生物多样性 2006, **14** (1): 48-54 doi: 10.1360/biodiv.050189
Biodiversity Science http: //www.biodiversity-science.net

利用线粒体DNA控制区序列分析细鳞鲑种群的遗传结构

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摘要: 细鳞鲑(*Brachymystax lenok*)是我国重要的经济鱼类, 由于过度捕捞、环境污染及其他因素的影响, 其种群已处于濒危状态。研究细鳞鲑种群的遗传结构对于探讨这一物种的形成与演化及其有效保护等问题具有十分重要的意义。本文测定了我国东部水系的细鳞鲑7个种群71个个体的线粒体DNA控制区序列片段(835 bp), 发现43个变异位点, 共计15个单倍型。AMOVA分析结果表明, 不同的地理区域之间存在显著的遗传分化(63.55%), 而区域内和种群内的遗传变异分别只有24.17%和12.28%。采用邻接法(NJ)构建分子系统树, 结果表明, 单倍型被分成3个与各自的地理区域相对应的族群, 各地理区域之间没有共享的单倍型。细鳞鲑的这种独特的遗传结构与其进化历史(例如地理隔离造成基因流的长期中断)和生物学特性(例如有限的散布能力和基因交换能力)有密切的关系。根据上述研究结果, 我们建议对这3个遗传分化显著的地理区域加以保护, 并按照不同的水系来保护种群, 避免不同区域的种群之间发生基因交流。

关键词: 遗传变异, 单倍型, 基因流, *Brachymystax lenok*

DNA sequence variation in the mitochondrial control region of lenok (*Brachymystax lenok*) populations in China

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Abstract: *Brachymystax lenok* (Salmonidae) is an economically important fish species in China whose population is currently declining due to overexploitation and environmental pollution. Recently it has been listed as a threatened species in the China Red Data Book of Endangered Animals. To study the genetic structure and phylogeographic pattern of its populations is important for addressing the systematics, evolution, and effective conservation of this species. Partial sequences of the mitochondrial control region (835 bp) were obtained by PCR amplification of 71 individuals of *Brachymystax lenok* from seven populations in China's eastern river systems. A total of 43 (5.1%) nucleotides were variable, resulting in a total of 15 haplotypes. Analysis of molecular variance indicated that a high proportion of the total genetic variance was attributable to variations among regions (63.55%), whereas 24.17% and 12.28% occurred among populations within regions and within populations, respectively. A molecular phylogenetic tree constructed using the neighbor-joining (NJ) method suggested that the 15 haplotypes were assigned to three clades associated with geographic regions. There were no shared haplotypes found among regions. The pattern of phylogenetic discontinuity, which is associated with spatial separation, is a result of both historical (long-term, zoogeographic barriers to gene flow) and contemporary (limited dispersal and gene flow capabilities) factors. Based on these results, we propose that each of the three evolutionarily distinct groups of lenok populations should be pro-

收稿日期: 2005-09-06; 接受日期: 2005-10-24
基金项目: 国家基础科学人才培养基金(NSFC-J0030092)和中国科学院院长基金(A2901046)
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tected from loss of biodiversity. It is highly recommended that management efforts should be focused on riverine conservation, avoiding translocations from the populations of different regions.
Key words: genetic variation, haplotype, gene flow, *Brachymystax lenok*

细鳞鲑(*Brachymystax lenok*)属于鲑科、鲑亚科(Salmoninae)、细鳞鲑属, 分布于西伯利亚东部、蒙古北部、中国及韩国等地(中国科学院水生生物研究所等, 1993)。由于细鳞鲑分布地区较广、严格营淡水生活、形态和生态特征复杂, 因而是研究东亚地区物种遗传分化、系统地理格局的形成和演化过程等问题的比较理想的模式生物。同时, 细鳞鲑肉味鲜美、营养丰富, 具有较高的经济价值。但由于过度捕捞、环境污染及其他因素的影响, 细鳞鲑种群数量下降很快, 已处于濒危状态(汪松, 1998; 杨德国和危起伟, 1999)。为保护物种和充分利用其自然资源, 目前正在积极进行人工繁殖(刘希泰等, 2000; 张建宏, 2003)。

了解现有种群的遗传背景对于制定有效的保护和管理策略十分重要。然而, 有关细鳞鲑的研究仍非常有限(Froufe *et al.*, 2004)。现有的研究主要利用传统的分类学和生物地理学方法, 所得出的结论往往存在争议, 如亚种划分问题(Kifa, 1976; 宋世良和方树淼, 1984; Alekseyev *et al.*, 2003; 马波等, 2005)、起源与演变问题(高玺章, 1980; 解玉浩, 1981; 李思忠, 1984; Mina, 1991; Froufe *et al.*, 2003; Alekseyev *et al.*, 2004)等。因此, 急需利用分子生物学手段对细鳞鲑种群的遗传结构、系统发育及生物地理学等方面开展全面、系统的研究。

在高等动物体内, 线粒体DNA(mtDNA)进化速率快, 主要为母系遗传, 这些优点使得mtDNA成为一种探讨种内分子系统地理学的非常有效的遗传标记(Avise *et al.*, 1987), 因而在鲑科鱼类的研究中得到了广泛应用(Brunner *et al.*, 2001; Weiss *et al.*, 2002; Asplund *et al.*, 2004; Stamford & Taylor, 2004)。本文对我国东部水系细鳞鲑7个种群71个个体的mtDNA控制区(D-Loop)片段进行了序列分析, 研究了细鳞鲑种群的遗传结构, 并根据研究结果对细鳞鲑种群的有效保护提出一些建议。

1　材料与方法

1.1　样品采集和DNA提取

细鳞鲑种群在我国东部水系基本呈连续分布(高玺章, 1980), 我们按由北向南顺序选择了7个种群, 分属于3个地理区域(黑龙江地区、长白山地区、古黄河地区), 共采集71份肌肉样品。由于采集难度较大, 我们对采集到的所有样品都进行了分析。采样地的具体地理位置和样本数见图1和表1。样品用酒精保存并带回实验室进行分析。

在每个装有100 mg粉碎样品的Eppendorf管中加入1 mL消化液(50 mmol/L Tris, pH 8.0; 100 mmol/L EDTA, pH 8.0; 1% SDS, 0.6%蛋白酶K), 室温消化16 h, 期间不停地轻轻摇动混匀。消化结束后用等体积氯仿:异戊醇(24:1)进行抽提, 并取上清液移至干净管中。在管中加入2.5倍体积的无水酒精, 室温下过夜沉淀, 然后经13,000转离心30 min, 回收总DNA。DNA中加入100–300 μL 无菌水, 放置在–20℃下保存备用。

1.2　PCR扩增和序列测定

扩增mtDNA控制区序列的引物: 正向引物为M13通用引物和引物t-pro (Shedlock *et al.*, 1992), M13/t-pro: 5′-TGT AAA ACG ACG GCC AGT CCC AAA GCT AAG ATT CTA AA-3′; 反向引物s-phe: GCT TTA GTT AAG CTA CG (Nielsen *et al.*, 1994)。反应体系为50 μL, 其中包括 0.2 mmol/L dNTPs, 1.5 μmol/L 每个引物, 2.5 U *Taq* 酶(Promega公司), 10 × buffer, 以及3 μL DNA模板。PCR反应在PTC-200 (MJ Research公司)上进行, 反应条件为: 94℃, 5 min; 之后进行40个循环 (94℃, 30 s, 49℃, 30 s, 72℃, 1 min); 反应结束后在72℃下再延伸5 min。利用QIAGEN 试剂盒纯化PCR产物, 测序工作由上海生工生物工程公司完成。

1.3　数据分析

利用CLUSTAL X (Thompson *et al.*, 1997) 程序对DNA序列进行多重对位排列并辅以手工校正, 参数设置为: gap-opening penalty=10.0, gap- extensionpenalty=5.0。利用DnaSP 2.0 (Rozas & Rozas, 1997)计算单倍型多样性 (*h*) (Nei & Tajima, 1981)和核酸多样性 (π)(Nei, 1987), 评价种群遗传多样性水平。为反映遗传分化在地区之间、地区内的种群之间以及种群内的分布情况, 利用单倍型间的欧氏

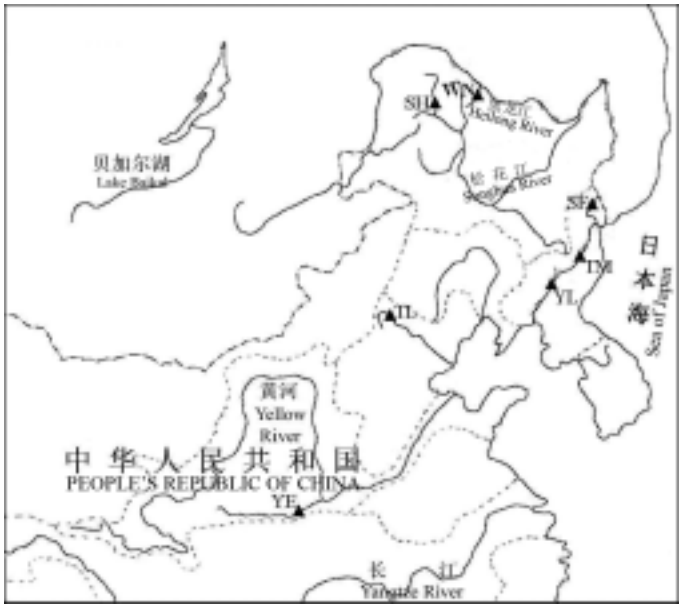

图1 细鳞鲑种群的采样地点
Fig. 1 Map showing *Brachymystax lenok* populations analyzed in this study

表1 细鳞鲑种群代号、采样地、采样大小及地理坐标
Table 1 Population codes, locality, sample size, and geographical coordinates of *Brachymystax lenok*

种群 Population	采样地 Locality	采样数 Sample size	纬度 Latitude	经度 Longitude
WN	卧牛河, 黑龙江地区 Woniuhe, Amur	10	50°05′ N	127°51′ E
SF	绥芬河, 黑龙江地区 Suifenhe, Amur	8	43°48′ N	131°12′ E
SH	松花江, 黑龙江地区 Songhua River, Amur	9	50°33′ N	125°49′ E
YL	鸭绿江, 长白山地区 Yalu River, Changbai Mountains	12	42°00′ N	127°22′ E
TM	图们江, 长白山地区 Tumen River, Changbai Mountains	14	42°05′N	129°00′ E
YE	黄河, 古黄河地区 Yellow River, old Yellow River	10	34°24′N	108°14′ E
TL	吐里根河, 古黄河地区 Tuligen River, old Yellow River	8	42°14′N	116°42′ E

种群代号同图1 Population codes are the same as in Fig. 1.

距离平方(squared Euclidean distance)矩阵进行分子变异分析(AMOVA)(Excoffier *et al.*, 1992)。以上的种群遗传分析均利用ARLEQUIN 2.0(Schneider *et al.*, 2000)程序完成。利用MEGA软件(Kumar *et al.*, 1994)构建基于Kimura双参数模型的系统发育树, 节点支持率使用1,000次bootstrap检验。

2 结果

我们从71个细鳞鲑个体中成功扩增出约835 bp的mtDNA控制区序列片段。序列分析发现变异位点43个, 其中含33个系统发育信息位点; 碱基含量的平均值(%)分别为: A=32.1, C=17.5, G=18.4, T＝

32.0, 其中(A+T)含量(64.1%)明显高于(C+G)含量(35.9%)。共计15个单倍型(GenBank号为AY960113, DQ017066-DQ017079), 种群之间不存在共享的单倍型, 这些单倍型在种群中的分布情况见表2。通过分析表明(表3), 种群WN和SF都仅存在一个单倍型; 在其他种群中, 种群TM的单倍型多样性最高(0.747), 种群核苷酸多样性指数为0.0005(种群SH)–0.0046(种群TL)。分子变异分析表明, 遗传变异主要发生在地理区域之间, 占63.55%, 而区域内和种群内分别只有24.17%和12.28%(表4)。

表2　15种单倍型在细鳞鲑种群中的分布情况
Table 2　Distribution of the 15 haplotypes in *Brachymystax lenok* populations

单倍型 Haplotype	种群 Population						
	WN	SF	SH	YL	TM	YE	TL
WN1	10	–	–	–	–	–	–
SF1	–	8	–	–	–	–	–
SH1	–	–	2	–	–	–	–
SH2	–	–	7	–	–	–	–
YL1	–	–	–	6	–	–	–
YL2	–	–	–	6	–	–	–
TM1	–	–	–	–	5	–	–
TM2	–	–	–	–	5	–	–
TM3	–	–	–	–	3	–	–
TM4	–	–	–	–	1	–	–
YE1	–	–	–	–	–	2	–
YE2	–	–	–	–	–	6	–
YE3	–	–	–	–	–	2	–
TL1	–	–	–	–	–	–	6
TL2	–	–	–	–	–	–	2

种群代号同表1　Population codes are the same as in Table 1.

表3　细鳞鲑种群的单倍型多样性(*h*)和核苷酸多样性(π)
Table 3　Haplotype diversity (*h*) and nucleotide diversity (π) of *Brachymystax lenok* populations

种群 Population	单倍型多样性(*h*) Haplotype diversity (*h*)	核苷酸多样性(π) Nucleotide diversity (π)
WN	0.000	0.0000
SF	0.000	0.0000
SH	0.389	0.0005
YL	0.545	0.0007
TM	0.747	0.0025
YE	0.622	0.0017
TL	0.429	0.0046

种群代号同表1　Population codes are the same as in Table 1.

表4　细鳞鲑种群分子变异分析结果
Table 4　Analysis of molecular variance (AMOVA) for the *Brachymystax lenok* populations

分子标记 Marker	变异来源 Source of variation	总变异百分比 Total variance (%)	*P*
线粒体DNA控制区 Control region	地理区域之间 Among regions	63.55	< 0.001
	地理区域内的种群之间 Among populations within regions	24.17	< 0.001
	种群内 Within populations	12.28	< 0.001

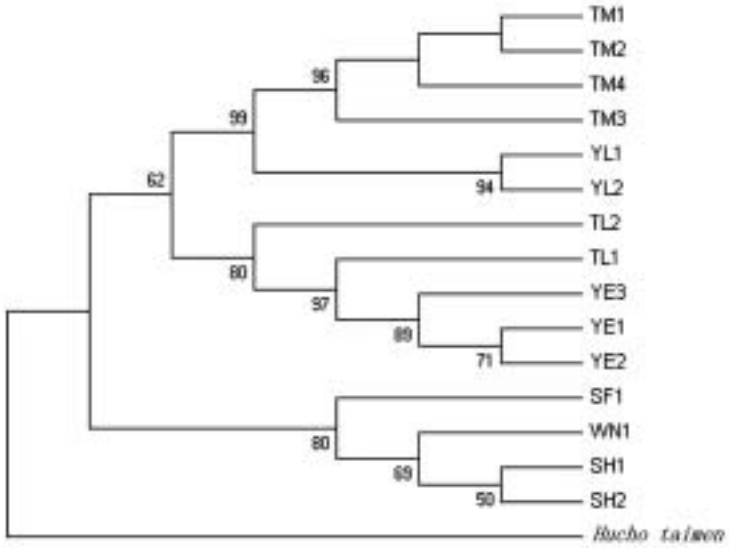

图2 通过邻接法构建的细鳞鲑**mtDNA**控制区序列单倍型的进化树。节点的数字为大于**50%bootstrap**重抽样支持率；以近缘属的哲罗鲑(*Hucho taimen*)作为外群

Fig. 2 Neighbor-joining tree of mtDNA D-loop haplotypes of *Brachymystax lenok*. Numbers at the nodes are bootstrap values above 50%. *Hucho taimen* is used as an outgroup taxon.

通过NJ分析得到的细鳞鲑种群分子系统树见图2，大多数节点的bootstrap支持率较高，15个单倍型被分成3个明显的族群(clade)，每个族群都与种群的地理分布区域相对应，即黑龙江地区、长白山地区、古黄河地区。

3 讨论

通过研究我们发现，高比例的遗传变异分布在地区之间，表明细鳞鲑种群具有显著的遗传分化。系统发育分析把单倍型分成3个与各自的地理分布区域相对应的族群，各地理区域之间没有共享的单倍型。这种独特的遗传结构与其进化历史(例如地理隔离造成基因流的长期中断)和生物学特性(例如有限的散布能力密切相关(Avise *et al.*, 1987; Avise, 2000)。Brunner 等 (2001) 报道了北极红点鲑(*Salvelinus alpinus*)种群具有显著的遗传分化，认为种群之间基因流较低的原因可能是由于北极红点鲑具有产卵地洄游行为和有限的海洋性分布的特点。Weiss等(2002)和Gum 等(2005)通过对欧洲茴鱼(*Thymallus thymallus*) 的生物地理学研究，推断流域间和流域内种群片断化的原因可能是其具有强烈的返家本能以及散布能力较差造成的。

同样，细鳞鲑是一种严格营淡水生活、具溯河产卵习性的鱼类，这些生物学特征会限制种群当前的基因流水平，而种群之间保持较低的基因流水平(即使种群间不存在自然地理障碍，或地理障碍可以穿越)是保持种群历史地理格局的先决条件(Avise *et al.*, 1987; Avise, 2000)。然而, Froufe等(2003)最近的研究表明，情况可能并非如此。他们发现莱纳河流域和黑龙江流域的细鳞鲑种群之间存在一个共享的单倍型，由此推断当西伯利亚地区东部和远东西伯利亚地区的主要河流水系之间发生交融时，为细鳞鲑这种冷水性鱼类提供了合适的通道，细鳞鲑有能力进行跨流域分布。因此，虽然我们的研究并没有发现种群间或地区间有共享的单倍型，但不排除有少量共享单倍型未被检出的可能性(尤其是在相邻水系)，今后需要进行大量的取样，并尝试结合其他mtDNA基因变异进行进一步分析，深入研究基因流和是否有天然杂交，以及是否有可能的杂交带等问题。

本研究揭示出的细鳞鲑种群的遗传结构特征对于细鳞鲑自然种群的保护以及人类经济活动(引种、人工繁殖、杂交等)有重要的指导意义。显然，忽略这3个遗传分化显著的地理区域中的任何一个都将造成遗传多样性的损失(Soltis & Gitzendanner, 1999)。关于细鳞鲑的分类问题一直存在争议：俄罗

斯学者认为西伯利亚地区的细鳞鲑在形态上可以分为两种形式, 即尖吻细鳞鲑(sharp-snouted lenoks)和钝吻细鳞鲑(blunt-snouted lenoks)(Kifa, 1976; Alekseyev *et al.*, 2003); 李思忠(1984)认为分布在秦岭太白山附近河流中的细鳞鲑应作为秦岭亚种(*B. lenok tsinlingensi*); 马波等(2005)认为黑龙江流域的细鳞鲑种群可以分为*B. tumensis*和*B. lenok*两种。因此, 在这3个区域中的细鳞鲑种群可能还有大量的遗传信息没有被揭示。在以提高种群数量为目的而进行的人工繁殖过程中, 不同区域的个体之间进行异位杂交将严重降低种群的适应潜能, 而且也将改变这些地理区域种群的独特进化轨迹。因此, 建议按照不同的水系来保护细鳞鲑种群, 避免不同区域的种群之间发生基因交流。

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