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北部湾水母类生态学研究及中国近海和平水母科
分子系统分析

Ecological Study on Medusae in Beibu Gulf
and Molecular Phylogenetic Analysis of
Eirenidae in Coastal Waters of China

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摘要

水母类是海洋浮游动物的重要类群之一，是海洋食物链的重要环节，在近岸海域或半封闭型海湾，水母往往是影响浮游动物种群数量和鱼类补充的重要因子，很容易成为干扰生态系统的主要类群，进而破坏海洋生态平衡，影响鱼类资源的可持续利用。北部湾是南海北部一个典型的半封闭型海湾，也是我国重要渔场之一。开展北部湾水母类的生态学研究，能够了解水母类在北部湾生态系统所扮演的角色及其对健康的或急剧变化的北部湾生态系统的影响，进而促进对整个北部湾生态系统动力学过程的全面认识。本研究利用2006—2007年北部湾海域调查资料，利用多种统计学分析和生态分析手段，首次对北部湾水母类的栖息环境、种类组成、数量时空分布、群落结构、多样性分布特征及其相应动力学等方面进行研究，充分提取了北部湾水母类资料所包含的信息，形成了对北部湾水母类生态学较为完整的认识体系。此外，本研究以中国近海分布的和平水母科主要属种为研究对象，首次将DNA序列分析的方法应用到和平水母科的系统发育研究中，探讨了和平水母科部分属间、和平水母属部分种间的DNA分子差异；同时，应用分子系统学技术和分析手段，基于核糖体18S rDNA和线粒体16S rDNA基因序列数据建立和平水母科分子水平系统演化关系，并基于线粒体16S rDNA、COI和核内ITS1基因序列数据建立和平水母属分子系统演化关系；其次，在重建的系统发育关系树的基础上，诠释现存的属、种分类问题，为和平水母科、和平水母属的客观分类和系统进化在分子水平提供证据，为今后整个和平水母科的系统演化与分类格局关系的研究提供了研究基础。

主要研究结果如下：

1. 综合环境因子各变量，通过聚类、非参数多变量排序（MDS）分析，将北部湾水母类的生境分成两种类型：一是近岸型，主要受受广西、越南沿岸江河径流以及由琼洲海峡入湾的南海北部沿岸流的影响；另一种是远岸型，主要受南海暖流的影响。
2. 四个航次共鉴定北部湾水母类219种，其中，水螅水母148种，管水母58种，钵水母6种，栉水母7种，包括6个水螅水母新种和3个北部湾水螅水母新纪录。水母类

种数存在明显的季节变化，夏季最高（159种），冬季次之（110种），春季（100种），秋季最少（91种），其中水螅水母种数季节变化最明显，夏季出现100种，而其他季节只有60~70种，管水母、钵水母也以夏季居多，只有栉水母类种类数各季变动不大。四季水母种类数均呈现南部高于北部，远岸高于近岸的分布特点。调查海区水母类的优势种主要是管水母类的拟细浅室水母 (*Lensia subtiloides*) 和双生水母 (*Diphyes chamissonis*)，栉水母类的球型侧腕水母 (*Pleurobrachia globosa*)，水螅水母类的半口壮丽水母 (*Aglaura hemistoma*) 和四叶小舌水母 (*Liriope tetraphylla*)。

3. 探讨了北部湾水母类种群数量变化特征和相应的动力学。北部湾四个季节水母类丰度均呈现北高南低，沿岸向远岸逐渐增高的平面分布特征。水母类丰度季节变化明显，其中以夏季最高 ($22.02 \pm 18.17 \text{ ind./m}^3$)，秋季次之 ($19.35 \pm 19.54 \text{ ind./m}^3$)，春季 ($14.55 \pm 14.06 \text{ ind./m}^3$)，冬季最低 ($11.47 \pm 13.12 \text{ ind./m}^3$)。北部湾各季水母类丰度主要来自优势种的贡献：春季，以拟细浅室水母和双生水母的贡献较大；夏季主要来自拟细浅室水母的贡献；秋季，以四叶小舌水母和异摇篮水母 (*Cunina peregrina*) 的贡献较大；冬季，以双生水母和半口壮丽水母的贡献较大。除了与优势种的生态适应特征相关外，盐度是影响水母类丰度变化的主要环境动力学因子，这主要与影响北部湾的两大流系——沿岸流和南海暖流的相互推移和消长相关。此外，北部湾饵料浮游动物及桡足类四季丰度分布呈现北部高，南部低的变化趋势，这与水母类丰度的分布特点相一致，说明丰富的饵料浮游动物也是水母类聚集并形成较高数量的原因之一。

4. 北部湾四季鱼卵、仔稚鱼高丰度和水母类的高丰度在空间分布上有良好的负相关关系。数量丰富的水母类和渔业资源衰退是北部湾生态环境的主要特点，暗示着北部湾生态体制可能朝着有利于水母类的方向变化。

5. 综合聚类、MDS标序和除趋势对应分析 (detrended correspondence analysis, DCA) 结果，可以将北部湾水母类划分为内湾群落和外湾群落，两个群落结构稳定，内湾群落主要由近岸暖水性种类构成，外湾群落主要由大洋暖水或大洋热带广布种构成。根据水母类的生态习性及其除趋势典范对应分析 (detrended canonical correspondence analysis, DCCA) 分析结果，北部湾水母类可分沿岸暖温性、近

岸暖水性、大洋暖水性和大洋热带性四个生态类群，其中以近岸暖水性类群为优势类群，其次是大洋暖水性类群。

6. 从环境因素与优势种的聚集强度等不同侧面探讨了北部湾水母类多样性指数 (H') 的分布特征及其成因。水母类多样性指数冬夏季高于春秋两季，夏季最高，春季最低；就不同海区比较，湾南部高于湾北部，远岸高于近岸；外湾群落多样性指数四季均高于内湾群落。分析原因如下：（1）多样性指数与物种数密切相关，但与丰度相关性不显著。优势种的高度聚集导致局部海域水母类多样性降低。春季拟细浅室水母、秋季四叶小舌水母、冬季双生水母在湾北部聚集，导致四季北部湾北部海域多样性均低于南部。（2）水温和盐度是影响多样性指数分布的主要环境因子，春季与表层水温正相关，秋冬季都与中层水温正相关；此外，夏、秋季还分别与底层盐度和中层盐度正相关。（3）北部湾四季水母类多样性指数等值线密集区反映了北部湾内海流和水团的走向和位置，是分析北部湾水团的良好标记。

7. 基于核内18S rDNA和线粒体16S rDNA两种基因序列探讨我国近海和平水母科的系统发育关系，使用MEGA软件构建了N-J和MP系统树，在忽略了小于50%的支持率后，重建的系统树所显示的拓扑结构具一致性，通过比较、分析，得到下列主要研究成果：

（1）和平水母属是本次研究的和平水母科四个属中最早分歧出来的一个分支，属较原始类群，且可能是侧丝水母属、真瘤水母属和Eugymnanthea属的共同祖先；但和平水母属是单系群还是并系群，还须作进一步的研究。

（2）真瘤水母属为一并系群，Eugymnanthea属则为单系群，但二者亲缘关系非常相近，而且，我们的研究结果显示与双壳类共生的真瘤水母属种类Euima sapinha与Eugymnanthea属聚为一个单系群，支持了Kubota（2000）基于形态学研究提出的将二者合并为一个属的观点，从分子学角度找到了较为合理的解释证据；至于真瘤水母属能否与Eugymnanthea属合并成一个属，还须作进一步研究。

（3）侧丝水母为一单系群，可能是和平水母属向真瘤水母属演变的过渡类群。

8. 基于核内ITS1和线粒体COI两种基因序列探讨我国近海和平水母属的系统发育关系，使用MEGA软件构建了N-J和MP系统树，在忽略了小于50%的支持率后，重建

的系统树所显示的拓扑结构具一致性，均以较高置信度支持将和平水母属分成两个单系群：塔状和平水母 (*Eirene Pyramidalis*)、蟹形和平水母 (*E. kambara*)、六辐和平水母 (*E. hexanemalis*) 和 *E. lacteoides* 共同构成宽胃柄类群，而锡兰和平水母 (*E. ceylonensis*)、细颈和平水母 (*E. menoni*) 和短柄和平水母 (*E. brevistylis*) 则构成窄胃柄类群；两类群间基于ITS1和mtCOI两种基因序列的平均遗传距离分别达到0.543和0.160，分子性状的界限分明。

关键词：水母类；生态学研究；和平水母科；分子系统发育

厦门大学博硕士学位论文摘要库

Abstract

Medusae[1] is one of the important groups in marine zooplankton and it is vital in the food chain of marine ecosystem. Medusae has a great influence on zooplankton population dynamics and fish recruitment in marine ecosystems, especially in marginal seas. In recent years, there has been a dramatic increase in Medusae biomass over the coastal areas around the world, and it can damage oceanic ecological balance and affect the sustainable utilization of fishery resource. Beibu Gulf is a semi-closed area in South China Sea, abundant in fishery resources, is one of the main fishery areas in China. Environmental protection and ecological preservation in this area is concerned by both government and scientists. In order to study the changing tendency of the ecological environment in Beibu Gulf, four cruises of survey were carried out, from July, 2006 to October, 2007. Based on the data from aforesaid four cruises, using several statistical methods and ecology analysis tools, the habitat, species composition, temporal and spatial variation of abundance and diversity, community characteristics of Medusae and their dynamics were firstly discussed this study, and aimed to show the important role of Medusae in Beibu Gulf ecosystem.

Another part of this study was to evaluate the molecular phylogenetic relationship of Eirenidae (Eirenidae, Leptomedusae, Hydrozoa, Cnidaria). Eirenidae is a highly diversified monophyletic group of Hydromedusae. In China sea, this group includes 6 genus 29 species, displaying diversified morphological form of hydroid status and pelagic medusa. The adult medusa have rather well differentiated gastric peduncle, 4- 6 simple radial canals. Polyps are always colonial, colonies either stolonial, erect, ramified, or comprising a single polyp budding totally into a single medusa (*Eirene hexanemalis*), and these colonies exhibit a great diversity

of organizations: Campanopsis type or Campanulina type. This variability makes their evolutionary history particularly interesting, but at the same time difficult to reconstruct. In this study, to evaluate the phylogenetic relationship of the 12 species belong to 4 genus from China Seas, which presented morphological specializations traditionally used in Eirenidae classification. A molecular phylogenetic approach was employed using two nuclear (18S rDNA and ITS1) and two mitochondrial (16S rDNA and cytochrome oxidase subunit I) genes. Phylogenetic analyses were performed under the maximum parsimony (MP) Neighbor Joining (N-J) criterion using MEGA 3.0. Goal of the present studies try to provide molecular evidence to the study of objective classification and phylogeny of Eirenidae.

The brief results of the present study are described as following:

1. Two type of habitat of medusa in Beibu Gulf was shown: alongshore type which was influenced mainly by the coastal current; offshore type which was influenced by the warm current from south China sea.
2. Based on data from four seasonal oceanographic cruises in Beibu Gulf in 2006-2007, a total of 219 medusa species were identified, in which, 148 are Hydrozoans, 58 are Siphonophores, 6 are Scyphozoans, and 7 are Ctenophore, including six new species and three new records in the Beibu Gulf. Species number exhibited obvious seasonal change: high in the summer, followed by winter and spring, low in autumn. Higher species number occurred, respectively, in the southern part of the gulf and offshore. Dominant species of Medusae include *Lensia subtiloides* and *Diphyes chamissonis* (Siphonophorae), *Pleurobrachia globosa* (Ctenophore), *Aglaura hemistoma* and *Liriope tetraphylla* (Hydromedusae).
3. Distribution and the seasonal variation of Medusae abundance and their dynamics are discussed. Medusae abundance peaked in summer (22.02 ± 18.17 ind./m³), and it was the second highest in autumn (19.35 ± 19.54 ind./m³), then in

spring (14.55 ± 14.06 ind./m³) and the lowest in winter (11.47 ± 13.12 ind./m³) with the horizontal distribution of abundance in the northern part of the gulf and alongshore being larger than in the southern part and offshore. Medusae abundance was due to the contribution of the dominant species: *L. subtiloides* and *D. chamissonis* for abundance in spring, *L. subtiloides* in summer, *Lir. tetraphylla* and *Cunina peregrine* in autumn, *D. chamissonis* and *A. hemistoma* in winter. Salinity is the main dynamical factor affecting the medusa abundance, and this was resulted from the status of interaction between coastal current and offshore water. Moreover, the abundance of prey zooplankton had the same horizontal distribution trend of abundance with Medusae's, indicating the food is also one of the important factors influencing the distribution of abundance of Medusae.

4. The high abundance of fish larvae and juveniles was mostly found at the edges of the concentrated region of medusa, it showed that there was a negative correlation between fish larvae and juveniles and medusa in distribution pattern. There were abundant medusa and a declining trend of fishery resources in Beibu Gulf ecosystem, suggesting that the regime shift of ecosystem may be beneficial to Medusae.

5. Based on the CLUSTER, MDS and DCA analysis, medusa in Beibu Gulf was divided into two community of stable structure: inner bay community and outer bay community. The former was mainly composed of coastal tropical species, the latter was mainly composed of warm-water species. According to the adaptability of Medusae to different temperature and salinity and DCCA analysis, the Medusae species in Beibu Gulf were classified into four ecological groups: neritic warm-temperate, neritic warm-water, oceanic eurythermal warm-water and oceanic tropical species.

6. The dynamics of medusa diversity and the cause were analyzed. Higher species diversity indices (H') of Medusae occurred, respectively, in the southern

part of the gulf, offshore, outer bay community, and in summer and winter. The number of species was closely correlated with H' value, whereas the abundance was not correlated with it significantly. The lower H' value in the northern part of the gulf resulted from the aggregation of *L. subtiloides* in spring and summer, *Lir. tetraphylla* in autumn, *D. chamissonis* in winter, respectively. Water temperature and salinity were main environmental factor influencing the distribution of species diversity. H' value was related to the surface water temperature in spring, while it is associated with middle layer temperature in autumn and winter. Moreover, it is associated with bottom salinity and middle layer salinity in summer and autumn respectively. The isoline distribution of H' value reflected the direction of currents and changes in water masses in the Beibu Gulf, and the H' value isoline was a good indicator for analyzing the water masses in the Beibu Gulf.

7. Based on the fragment of small subunit rDNA (18S rDNA) and mitochondrial 16S rDNA gene data, the 50% consensus tree of neighbor-joining (N-J) and maximum parsimony (MP) were constructed, showed a consistent topological structure. Conclusions were drawn as follow:

(1) All the phylogenic trees suggested that genus *Eirene* is the most primitive group among *Eirenidae* in this study, and it may be the common ancestors of genus *Helgicirra*, *Eutima* and *Eugymnanthea*; There were two parallel evolutionary sister clades existing (with high bootstrap value support) in genus *Eirene*, and a further study was called for to evaluate the monophyly or paraphyly of *Eirene*.

(2) Genus *Eutima* was a paraphyletic group, and genus *Eugymnanthea* was a monophyletic group, and they showed close relationship. *Eutima sapinhua* should be included in genus *Eugymnanthea* because it emerged as a cluster within the clade of *Eugymnanthea* and had a close relationship with *Eugymnanthea inquilina* and *Eug. japonica*. Our result suggested that taxonomic treatment of assigning all the bivalve-inhabiting *Eutima* and *Eugymnanthea* into the one genus is

reasonable, and further research should be carried out to evaluate the relationship between Eutima and Eugymnanthea.

(3) The monophyly of Genus Helgicirrho was also strongly supported, and the evolutionary status of Helgicirrho is between Eirene and Eutima.

8. The phylogenetic trees obtained by MP and N-J methods based on ITS1 and mtCOI got a consistent topological structure indicating that all species of Eirene were clustered together and divided into two strongly supported major clades.

One group with “peduncle wide”: E. Pyramidalis, E. hexanemalis, E. lacteoides and E. kambara indicated a closer relationship. A second clade, E. ceylonensis and E. menoni show closer relationship, forming a monophyletic group, then E. brevistylis is a sister lineage to them as basal clade in another group with “Peduncle slender”. This preliminary research shows that the traditional view may be challenged by molecular data. Our molecular trees are sufficiently resolved to set up a framework for a phylogenetic classification of the Eirene.

[1] (Hydrozoans) (Siphonophores) (Scyphozoans)(Ctenophores)“Medusae”

Keywords: Medusae; ecological study; Eirenidae; molecular phylogeny

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