上蓄水区鱼类群落与流水河段差异显著, 表现为亲流性鱼类减少而非亲流性鱼类增多; 进一步, Chu等(2015)在根据鱼类的生活习性及生境选择特点将该区域河源溪流鱼类分为"本地入侵种"和土著种之后, 发现入侵种(如麦穗鱼等)对土著鱼类群落结构有着显著的负面影响。因此, 我们认为, 本研究结果中的蓄水区鱼类群落同质化现象是因本地入侵种扩散和土著种减少而起; 但就那些初始相似性较高的鱼类群落而言, 可能是因为不同蓄水区的坝体大小不一致且修建时间不同, 其入侵种扩散及土著种消亡的生态进程不同, 进而导致群落间不相似性的上升并呈现出生物异质化现象。由此可见, 针对山区溪流中普遍存在的低头坝这一人为干扰, 在后续的相关研究工作中, 十分有必要进一步拓展研究的时间和空间尺度大小, 以更为客观地揭示低头坝驱动溪流鱼类群落同质化作用对时间和空间尺度的依赖性, 也有必要剖析入侵种扩散和土著种消亡这2个生态过程在鱼类群落同质化/异质化中的相对重要性, 进而为山区溪流鱼类多样性的保护、管理和可持续利用提供必要的科学基础。

参考文献

Allan JD (2004) Landscapes and riverscapes: the influences of land use on stream ecosystems. Ecology, Evolution, and Systematics, 35, 257–284.

Bain MB (1999) Substrate. In: Aquatic Habitat Assessment: Common Methods (eds Bain MB, Stevenson NJ), pp. 95–103. American Fisheries Society, Bethesda, Maryland.

Beisner BE, Ives AR, Carpenter SR (2003) The effects of an exotic fish invasion on the prey communities of two lakes. Journal of Animal Ecology, 72, 331–342.

Buisson L, Grenouillet G (2009) Contrasted impacts of climate change on stream fish assemblages along an environmental gradient. Diversity and Distributions, 15, 613–626.

Casatti L, Veronezi JL, Ferreira CDP (2009) Diet of the armored catfish *Aspidoras fuscoguttatus* (Ostariophysi, Callichthyidae) in streams with different limnological and structural features. Biota Neotropica, 9, 113–121.

Chen XY (2013) Checklist of fishes of Yunnan. Zoological Research, 34, 281–343. (in Chinese with English abstract) [陈小勇 (2013) 云南鱼类名录. 动物学研究, 34, 281–343.]

Chu L, Wang WJ, Yan LL, Yan YZ, Zhu R, Si C (2015) Fish

assemblages and longitudinal patterns in the headwater streams of the Chencun Reservoir in the Huangshan Area. Acta Ecologica Sinica, 35, 900–910. (in Chinese with English abstract) [储玲, 王文剑, 闫莉莉, 严云志, 朱仁, 司春 (2015) 黄山陈村水库上游河源溪流的鱼类群落及其纵向梯度格局. 生态学报, 35, 900–910.]

Chu L, Wang WJ, Zhu R, Yan YZ, Chen YF, Wang LZ (2015) Variation in fish assemblages across impoundments of low-head dams in headwater streams of the Qingyi River, China: effects of abiotic factors and native invaders. Environmental Biology of Fishes, 98, 101–112.

Daga VS, Skóra F, Padial AA, Abilhoa V, Gubiani EA, Vitule JRS (2015) Homogenization dynamics of the fish assemblages in Neotropical reservoirs: comparing the roles of introduced species and their vectors. Hydrobiologia, 746, 327–347.

Dar PA, Reshi ZA (2014) Components, processes and consequences of biotic homogenization: a review. Contemporary Problems of Ecology, 7, 123–136.

Erös T, Grossman GD (2005) Effects of within-patch habitat structure and variation on fish assemblage characteristics in the Bernecei stream, Hungary. Ecology of Freshwater Fish, 14, 256–266.

Gillette DP, Tiemann JS, Edds DR, Wildhaber ML (2005) Spatiotemporal patterns of fish assemblage structure in a river impoundment by low-head dams. Copeia, 2005, 539–549.

Głowacki ŁB, Penczak T (2013) Drivers of fish diversity, homogenization/differentiation and species range expansions at the watershed scale. Diversity and Distributions, 19, 907–918.

Graf WL (2006) Downstream hydrologic and geomorphic effects of large dams on American rivers. Geomorphology, 79, 336–360.

Jaramillo-Villa U, Maldonado-Ocampo JA, Escobar F (2010) Altitudinal variation in fish assemblage diversity in streams of the central Andes of Colombia. Journal of Fish Biology, 76, 2401–2417.

Kornis MS, Weidel BC, Powers SM, Diebel MW, Cline TJ, Fox JM, Kitchell JF (2015) Fish community dynamics following dam removal in a fragmented agricultural stream. Aquatic Sciences, 77, 465–480.

Li X, Li YR, Chu L, Zhu R, Wang LZ, Yan YZ (2016) Influences of local habitat, tributary position, and dam characteristics on fish assemblages within impoundments of low-head dams in the tributaries of the Qingyi River, China. Zoological Research, 37, 67–74.

Li Y, Tao J, Chu L, Yan YZ (2017) Effects of anthropogenic disturbances on α and β diversity of fish assemblages and their longitudinal patterns in subtropical streams, China. Ecology of Freshwater Fish, doi: 10.1111/ eff.12358.

Magurran AE, Dornelas M, Moyes F, Gotelli NJ, Mcgill B (2014) Rapid biotic homogenization of marine fish assemblages. Nature Communications, 6, 8405.

March JG, Benstead JP, Pringle CM, Scatena FN (2003) Damming tropical island streams: problems, solutions, and alternatives. BioScience, 53, 1069–1078.

Marchetti MP, Moyle PB (2001) Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications, 11, 530–539.

Marchetti MP, Lockwood JL, Light T (2006) Effects of urbanization on California's fish diversity: differentiation, homogenization and the influence of spatial scale. Biological Conservation, 127, 310–318.

McCully P (1996) Silenced Rivers: the Ecology and Politics of Large Dams. Zed Books, London.

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution, 14, 450–453.

McKinney ML (2008) Do humans homogenize or differentiate biotas? It depends. Journal of Biogeography, 35, 1960–1961.

Meyer JL, Strayer DL, Wallace JB, Eggert SL, Helfman GS, Leonard NE (2007) The contribution of headwater streams to biodiversity in river networks. Journal of the American Water Resources Association, 43, 86–103.

Moyle PB, Mount JF (2007) Homogenous rivers, homogenous faunas. Proceedings of the National Academy of Sciences, USA, 104, 5711–5712.

Nelson JS (2006) Fishes of the World, 4th edn. John Wiley & Sons, Hoboken, New Jersey.

Olden JD (2006) Biotic homogenization: a new research agenda for conservation biogeography. Journal of Biogeography, 33, 2027–2039.

Olden JD, Poff NL (2003) Toward a mechanistic understanding and prediction of biotic homogenization. The American Naturalist, 162, 442–460.

Olden JD, Poff NL, Douglas MR, Douglas ME, Fausch KD (2004) Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution, 19, 18–24.

Petesse ML, Petrere M (2012) Tendency towards homogenization in fish assemblages in the cascade reservoir system of the Tietê River basin, Brazil. Ecological Engineering, 48, 109–116.

Petsch DK (2016) Causes and consequences of biotic homogenization in freshwater ecosystems. International Review of Hydrobiology, 101, 113–122.

Poff NL, Hart DD (2002) How dams vary and why it matters for the emerging science of dam removal? BioScience, 52, 659–668.

Pool TK, Olden JD (2012) Taxonomic and functional homogenization of an endemic desert fish fauna. Diversity and Distributions, 18, 366–376.

Poulet N (2007) Impact of weirs on fish communities in a piedmont stream. River Research and Applications, 23, 1038–1047.

Qian H, Mcglone M (2009) Beta diversity in relation to disper-

sal ability for vascular plants in North America. Global Ecology and Biogeography, 18, 327–332.

Rahel FJ (2003) Homogenization of freshwater faunas. Annual Review of Ecology and Systematics, 33, 291–315.

Rahel FJ (2010) Homogenization, differentiation, and the widespread alteration of fish faunas. American Fisheries Society Symposium, 73, 311–326.

Rasmussen JJ, Mcknight US, Loinaz MC, Thomsen NI, Olsson ME, Bjerg PL, Binning PJ, Kronvang B (2013) A catchment scale evaluation of multiple stressor effects in headwater streams. Science of the Total Environment, 442, 420–431.

Rosenberg DM, McCully P, Pringle CM (2000) Global-scale environmental effects of hydrological alterations. BioScience, 50, 746–751.

Schlosser IJ (1982) Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs, 52, 395–414.

Scott MC, Helfman GS (2001) Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries, 26, 6–15.

Stockwell CA, Mulvey M, Vinyard GL (1996) Translocations and the preservation of allelic diversity. Conservation Biology, 10, 1133–1141.

Storfer A (1999) Gene flow and endangered species translocations: a topic revisited. Biological Conservation, 87, 173–180.

Sui XY, Lu Z, Yan YZ, Chen YF, Jia YT (2014) Influence of a large dam on the longitudinal patterns of fish assemblages in Qingyi Stream. Zoological Research, 35, 362–372.

Tiemann JS, Gillette DP, Wildhaber ML, Edds DR (2004) Effects of lowhead dams on riffle-dwelling fishes and macroinvertebrates in a midwestern river. Transactions of American Fisheries Society, 133, 705–717.

Torgersen CE, Close DA (2004) Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (*Lampetra tridentata*) at two spatial scales. Freshwater Biology, 49, 614–630.

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences, 37, 130–137.

Vitule JRS, Skóra F, Abilhoa V (2012) Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. Diversity and Distributions, 18, 111–120.

Wang GM, Yang JC, Jiang CD, Zhao HT, Zhang ZD (2009) A literature review on biotic homogenization. Biodiversity Science, 17, 117–126. (in Chinese with English abstract) [王光美, 杨景成, 姜闯道, 赵洪涛, 张志东 (2009) 生物同质化研究透视. 生物多样性, 17, 117–126.]

Wang WJ, Chu L, Si C, Zhu R, Chen WH, Chen FM, Yan YZ (2013) Spatial and temporal patterns of stream fish assemblages in the Qiupu Headwaters National Wetland Park. Zoological Research, 34, 417–428. (in Chinese with English abstract) [王文剑, 储玲, 司春, 朱仁, 陈文豪, 陈方明, 严云志 (2013) 秋浦河国家湿地公园溪流鱼类群落的时空格局. 动物学研究, 34, 417–428.]

Yan YZ, Wang H, Zhu R, Chu L, Chen YF (2013) Influences of low-head dams on the fish assemblages in the headwater streams of the Qingyi watershed, China. Environmental Biology of Fishes, 96, 495–506.

Zhu R, Si C, Chu L, Rui M, Wu TT, Yan YZ (2015) The spatio-temporal distribution of fish population in the headwaters of the Qingyi River: a study based on the habitat patches. Acta Hydrobiologica Sinica, 39, 686–694. (in Chinese with English abstract) [朱仁, 司春, 储玲, 芮明, 吴添天, 严云志 (2015) 基于栖息地斑块尺度的青弋江河源溪流鱼类群落的时空格局. 水生生物学报, 39, 686–694.]

(责任编委: 陈小勇 责任编辑: 闫文杰)