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Length at first sexual maturity of female mantis shrimp (*Oratosquilla oratoria*) in Bohai Bay based on gonadal development

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摘 要：为准确掌握渤海湾雌性口虾蛄初次性成熟体长信息，以 2018 年 4—11 月渤海湾渔业资源科学调查期间逐月拖网渔获物为对象，通过观察雌性口虾蛄性腺的发育阶段，分别以性腺发育Ⅱ期、Ⅲ期和Ⅳ期作为性成熟的判别标准，采用 2 种逻辑斯蒂模型进行初次性成熟体长估算。结果显示，体长为 7.00~7.99 cm 的雌性口虾蛄即可达到性成熟并完成产卵行为，体长为 9.00~11.99 cm 的个体在数量上对繁殖亲体起着主要贡献作用。当逻辑斯蒂模型中性成熟比例渐近值为待估参数时，以性腺发育Ⅱ期、Ⅲ期和Ⅳ期作为性成熟标志得到的雌性口虾蛄初次性成熟体长分别为(9.42±0.02) cm、(10.44±0.04) cm 和(12.03±0.17) cm。当逻辑斯蒂模型中性成熟比例渐近值取固定值时，以性腺发育Ⅱ期、Ⅲ期和Ⅳ期作为性成熟标志得到的初次性成熟体长分别为(9.44±0.02) cm、(10.50±0.04) cm 和(11.74±0.08) cm。研究表明，采用可变性成熟比例渐近值逻辑斯蒂模型的拟合结果优于采取固定值形式的模型。建议渤海湾口虾蛄的开捕最小体长不小于9.42 cm。

关键词：口虾蛄；初次性成熟体长；性腺发育；渤海湾

中图分类号：S 932 **文献标志码：**A

性成熟是渔业资源发育过程的重要阶段，是渔业资源从幼体发育到成体并开始参与繁殖活动的重要转折[1]。初次性成熟体长(群体中处于该体长的个体已有 50%性成熟，L_{50})作为普遍使用的性成熟指标[2]，被广泛应用于渔业资源的生长模式变动分析[3]、最大体长估算[4]、最小开捕规格确定[5]等方面，是渔业资源评估和管理策略风险评价的关键参数之一[6-7]，为渔业资源的可持续利用提供了重要参考。

为获得初次性成熟体长的可靠信息，学者们构建了各种形式的估算方法[8]。KORANTENG[9]基于性腺发育特征估算了欧洲鳀(*Engraulis encrasicolus*)的初次性成熟体长，并提出该种类商业捕捞使用渔具的最小网目规格；FONTOURA 等[10]认为在生长过程中，性成熟会影响渔业资源的体长-体质量关系，从而建立了包含初次性成熟体长的多项式体长-体质量关系，并用于巴西宝莲灯鱼(*Cheirodon ibicuhiensis*)初次性成熟体长估算；MESQUITA 等[11]指出雌性普通黄道蟹(*Cancer pagurus*)的性成熟会引起身体形态变化，进而应用广义线性模型估算初次性成熟头胸甲宽；FROESE 等[12]利用世界鱼类数据库(http://www.fishbase.org)中 265 个种类的 467 组成对的初次性成熟体长和 von Bertalanffy 生长方程参数渐近体长数据建立相关关系，以用于在缺少恰当信息时的渔业资源初次性成熟体长估算。其中基于性腺发育的初次性成熟体长估算方法，因其具有较好的精度[13]，在渔业资源研究中被广泛使用。

口虾蛄(*Oratosquilla oratoria*)隶属节肢动物门(Arthropoda)甲壳纲(Crustacea)口足目(Stomadistaloda)虾蛄科(Squillidae)口虾蛄属(*Oratosquilla*)，是多年生海产经济甲壳类[14]，为西北太平洋沿海各国重要的渔业捕捞对象之一[15]。口虾蛄 1 龄即可性成熟[16]，繁殖群体以 2 龄和 3 龄个体为主[17]，繁殖期从 5 月初到 8 月

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初[18]。口虾蛄渔业是我国近海渔业的重要组成部分,其渔获量在我国近海渔获中占有重要比例[19]。有资料显示,我国近海口虾蛄资源已呈明显的小型化趋势[20],资源利用正面临逐渐增加的压力。国内学者对口虾蛄开展了广泛的研究[14,16],但尚未有基于性腺发育信息的初次性成熟体长的报道。本研究基于性腺发育估算雌性口虾蛄初次性成熟体长(L_{50}),以丰富口虾蛄繁殖生物学信息,为开展渤海湾口虾蛄资源评估、确定最小可捕体长和渔业管理提供科学依据。

1 材料与方法

1.1 数据来源

研究用口虾蛄来源于渤海湾(117°30′E~118°20′E,38°25′N~39°20′N)渔业资源科学调查获得的渔获物样品,调查以单船底层拖网的形式在 2018 年 4—11 月(除 5 月)逐月开展,累计获得口虾蛄 6 731 尾。调查船总吨位 64 t,主机功率 176 kW,拖网网口宽度 10 m,囊网网目尺寸 20 mm,拖网调查作业平均拖速 2.5 kn,拖曳时间 1 h。口虾蛄样品在低温状态下运回实验室,经性别鉴定后进行头胸甲长、体长、全长和体质量等性状测量[21];对雌性口虾蛄个体解剖,根据 KODAMA 等[22]的方法确定性腺发育分期,称量性腺质量。指标测量时,长度测量精确到 0.1 cm,质量测量精确到 0.01 g。

1.2 研究方法

1.2.1 逻辑斯蒂模型

基于雌性口虾蛄性腺发育分期,确定性成熟的性腺发育分期判别标准[23-26]。个体性腺发育分期低于标准的为性未成熟,性腺发育分期处于或者高于标准的为性成熟[27-28]。以普遍采用的长度间隔 1 cm[14,23]对口虾蛄体长进行分组,统计各体长组中雌性性成熟个体数量占相应体长组雌性个体总量的比例。应用逻辑斯蒂方程拟合各体长组的性成熟比例与对应体长组的体长中值[2,29],以估算雌性口虾蛄初次性成熟体长。逻辑斯蒂模型如下:

$$P_i = \frac{A}{1 + e^{[-r(L_i - L_{50})]}} \quad (1)$$

式中:P_i 和 L_i 分别为第 i 体长组对应的雌性口虾蛄性成熟个体的比例及该组的体长中值;A 为性成熟比例渐近值;r 为性成熟曲线系数;L_{50} 为 50% 雌性个体性成熟的体长(即初次性成熟体长)。

1.2.2 模型中性成熟比例渐近值

以往的渔业资源初次性成熟体长研究,逻辑斯蒂模型中性成熟比例渐近值多取为固定值 1[30-31],但有学者指出,因种类而异,该值并不总是为 1[2,8]。本研究为更加准确地揭示渤海湾雌性口虾蛄性成熟比例特征,对于性成熟比例渐近值(A)的取值采用 2 种方法,一种是取为固定值 1,另一种是将其作为待估参数,与性成熟曲线系数(r)和初次性成熟体长(L_{50})同样处理,在使用模型进行数据拟合的过程中一并进行估算[2,24]。

1.2.3 性成熟判别标准

普遍认为性成熟群体应包括在繁殖季节全部潜在的产卵个体[8,32]。但是,在已开展的性成熟研究中,尚未有统一的性成熟判别标准[32-33]。以往基于性腺发育阶段判别个体是否处于性成熟时,不同研究中采取的性成熟判别标准也不同[30,33]。即使研究对象是同一种生物,判别标准的差异也存在于各研究之间[23-26]。尽管这些差异与性腺发育被划分的阶段数有关[28,34],但标准的确定更多时候是因研究者的理解而异的[35-36]。大量文献[23,25,37]显示,渔业资源性未成熟和性成熟的判别常以Ⅱ期、Ⅲ期或Ⅳ期为划分标准,相对应的是性腺发育阶段为Ⅱ期及以上、Ⅲ期及以上或Ⅳ期及以上的个体为性成熟。本研究为更丰富地提供渤海湾雌性口虾蛄性成熟信息,分别采取上述 3 种性成熟判别标准进行初次性成熟体长估算。

1.2.4 数据分析

为计算逻辑斯蒂模型中参数的标准误,对雌性口虾蛄样本采取无放回取样,取样量为原始样本量的 50%,进行性成熟比例和对应体长组体长中值拟合,重复 30 次,30 次估计值的标准差作为参数的标准误[10,38]。

不同建模方法的待估计参数数量存在差异,因此使用赤池信息准则(akaike's information criterion, AIC)[39]作为逻辑斯蒂曲线拟合效果的评价标准。所有的数据分析使用 R 4.1.2 软件[40]完成。

2 结果

2.1 样本结构及体长特征

本研究累计收集雌性口虾蛄样本 3 690 尾,

约占样本总量的 54.82%。各月雌性个体样本量中 10 月最少,11 月与 10 月的样本量相当,7 月份的样本最多。雌性口虾蛄头胸甲长为 0.08～0.34 cm,体长为4.02～15.83 cm,全长为 4.21～16.58 cm,体质量为 0.86～59.72 cm。其中,雌性口虾蛄主要集中在体长中值为 6.50～11.50 cm 的体长组,其中 7 月份的优势体长为中值 5.50～8.50 cm 组,其他月份的优势体长组主要分布在中值7.50～11.50 cm 组(图 1)。

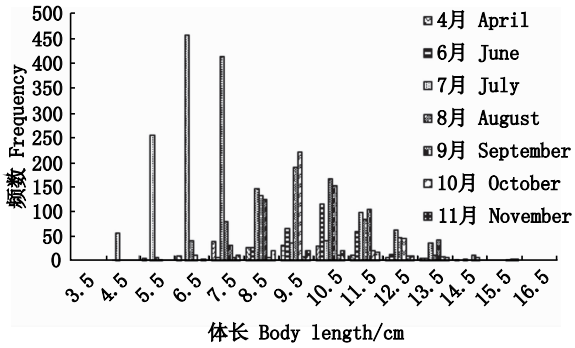

图 1　雌性口虾蛄的体长分布

Fig.1　Frequency distribution of length of female mantis shrimp

2.2　性腺发育分期的结构特征

性腺发育处于Ⅰ～Ⅵ期的雌性口虾蛄个体在样本中均有发现。性腺发育处于完全成熟、临近产卵的Ⅴ期个体数量最少,仅占 0.16%,处于Ⅰ期的个体数量最多,约为 58.26%(图 2)。统计各期的雌性口虾蛄来源,性腺发育处于Ⅰ期的样本主要来源于 7 月,贡献率达 62.94%,约占当月雌性口虾蛄个体数量的 85.01%。性腺发育处于Ⅵ期的样本主要来源于 6—8 月,贡献率为28.93%±1.72%,其中 7 月的贡献率最大,为30.53%,6 月和 8 月的Ⅵ期样本分别占各自月份雌性口虾蛄个体数量的 41.90%和 17.23%。4 月未发现性腺发育处于Ⅴ期和Ⅵ期的雌性口虾蛄。

处于不同性腺发育期的雌性口虾蛄个体组成具有明显的体长特征(表 1)。性腺发育各期口虾蛄的体长范围相比较而言,性腺发育Ⅰ期个体的体长范围最大,覆盖了除两个最大体长组的其他全部 10 个,以中值为 5.50～9.50 cm 的体长组为主,约占该发育期个体总量的 92.96%。性腺发育Ⅱ期、Ⅲ期和Ⅳ期个体体长最小值全部位于中值为 7.50 cm 体长组。Ⅱ期个体体长以 9.50～11.50 cm 为主,Ⅲ期以 10.50～12.50 cm 为主,Ⅳ期以 11.50～13.50 cm 为主,分别占各自性腺发育期个体数量的 85.94%、82.99%和 76.45%。Ⅴ期的体长范围最小,仅包含了中值为 10.50～12.50 cm的体长组。Ⅵ期个体体长范围从中值 6.50 cm到中值 14.50 cm 组,以 9.50～11.50 cm 体长中值组为主。

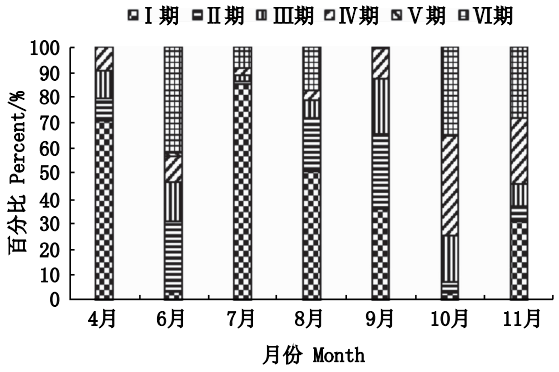

图 2　各月的性腺发育阶段状况

Fig.2　Composition of gonadal development stages for female mantis shrimp in each month

表 1　各性腺发育阶段的体长组成

Tab.1　Distribution of length at each gonadal development stage for female mantis shrimp　　%

体长组中值 Mid value of each size class	性腺发育阶段 Gonadal stage					
	Ⅰ	Ⅱ	Ⅲ	Ⅳ	Ⅴ	Ⅵ
4.50	2.56	–	–	–	–	–
5.50	12.21	–	–	–	–	–
6.50	23.96	–	–	–	–	0.23
7.50	25.97	1.00	0.60	0.39	–	3.42
8.50	18.60	7.23	1.79	0.77	–	6.83
9.50	12.21	38.96	8.06	2.32	–	16.86
10.50	3.45	34.74	31.64	11.97	33.33	32.12
11.50	0.79	12.25	37.31	27.03	50.00	25.51
12.50	0.19	4.42	14.03	25.48	16.67	10.71
13.50	0.05	1.41	5.97	23.94	–	3.87
14.50	–	–	0.60	6.18	–	0.46
15.50	–	–	–	1.93	–	–

注:“–”表示该性腺发育阶段未有对应体长组的雌性口虾蛄个体发现。

Notes: “–” indicates that sample with specific gonadal development had not been found in corresponding size class.

2.3　初次性成熟体长

基于不同性成熟判定标准及性成熟比例渐近值处理方式的逻辑斯蒂模型拟合结果见表 2。

当模型中性成熟比例渐近值为待估参数时,以性腺发育Ⅱ期、Ⅲ期和Ⅳ期作为性成熟标志,得到的雌性口虾蛄初次性成熟体长分别为(9.42±0.02) cm,(10.44±0.04) cm 和(12.03±0.17) cm。当模型中性成熟比例渐近值取 1 时,各性成熟标准下得到的初次性成熟体长分别为(9.44±0.02) cm,(10.50±0.04) cm 和(11.74±0.08) cm。性成熟判定标准选取的性腺发育分期越大,模型的拟合效果逐渐降低。对比两种性成熟比例渐近值处理方法,采用可变性成熟比例渐近值建模,得到的模型拟合效果均优于采取固定值 1 的处理方式。基于赤池信息准则,将性腺发育Ⅱ期作为性成熟判定标准,采用可变性成熟比例渐近值得到的模型拟合结果最优(AIC = −79.21),雌性口虾蛄初次性成熟体长(L_{50})为(9.42±0.02) cm。

表 2 性成熟曲线模型的参数及比较

Fig.2 Estimates of the size at first maturation (L_{50}) for female mantis shrimp using different maturation criteria and asymptote

性腺发育阶段 Gonadal stage	性成熟比例渐近值 A	性成熟曲线系数 r	初次性成熟体长 L_{50}	AIC
Ⅱ	0.99±0.00	1.75±0.06	9.42±0.02	−79.21
Ⅱ	1	1.71±0.06	9.44±0.02	−75.04
Ⅲ	0.98±0.01	1.29±0.05	10.44±0.04	−46.95
Ⅲ	1	1.21±0.04	10.50±0.04	−46.79
Ⅳ	1.07±0.04	0.67±0.03	12.03±0.17	−46.56
Ⅳ	1	0.74±0.04	11.74±0.08	−45.55

3 讨论

逻辑斯蒂模型被广泛用于渔业资源初次性成熟体长估算[41-42]。以往普遍认为随着体长的增加,性成熟比例也增加并逐渐达到最大值 100%[9,22]。因此在研究过程中,性成熟比例渐近值通常固定取值为 1[22-23,25]。但是,有学者指出,由于摄食不足、营养条件差或疾病等因素,潜在性成熟个体而不能性成熟或跳过产卵阶段的现象在许多生物中存在[43]。这些种类的生物即使在繁殖盛期,总是存在具有完全满足参与繁殖行为体长特征的个体仍有性未成熟的现象,或是基于最严谨的性腺发育标准被判定为性成熟的个体仍不发生产卵行为[8]。因此应用逻辑斯蒂模型估算渔业资源初次性成熟体长时,性成熟比例渐近值并不一定都是 1。另外,在各性腺发育期内,随着体长增加,渔业资源的数量普遍呈先增加后减小的倒扣钟特点[2,11]。当采用逻辑斯蒂模型进行性成熟比例与体长关系拟合时,即使最大体长的个体也存在不能被全部识别为 100%性成熟的可能[2]。因此,在估算初次性成熟体长时,机械地将逻辑斯蒂模型中性成熟比例渐近值取为 1,必然会造成结果的偏差[2,8]。本研究发现,在繁殖盛期存在大个体的雌性口虾蛄性腺发育处于Ⅰ期的现象;因此,认为使用逻辑斯蒂模型拟合雌性口虾蛄性成熟比例与体长关系时,模型中性成熟比例渐近值设定为待估参数是更恰当的。本研究建模的结果也证实了这点,对比 2 种性成熟比例渐近值(A)赋值方法的拟合效果,3 种性成熟判定标准下,均呈现出 A 为待估参数时的 AIC 值小于固定值 1 时的值。尽管增加待估参数的数量能够改善拟合结果[44],但是赤池信息准则作为评价模型拟合效果的标准,权衡了模型的复杂度和模型拟合数据的优良性[39]。本研究中,当以性腺发育Ⅳ期为性成熟判别标准,使用可变性成熟比例渐近值逻辑斯蒂模型拟合性成熟比例和体长关系时,性成熟比例渐近值估计值为 1.07±0.04,拟合结果出现了过拟合的现象。因此,为避免因性腺发育分期鉴定和性成熟判别偏差[45-46],以及过拟合现象的发生[37],在可变性成熟比例渐近值逻辑斯蒂模型参数估算过程中,应引入性成熟比例渐进值不大于 1 的限制[2,8],以确保参数的估计值具有生物学意义。

性腺发育程度是渔业资源繁殖行为发生的基础[33,47],与体长关系密切[9],因此体长结构特征可以间接地反映渔业资源的性成熟及繁殖行为的相关信息[26,28]。本研究显示,性腺发育处于Ⅱ期、Ⅲ期和Ⅳ期的雌性口虾蛄个体最小体长均处于 7.00~7.99 cm 组,同时,该体长组内也存在性腺发育Ⅵ期的个体;说明无论是以性腺发育Ⅱ期,还是以Ⅲ期或Ⅳ期作为雌性口虾蛄性未成熟和性成熟的界定标准,渤海湾雌性口虾蛄最小性成熟体长[28]均介于 7.00~7.99 cm 并可完成产卵行为,这与黄渤海海域其他相关研究的结果一致[16,48]。雌性口虾蛄繁殖行为发生前,性腺发育Ⅱ期个体体长以 9.00~11.99 cm 为主,Ⅲ期以 10.00~12.99 cm 为主,Ⅳ期以 11.00~13.99 cm 为主,各期的优势体长均呈现随性腺发育逐渐增加

的趋势,说明在同一繁殖季节,繁殖群体中大个体雌性口虾蛄的性腺发育较小个体早[22]。性腺发育Ⅵ期的个体中,体长中值为 10.50 cm、11.50 cm 和 12.50 cm 组的个体量占各对应体长组样本总量的 26.92%±1.87%,其他体长组的个体量比例值最大仅为 13.14%(出现在体长中值 9.50 cm 组)。说明体长 10.00~12.99 cm 的个体较其他体长组参与产卵活动的时间早[23],在繁殖季节早期更适于被选作为人工繁育的亲体。而就性腺发育Ⅵ期的雌性口虾蛄,体长以 9.00~11.99 cm 为主,占该发育期个体总量的 74.49%,说明在自然环境条件下,该体长范围的雌性口虾蛄对繁殖亲体起着主要贡献作用,这与 HAMANO 等[15]的研究结果一致。通过描述性腺发育特征确定性成熟被认为是估算初次性成熟体长的最有效且普遍适用的方法[33,37],但在实际工作中,采用的性腺发育分期标准存在较大差异[49-52]。就雌性口虾蛄而言,存在 5 期[25,34]和 6 期[22]两种性腺发育阶段划分方法,因此选择恰当的性腺发育阶段作为性成熟判别标准就成为影响初次性成熟体长研究结果的关键因素之一。对比已知的两种性腺发育阶段划分方法,尽管分期数量不同,但对Ⅰ期的性腺发育特征描述基本一致[22,25]。因此将Ⅰ期作为性未成熟,Ⅱ期及以上作为性成熟的判别标准估算雌性口虾蛄初次性成熟体长同时适用于两种不同的性腺发育阶段划分方法。

性成熟过程作为渔业资源从幼体发育到成体的重要阶段[38],即包含了生长模式和繁殖器官等的外部形态学特征变化[10,30],也涉及性腺质量和颜色等的内部生理学特征变化[22-23],这些可观察并可量化的改变为确定性成熟类型提供了依据[24,38]。根据开展研究所依赖的生物学特征[45,53],性成熟分别被定义为生理学性成熟和形态学性成熟[1]。内部生理学特征变化标志着渔业资源繁殖行为的开始,外部形态学特征变化则是渔业资源能够完成繁殖活动的基本保障[47]。从繁殖活动的开始到完成,尽管渔业资源的生长通常会减缓,但并未完全停止[26],因此基于两类生物学特征得到的初次性成熟体长在多数情况下是不同的[1]。本研究得到的初次性成熟体长(9.42 cm±0.02 cm)小于基于生长模式变化得到的初次性成熟体长(11.01 cm)[38],符合生理学初次性成熟体长小于形态学初次性成熟体长的基本规律[54]。渔业资源利用过程中,大量的小规格或性未成熟个体被捕捞的现象在许多渔业中普遍存在[55-56],一直是渔业管理重点解决的问题之一,对渔业资源的结构稳定和可持续利用带来严重危害[57-58]。为保障有足够的亲体参与繁殖活动而使资源得以可持续利用,初次性成熟体长被认为是渔业开发过程中可被容许的最小捕捞体长[55,57,59]。根据本研究结果,建议渤海湾口虾蛄的开捕最小体长不小于 9.42 cm。

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Length at first sexual maturity of female mantis shrimp (*Oratosquilla oratoria*) in Bohai Bay based on gonadal development

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Abstract: The mantis shrimp (*Oratosquilla oratoria*) is a benthic, megafaunal burrower and a predatory species. As an important commercial fishery species, its abundance is significantly correlated to sediment type. To understand the size at first maturity of female mantis shrimp widely distributed in Bohai Bay, the biological data, such as carapace length, kubo's standard length, total length, weight, gonadal development and ovarian weight, of female individuals were collected monthly from April to November except May in 2018 from research surveys on the board of fishing vessels. The determination of the immature and mature stages was performed based on the gonadal development, and then the size at first maturity was estimated using a logistic model with specific asymptote or variable asymptote. The results showed that: Female mantis shrimp could develop to maturity and complete reproduction at a standard length of 7.00−7.99 cm; Female individuals with 9.00−11.99 cm standard length made a great contribution to reproduction in quantities; There was a bias for estimates of the size at first sexual maturity between different sexual maturities judged by gonadal development, as well as models with different asymptotes; Estimates of size at first sexual maturity based on a logistic curve with variable asymptote were (9.42 ± 0.02) cm, (10.44 ± 0.04) cm and (12.03 ± 0.17) cm respectively by using gonad stage of Ⅱ, Ⅲ and Ⅳ as criteria of mature for female mantis shrimp in Bohai Bay. And while the asymptote was assigned to 1 in the logistic model, the estimates of the size at first sexual maturity were (9.44 ± 0.02) cm, (10.50 ± 0.04) cm and (11.74 ± 0.08) cm, respectively. This study enhanced our understanding of the relationships between the proportion of maturity and standard length of female mantis shrimp. While female mantis shrimp with gonadal development stages Ⅰ were treated as immature and individuals with gonadal development stages Ⅱ and above as mature, the size at first sexual maturity could be robustly estimated by using a logistic curve with variable asymptote through describing the relationship between the proportion of maturity and standard length. Based on these findings, it was suggested that the regional fishery should operate with a minimum legal size of 9.42 cm for mantis shrimp.

Key words: *Oratosquilla oratoria*; size at first sexual maturity; gonadal development; Bohai Bay