# 牙鲆遗传连锁图谱的构建

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摘要:利用基因组测序得到的大量微卫星序列,以 681383B 为父本、6812E36 为母本杂交获得的 F<sub>1</sub> 为作图群体,构 建了牙鲆(*Paralichthys olivaceus*)微卫星标记(SSR)遗传连锁图谱。雌雄图谱共定位 SSR 标记 529 个,其中雄性连锁 图谱包括 418 个标记,分布在 24 个连锁群上,总长度 1 418.1 cM,标记平均间隔 3.62 cM,图谱覆盖率为 88.7%;雌 性连锁图谱包括 437 个标记,分布在 24 个连锁群上,总长度 1 298.1 cM,标记平均间隔为 3.16 cM,图谱覆盖率为 89.1%。牙鲆中密度遗传图谱的构建为 QTL 分析以及分子标记辅助育种进一步奠定基础,并可以有效推动牙鲆的 遗传改良工作,推动牙鲆养殖业的可持续发展。

关键词:牙鲆; SSR 分子标记;遗传连锁图谱 中图分类号: S96 \_\_\_\_\_文献标志码: A \_\_\_\_\_\_文章编号: 1005

牙鲆(Paralichthys olivaceus), 属鲽形目(Pleuronectiformes)、 鲽 亚 目 (Pleuronectoidei)、 鲆 科 (Bothidae)、牙鲆属(Paralichthys), 是中国重要的 水产养殖种类、主要分布在渤海、黄海、南海以 及朝鲜、日本、俄罗斯远东海域<sup>[1]</sup>。由于牙鲆个 体硕大,肉质鲜嫩,营养丰富,深受广大消费者 青睐,极具养殖前途。近几年牙鲆市场愈加广阔, 已经成为中国重要的海水增养殖鱼类之一。但是 由于人工育苗的累代养殖, 牙鲆养殖群体的遗传 多样性明显降低;加之近年来的过度养殖和日益 恶化的近海环境, 牙鲆种质退化严重, 因此急切 需要培育优质、高产的新品种、使牙鲆的养殖呈 良性持续发展。传统的鱼类遗传育种易受环境影 响、育种周期长、而利用分子标记进行辅助选育 可以快速获得优良品种。分子标记技术已在遗传 图谱构建、重要目标基因定位、种质资源鉴定、 遗传多样性、系统与进化、分子生态学等方面得到

文章编号:1005-8737-(2012)06-0930-09

了广泛应用。遗传连锁图谱是用遗传距离来反映 多态性的遗传标记在染色体上相对位置的基因作 图,是系统的进行基因组学研究和数量性状定位 研究的基础,同时也是分子标记辅助育种及分子 克隆等应用研究的理论依据。由于没有高密度的 遗传连锁图谱,家系的选育工作还处于初级阶段, 还无法完成数量性状位点的定位,因此获得较高 密度的遗传连锁图谱是目前遗传育种、分子标记 辅助育种及基因组学研究的基础和有效工具之一。

近年来,各国学者已建立了多种鱼类的遗传 连锁图谱,包括红鳍东方鲀(Takifugu rubripes)、 剑鱼(Porado)、斑马鱼(Danio retio)、鲤(Cyprinus carpio)、虹鳟(Oncorhynchus mykiss)、罗非鱼 (Tilapia)、青鳉(Oryzias latipes)、金头鲷(Sparusaurata)、大菱鲆(Scophthalmus maximus)、黄尾 鲫(Seriola lalandi)、尖吻鲈(Lates calarifer)、慈鲷 (Cichlid)、半滑舌鳎(Cynoglossus semilaevis)<sup>[2-15]</sup>

收稿日期: 2012-03-02; 修订日期: 2012-04-09.

基金项目:国家 973 计划项目(2010CB126303);国家 863 计划项目(2012AA10A408);山东省泰山学者工程专项资助项目.

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等。在牙鲆遗传连锁图谱构建方面,日本 Coimbra 等<sup>[16]</sup>首次构建了牙鲆低密度遗传连锁图谱,共定 位了 111 个 SSR 标记、352 个 AFLP 标记;韩国 Kang 等<sup>[17]</sup>采用 180 个微卫星标记和 31 个 EST 来 源的标记构建了牙鲆遗传连锁图谱,该图谱由 24 个连锁群组成,标记间平均间隔为 4.7 cM。Castaño-Sánchez 等<sup>[18]</sup>用 1 268 个 SSR 标记,105 个 SNP 标 记和 2 个基因构建了牙鲆第二代遗传连锁图谱, 雄性和雌性图谱总长度分别为 1 147.7 cM 和 833.8 cM,覆盖率分别为 79%和 82%。宋文涛等<sup>[19]</sup> 用 307 个微卫星标记构建了国内第一张牙鲆遗传 连锁图谱,雄性和雌性图谱总长度分别达到了 1 361 cM 和 1 320 cM,图谱的平均间隔分别为 7.8 cM 和 7.0 cM,已经可以初步进行 QTL 的定位分 析和分子标记辅助育种。

本文利用微卫星标记,使用 JoinMap4.0 软件, 构建了牙鲆雌、雄遗传连锁图谱。图谱共定位微 卫星标记 529 个,雌、雄连锁图谱的总长度分别 达到 1 298.1cM 和 1 418.1cM,雌、雄图谱覆盖率 分别达到了 89.11%和 88.70%,图谱的总长度和 覆盖率均达到较高水平,进一步为牙鲆重要基因 的定位、图谱克隆及分子标记辅助育种奠定基础。

1 材料与方法

#### 1.1 实验材料

牙鲆家系的构建在山东海阳市黄海水产有限 公司按已报道方法<sup>[20]</sup>进行。2009 年 5 月,对各家 系亲本用 8~10 对微卫星引物进行筛选,以亲本 间遗传距离较大家系为作图群体。选择了父本为 681383B、母本为 6812E36 的 10 号家系为作图群 体。2009 年 10 月随机抽取 200 尾个体,使用 10 对微卫星引物进行分析,分别从雌雄鱼中抽取雌 雄比例基本一致群体作为作图个体,共使用 80 尾, 同时记录其体长、体质量等性状。

### 1.2 基因组 DNA 提取

用传统的酚氯仿法对牙鲆家系个体和亲本进 行 DNA 提取,用 1%的琼脂糖凝胶电泳检测 DNA 的纯度,然后用 ddH2O 将 DNA 稀释成 100 ng/μL 的最终浓度后冷冻保存。

1.3 PCR 反应体系及产物检测

**1.3.1** PCR 反应体系 基因组 DNA 1.0 μL, dNTPs (2.5 mmol/L) 0.6 μL, 10×PCR buffer (含 Mg<sup>2+</sup>)1.5 μL, 上游引物 (10 μmol/L) 0.5 μL, 下游引物 (10 μmol/L) 0.5 μL, Taq DNA polymerase (5 u/μL) 0.1 μL, ddH2O10.8 μL, 总体积 15 μL。

**1.3.2** PCR 反应程序 95℃ 5 min 1 个循环; 95℃ 30 s, 57.5℃ 30 s, 72℃ 35 s, 32 个循环; 72℃ 5 min 1 个循环; 4℃保存。PCR 产物经变性后用 6%的聚 丙烯酰胺凝胶电泳于电压 1 500 V, 功率 150 W, 电流 150 mA 下进行电泳, 电泳时间约 2 h。然后 用银染法染色固定后拍照保存。

**1.4** 遗传图谱的观测长度、估算长度和图谱覆盖率的计算

图谱的观测长度由框架图长度( $G_{of}$ )和图谱总 长度( $G_{oa}$ )组成,  $G_{of}$ 包括至少含有 4 个或以上标记 的连锁群的长度之和;  $G_{oa}$ 包括三联体和连锁对在 内的图谱长度。 $G_{oa}=G_{of}+$ 连锁对和三联体的长度。

图谱的估算长度 $(G_e)$ ,通常使用两种方法进行计算 $G_{e1}$ 和 $G_{e2}$ :

(1)*G*<sub>el</sub>:每个连锁群的观察长度加上整个连锁群 的平均间隔(*s*)的 2 倍,来补偿连锁群最末端的标 记与端粒之间的距离。其中平均间隔(*s*)为图谱总长 度(*G*<sub>oa</sub>)除以总间隔数(标记总数减去连锁群总数)。

 $G_{e1} = G_{oa} + 2 \times s \times n (n$  为连锁群数)

(2)G<sub>e2</sub>: 各个连锁群的估算长度之和。每个连
 锁群的估算长度为其观察长度乘以系数(*m*+1)/
 (*m*-1), *m* 为某个连锁群的有效基因位点数目。

遗传连锁图谱的估算长度 $(G_e)$ 为 $G_{e1}$ 和 $G_{e2}$ 的 平均值,  $G_e = (G_{e1} + G_{e2})/2$ 

图谱覆盖率  $C_{oa} = G_{oa}/G_{e}$ 

#### 1.5 遗传图谱的构建

本研究使用 JoinMap4.0 软件构建牙鲆遗传连 锁图谱。具体操作如下:使用"new project"命令创 建新的文件,并使用"Creat New Dataset"将雌、雄 微卫星标记源数据分别添加到数据库中。使用  $\chi^2$ 检验来检测遗传标记在子代中是否符合 1:1 孟德 尔分离规律,并获得标记偏分离信息,将符合分

离规律(P>0.05)的标记用于初步连锁分析构建连 锁图谱框架图、同时将所有分离标记全部进行连 锁分析,观察偏分离标记对图谱框架的影响。群 体类型设置为CP(cross-pollinating), LOD值为3~ 10。使用"Creat Population Node"分别建立雌、雄 群体数据。使用"Individual genot. freq."命令去掉 缺失了较多基因型的个体、使用"Locus genot. freq."和"Exclude selected items"命令去掉不符合 分离规律的标记、使用"Similarity of loci"命令(the value=1)去掉相似的位点, 使用"Similarity of individuals"命令(the value>0.95)去掉相似的个体、使 用 "Grouping tree"和"Calculate" 命令将所有作 图标记分群;右键选中已分群的标记组,使用 "Population"选项中的"Create Groups Using the Groupings Tree"命令建立连锁群;依次选中连锁 群使用"Calculate"使用绘制连锁图。雌、雄图 谱构建完成之后, 使用 JoinMap4.0 的"Join"选 项中的"Combine Groups For map Integration"命 令进行雌、雄图谱的整合。图谱整合的原理是将 同时定位在两个连锁图的标记作为锚定标记、将 其他标记通过锚定标记加入到连锁图谱中、每个 连锁中至少有两个锚定标记. 才能确定标记间的 相对方向。

2 结果与分析

2.1 多态性分析

使用 80 个个体对 2 000 个 SSR 标记进行多态 性筛选, 共筛选出多态性标记 640 对, 多态比例 为 32%, 所有引物序列均来源于本实验室基因组 测序。图 1 为标记 scaffold345\_39354 的 PCR 扩 增结果, 两侧分别  $F_1$ 个体, 中间为亲本。

2.2 偏分离分析

χ<sup>2</sup> 检验结果表明, 雌、雄亲本中无多态而在 后代中出现分离的标记 76 个(亲本基因型为 HK×HK), 其中 20 个不符合孟德尔分离定律 (*P*<0.05), 表现偏分离; 父本分离标记有 418 个, 其中偏分离标记 131 个; 母本分离标记有 437 个, 其中偏分离标记 137 个。

2.3 遗传连锁图谱

对 640 个多态性标记进行连锁分析, 分别构建 了牙鲆雌、雄遗传连锁图谱(图 1, 图 2)。其中雄性 连锁图谱包括 418 个标记, 24 个连锁群, 平均间隔 为 3.62 cM, 连锁群的长度范围从 34.8~75.2 cM, 连锁群上的标记数为 11~33 个, 平均每个连锁群 含有 17.4 个标记, 图谱观测长度为 1 418.1 cM, 估 算长度为 1 598.7 cM, 图谱覆盖率为 88.7%。雌性连 锁图谱包括 437 个标记, 24 个连锁群, 平均间隔为 3.16 cM, 连锁群的长度范围从 29.9~73.0 cM, 连 锁群上的标记数 10~32 个, 平均每个连锁群含有 18.2 个标记。图谱观测长度为 1 298.1 cM, 估算长 度为 1 456.77 cM, 覆盖率为 89.11%(表 1, 表 2)。

#### 3 讨论

3.1 作图标记的选择

构建遗传连锁图谱的主要分子标记有 AFLP、 SNP和 SSR 等标记, AFLP 分子标记操作技术难度



图 1 第 16~58 个标记 PCR 产物电泳分析截图 A、B、C 表示等位基因;双亲分别是 BC×AB;按孟德尔分离定律,F1基因型为 AB、BB、AC、BC. Fig.1 Electrophoresis analysis of PCR products A, B and C mean alleles, respectively; parents are BC×AB; the genotypes of F1 are AB, BB, AC and BC

雌性图谱 female map		雄性图谱 male map			
连锁群	标记数	连锁群长度/cM	连锁群	标记数	连锁群长度/cM
linkage group	number of markers	length	linkage group	number of markers	length
1f	31	49.9	1m	32	55.2
2f	16	44	2m	25	73.1
3f	31	62.9	3m	21	68.4
4f	14	44.5	4m	19	61.2
5f	32	66.5	5m	19	64.9
6f	26	59.7	6m	19	73.9
7f	27	67.6	7m	16	75.2
8f	19	53.7	8m	18	61.8
9f	16	49.4	9m	15	64.2
10f	17	57.6	10m	14	37.7
11f	18	64.1	11m	12	28.8
12f	15	55.6	12m	13	70.2
13f	15	44.8	13m	12	54.8
14f	14	42.8	14m	11	60.3
15f	11	53.9	15m	33	61.8
16f	10	60.4	16m	15	58.9
17f	17	60.9	17m	25	58.5
18f	15	38.6	18m	12	68.3
19f	14	29.9	19m	15	50.8
20f	12	73	20m	16	54.6
21f	21	64	21m	14	62.1
22f	19	60.2	22m	16	72.5
23f	15	63.3	23m	15	34.9
24f	12	30.8	24m	11	46
总数 total	437	1298.1	总数 total	418	1418.1

表 1 牙鲆遗传连锁图谱的特点 Tab. 1 The characterization of genetic linkage map of *Paralichthys olivaceus* 

#### 表 2 牙鲆遗传连锁图谱的简要信息

 Tab. 2
 The information of genetic linkage map of Paralichthys olivaceus

项目 item	雌性图谱 female map	雄性图谱 male map
定位的标记总数 total number of markers	437	418
有效座位的数目 number of effective locus	434	416
连锁群数目 number of linkage groups	24	24
平均标记数目 average number of marker	18.2	17.4
最大标记数目 maximum number of makers	32	33
最小标记数目 minimum number of makers	10	11
平均间隔/cM average marker interval	3.16	3.62
连锁群的最大长度/cM maximum length of linkage groups	73.0	73.9
图谱观测长度/cM observed consensus map length	1298.1	1418.1
图谱预期长度/cM estimated consensus map length	1456.8	1598.7
图谱覆盖率/% coverage	89.11	88.70

LG 1f	LG 2f	LG 3f	LG 4f	LG 5f	LG 6f
0.0 - scaffold 1159_75853	0.0	0.0 scaffolde263_77403	0.0 scaffold343_37432	0.0 3.2 scaffold289_32576 3.2 scaffold289_32507	0.0
3.9 scaffold 880_68444		3.9 scaffold 595_53946 7.5 scaffold 199_23892	5.3 scaffold67_112	5.5 Scaffold289_32535 9.6 Scaffold772_60963	
11.3 14.4 10.6 10.6 10.6 10.6 10.6 10.6 10.6 10.6	8.2 scaffold645_57852	21.2 3 ( scaffold624_58810		13.2 1 // scaffold 123 22000 22.4 1 // scaffold 123 22000 22.4 1 // scaffold 123 56496	14.1
22.4 1 // scaffold 1386_78494 26.0 1 // scaffold 538 50478	9.3 scattold240_30554 12.0 scattold114_13593	23.0 - scaffold472_46619 23.7 - scaffold384_40712		24.8 T // scaffold 331_39635 27.0 T // scaffold 548_50951	16.1 scaffold525_49696 21.8 c scaffold152 17986
27.1 scaffold 876_68345 28.1 scaffold 383_42014	13.2	25.7	13.8 scaffold570_52520	29.4 3 scaffold548_50945 31.1 - scaffold1352_78298	25.5 scaffold292_35193 26.6 scaffold152_17980
28.6 W - W scattold 921_69859 30.1 W scattold 350_40278 31.4 W scattold 44_5253	18.8 - scaffold 112_13083	28.7 - scaffold414_48885 29.5 - scaffold370_39921	17.6 scaffold339_43856 18.4 scaffold735_61277	33.7 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	29.9 - r scaffold 779_63661 31.5 - r scaffold 779_63660
32.8 v cr scaffold224_26330 33.2 v cr scaffold224_26315	19.7 scaffold194_23178 scaffold423_43798 21.3 scaffold15_1376	30.9 scaffold 370_39899 31.6 scaffold 1944_79163	21.4 scaffold415_48711 22.7 scaffold94_11057	42.2 n	33.8 1 r scaffold 490 53932 34.2 r scaffold 64 7105 35.1 r scaffold 150 23522
34.5 1 = 1 scaffold 1585_79029 35.3 1 = 1 scaffold 1326_78007	22.9 scaffold530_50163 25.1 scaffold296_33277	33.6 scaffold 949_70805 34.2 scaffold 5_2054	24.1 scattoki67_96	44.3 + TA scaffold857_67453 45.0 + Scaffold478_52180	35.7 scaffold247_28440 36.2 scaffold227_28657
35.6 w scatfold 210_24614 36.5 w scatfold 1191_76393 37.0 w // scatfold 1086_74309		35.2 - Scaffold 762_62836 36.0 - Scaffold 1016_72669	28.4 scaffold346_37702	46.5 m scattoldo57_57444 47.1 m scattold645_56554 49.0 scattold1623_79065	37.3 scaffold 152_17972 38.2 scaffold 152_17971 40.4 scaffold 152_17971
37.6 scaffold 587_1462 37.8 scaffold 619_57730	33.1 scaffold699_59701	39.2 - 1 - 1 - scaffold 307_35970 39.2 - 1 - 1 - scaffold 60_10247 39.9 - 1 - 1 - scaffold 165_19721		49.2 49.4 scaffold 1902_79152 49.4 scaffold 294_35008	42.5 scaffold815_65508 43.0 scaffold815_65481
38.8 scatfold 784_63815 39.9 scatfold 812_65243 40.6 scatfold 10.10_72348	37.0 scaffold 1380_78437	42.8 - 4 scaffold 60_10489 44.7 - 4 scaffold 16_1588	36.6 scaffold781_63716 38.3 scaffold465_46245	51.0 scaffold202_23987 51.1 scaffold870_68096	43.6 scaffold815_65496 44.2 scaffold1249_77187
41.7 42.6 scaffold 92 1_69868 scaffold 30 1_34693		45.6 - 47 - 41 - 41 - 41 - 41 - 41 - 41 - 41	39.1 scaffold210_24612	55.7 55.7 56.4 56.4 56.4 56.4 56.4 56.4 56.4 56.4	45.3
43.9 46.3 scaffold666_57505 scaffold224_26328	44.0 scaffold575_56471	53.7 scaffold 126_15449 55.8 scaffold 865_67898	44.5 - scaffold 163_19588	58.5 scaffold 1317_77975 61.5 scaffold 1162_75878-1	51.3 54.3 scaffold134_16598 scaffold284_32111
49.9 (scalfold 1433_78685		58.4 scaffold66_7572 62.4 scaffold391_1095		64.9 cscatfold 1138_/5429 66.5 scatfold 121_13392	59.7 Scaffold1249_77184
LG 7f	LG 8f	LG 9f	LG 10f	LG 11f	LG 12f
0.0 scaffold 1274_77523 2.3 scaffold 209 23945	0.0 scaffold843_66608	0.0 scaffold274_30815	0.0 - scaffold21_2496	0.0	0.0 scaffold557_51574
	5.6 scaffold843_66624	5.9 scaffold56 6340		7.5 scaffold878_68370	3.2 scattold792_64200
14.6 18.0 /r scaffold108_14497 scaffold437_49694	9.5 scaffold843_66583 11.1 scaffold843_66583	10.2	11.3 scaffold357 42337	12.2 scaffold45_4452	0.6 scaffold497_48029
20.0	13.0 scaffold 1030_72976 14.2 scaffold 179_24828	12.4 scaffold568_52341		19.8	5.2 scaffold185_22112
24.7 scaffold253_29170 25.2 scaffold765_62882	16.0 scaffold541_56017 17.9 scaffold833_66211	15.7 scaffold1338_78201 17.7 scaffold639_56229	20.4 scaffold 336 37020	19.6 scaled 130_14071	6.8 scaffold823_65878 9.0 scaffold11_122
26.4 scaffold 1000_72180 27.0 scaffold 929_70198	20.5 scaffold64_6455 21.6 scaffold64_6455	19.2 scaffold111_12997 20.8 scaffold1194_76439	24.5 scaffold 1304_77821 25.9 scaffold 21 2927	27.6	2.6 scaffold804_64865 3.6 scaffold771_60639
28.2	24.0 scaffold 345_39354 26.1 scaffold 179_25109	24.0 scaffold719_60576	29.5 30.1 scaffold956_71004	32.5 scaffold151_17947 36.5 scaffold502_48282	14.6 scaffold 391_41147 16.3 scaffold 1334_78084
30.9 scaffold279_31523 32.4 scaffold1441_78705	31.8 scaffold473_56994	28.5 scaffold3_352	30.8 scaffold 226_26507 31.9 scaffold 220_25817	37.3 - scaffold 1 183 76308 39.7 - scaffold 658_590 18	14.4 scaffold1615 79059
35.2 - scaffold 1024_72855 38.2 - scaffold 547_50927		33.6 - scaffold727_61047	36.9 scaffold 1727_79118 39.2 scaffold 635_56116	41.0 scaffold396_45547 scaffold1066_73956 42.1 scaffold396_45575	10.4
44.2 scaffold551_55114 45.4 scaffold498 48138	40.5 scaffold609_54901	34.4 - scallold / 2/_61032	41.6 - scaffold 103_12085 44.3 - scaffold 678_58232	44.9 - Scalfold 100 5 - 72254 49.9 - scalfold 100 5 - 72254	19.4 scattold 320_36627
47.1 49.7 scaffold 1430_78672 scaffold 1305_77853	44.6	56.9 scalloliz 02_23740	45.6	56.5 scaffold394_48271	
51.6 7 52.7 scaffold 1084_74297 scaffold 1084_74297	45.9				
67.6 scaffold697_59597	53.7 scaffold241_32740	49.4	57.6 scaffold 30_3929	64.1 - Scaffold714_60493	5.6 scaffold1082_74230
LG 13f	LG 14f	LG 15f	LG 16f	LG 17f	LG 18f
0.0	0.0 scaffold492_47464	0.0 caffold553_55885	0.0 scaffold500_48177	0.0 scaffold 319_39135	0.0 - scaffold117_14552
6 1 scaffold 991 71823			7 7 scaffold309 34532	6.6 scaffold804_64892	
	9.2 scaffold 1133 75278	8.5 scaffold 1035_73111		9.5 scaffold804_64852	6.7 scaffold419_43528
			16.8 scaffold343_40722	15.5 scaffold 55_1266 15.5 scaffold 560_56685	
15.5 scaffold841_66516	14.2 scaffold 299_36547 15.5 scaffold 1350_78279	17.0 scaffold 1093_74471	18.4 scattold414_43382	20.3 scaffold800_60902 22.7 scaffold81 11159	14.5 scaffold1114_74931
19.8 scaffold619_55335	19.4 scaffold 634_56015	22.6 scaffold 1027_72925			18.8 scaffold951 70894
24.0 scaffold664_58753	21.7 scaffold 56 8 8663 22.5 scaffold 513 49143	25.5 scanoid / 42_61599	22.2 anoffe bit 152, 19020	32.1 scaffold939_70453	19.8 scaffold17_1776 19.9 scaffold1114_74878
27.1 scaffold560_51836 28.7 scaffold293_34662	24.0 scaffold513_49203 25.6 scaffold552_51132	30.5 scaffold 679_58354 33.1 scaffold 146_17513	37.8 scaffold460_53605	36.2 scaffold 1306_77868 37.5 scaffold 16 2029	22.1 scaffold1114_74869
29.1	28.1 scaffold 638_56169	35.6 scaffold 1483_78801	42.5 scaffold 121 14985	40.2 scaffold 346_39699	26.2 scaffold103_11003
33.4 scaffold1045_73528 35.9 scaffold761_62829	33.0 scaffold443_44729	30.0    Scalloid / 5_0 124	47.6 scaffold229_28411	47.6 scaffold 172_24561	28.4 scaffold657_59041 29.9 scaffold280_32215
36.2 scaffold269_30349 38.7 scaffold115_13516	34.9 scanola 1058_/3/22	45.7 scaffold467_52810		51.8 scaffold854_67343	32.8 scaffold905_69394
			56.5 scaffold59_6564		36.9 scaffold577_56325
44.8 U scaffold 912_69534	42.8 - scaffold254_33077	53.9 U scaffold293_32994	60.4	60.9 - scaffold558_56416	38.6 - U- scaffold147_15618
LG 19f	LG 20f	LG 21f	LG 22f	LG 23f	LG 24f
0.0 scaffold249_28678	0.0 scaffold704_59923	0.0 scaffold192_23107	0.0 scaffold1290_77648	0.0 scaffold162_19489	0.0 scaffold379_46278 1.3 scaffold379_46179
		6.3 scaffold567_52284		7.7 scaffold184_20694	
6 7 ecoffold1216_76693	15.3 scaffold299_33764		12.5 scaffold1131_75238	12.3 - scaffold 35_4096	
8.5 scaffold987_71723	_	15.5 scaffold32_6886 19.2 scaffold482_47066	15.6 scaffold915_69571	16.5 scaffold750_60314 17.9 scaffold315_34907	
10.1 scaffold61_6403 11.1 scaffold61_6409		20.6	21.9 scaffold915_69566 24.9 scaffold725_60932	19.8 scaffold 387_47357 24.1 scaffold 749_61895	12.4 - scaffold518 54414
12.8 scaffold 1262_77386	31.0 scaffold791_64165	27.7 scaffold147_17514 28.6 scaffold85_10316	25.3 scaffold 1154_75679 26.5 scaffold 915_69572 28.5 conffold 915_69572	25.1 - scattoid1386_78493 29.8 - scattoid810_65165	12.9 scaffold518_54456
16.3	38.7 scaffold487_47127	32.2 scaffold 137_16826	29.8 scaffold78_9895 31.4 scaffold535 55676		15.6 scattoid893_68922 16.6 scattoid893_7845 17.5 scattoid1381_7845
17.5 scaffold464_46166 18.0 scaffold1531_78950	41.7 scaffold658_57211 44.2 scaffold281_31690	36.7	34.0 scaffold988_71725 36.7 scaffold728_60506	36.3 - scaffold953_70904	17.9 scaffold705_59948
20.5 scaffold656_59185	50.4 scaffold257_30957 50.6 scaffold1170 76103	47.5	38.8 39.9 42.0 scaffold442_44562 scaffold442_48562	46.0 eco#6ki1304_77707	
	55.2 scaffold526_49786	47.6 47.6 48.2 scaffold 660_57300 scaffold 192_24152	44.6 scaffold 771_63294 48.4 scaffold 333_37444	48.8 scaffold852_67256 50.5 scaffold827_48573	23.2 scaffold1447_7872 24.5 scaffold191_22964
24.9 scaffold694_59485		50.5 scaffold863_67755 54.2 scaffold1201_76581			26.0 scaffold7_3296
27.6 scaffold694_59459	66.1 scaffold1167_75960	55.7 - scatfold 1272_77503 59.3 - scatfold 1157_75730			
		and the second second	60.2 - conffedd 1724 70116	C2 2	30.8 - coaffold643 56522

## 图 2 雌性牙鲆连锁图谱

Fig. 2 The female genetic linkage map of Paralichthys olivaceus

# 庞仁谊等: 牙鲆遗传连锁图谱的构建

LG 1m	LG 2m	LG 3m	LG 4m	LG 5m	LG 6m
0.0 0.8 1.7 1.7 1.7 1.7 1.7 1.7 1.7 1.7 1.7 1.7	0.0 scaffold1623_79065 2.8 scaffold1138_75429	0.0 scaffold79_8198	0.0 scanold 1362_78380	0.0 scanold207_23021	6.6 scaffold45 4452
5.7 1 scaffold 329_37433 6.7 1 scaffold 159_18917 9.7 1 scaffold 1119_74976	8.5 scaffold374_40228 12.8 scaffold123_22000	8.7 - scaffold 24_2845 11.3 - scaffold 192_23107	11.6 rcn#pH332_47850	12.8 - cereffold 334, 3780.9	10.9 scaffold 878_68370
12.5 + / // scaffold44_5286 15.7 + // scaffold224_26328 17.5 + // scaffold176_20941	13.9 scaffold289_32535 15.3 scaffold289_32576 18.0 scaffold772_60963	14.2 scaffold 147_17515 16.8 scaffold 567_52284 18.5 scaffold 566_50439	14.3 scaffold 79_10045 16.4 scaffold 422_43752	14.7 - scaffold207_23035 15.5 - scaffold207_35322	17.7 scaffold138_14871 20.8 scaffold846_66755
18.6 V r scaffold 876_68345 19.1 V A scaffold 1200_76580 19.3 V c scaffold 927_70003	20.5 scaffold289_32507 23.6 scaffold572_56496 27.0 scaffold331_39635	21.4 scaffold37_4241 24.5 scaffold32_6886 25.5 scaffold660_57301	18.9 scaffold 108_14497	24.3 scaffold473_56994	26.5
20.0 v scaffold538_50478 20.9 v scaffold921_69859 21.7 v scaffold921_69859	28.7 scaffold548_50951 32.1 scaffold548_50945 33.6 scaffold548_50945	27.1 scaffold1107_74719 28.9 scaffold482_47066	25.7 scaffold 1123_75036 29.2 scaffold 1000_72180	26.0 scaffold301_33889 31.0 scaffold514 55541	31.5 scaffold 1183 76308 34.0 scaffold 658 59018 36.6 scaffold 396 45575
22.9 scaffold224_26315 23.7 scaffold224_26330	37.0 scaffold478_52144 41.8 scaffold450_44890	35.1 scaffold85_10316	30.9 scaffold765_62882 32.9 scaffold279_31523 35.0 scaffold1441_78705	35.6 scaffold179_25109	39.2 scaffold 151 17947 42.3 scaffold 89 8557 43.2 scaffold 189 22532
25.5 scaffold 1326 78007 25.8 scaffold 1326 78007 25.8 scaffold 210 24614	47.9 scaffold30_3927	41.1	36.7	40.6 scaffold179_24828 42.9 scaffold541_56017 44.2 scaffold541_76017	49.0 scaffold 301_33874
26.4 97 Scaffold587_1462 27.6 7 scaffold587_1462 27.9 7 scaffold619_57730	51.7 scattold857_67444 52.8 scattold857_67453 56.1 scattold870_68096	47.2 scaffold 947_70672	44.6 scaffold547_50927	46.4 scaffold533_50338 48.5 scaffold60_6605	52.5 scattold 295_33190 54.7 scattold 502_48282 59.4
28.7 4 14 scattold / 84_63815 29.7 4 scattold 812_65243 31.7 4 scattold 1086_74309	59.3	59.6	51.3 scaffold370_41021	53.6	60.6 scaffold714_60493
33.3 34.8 36.4 scaffold 301_34693 scaffold 666_57505	67.0	65.5 scaffold 1201_76581	56.0 scaffold817_65532 60.8 scaffold209_23945	62.9 scaffold843_66608	73.9 ecaffold384_43780
41.8 scaffold1433_78685 51.8 scaffold968_71269	73.1 scattold121_13392	68.4 — scaffold 1272_77503	61.2 ->>> scaffold 1274_77523	64.9 scallold 1015_72650	73.5 O ataliou304_43700
55.2 → scaffold34_5087	IG 8m	LG 9m	LG 10m	IG 11m	I.G.12m
0.0 scaffold274_30813	0.0 scaffold991_71823	0.0	0.0 scaffold 1114_74869	0.0 scaffold249_28703	0.0 - scaffold807_65101
	4.8 scaffold841_66516	2.1 scaffold21_2496	2.0 scaffold 1114_74931	2.0 scaffold249_28678	2.1 Scalloudor_05100
16.6 - ecoffold600 50670	12.2 scaffold965_71222	9.8 scaffold408_42926	7.2 scaffold117_14552		16.5 ecaffold553.55885
19.8 scaffold 32_4004		14.7 scaffold357_42337 19.7 scaffold636 58399 scaffold1179 76240	40.0	7.0 scaffold1216_76693	16.5 scallou555_55665
27.3	24.3 26.4 scaffold 664_58753 scaffold 362_39390	24.8 scaffold336_37020	12.2 scallod 1029_12913	9.8 scattold61_6403 11.1 scattold1262_77386	24.7 scaffold1035_73111
33.8 scalfold 56 5340 36.0 scaffold 505 53887 38.6 scaffold 568 52341	27.7 scattold293_34662 29.5 scattold1339_78219 30.1 scattold560_51836	30.2 - scaffold 1304_77821 31.5 - scaffold 21_2927		14.7 scaffold903_69232	33.3 scaffold1093_74471
39.3	32.3 33.7 34.6 scaffold1045_73528 scaffold233_27183	35.3 scaffold226_26507 37.2 scaffold220_25817	20.1 scaffold 951_70894	15.7 scaffold1531_78950 16.8 scaffold464_46166	38.9 scaffold1027_72925 41.6 scaffold742_61599
45.3 Scaffold111_12997	36.3 36.9 38.8 scaffold269_30349 38.8 scaffold115_13516	45.5 scaffold635 56116	24.6 scaffold.657_59041 25.6 scaffold.280_32222 26.4 scaffold.1598_79036	19.2 scaffold656_59185	46.7 scaffold679_58354 49.4 scaffold146_17513 51.0 scaffold1483_78801
61.1 scaffold727_61047	43.9 Scaffold 912_69534	49.9 scaffold678_58232	27.3 - scaffold 103_11003	23.7 scaffold694 59485	55.0 scaffold73_8124
62.0 Scattold / 27_61032	54.2		32.8 scaffold 147_15618	26.5 scaffold694_59459	61.9 scaffold467_52810
		C4.0	35.7	28.8 ccaffold694_59453	70.2 scaffold293 32994
75.2 - scatfold 727_61030	61.8 scattold55_6429	64.2 scanolo30_3929	37.7 - scaffold419_43528	20.0 () 8081010034_55455	
LG 13f	61.8 scattold55_6429 LG 14f	LG 15f	LG 16f	LG 17f	LG 18f
LG 13f 0.0	LG 14f	LG 15f	37.7	LG 17f	LG 18f
LG 13f 0.0 scaffold/22_61030 2.4 scaffold/299_33764 2.4 scaffold/299_33520	61.8 - scattold55_6429 LG 14f 0.0 - scattold500_48177 7.7 - scattold309_34532	LG 15f 00 scalob10_323 LG 15f 01 scalob1263_77403 56 scalob1263_77403 56 scalob1263_77403 56 scalob1264_545663 192 scalob1264_56663 192 scalob1264_56663 192 scalob1264_56663	37.7 scaffold 19_43528 LG 16f 0.0 + scaffold 343_37432 scaffold 67_112	LG 17f 0.0 scaffold1219.76726 1.9 scaffold1429.76726 3.9 scaffold145_77427 3.9 scaffold145_77427 6.3 scaffold1189.76355	LG 18f
LG 13f 0.0 = scaffold/29_33764 2.4 = scaffold/299_33764 10.5 = scaffold/299_33520 10.5 = scaffold/791_64165 13.2 = scaffold/15_7596	61.8 scattold55_6429 LG 14f 0.0 scattold500_48177 7.7 scattold500_48177 16.7 scattold309_34532 16.7 scattold309_34532	LG 15f 	37.7	LG 17f LG 17f 0.0	LG 18f
15.2         scattold /22_61030           LG 13f            0.0         scattold /299_33764           2.4         scattold /299_33520           10.5         scattold /91_64165           13.2         scattold /5796           18.2         scattold /42_47127	LG 14f 0.0 scaffold50_6429 7.7 scaffold309_34532 16.7 scaffold309_34532 18.4 scaffold343_40722 18.4 scaffold343_40722	Call C and	377	LG 17f 0.0 scatbul 1219_76726 19 scatbul 145_17427 3.9 scatbul 145_17427 6.3 scatbul 145_17427 15.4 readbul 145_17427 15.4 readbul 145_17427 15.4 readbul 145_17425 15.4 readbul 145_174853 22.4 readbul 145_174853 22.5 readbul 145_17300	LG 18f 0.0 caffold1306_77868 10.4 caffold1306_77868 13.4 caffold804_64892 13.6 caffold804_64892 13.6 caffold80_64852 18.0 caffold81_1159 24.4 caffold81_1159
15.2         scatfold/22_61030           LG 13f         0.0         scatfold/299_33764           2.4         scatfold/299_33520         scatfold/791_64165           10.5         scatfold/791_64165         scatfold/15_7596           18.2         scatfold/15_7596         scatfold/86568_57211           2.1.1         scatfold/821_31690         scatfold/821_31690	61.8 scattold55_6429 LG 14f 0.0 scattold50_6429 7.7 scattold309_34532 16.7 scattold309_34532 16.7 scattold343_40722 18.4 scattold343_40722 25.0 scattold253_29287	LG 15f LG 15f safbidz63,77403 56 192 192 197 197 197 197 201 201 201 201 201 201 201 201	37.7	LG 17f LG 17f 0 = scatbil 1219.76726 19 = scatbil 1219.77184 10 = scatbil 1219.77184 10 = scatbil 121.77184 10 = scatbil 121.77185 10 = scatbil 121.77855 10 = s	LG 18f 0.0 caffold306_77868 10.4 scaffold304_64832 13.4 scaffold304_64832 18.0 scaffold304_64852 18.0 scaffold33_10266 21.3 scaffold33_10266 26.5 scaffold304_663055 26.5 scaffold304_663055
LG 13f LG 13f 	61.8         scathold55_6429           LG 14f           0.0         scathold500_48177           7.7         scathold309_34532           16.7         scathold341_40722           18.4         scathold343_20722           25.0         scathold253_29287           33.5         scathold153_18238	LCG 15f LCG 15f scafbid253 77403 scafbid253 77403 scafbid253 77403 scafbid259 53946 scafbid395 53946 scafbid395 53946 scafbid392 50810 scafbid392 50810 scafbid392 50810 scafbid392 50810 scafbid392 50810 scafbid392 50810 scafbid392 50810 scafbid392 50810 scafbid392 50810 scafbid392 50820 scafbid392 5	37.7	LG 17f LG 17f 0 carlbul 1219_76726 19 carlbul 1219_76726 19 carlbul 135_71427 39 carlbul 135_71427 39 carlbul 135_71427 39 carlbul 135_71427 154 carlbul 135_71855 154 carlbul 145_77184 214 carlbul 145_77184 215 carlbul 145_77184 216 carlbul 145_77187 216 carlbul 145_77170 216 carlbul	LG 18f 0.0 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold804_64892 13.4 scaffold804_64892 13.4 scaffold804_64852 18.0 scaffold804_64852 21.3 scaffold804_64852 21.3 scaffold806_60902 26.5 scaffold806_60902 36.8 scaffold939_70453
15.2         scaffold/22_61030           LG 13f         0.0           0.0         scaffold/299_33764           2.4         scaffold/299_33764           10.5         scaffold/299_33520           10.5         scaffold/91_64165           13.2         scaffold/15_7596           18.2         scaffold/858_57211           24.0         scaffold/868_57211           24.0         scaffold/81_31690           31.2         scaffold/826_39786	61.8         scathold 55_6429           LG 14f           0.0         scaffold 500_48177           7.7         scaffold 309_34532           16.7         scaffold 309_34532           16.7         scaffold 343_40722           18.4         scaffold 253_29287           33.5         scaffold 153_18238           37.8         scaffold 460_53605	LG 1 5 f Scattor 10, 2323 LG 1 5 f Scattor 10, 2323 Scattor 10, 2333 Scattor 10, 2333 Scattor 10	37.7	LG 17f LG 17f 0 scatbild 219_76726 19 scatbild 217427 3.3 scatbild 219_7635 154 scatbild 249_77184 scatbild 249_77182 231 scatbild 249_77184 scatbild 249_77182 232 233 234 235 235 235 235 235 235 235 235	LG 18f 0.0 scaffold1006_77868 10.4 scaffold1006_77868 10.4 scaffold804_64892 13.4 scaffold804_64852 18.0 scaffold80_64852 18.0 scaffold80_64852 18.0 scaffold80_60902 36.8 scaffold80_60902 36.8 scaffold939_70453 41.9 scaffold16_2029 36.9 scaffold16_2029
15.2         scattold /22_61030           LG 13f            0.4         scattold /299_33764           2.4         scattold /299_33520           10.5         scattold /291_64165           13.2         scattold /291_64165           13.2         scattold /29_6796           18.2         scattold /87_47127           21.1         scattold /87_47127           21.1         scattold /87_47127           21.1         scattold /87_6711           24.0         scattold /87_6103           31.2         scattold /26_6476           33.6.4         scattold /74_61883	61.8         scathold 55_6429           LG 14f         0.0           orafio kl500_48177           7.7         scathold 309_34532           16.7         scathold 343_40722           18.4         scathold 343_40722           18.4         scathold 14_4_3382           25.0         scathold 16_3_18238           33.5         scathold 153_18238           37.8         scathold 163_5805           42.5         scathold 161_114985	LC 1 5 C 1 5	37.7	LG 17f LG 17f 0 scatbild 219 76726 19 scatbild 5 77427 39 scatbild 5 77427 30 scatbild 5 77427 30 scatbild 24 7211 30 scatbild 24 7211 31 scatbild 24 7211 32 scatbild 24 7211 32 scatbild 24 7211 32 scatbild 24 7211 32 scatbild 25 77470 32 scatbild 25 77470 33 scatbild 25 77470 34 scatbild 25 77470 35 scatbild 25 77470 36 scatbild 25 77470 36 scatbild 25 77470 37 scatbild 25 77470 38 scatbild 25 77470 39 scatbild 25 77470 30 scatbild 25 56341 31 scatbild 27 7770 30 scatbild 25 77470 30 scatbild 25 7	LG 18f 0.0 caffold 1306_77868 10.4 scaffold 1306_77868 10.4 scaffold 1306_77868 10.4 scaffold 30_64892 13.4 scaffold 30_6482 18.0 scaffold 30_10266 21.3 scaffold 30_10266 21.3 scaffold 30_52 26.5 scaffold 30_5022 36.8 scaffold 16_2023 41.9 scaffold 16_2023 47.3 scaffold 46_4553
15.2         scatfold /2/_61030           LG 13f            0.0         scatfold /299_33764           2.4         scatfold /299_33520           10.5         scatfold /299_33520           10.5         scatfold /191_64 165           13.2         scatfold /15_7596           18.2         scatfold /15_7596           18.2         scatfold /16_7596           18.2         scatfold /16_7696           18.2         scatfold /16_7696           18.2         scatfold /16_7696           18.2         scatfold /16_76103           36.4         scatfold /170_76103           36.4         scatfold /170_76183           19.6         scatfold /170_76103	61.8         scathold55_6429           LG 14f           0.0         scathold500_48177           7.7         scathold500_34532           16.7         scathold309_34532           16.7         scathold263_29287           33.5         scathold263_29287           33.5         scathold51_532           42.5         scathold263_29287           37.8         scathold263_5305           42.5         scathold211_14985           47.5         scathold229_28411	LC I Samo Log 1323 LC I Sf scaffold 263 77403 scaffold 263 77403 scaffold 263 77403 scaffold 295 153946 scaffold 395 153946 scaffold 395 153946 scaffold 395 153946 scaffold 395 153946 scaffold 395 153946 scaffold 395 15366 scaffold 395 1566 scaffold 395 1566 scaffo	37.7	LG 17f LG 17f 0 cardiol 1219_76766 19 cardiol 1219_76766 19 cardiol 133_40093 6.3 cardiol 133_712477 3.9 cardiol 133_70295 15.4 cardiol 124_77184 15.4 cardiol 125_56486 13.3 cardiol 125_56486 13.3 cardiol 125_56486 13.4 cardiol 125_56486 13.5 cardiol 125_57840 14.4 cardiol 126_77872 15.4 cardiol 126_778400 15.4 cardiol 1	LG 18f 0.0 scaffold1306_77868 10.4 scaffold804_64892 13.4 scaffold804_64892 13.4 scaffold80_1266 21.3 scaffold8_12026 21.3 scaffold8_1026 24.4 scaffold8_0305 26.5 scaffold939_70453 41.9 scaffold16_2029 47.3 scaffold46_4563
15.2         scatfold /2/_61030           LG 13f         0.0           0.0         scatfold /2933764           2.4         scatfold /2933520           10.5         scatfold /3964165           13.2         scatfold /3964165           13.2         scatfold /658_57211           2.4         scatfold /167596           18.2         scatfold /17076103           31.2         scatfold /17076103           36.4         scatfold /2649786           39.6         scatfold /1675960	61.8         • scathold 55_6429           LG 14f           0.0         • scaffold 500_48177           7.7         • scaffold 309_34532           16.7         • scaffold 309_34532           16.7         • scaffold 263_29287           33.5         • scaffold 253_2827           33.5         • scaffold 153_18238           37.8         • scaffold 460_53605           42.5         • scaffold 229_28411           56.3         • scaffold 59_6564	LG 1 5 1 LG 1 5 1 C 1 C 1 C 1 C 1 Scaffold 263 77403 Scaffold 395 53946 Scaffold 395 53946 Scaffold 395 53946 Scaffold 395 53946 Scaffold 395 53946 Scaffold 395 53946 Scaffold 395 78626 Scaffold 395 78626 Scaffold 394 79626 Scaffold 394 79777 Scaffold 394 797777 Scaffold 394 79777 Scaffold 394 797777 Scaffold 394 79777777777 Scaffold 394 79777777	37.7	LG 17f LG 17f 0 scafful 1219_76766 19 scafful 1219_76766 10 scafful 1219_77184 10 scafful 1219_77184 10 scafful 1219_77184 10 scafful 1219_77182 10 scafful 121_77182 10 scaf	LG 18f 0.0 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold804_64892 13.4 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_026 26.5 scaffold83_70453 41.9 scaffold46_4553 61.5 scaffold373_41742
75.2         scatfold /2/_61030           LG 13f         0.0           0.1         scatfold /2933764           2.4         scatfold /2933520           10.5         scatfold /295796           13.2         scatfold /17076103           36.4         scatfold /7461883           48.5         scatfold /16775960           54.8         scatfold /187479149	61.8         • scathold 55_6429           LG 14f         0.0         • scathold 50_6429           16.7         • scathold 309_34532         •           16.7         • scathold 343_40722         •           18.4         • scathold 343_40722         •           18.4         • scathold 141_43382         •           25.0         • scathold 163_18238         •           33.5         • scathold 163_18238         •           37.8         • scathold 163_18238         •           42.5         • scathold 121_14986         •           47.5         • scathold 59_6564         •           60.3         • scathold 59_6564         •	LC 1 5 1 LC 1 5 1 C 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	37.7	LG U Dankots, JAGS LG 17f 19 scaffbil1219_76726 19 scaffbil1219_76726 19 scaffbil1219_76726 19 scaffbil1219_76726 19 scaffbil123_7027 10 scaffbil123_7028 10 scaffbil123_7028 10 scaffbil123_7028 10 scaffbil123_7028 10 scaffbil131_78955 10 scaffbil131_78955 10 scaffbil131_78955 10 scaffbil131_78955 10 scaffbil131_78955 10 scaffbil131_78955 10 scaffbil131_78955 10 scaffbil131_78955 10 scaffbil131_78955 10 scaffbil135_77132 10 scaffbil135_77132 10 scaffbil135_77132 10 scaffbil135_56481 10 scaffbil135_56508 10 scaffbil135_56481 10 scaffbil135_56508 10 scaffbil110_78_3666 10 scaffbil110_78_3666 10 scaffbil110_74816 10 scaffbil11	LG 18f 0.0 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold804_64892 13.4 scaffold804_64852 18.0 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold83_12026 21.5 scaf
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12.2	LG 14f 0.0 scaffold55_6429 LG 14f 0.0 scaffold50_48177 7.7 scaffold309_34532 16.7 scaffold309_34532 16.7 scaffold343_40722 18.4 scaffold343_40722 18.4 scaffold343_40722 18.4 scaffold343_40722 18.4 scaffold343_40722 18.4 scaffold34_0722 18.4 scaffold34_0722 19.4 scaffold55_664 0.0 scaffold75_6651 LG 20m 0.0 scaffold75_6651	LG 151 C	37.7	LG US C Balances, 2403 LG 17f 0 = scaffield 1219,76726 19 = scaffield 1219,777184 10 = scaffield 121,7273 10 = scaffield 121,78853 24 = scaffield 121,78853 25 = scaffield 121,78853 26 = scaffield 121,78853 27 = scaffield 121,78853 28 = s	LG 18f 0.0 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold1306_78868 21.3 scaffold1301_159 24.4 scaffold131_1159 24.4
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15.2	61.8         scathol55_6429           LG 14f         0.0           scathol55_6429           LG 14f           0.0         scathol50_48177           7.7         scathol309_34532           16.7         scathol343_40722           18.4         scathol414_43382           25.0         scathol414_1838           25.0         scathol416_53005           33.5         scathol415_18238           37.8         scathol412_14985           47.5         scathol412_14985           47.5         scathol472_28411           56.3         scathol479_6564           60.3         scathol479_6564           0.0         scathol472_6264200           1.3         scathol477_372           10.4         scathol477_144           20.2         scathol471_122           25.6         scathol471_16039           25.6         scathol471_16039	LG 151 LG 152 Comparison of the second start	37.7	LG 23 C 2600000000000000000000000000000000000	LG 18f 0.0 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold804_64892 13.4 scaffold804_64852 18.0 scaffold83_10266 21.3 scaffold83_10266 21.3 scaffold939_70453 41.9 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold568_56416 LG 24m 0.0 scaffold482_47464 9.9 scaffold133_75278 14.5 scaffold133_75278 14.5 scaffold133_75278 14.5 scaffold133_75278 14.5 scaffold133_75278 14.5 scaffold133_75278 14.5 scaffold135_78279 19.8 scaffold135_78279
15.2         Scatfold /2/_61030           LG 13f         0.0         scatfold /29_33764           2.4         scatfold /29_33764         2.4           10.5         scatfold /29_33520         10.5           11.2         scatfold /29_5761         12.7           21.1         scatfold /20_571         12.4           24.0         scatfold /20_571         12.4           24.0         scatfold /20_571         13.6           36.4         scatfold /20_578         18.3           48.5         scatfold /167_75960         54.8           54.8         scatfold /1874_79149         13.3           13.5         scatfold /1874_79149         13.3           13.5         scatfold /17.05397         13.331           13.5         scatfold /17.05397         13.331           13.5         scatfold /10.7057         17.4250           20.6         scatfold /10.7057         17.4250	61.8         — scathold55_6429           LG 14f         0.0           0.0         — scathold55_6429           LG 14f         0.0           0.0         — scathold50_6429           16.7         — scathold309_34532           16.7         — scathold343_40722           18.4         — scathold343_40722           18.4         — scathold141_43382           25.0         — scathold153_18238           37.8         — scathold153_18238           37.8         — scathold153_18238           37.8         — scathold121_14985           47.5         — scathold59_6564           60.3         — scathold715_00551           LG 20m         1.3           10.4         — scathold37_6091           15.8         — scathold31_47084           25.6         — scathold31_4714           26.6         — scathold31_47084           27.6         — scathold31_47084           28.6         — scathold31_4714           29.0         — scathold31_47084           29.0         — scathold76_6331           31.4         — scathold76_6331	LC 1 1 5 1 5 1 5 1 5 1 5 1 5 1 5 1 5 1 5	37.7	LG 23 LG 17f 0 0 0 0 0 0 0 0 0 0 0 0 0	LG 18f 0.0 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold1306_77868 10.4 scaffold301_64829 13.4 scaffold301_0266 21.3 scaffold301_1159 24.4 scaffold301_0266 21.3 scaffold301_0266 21.3 scaffold11159 24.4 scaffold302_069302 36.8 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold16_2029 47.3 scaffold458_4744 0.0 scaffold452_47464 9.9 scaffold133_75278 14.5 scaffold133_75278 14.5 scaffold130_75279 19.8 scaffold104_72228 21.8 scaffold104_72228 21.8 scaffold104_72228 21.8 scaffold131_4203 21.8 scaffold131_4203
15.2         scatfold /2/_61030           LG 13f         0.0         scatfold /2933764           2.4         scatfold /2933764         2.4           10.5         scatfold /2933764         2.4           11.2         scatfold /217560         3.2           31.2         scatfold /2461883         3.4           48.5         scatfold /1677560         3.4           54.8         scatfold 16775760         3.4           13.5         scatfold 16176760         3.3           13.5         scatfold 16077690         3.2           13.5         scatfold 16077600         3.2           13.5         scatfold 16077600         3.2           13.6         scatfold 16077600         3.2           13.6         scatfold 16077760         3.2           23.5         scatfold 16273654         3.2           23.5         scatfold 16374265         3.2 <td>61.8         scathold55_6429           LG 14f         0.0           0.0         scathold55_6429           LG 14f         0.0           0.0         scathold50_843           16.7         scathold309_34532           16.7         scathold343_40722           18.4         scathold253_29287           33.5         scathold253_29287           33.5         scathold253_29287           33.5         scathold253_18238           37.8         scathold460_53605           42.5         scathold59_6564           60.3         scathold716_60551           LG 20m         1.3           0.0         scathold77_372           10.4         scathold77_144           20.2         scathold77_144           22.5         scathold77_6039           27.5         scathold77_6039           27.6         scathold16_70639           37.8         scathold77_6039           28.0         scathold16_70639           3.3         scathold77_6039</td> <td>LG 1 51 LG 1 51 </td> <td>37.7 -&gt;&gt; scaffold 19_43528           LG 16f           0.0         +iscaffold 343_37432 scaffold 67_112           12.2         scaffold 343_37432 scaffold 67_112           12.2         scaffold 343_37429           14.5         scaffold 343_3716           17.0         scaffold 163_1158           28.7         scaffold 13_1958           44.6         scaffold 13_1958           44.6         scaffold 337_37032           15.1         scaffold 337_37032           15.1         scaffold 337_37032           15.1         scaffold 1724_79116           29.4         scaffold 337_12590           31.0         scaffold 1724_4452           32.0         scaffold 1726_9956           31.0         scaffold 172_9956           32.0         scaffold 172_9956           34.0         scaffold 172_9956           31.0         scaffold 172_99572<td>LG 23 C 2440000_0403 LG 17f 0</td><td>LG 18f 0.0 scaffold 1306_77868 10.4 scaffold 1306_77868 10.4 scaffold 804_64892 13.4 scaffold 804_64892 13.4 scaffold 803_6482 13.6 scaffold 803_70453 41.9 scaffold 16_2029 47.3 scaffold 16_2029 47.4 scaffold 132_75278 14.5 scaffold 1133_75278 14.5 scaffold 1135_78279 19.8 scaffold 13_49143 28.5 scaffold 13_49143 28.5 scaffold 13_49143 28.5 scaffold 13_6263 28.5 scaffold 13_6265 28.5 scaffold</td></td>	61.8         scathold55_6429           LG 14f         0.0           0.0         scathold55_6429           LG 14f         0.0           0.0         scathold50_843           16.7         scathold309_34532           16.7         scathold343_40722           18.4         scathold253_29287           33.5         scathold253_29287           33.5         scathold253_29287           33.5         scathold253_18238           37.8         scathold460_53605           42.5         scathold59_6564           60.3         scathold716_60551           LG 20m         1.3           0.0         scathold77_372           10.4         scathold77_144           20.2         scathold77_144           22.5         scathold77_6039           27.5         scathold77_6039           27.6         scathold16_70639           37.8         scathold77_6039           28.0         scathold16_70639           3.3         scathold77_6039	LG 1 51 LG 1 51 	37.7 ->> scaffold 19_43528           LG 16f           0.0         +iscaffold 343_37432 scaffold 67_112           12.2         scaffold 343_37432 scaffold 67_112           12.2         scaffold 343_37429           14.5         scaffold 343_3716           17.0         scaffold 163_1158           28.7         scaffold 13_1958           44.6         scaffold 13_1958           44.6         scaffold 337_37032           15.1         scaffold 337_37032           15.1         scaffold 337_37032           15.1         scaffold 1724_79116           29.4         scaffold 337_12590           31.0         scaffold 1724_4452           32.0         scaffold 1726_9956           31.0         scaffold 172_9956           32.0         scaffold 172_9956           34.0         scaffold 172_9956           31.0         scaffold 172_99572 <td>LG 23 C 2440000_0403 LG 17f 0</td> <td>LG 18f 0.0 scaffold 1306_77868 10.4 scaffold 1306_77868 10.4 scaffold 804_64892 13.4 scaffold 804_64892 13.4 scaffold 803_6482 13.6 scaffold 803_70453 41.9 scaffold 16_2029 47.3 scaffold 16_2029 47.4 scaffold 132_75278 14.5 scaffold 1133_75278 14.5 scaffold 1135_78279 19.8 scaffold 13_49143 28.5 scaffold 13_49143 28.5 scaffold 13_49143 28.5 scaffold 13_6263 28.5 scaffold 13_6265 28.5 scaffold</td>	LG 23 C 2440000_0403 LG 17f 0	LG 18f 0.0 scaffold 1306_77868 10.4 scaffold 1306_77868 10.4 scaffold 804_64892 13.4 scaffold 804_64892 13.4 scaffold 803_6482 13.6 scaffold 803_70453 41.9 scaffold 16_2029 47.3 scaffold 16_2029 47.4 scaffold 132_75278 14.5 scaffold 1133_75278 14.5 scaffold 1135_78279 19.8 scaffold 13_49143 28.5 scaffold 13_49143 28.5 scaffold 13_49143 28.5 scaffold 13_6263 28.5 scaffold 13_6265 28.5 scaffold
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15.2       — scaffold/22_61030         LG 13f         0.0       — scaffold/299_33764         2.4       — scaffold/299_33520         10.5       — scaffold/299_33520         10.5       — scaffold/791_64165         13.2       — scaffold/791_64165         13.2       — scaffold/87_47127         21.1       — scaffold/87_47127         21.1       — scaffold/86_65_67211         24.0       — scaffold/281_31690         31.2       — scaffold/281_31690         31.2       — scaffold/74_61883         48.5       — scaffold/187_4_9149         LG 19m       0.0         0.0       — scaffold/390_44483         15.3       — scaffold/180_77637         20.5       — scaffold/20_3054         21.5       — scaffold/30_47265         22.5       — scaffold/30_47265         23.5       — scaffold/30_5054         24.4483       — scaffold/30_50561         25.5       — scaffold/30_505613         26.5       — scaffold/30_5056153	61.8       — scaffold55_6429         LG 14f       0.0         0.0       — scaffold50_48177         7.7       — scaffold309_34532         16.7       — scaffold309_34532         16.7       — scaffold309_34532         16.7       — scaffold314_40722         18.4       — scaffold253_29287         33.5       — scaffold253_29287         33.5       — scaffold153_18238         37.8       — scaffold253_29281         42.5       — scaffold229_28411         56.3       — scaffold59_6564         60.3       — scaffold79_56564         60.3       — scaffold77_572         10.4       — scaffold3_6091         15.8       — scaffold3_4084         25.6       — scaffold3_34_7004         25.6       — scaffold3_34_7034         26.6       — scaffold3_406665         16.7       — scaffold3_406665         27.5       — scaffold31_7064         28.6       — scaffold31_6391_4112         28.7       — scaffold31_6391_4114         29.8       — scaffold31_412         31.3       — scaffold31_5,79059         32.4       — scaffold31_4112         31.4       — scaffold331_41140     <	LG 1 51 LG 1 51 C 1	37.7 ->> scaffold 19_43528           LG 16f           0.0         + scaffold 343_37432 scaffold 67_112           12.2         scaffold 343_37429           14.5         scaffold 343_57432 scaffold 67_112           12.2         scaffold 343_37429           14.5         scaffold 343_57432 scaffold 67_112           12.2         scaffold 343_57432           16.7         scaffold 781_63723           11.0         scaffold 781_63723           28.7         scaffold 781_63723           30.8         scaffold 781_63723           31.6         scaffold 71_24612           32.6         scaffold 73_1568           44.6         scaffold 13_1985           58.9         scaffold 337_37032           15.1         scaffold 333_3_77444           32.6         scaffold 333_3_77444           32.6         scaffold 333_3_77444           32.6         scaffold 333_3_77444           32.6         scaffold 315_690           33.2         scaffold 315_690           33.2         scaffold 315_6972           33.2         scaffold 315_6972           33.2         scaffold 315_6972           33.2         scaffold 315_6972           33.2         sca	LG 25 LG 17f 0 scatbill 219 76726 19 scatbill 219 76726 10 scatbill 219 77427 10 scatbill 219 77184 10 scatbill 219 77185 10 scatbill 219 7726 20 scatbi	LG 18f 0.0 scaffold 1306_77868 10.4 scaffold 1306_77868 10.4 scaffold 1306_77868 10.4 scaffold 1306_77868 10.4 scaffold 1159 10.4 scaffold 1159 10.5 scaffold 158_52 10.6 scaffold 158_52 10.6 scaffold 158_52 10.6 scaffold 1013_75278 10.6 scaffold 1133_75278 10.6 scaffold 1133_75278 10.8 scaffold 1133_75278 10.8 scaffold 1350_78279 10.8 scaffold 1350_78279 10.8 scaffold 1350_78279 10.8 scaffold 1351_4203 22.8 scaffold 135_73222 10.8 scaffold 135_73722

## 图 3 雄性牙鲆连锁图谱

Fig. 3 The male genetic linkage map of *Paralichthys olivaceus* 

大,对 DNA 纯度和质量要求高,微量的 DNA 污 染即可导致很大的偏差,作为显性标记无法对种 群的遗传变异和遗传结构的分析提供较多的统计 信息<sup>[20]</sup>。作为继 SSR 后的第三代标记 SNP 标记, 虽杂合期望度低,容易定位于基因组的大多数拷 贝区域<sup>[21]</sup>,但是其费用成本相对更高。本实验使 用的 SSR 分子标记由于作图遗传信息量大、稳定 性和多态性高、共显性分离、在基因组中平均分 布,在种群内不同的群体之间比较和整合能起到很 好的桥梁作用<sup>[22]</sup>,被公认为是最理想的作图标记。

3.2 图谱的分析与探讨

Castaño-Sánchez<sup>[18]</sup>构建的日本牙鲆第二代 高密度遗传连锁图谱, 雌雄图谱定位上的微卫星 标记数目达到了1067个和1167个、但有效座位 只有184个和235个, 覆盖率也仅为79%和82%。 本研究构建的牙鲆图谱虽然标记数目不及日本牙 鲆第二代图谱, 但实际有效座位却达到了 434 个 和 416 个, 只在 LG3f、LG11f、LG9m、LG16m 连锁群出现少量标记定位在同一座位上、而雌、 雄图谱的覆盖率也分别达到了 89.11%和 88.70%, 从而很大程度上达到了较高图谱的密度的标准。 本实验所构建的牙鲆遗传连锁图谱相比于宋文涛 等<sup>[19]</sup>国内构建的牙鲆第一张遗传图谱标记的数 量、图谱覆盖率等方面也均有所提高,定位到图 谱上的标记总数由 307 个提高到了 529 个、雌、 雄图谱的覆盖率分别从之前的 77.7%和 71.1%提 高到了 89.1%和 88.7%,从而使得图谱的质量、可 信度及应用价值都得到了相应提高。

本研究中, SSR 标记在构建的遗传连锁群上 大多数分布比较均匀, 但在个别连锁群中仍有明 显的成簇分布现象(LG1f、LG5f、LG1m、LG15m 连锁群)。SSR 标记在很多已经构建的水产动物连 锁群上往往有明显的聚集分布现象, 宋文涛等<sup>[19]</sup> 构建的国内第一代牙鲆遗传图谱中, 提到了在牙 鲆雌、雄图谱的第4、7和第22号连锁群上还存 在超过 30 cM 区段找不到多态性标记, 而第1、3 和 8 号连锁群一些区段标记非常密集, 本研究构 建的图谱不论在图谱密度还是标记数目都得到了 很大的提升。 本实验中微卫星标记存在偏分离现象, 雌、 雄牙鲆图谱的偏分离位点分别达到了 131 个和 137 个。偏分离现象在水产动物界广泛存在, 在 Launey 和 Hedgecock 等<sup>[23]</sup>利用 SSR 标记构建的 太平洋牡蛎图谱、Young 等<sup>[24]</sup>利用 AFLP、RAPD、 SSR 和 VNTR 标记构建虹鳟的图谱中均检测到 偏分离现象。本次构建图谱的作图群体个体只有 80 个, 样本容量数目的限制导致数据统计产生了 偏差。遗传图谱的分辨率和精度, 很大程度上取 决于群体大小; 群体越大, 则作图精度越高, 出 现偏分离标记的几率越小。另外较高的遗传负荷 和致死基因的存在也会直接导致某些性状表现不 出来, 造成标记分离偏离孟德尔分离定律<sup>[21]</sup>。

遗传连锁图谱显示遗传标记位点在染色体的 相对位置,定位的分子标记反映出相应染色体座 位上的遗传多态性状态。理论上,所构建的牙鲆 遗传图谱的连锁群总数应与该物种的单倍体染色 体总数一致<sup>[25]</sup>,本研究构建的雌雄遗传连锁图谱 框架图均由 24 个连锁群组成,与牙鲆的单倍体染 色体总数完全相等。同时,该图谱的标记数目和 密度都达到了很高的水平,已经可以进行重要经济 性状的 QTL 定位分析和重要基因定位的研究,从 而可以在一定程度上指导牙鲆的遗传育种工作。

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# Construction of genetic linkage map in Japannese flounder (*Paralich-thys olivaceus*)

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**Abstract:** Using the microsatellite sequence got from genome sequencing, we constructed genetic linkage map with SSR markers for Japanese flounder (*Paralichthys olivaceus*), in which 681383B is the male parent and 6812E36 is the female parent. The male linkage map included 418 markers, which were distributed in 24 linkage groups, with 88.7% coverage. The length reached 1 418.1 cM, and the average marker interval was 3.62 cM. The female linkage map distributed in 24 linkage groups included 437 markers, with 89.1% coverage.spanning. The length reached 1 298.1 cM, and the average marker interval was 3.16 cM,. The medium density genetic linkage maps laid the groundwork for QTL analyses and marker-assisted selection breeding programs, and effectively promote the genetic improvement of Paralichthys, make flounder aquaculture sustainable development.

Key words: *Paralichthys olivaceus*; SSR molecular markers; genetic linkage map Corresponding author: CHEN Songlin. E-mail: chensl@ysfri.ac.cn

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