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卵胎生入侵种食蚊鱼的两性异形和雌性繁殖输出

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摘要:检测了卵胎生入侵种食蚊鱼(*Gambusia affinis*)繁殖期个体大小和形态特征的两性异形以及雌性繁殖输出。结果表明,繁殖期,雌性个体的数量显著大于雄性个体,雌性个体的体长显著大于雄性个体,食蚊鱼属于偏向雌性的两性异形。以体长为协变量的 One-way ANCOVA 及后续的 Tukey's 检验显示,特定体长食蚊鱼的雌性个体的头宽、眼间距、体宽和体重均显著大于雄性个体;头长和尾鳍长的两性间差异不显著。6 个形态特征变量的主成分分析(Eigenvalue ≥ 1)发现,前 2 个主成分共解释 65.1% 的变异。头宽、眼间距、体宽和体重在第一主成分有较高的正负载系数(解释 45.4% 变异),头长在第二主成分有较高的负负载系数(解释 19.7% 变异)。食蚊鱼的繁殖输出与母体个体大小的线性回归显示,窝仔数和窝仔重均与母体体长、体重呈显著的正相关;食蚊鱼的繁殖输出与母体局部特征的线性回归显示,窝仔数和窝仔重均与母体头宽、眼间距和体宽呈显著的正相关。窝仔数与后代个体的平均体长呈显著的正相关、与后代个体的平均体重相关不显著,后代个体大小与数量不发生权衡。食蚊鱼繁殖期的性别比例、个体大小和局部形态特征的两性异形受生育力选择、性选择、生态位分化、食物竞争等多种选择压力的作用,也有利于该物种种群扩张和快速入侵。

关键词:食蚊鱼;卵胎生;两性异形;性别比例;繁殖输出

Sexual dimorphism and female reproductive outputs of the ovoviparous and invasive mosquitofish *Gambusia affinis*

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Abstract: In this study, we measured the sexual dimorphism in body size and six other morphometrical variables along with the individual fecundity in females of ovoviparous and invasive mosquitofish *Gambusia affinis*, collected in Lishui (Zhejiang, eastern China), during the reproductive season. The results showed that the number of adult females was more than that of the males during the breeding season, and the body length of adult females was significantly longer than that of adult males. Therefore, *G. affinis* is a species with highly female-biased sexual size dimorphism. One-way analysis of variance with body length as a covariate showed significantly higher ($P < 0.0001$) head width, interorbital width, body width, and body mass for *G. affinis* females than males, while no significant sexual differences were identified based on the head length or caudal fin length. A principal component analysis resolved two components (with Eigenvalues ≥ 1) from six morphometrical variables, accounting for 65.1% of variation in the original data. The first component (45.4% variance explained) had high positive loading for size-free values of head width, interorbital width, body width, and body mass; and the second component (19.7% variance explained) had high negative loading for the size-free value of head length. Analysis of unary linear regression showed that the reproductive outputs (including brood size and mass) of *G. affinis* positively

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correlated with the female body length, body mass, head width, interorbital width, and body width. Brood size positively correlated with the average body length of offspring, but there was no correlation between the brood size and the average body mass. No trade-off was identified between the size and number of offspring. Sexual dimorphism in sex ratio, body size, and local characteristics of *G. affinis* was influenced by a variety of selection pressure parameters, including fecundity selection, sexual selection, niche differentiation, and food competition during the breeding season. Sexual dimorphism also contributed to population expansion and rapid invasion of the species. Our results have provided some basic data for further studies on the evolution mechanisms of fish sexual dimorphism.

Key Words: *Gambusia affinis*; ovoviviparity; sexual dimorphism; sex ratio; reproductive outputs

鱼类雌雄个体在大小、体色和其他局部特征的两性异形与繁殖、生长和资源的可得性等具有显著的相关性^[1-4]。例如,鱼类普遍存在个体大小的两性异形,雌性个体大于雄性个体,如似刺鲃(*Paracanthobrama guichenoti*)^[5];雄性个体大于雌性个体,如黄颡鱼(*Pseudobagrus fulvidraco*)^[6]、棒花鱼(*Abbottina rivularis*)^[7]、沙塘鳢(*Odontobutis obscurus*)^[8]、凯利贝(*Lamprologus callipterus*)^[9]、胡子鲶(*Clarias fuscus*)^[10]、*Pseudomugil signifier*^[11];雌雄个体大小相似,如花鲮(*Hemibarbus maculatus*)^[12]、温州厚唇鱼(*Acrossocheilus wenchowensis*)^[13]、鲶鱼(*Silurus asotus*)^[10]。第一种类型有利于雌体提高繁殖输出,表现出生育力选择的强烈作用,第二、第三种类型与雄体追逐配偶,提高受精和繁殖成功率有关^[12, 14-15]。在某些鱼类中,特定体长的雌性个体的体高、腹鳍基前端到吻端的水平距离、胸鳍腹鳍间距和腹鳍臀鳍间距等与增大腹腔容积、增加个体生育力相关的局部特征显著大于雄性个体^[7-8, 10]。发生口腔孵卵行为的蓝首鱼属(*Tropheus*)的雌鱼比雄鱼具有更大的口腔^[16]。已有这些形态特征的定量研究主要涉及卵生鱼类,较少涉及卵胎生鱼类,如姥鲨(*Cetorhinus maximus*)^[17]、许氏平鲉(*Sebastes schlegeli*)^[18]。

食蚊鱼(*Gambusia affinis*)是原产于北美洲大西洋沿岸低洼地和沟渠等的一种暖水性(25—30℃)营卵胎生的小型硬骨鱼类,隶属于鲶形目(Cyprinodontiformes),食蚊鱼属(*Gambusia*)^[19]。在繁殖期,性成熟雄性个体的臀鳍特化形成交配器,卵子在雌性体内受精并发育成仔鱼产出^[20-21],一尾雌鱼能同时贮存多个雄性个体的精子发生多批次产仔,产出仔鱼能够自由游动和摄食^[22-24]。1927年食蚊鱼引入我国^[25],目前普遍存在于在中国长江以南地区的水体中^[26],甚至出现在云南高原湖泊中^[27]。全球范围来看,该物种已扩散到全球温带和热带地区(除南极洲以外)^[28-29]。大量研究表明,入侵种食蚊鱼通过竞争和捕食等机制对当地土著种和生物多样性产生了严重影响^[30-34]。因此,食蚊鱼已经被纳入由世界自然保护联盟公布的全球100种最具威胁的外来入侵种名单^[35]。

本文以食蚊鱼为材料,检测繁殖期形态特征的两性异形,利用其卵胎生的特点实现雌性繁殖特征的有效收集,探讨该物种两性异形的形成原因,以及食蚊鱼的全球入侵和扩散的相关机制。

1 材料与方法

1.1 实验动物的采集与形态测定

2014年3月5日—10日,11:00—13:00,从浙江省丽水学院持久性池塘(28°27'N, 119°53'E)的水面表层用聚乙烯加工的手捞网(网目3×3 mm²)捕获食蚊鱼(*N*=92),带回两栖爬行动物实验室,混养在25℃人工气候室内的塑料箱(70×50×40 cm³)中,箱内放置一些金鱼藻(*Ceratophyllum demersum*)。

用Sartorius分析天平分别称取成鱼的体重(±0.001 g,雌鱼为产前体重),用Sony DSC-T100数码相机记录亲鱼形态,用ImageJ 1.44p软件测定亲鱼的体长(从吻端到尾椎终端的距离)、头长(由吻端到鳃盖骨后缘的水平距离)、头宽(眼眶后缘处头部的水平宽度)、眼间距(左右两侧眼背缘之间的最小距离)、体宽(背鳍起始处左右两侧身体之间的距离)以及尾鳍长(尾鳍起始处到尾鳍末端的距离)(±0.01 mm)。记录性别,臀鳍的第3、4、5鳍条延长特化形成具有固着小勾、感觉小棘和输精管沟的交配器(也称生殖足)的个体为雄鱼^[20],

躯干两侧具有黑色胎斑的个体为雌鱼^[36]。

1.2 雌性繁殖输出

怀仔雌鱼单独饲养在透明塑料碗(直径约 150 mm)内,水深 120 mm,放置一定数量金鱼藻,碗口盖 1 mm 网眼的防逃网罩,每天定量喂食鱼饲料。仔鱼一旦产出,记录产仔数,随机挑出 10 条仔鱼记录其体长、体重,同时称取雌鱼产后体重(± 0.001 g)。实验结束后,实验动物放回原先捕获水体。

1.3 数据分析

所有数据的统计分析用 Statistica 统计软件包完成。数据在作进一步统计分析前检验其正态性(Kolmogorov-Smirnov test)和方差同质性(F-max test)。经检验,部分形态学数据经 Ln 转换后符合参数统计条件。用线性回归、方差分析(One-way ANOVA)、协方差分析(One-way ANCOVA)、主成分分析等处理和比较相应的数据,比较矫正平均值前检验斜率的均一性。文中涉及的非参数统计为 G-检验。描述性统计值用平均值 $\pm$ 标准误(范围)表示,显著性水平设置为 $\alpha=0.05$ 。

2 结果

2.1 个体大小和局部形态特征的两性异形

共采集食蚊鱼 92 尾,雌性 62 尾,均有产仔行为,雄性 30 尾,均有延长具勾的臀鳍,雌性个体的数量显著大于雄性个体(G -检验, $G=11.37$, $df=1$, $P<0.001$)。记录了其中 38 尾雌性个体完整的形态和繁殖特征,该数据用于形态特征的比较和分析,食蚊鱼雌雄形态特征的描述性统计见表 1。数据经 Ln 转换后,符合参数统计的条件。One-way ANOVA 显示,雌性个体的体长显著大于雄性个体(图 1,表 1),最小的雌性个体大于最大的雄性个体;以体长为协变量的 One-way ANCOVA 及后续的 Tukey's 检验显示,特定体长食蚊鱼的雌性个体的头宽、眼间距、体宽和体重均显著大于雄性个体(all $P<0.001$,图 2,表 2);头长和尾鳍长的两性间差异不显著(表 1)。6 个形态特征变量的主成分分析(Eigenvalue ≥ 1)发现,前 2 个主成分共解释 65.1%的变异(表 3)。头宽、眼间距、体宽和体重在第一主成分有较高的正负载系数(解释 45.4%变异),头长在第二主成分有较高的负负载系数(解释 19.7%变异)。

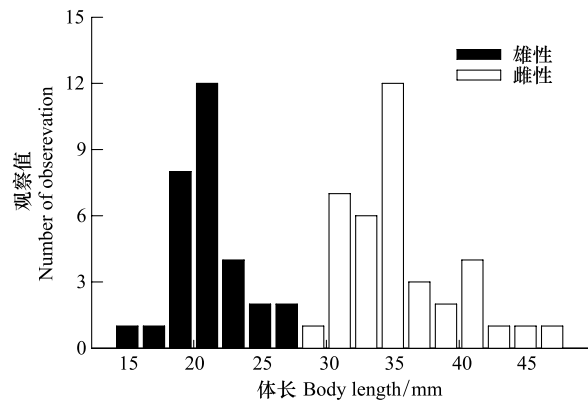


图 1 食蚊鱼雌雄个体体长的频数分布图
Fig. 1 Body length frequency distributions of female and male mosquitofish, *G. affinis*

表 1 食蚊鱼形态特征的描述性统计值

Table 1 Descriptive statistics of morphological traits of mosquitofish, *Gambusia affinis*

形态变量 Morphological variables	雌性成体 Adult females (n=38)	雄性成体 Adult males (n=30)	显著性水平及多重比较结果 Significant levels and results of multiple comparisons
体长 Body length/mm	35.66 $\pm$ 0.710 (28.33—47.62)	21.20 $\pm$ 0.469 (15.37—27.96)	$F_{1,66} = 318.94, P<0.0001, F>M$
头长 Head length /mm	7.70 $\pm$ 0.181 (5.36—10.05)	4.87 $\pm$ 0.108 (3.76—5.91)	$F_{1,65} = 0.44, P = 0.508$
头宽 Head width /mm	5.90 $\pm$ 0.128 (4.45—7.91)	2.96 $\pm$ 0.077 (2.28—3.77)	$F_{1,65} = 19.66, P<0.0001, F>M$
眼间距 Interorbital width/mm	4.95 $\pm$ 0.098 (3.90—6.37)	2.53 $\pm$ 0.061 (1.85—3.16)	$F_{1,65} = 27.51, P<0.0001, F>M$
体宽 Body width /mm	7.26 $\pm$ 0.160 (5.28—10.25)	2.74 $\pm$ 0.092 (1.86—3.80)	$F_{1,65} = 58.13, P<0.0001, F>M$
尾鳍长 Caudal fin length /mm	7.53 $\pm$ 0.189 (5.52—10.48)	4.33 $\pm$ 0.123 (3.03—6.12)	$F_{1,65} = 1.33, P = 0.253$
体重 Body mass/mg	665.80 $\pm$ 41.93 (317.50—1500.40)	109.06 $\pm$ 5.49 (24.30—170.00)	$F_{1,65} = 17.65, P<0.0001, F>M$

表中数据用平均值 $\pm$ 标准误(范围)表示,所有长度单位为 mm,重量单位为 mg;表中显示 One-way ANOVA(体长)或 ANCOVA(其余形态变量以体长为协变量)的 F 值和显著性水平(数据经 Ln 转换); F :成年雌体; M :成年雄体

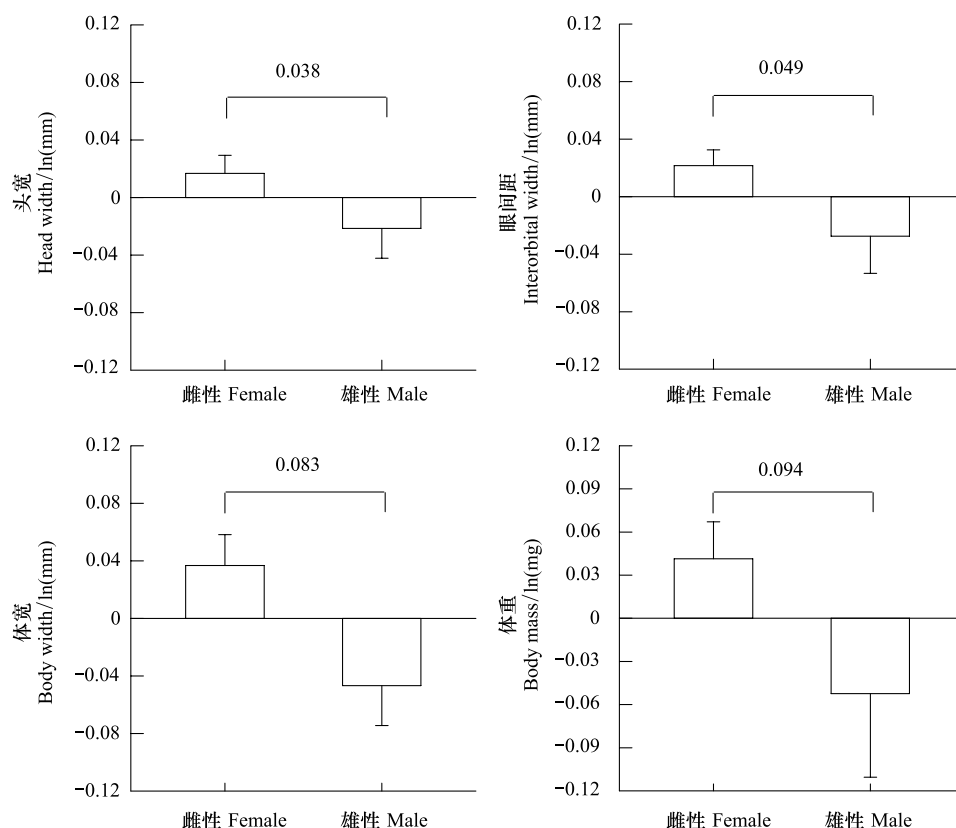


图2 以体长为自变量的食蚊鱼头宽、眼间距、体宽和体重的回归剩余值(数据经Ln转换),图中数值表示两性间回归剩余值的差值
 Fig. 2 Mean values ($\pm$ SE) for regression residuals of head width, interorbital width, body width and body mass against body length of *G. affinis*. Numbers in each plot are differences in mean regression residual between the sexes.

表2 食蚊鱼繁殖特征的描述性统计值

Table 2 Descriptive statistics, expressed as means, standard error and ranges, for female reproductive traits of *G. affinis* (n=38)

形态变量 Morphological variables	平均值 Mean	标准误 Standard error	最小值 Minimum	最大值 Maximum
体长 Body length/mm	35.66	0.710	28.33	47.62
产仔后体重 Postpartum body mass/mg	503.98	33.243	233.20	1107.20
窝仔重 Litter mass/mg	151.82	10.825	57.60	393.20
窝仔数 Litter size	21.21	1.303	10	47
仔鱼平均体长 Mean litter body length /mm	7.01	0.080	6.12	8.23
仔鱼平均体重 Mean litter body mass /mg	7.23	0.301	3.90	10.94

2.2 雌体繁殖输出

食蚊鱼的繁殖输出与母体个体大小的线性回归显示(图3),窝仔数与母体体长($F_{1,36} = 28.24$, $P < 0.0001$)、体重($F_{1,36} = 39.94$, $P < 0.0001$)呈显著的正相关;窝仔重与亲本的体长($F_{1,36} = 56.60$, $P < 0.0001$)、体重($F_{1,36} = 92.31$, $P < 0.0001$)呈显著的正相关。

食蚊鱼的繁殖输出与母体局部特征的线性回归显示(图4),窝仔数与母体头宽($F_{1,36} = 15.32$, $P < 0.0001$)、眼间距($F_{1,36} = 18.64$, $P < 0.001$)和体宽($F_{1,36} = 21.80$, $P < 0.0001$)呈显著的正相关;窝仔重与母体的头宽($F_{1,36} = 35.56$, $P < 0.0001$)、眼间距($F_{1,36} = 28.88$, $P < 0.001$)和体宽($F_{1,36} = 48.09$, $P < 0.0001$)呈显著的正相关。

窝仔数与后代个体的平均体长呈显著的正相关($r^2 = 0.11$, $F_{1,36} = 4.45$, $P < 0.042$, 图5)、与后代个体的平均体重相关不显著($r^2 = 0.01$, $F_{1,36} = 0.39$, $P = 0.536$)。

3 讨论

繁殖期食蚊鱼性别比例偏离 1:1,雌性个体显著多于雄性个体,这与已有结果一致^[20],雄性个体一旦完成授精后就从种群中消失,这可能是完成繁殖后,给雌性个体留下更多的环境资源和空间^[22],有利于雌性个体提高后代的数量和成活率,可能是造成该物种种群扩张和快速入侵的原因之一。

鱼类普遍存在的个体大小的两性异形,主要受生育力选择、性选择、生态位分化、食物竞争等多种选择压力的作用^[5, 14, 16, 37-39]。食蚊鱼的雌性个体显著大于雄性(表 1,图 1),首先与食蚊鱼的摄食和生长的性别分化有关,食蚊鱼在 6 日龄臀鳍开始分化时,雄鱼的摄食量和生长速度开始低于雌鱼,且随着日龄的增加差异加大^[40],雄性个体在性成熟后生长便接近于停滞^[25],此阶段将身体主要能量用在对雌鱼的争夺及交配行为上^[25, 41-44]。其次,食蚊鱼在生长发育、性成熟和能量分配等应对策略上的性别差异在一定程度上促进了生态位的分化、减少了种内的资源竞争,使种群内的雌鱼有更多机会获得生长发育所需的食物资源,这也为其生态

表 3 6 个成体形态特征变量的主成分分析的负载系数

Table 3 Loading of the first two axes of a principal component analysis on six adult morphological variables

形态变量 Morphological variables	负载系数 Factor loading	
	PC1	PC2
头长 Head length	-0.005	-0.967
头宽 Head width	0.756	-0.357
眼间距 Interorbital width	0.758	-0.319
体宽 Body width	0.797	0.044
尾鳍长 Caudal fin length	0.588	0.115
体重 Body mass	0.773	0.005
解释变异 Variance explained	45.4%	19.7%

用变量与体长的回归剩余值去除大小差异的影响,对每个主成分有主要贡献的变量用黑体注明

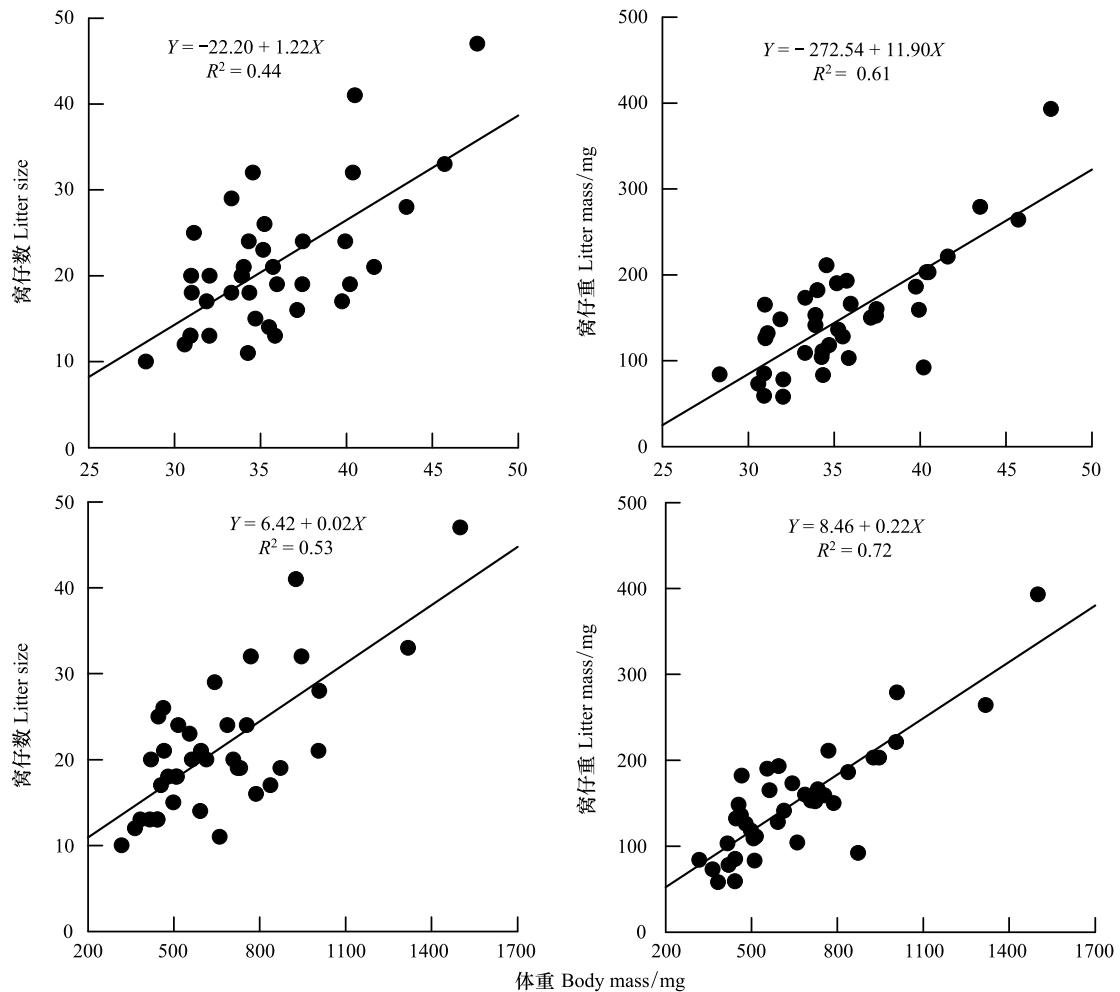


图 3 食蚊鱼的繁殖输出与母体个体大小的相关性

Fig. 3 Correlation between female body size and reproductive output of *G. affinis*

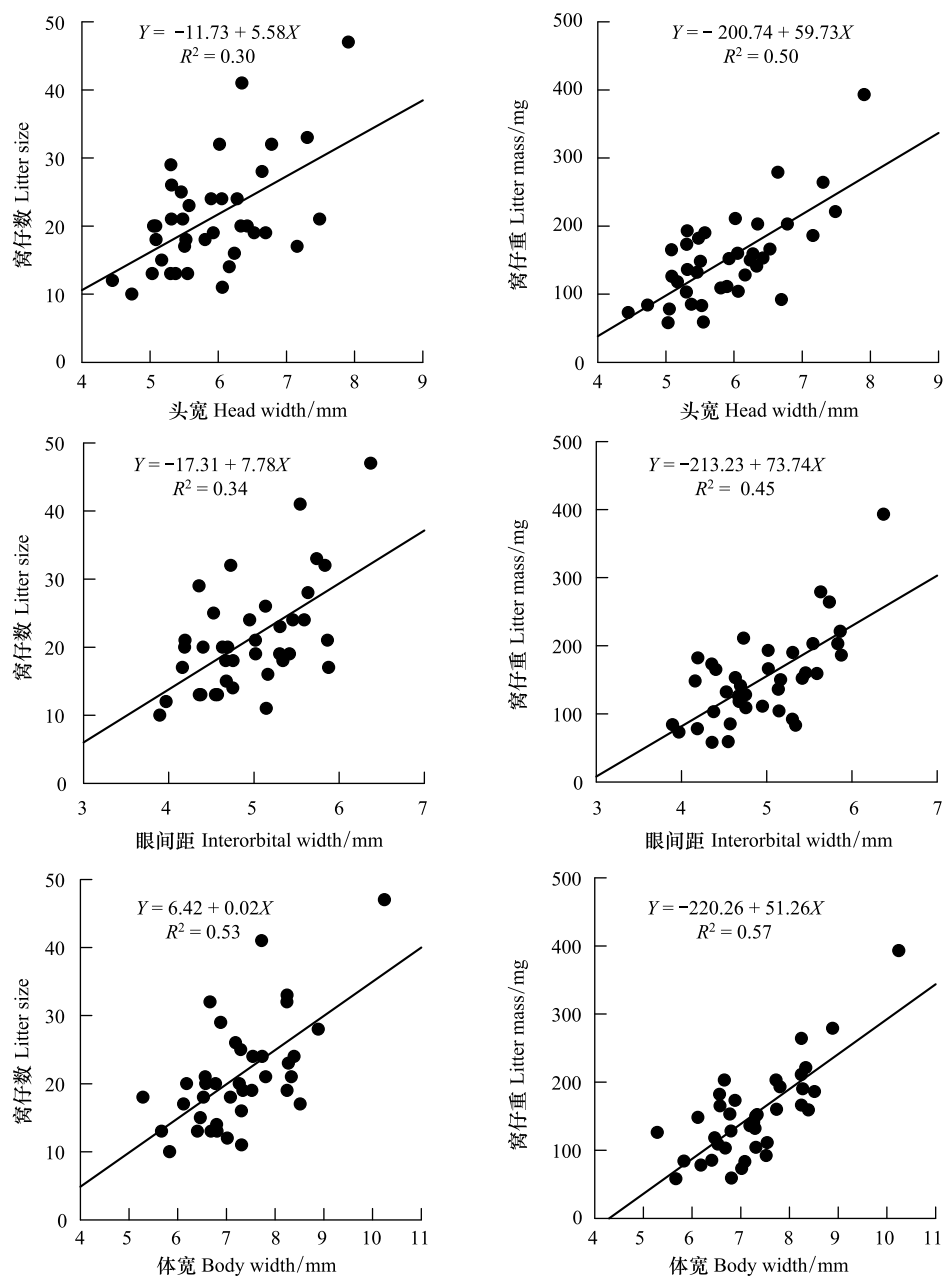


图4 食蚊鱼的繁殖输出与母体局部特征的相关性

Fig. 4 Correlation between local features and reproductive output of *G. affinis*

入侵提供了有利的条件^[1, 40, 45]。再次,食蚊鱼的繁殖输出(窝仔数与窝仔重)均与雌体大小(体长和体重)呈显著的正相关(图3),这一结果与已有研究^[20]的实验结果相吻合,也类似于卵胎生密点麻蜥(*Eremias multiocellata*)^[46]和蝮蛇(*Sphenomorphus indicus*)^[47]等动物的情况。据此可以推断:(1)食蚊鱼增大繁殖输出的主要途径是增加窝仔数及相应的窝仔重;(2)当食物可得性和雌体贮能状况不成为限制因素时,雌体大小是繁殖输出的主要决定因子。这也意味着雌性亲鱼个体越大,产下后代仔鱼也越多(或质量越好),这正如先前报道的许多其他鱼类一样^[5, 48-50]。故生育力选择是促使食蚊鱼大个体雌性形成的选择压力。

在本研究中,特定体长的食蚊鱼雌性个体的头宽与眼间距均显著大于雄性个体(表1,图2)。雌性个体拥有较宽头部和眼间距有利于雌性个体获取更多的食物资源来满足繁殖期连续多次产仔的能量需求,配偶竞争中更多的受精机会^[51]。母体内的胚胎发育过程中重量和体积的增加,使得腹腔空间成为增加繁殖输出的限制因子^[47]。食蚊鱼雌性个体的体宽显著大于雄性个体(表1,图2),因而形成较大的腹腔容量,雌性个体通

过局部特征的扩大来增加腹腔容量, 提高怀仔量, 从而增加雌性个体的繁殖输出, 这同时也反映了生育力选择对局部特征两性异形的影响^[7-8]。食蚊鱼繁殖输出(窝仔数与窝仔重)也与雌体的头宽、眼间距和体宽这 3 个局部形态特征呈显著的正相关(图 4), 进一步证实了食蚊鱼局部形态特征与雌性个体繁殖特征的相关性。

初产仔鱼个体大小通常直接影响到它的存活、生长速度、竞争能力等一系列的适合度, 故它被认为是卵胎生(或胎生)生物生活史特征的一个重要参数^[52-55]。在本研究中, 食蚊鱼的窝仔数与初产仔鱼个体大小呈显著正相关(图 5), 这表明雌体食蚊鱼生育力的提高, 并不以减少后代的个体大小为代价, 即卵胎生食蚊鱼的后代个体大小与数量之间不发生权衡, 这也是食蚊鱼种群扩张和快速入侵的一个优势。

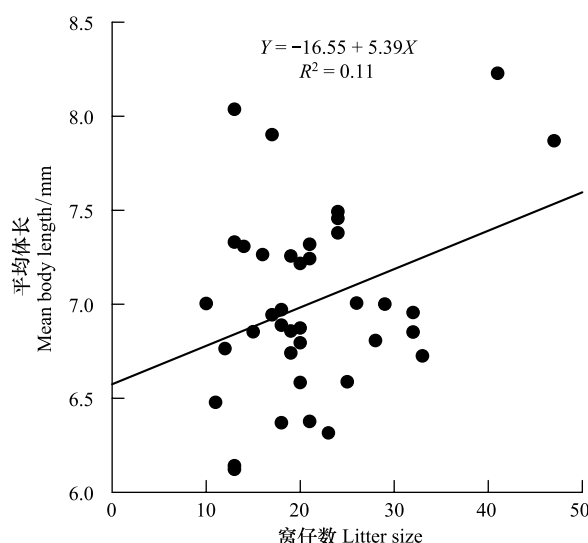


图 5 食蚊鱼窝仔数与仔鱼平均体长的相关性

Fig. 5 Correlation between litter size and mean litter body length of *G. affinis*.

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