View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by Xiamen University Institutional Repository

第 24 卷第 3 期
2004 年 3 月

生 态 学 报
ACTA ECOLOGICA SINICA

Vol. 24, No. 3
Mar., 2004

桡足类滞育规律研究

姜晓东, 王桂忠, 李少菁, 孔祥会, 管卫兵
(厦门大学海洋系、亚热带海洋研究所, 厦门 361005)

摘要: 首次提出用滞育指数对桡足类滞育能力进行相对量化处理, 并对 102 种桡足类的滞育能力同迁移能力、体长、栖息地之间的关系进行了数学分析, 初步得出了滞育在桡足类中的分布规律: 在桡足类中滞育与迁移呈负相关, 两者之间存在一定程度的置换; 个体较小的桡足类一般具有较强的滞育能力和较弱的迁移能力, 个体较大的桡足类一般具有较弱的滞育能力和较强的迁移能力; 淡水桡足类一般比海洋桡足类具有较强的滞育能力。最后探讨了这种分布模式的成因。

关键词: 滞育; 桡足类

Preliminary studies on the rule of copepod diapause

JIANG Xiao-Dong, WANG Gui-Zhong, LI Shao-Jing, KONG Xiang-Hui, GUAN GWei-Bing (*Department of Oceanography, Institute of Subtropical Oceanography, Xiamen University, Xiamen* 361005). Acta Ecologica Sinica, **2004**, **24**(3): **517～523**.

Abstract: Many copepods have integrated a state of diapause in their life history to avoid the critical conditions. It has been showed that the diapause trait is by no means evenly distributed within copepods, such as different diapausing forms (Diapause occurs in eggs, copepidites or adults) and different diapausing locations (in water column or in sediment). In this paper we attempt to investigate the distribution of diapause among copepods based on the published data of 102 species from 3 orders of pelagic copepods. The index of diapause and the index of migration are adopted in order to mathematically analyze. The index of diapause is described as follow: (1) lowest diapause, species diapausing with the form of copepidites or adults in the water column; (2) moderate diapause, species diapausing with the form of copepidites or adults in the sediment; (3) highest diapause, species diapausing with the form of eggs in the sediment. The index of migration is ranked as follow: (1) lowest migration, pond and lake dwelling species; (2) moderate migration, species living in the coastal areas; (3) highest migration, species living in the open sea.

The relationship between the index of diapause and the index of migration is highly negatively significant (R^2= 0.3932, $P \ll 0.00001$, n= 102). It suggests that there is a highly negative relationship and a trade-off between the diapause ability and the migratory ability among copepods. The relationship between the index of migration and the body length is highly positively significant (R^2= 0.3220, $P \ll 0.00001$, n= 102). And the index of diapause negatively covaries with the body length (R^2= 0.1871, $P < 0.00001$, n= 102). The results show that strong diapause and weak migration are more common among small copepods, whereas large species have weak diapause and strong migration. The index of diapause of freshwater copepods is higher 25.3% than that of marine copepods. It suggests that species with prolonged diapause tend to be found in inland water.

Two possible explanations for those uneven distribution of diapause are discussed. The one is microevoluntionary. The patterns reflect selection pressure exerted on copepods by the environment in which they live: diapause is favored in some habitats and not in others. Another explanation is macroevoluntionary. The patterns are the result of phylogenetic history: if the ancestors of some taxa did not evolve diapause, their descendants may also lack the trait whatever the selection pressure may have been.

Key words: diapause; copepod

基金项目: 国家自然科学基金资助项目(40076034)
收稿日期: 2003-02-19; **修订日期**: 2003-06-18
作者简介: 姜晓东(1978～), 男, 江苏人, 硕士生, 主要从事浮游动物生态学研究。E-mail: planktoncn@yahoo.com.cn
Foundation item: National Natural Science Foundation of China (No. 40076034)
Received date: 2003-02-19; **Accepted date**: 2003-06-18
Biography: JIANG Xiao-Dong, Master candidate, main research field: plankton ecology. E-mail: planktoncn@yahoo.com.cn

© 1994-2006 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

文章编号: 1000-0933(2004)03-0517-07 中图分类号: Q958 文献标识码: A

在水生生态系统中, 生命的成功与否受制于系统中捕食者的数目, 食物的可获得性, 同年龄组的数量, 以及水量(是否干枯或结冰)等诸多生物因子和非生物因子。为了避开这些严峻条件, 许多水生无脊椎动物在生活史中出现滞育阶段。作为水生生态系统重要组成部分的桡足类同样具有这种典型特征。有关桡足类滞育现象的研究已受到越来越多学者的重视[1~4]。众多研究表明, 桡足类的滞育特征呈现多样化, 如滞育形式有卵滞育、幼体滞育、成体滞育, 有些种类还形成胞囊; 滞育的场所有的为近海和湖泊的底层沉积物, 有的为大洋深水层。在如此纷繁复杂的现象背后是否存在一定规律是众多桡足类研究者共同关心的问题。本文利用已报道的 102 种桡足类的滞育研究资料对该问题进行了一定的研究探讨。

1 材料与方法

1.1 滞育能力(Diapause ability) 对术语"滞育"本文采用 Danks 的定义[5]: 指发育过程的明显中断, 受神经激素控制, 在自然界早于不利环境出现。由于对桡足类在不同季节或生活史中的神经激素状况知之甚少, 所以尚无法通过神经激素分泌状况来直接定量分析桡足类的滞育能力。但注意到下面 3 个事实: 其一, 在沉积物中滞育卵有较长的存活能力, 如 Marcus 等[6]报道河口海区两种桡足类滞育卵的平均存活年龄分别为 5a 和 14a, Hairston 等[7]利用放射性同位素技术研究发现淡水桡足类 Diaptomus sanguinens 滞育卵存活能力更强, 平均为 70a, 最高可达 330a; 其二, 在大洋深水层中以个体(桡足幼体或成体)形式进入滞育状态过冬或度夏的桡足类, 当冬天或夏天结束时即全部结束滞育状态, 故滞育时间一般为数个月。典型例子为飞马哲水蚤(*Calanus finmarchicus*)在挪威海深层水中以桡足幼体第 4 期或第 5 期形式滞育越冬, 春夏季节种群全部停止滞育继续生长发育[8]。其三, 在沉积物中以个体(桡足幼体或成体)形式滞育的桡足类由于有沉积物的覆盖, 抵抗外界不良环境能力显著增强, 最直接的证据就是在干枯的沉积物中也有活的处于滞育状态的桡足类存在[9]。根据上述事实将桡足类划分为 3 类: 第 1 类, 在大洋深水层中以个体形式滞育的种类; 第 2 类, 在沉积物中以个体形式滞育的种类; 第 3 类, 在沉积物中以滞育卵形式滞育的种类。这 3 类桡足类滞育能力依次增强, 提出采用滞育指数(the index of diapause)1、2、3 分别记之。滞育指数越高代表该种滞育能力越强。形成胞囊在沉积物中滞育的种类, 由于又受胞囊的保护, 所以滞育指数记为 2.5。通过上述办法对桡足类滞育能力进行相对量化处理, 便于下面数学分析。

1.2 迁移能力(Migratory ability) 有关桡足类的迁移能力的研究鲜有报道, 因此不可能直接量化处理。将 Hairston 等[10]提出的划分甲壳动物迁移能力的方法作修改后, 将桡足类划分为 3 类: 第 1 类, 生活于池塘湖泊的淡水种类; 第 2 类, 生活于沿岸近海的种类; 第 3 类, 生活于大洋的种类; 这 3 类桡足类迁移能力依次增强, 采用迁移指数(the index of migration)1、2、3 依次记之。对于生活于水深超过 20m 的湖泊中的种类, 其迁移能力有所提高, 记为 1.5。

1.3 体长: 将文献中雌雄个体体长取平均记之。

2 结果

102 种桡足类的体长、迁移指数、滞育指数、栖息地数据如表 1 所示。

102 种桡足类的滞育指数与迁移指数关系如图 1 所示, 图中各圆大小代表在该点处的种类数, 也即采取此点所对应的滞育能力与迁移能力的桡足类的种类数。面积越大, 代表采取此种生态对策的桡足类的种类数越多。由图 1 可知, 滞育指数(D)与迁移指数(M)呈明显的负相关, 其回归方程为 $D = -0.6767M + 3.6044$ ($R^2 = 0.3832$, $n = 102$, $P \ll 0.00001$)。由此可知桡足类的滞育能力与迁移能力呈负相关, 桡足类或者具有较高的滞育能力, 或者具有较高的迁移能力。

102 种桡足类体长与迁移能力的关系如图 2 所示, 对二者进行回归, 结果表明体长与迁移指数之间呈明显的正相关($R^2 = 0.322$, $n = 102$, $P \ll 0.00001$)。这说明桡足类的体长与迁移能力正相关, 也即个体较大的桡足类比个体较小的桡足类具有较强的迁移能力。

102 种桡足类体长与滞育指数关系如图 3 所示, 回归分析表明体长与迁移指数之间呈明显的负相关($R^2 = 0.1871$, $n = 102$, $P < 0.00001$), 这表明桡足类的体长与滞育能力负相关, 个体较大的桡足类一般滞育能力较弱, 而个体较小的桡足类一般具有较强的滞育能力。

按照公式 $D = \sum f_i D_i$(其中 f_i 代表具有滞育指数 D_i 的桡足类占总种类数的百分比), 分别计算淡水桡足类和海洋桡足类的滞育指数: 淡水桡足类滞育指数 $D_f = 2.5198$, 海洋桡足类的滞育指数 $D_m = 2.0106$, 淡水桡足类的滞育指数比海洋桡足类的滞育指数高出 25.3%, 这表明生活于淡水中桡足类比生活于海洋中的桡足类具有较高的滞育能力。

3 讨论

探讨滞育分布规律, 首先要解决的关键问题是对不同物种滞育能力的量化处理, 本文根据滞育形式及滞育场所首次将桡足类分为三大类, 用相应滞育指数表示, 这是一种相对量化处理的方法。虽然这种相对量化方法仍无法明确定量桡足类滞育能力的绝对数值, 但这种相对量化法已符合本研究的需要, 因为本研究并不需要知道桡足类滞育能力的绝对数值。最后分析结果表

© 1994-2006 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

表 1　102 种桡足类的体长、迁移指数、滞育指数列表

Table 1　List of the 102 copepods species and their body length, index of migration, index of diapause and habits

种名 Taxa	体长(cm) Length	迁移指数 The index of migration	滞育指数 The indexof diapause	栖息地 Habit	参考文献 Reference
Cyclops scutifer	1.19	1.5	2	淡水 freshwater	[11]
C. bicolor	1.6	1.5	2	淡水 freshwater	[3]
C. abyssorum	1.8	1	2	淡水 freshwater	[12]
C. bohater	2.03	1	2	淡水 freshwater	[12]
C. abyssorum tatricus	1.7	1.5	2	淡水 freshwater	[13]
C. vicinus vicinus	2.04	1.5	2	淡水 freshwater	[3]
C. strenuus strenuus	1.69	1.5	2	淡水 freshwater	[14]
C. lacustris	1.67	1.5	2	淡水 freshwater	[15]
C. kolensis	1.3	1.5	2	淡水 freshwater	[15]
Diacyclops thomasi	1.13	1	2	淡水 freshwater	[3]
Mesocyclops leuckarti	0.88	1.5	2	淡水 freshwater	[16]
Thermocyclops oithonoides	0.8	1.5	2	淡水 freshwater	[15]
T. crassus	0.75	1.5	2	淡水 freshwater	[3]
Acanthocyclops robustus	1.2	1	2	淡水 freshwater	[17]
Pontella mediterranea	2.69	2	3	海洋 marine	[18]
P. meadi	2.73	2	3	海洋 marine	[1]
Anomalocera patersoni	2.94	2	3	海洋 marine	[3]
Calanopia thompsoni	1.7	2	3	海洋 marine	[19]
C. americana	1.83	2	3	海洋 marine	[20]
Labidocera aestiva	1.94	2	3	海洋 marine	[3]
L. wollastoni	2.32	2	3	海洋 marine	[21]
L. bipinnata	2.09	2	3	海洋 marine	[22]
L. trispinosa	2.33	2	3	海洋 marine	[22]
L. scotti	2.2	2	3	海洋 marine	[3]
Epilabidocera amphritrites	2.5	2	3	海洋 marine	[20]
E. longipedata	2.45	2	3	海洋 marine	[3]
Temora longicornis	1.21	2	3	海洋 marine	[21]
Eurytemora affinis	1.33	2	3	海洋 marine	[3]
E. pacifica	0.85	2	3	海洋 marine	[22]
E. velox	1.63	2	3	海洋 marine	[3]
Centropages ponticus	1.31	2	3	海洋 marine	[3]
C. hamatus	1.12	2	3	海洋 marine	[21]
C. abdominalis	1.5	2	3	海洋 marine	[19]
C. yamadai	1.42	2	3	海洋 marine	[19]
C. velificatus	1.37	2	3	海洋 marine	[23]
Sinocalanus tenellus	1.6	2	3	海洋 marine	[22]
Acartia clausi	1.08	2	3	海洋 marine	[19]
A. tonsa	1.23	2	3	海洋 marine	[24]
A. hudsonica	1.39	2	3	海洋 marine	[25]
A. josephinae	1.37	2	3	海洋 marine	[26]
A. californiensis	1.26	2	3	海洋 marine	[3]
A. erythraea	1.43	2	3	海洋 marine	[19]
A. pulmosa	1.09	2	3	海洋 marine	[19]
A. pacifica	1.19	2	3	海洋 marine	[27]
A. latisetosa	1.4	2	3	海洋 marine	[26]
A. steueri	1.32	2	3	海洋 marine	[28]
A. bifilosa	1.1	2	3	海洋 marine	[29]
A. tseunsis	1.33	2	3	海洋 marine	[22]
A. longiremis	1	2	3	海洋 marine	[20]
Tortanus forcipatus	1.2	2	3	海洋 marine	[19]
T. discaudatus	2.5	2	3	海洋 marine	[20]
Calanus finmarchicus	3.7	3	1	海洋 marine	[30]
C. helgolandicus	2.75	3	1	海洋 marine	[3]

© 1994-2006 China Academic Journal Electronic Publishing House. All rights reserved.　http://www.cnki.net

续表 1

种名 Taxa	体长(cm) Length	迁移指数 The index of migration	滞育指数 The indexof diapause	栖息地 Habit	参考文献 Reference
C. hyperboreus	2.75	3	1	海洋marine	[31]
C. glacialis	2.9	3	1	海洋marine	[30]
C. pacificus	2.7	3	1	海洋marine	[3]
C. pacificus californicus	3.17	3	1	海洋marine	[32]
C. australis	3.5	3	1	海洋marine	[3]
C. propinquus	3.1	3	1	海洋marine	[33]
C. marshallae	3.2	3	1	海洋marine	[3]
Calanoides acutus	2.5	3	1	海洋marine	[3]
C. carinatus	2.6	3	1	海洋marine	[31]
Pseudocanalus acuspes	1	3	1	海洋marine	[30]
P. elongatus	1.4	3	1	海洋marine	[34]
P. minutus	1.5	3	1	海洋marine	[35]
Neocalanus plumchrus	3.12	3	1	海洋marine	[30]
N. plumchrus	2.05	3	1	海洋marine	[36]
N. flemingeri	3.25	3	1	海洋marine	[36]
N. cristatus	3.16	3	1	海洋marine	[37]
Metridia longa	4	3	1	海洋marine	[30]
M. lucens	2.25	3	1	海洋marine	[3]
A. longiremis	1.2	3	1	海洋marine	[35]
Onychodiaptamus sanguineus	0.53	1	3	淡水freshwater	[38]
O. bergei	0.61	1	3	淡水freshwater	[39]
Leptodiaptamus minutus	0.45	1	3	淡水freshwater	[40]
Acanthodiaptamus denticornis	1.6	1	3	淡水freshwater	[41]
Aglaodiaptamus leptopus	1.68	1	3	淡水freshwater	[42]
A. clavipes	1.56	1	3	淡水freshwater	[43]
Diaptamus sicloides	2.45	1	3	淡水freshwater	[44]
D. cyaneus intermedius	2.65	1	3	淡水freshwater	[3]
Hemidiaptamus ingens provincae	4.5	1	3	淡水freshwater	[3]
Epischura nordeskiolki	0.91	1	3	淡水freshwater	[45]
Thermodiaptamus galebi	1.21	1	3	淡水freshwater	[46]
Arctodiaptamus bacillifer	1.48	1	3	淡水freshwater	[3]
A. wierzejskii	1.51	1	3	淡水freshwater	[3]
Sinocalanus tenellus	1.23	1	3	淡水freshwater	[47]
Mixodiaptamus kupelwieseri	1.92	1	3	淡水freshwater	[3]
M. laciniatus	1.3	1	3	淡水freshwater	[3]
Canthocamptus staphylinus	0.75	1	2.5	淡水freshwater	[3]
C. staphlinoides	0.76	1	2.5	淡水freshwater	[3]
C. microstaphylinus	0.67	1	2.5	淡水freshwater	[3]
C. robertcokeri	0.71	1	2.5	淡水freshwater	[3]
Attheyella northumbrica	0.71	1	2.5	淡水freshwater	[3]
A. wulmeri	0.75	1	2.5	淡水freshwater	[3]
A. americana	0.68	1	2.5	淡水freshwater	[3]
Mosochra sp.	0.76	1	2.5	淡水freshwater	[3]
Cletocamptus retrogressus	0.71	1	2	淡水freshwater	[3]
Heteropsyllus nunni	0.56	2	2.5	海洋marine	[3]
H. pseudonunni	0.63	2	2.5	海洋marine	[3]
Tigriopus fulvus	0.75	1	2	海洋marine	[48]
T. brevicornis	1.05	1	2	海洋marine	[49]
T. japonicus	0.95	1	2	海洋marine	[19]

明这种方法确实有一定的可行性。Hairston 等[10]在研究滞育在甲壳动物(其中包括 50 种桡足类)中分布情况时,采用滞育持续时间来表示滞育能力,虽然这种思路可行,但在处理桡足类数据时陷入了困境,因为至今对桡足类滞育持续时间研究较少,没有足够的实验数据可供使用,在处理时作者不得不对许多桡足类的滞育持续时间进行主观估算,因而带来许多偏差,正如作者在

© 1994-2006 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

讨论中所言, 应该对桡足类滞育能力重新考虑。本文提出滞育指数对桡足类滞育能力进行相对处理, 较好地解决了这个问题, 同时为解决同类问题提供了新的思路。

进化生态学的一个重要研究领域就是生活史策略, 这其中就包括滞育和迁移。Venable 等[50]和Levin 等[51]提出, 在植物的生活史中存在种子休眠能力和扩散能力之间的可选择性置换(trade off), 他们认为当环境变化时, 植物或者通过种子休眠或者通过种子扩散而避开不利环境, 随着扩散能力的增强, 休眠能力就相对下降, 反之亦然。本文对 102 种桡足类研究表明, 其滞育能力与迁移能力呈显著负相关, 迁移能力弱的种类的滞育能力比迁移能力强的种类的滞育能力要高, 这与在植物中的结论相符。可以认为滞育和迁移是桡足避开不利环境的两大对策, 并且这两种对策存在一定程度的置换。桡足类或者采取强滞育弱迁移方式, 或者采取弱滞育强迁移方式来适应环境变化而达到避免种群灭绝的目的。不同种类的桡足类采取的置换比例往往不同, 这也就表现为不同桡足类采取不同的滞育方式, 这在一定程度上解释了桡足类滞育形式的多样性。Templeton 等[52]提出滞育可看作是时间上的迁移, 按此观点, 滞育和迁移这两种表面上有较大区别的生态对策从某种角度看可达到统一, 一种为时间上的迁移, 另一种为空间上的迁移, 物种通过迁移(时间或空间), 达到避开生活周期中遇到的恶劣条件, 维持种群的沿续。

通过数学模型研究表明, 理论上滞育在桡足类中的分布可能存在如下规律: 桡足类滞育能力与迁移能力负相关; 个体较小的桡足类一般具有较强的滞育能力和较弱的迁移强力, 个体较大的桡足类一般具有较弱的滞育能力和较强的迁移能力; 淡水桡足类的滞育能力明显比海洋桡足类的滞育能力要高。对这种分布规律可能有两种解释: 其一为微进化(microevolution)解释, 滞育在桡足类中的分布模式反映了桡足类所生活的环境对桡足类的选择压力, 在有些生境中滞育对桡足类生存有利, 在另一些生境中可能并不一定有利, 或者有利的程度较小。如淡水生态系统的环境条件波动一般比海洋生态系统要剧烈, 在这种情况下, 在进化中出现较强滞育能力的桡足类可能在竞争中就具有较大的优势。其二为大进化(macroevolution)解释, 这种模式可能是桡足类系统发育史(phylogenetic history)的结果, 也即在桡足类形成不同种类时, 不同种就具有了不同的滞育形式, 因此它们的后代就表现出滞育多样性。虽然还无法对这两种解释进行验证, 但可以认为这两种解释可能并不是绝对独立的, 因为选择的方向和力量与生物已具有的特征有关, 这些特征又与过去的选择压力有关, 两者可能是互相促进, 互相作用[10]。

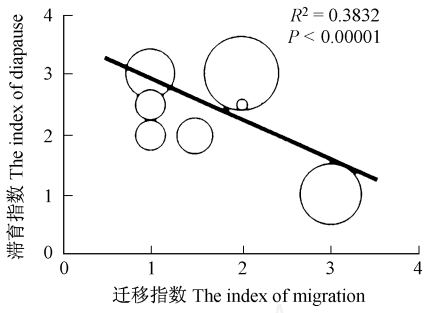

图 1　102 种桡足类滞育能力与迁移能力的关系

Fig. 1　The relationship between diapause ability and migratory ability for 102 copepods species

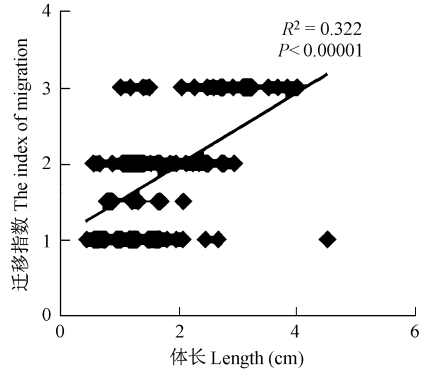

图 2　102 种桡足类体长与迁移能力的关系

Fig. 2　The relationship between migratory ability and body length for 102 copepods species

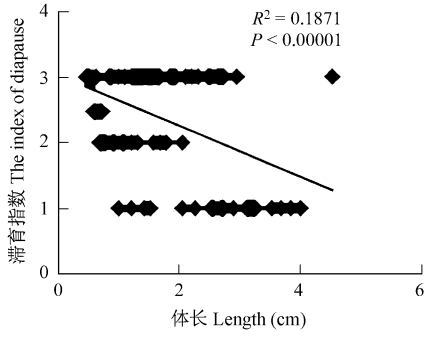

图 3　102 种桡足类体长与滞育能力的关系

Fig. 3　The relationship between diapause ability and body length for 102 copepods species

有关桡足类的进化生态学的研究正处于起步阶段, 但由于桡足类个体发育各期容易区分以及容易获得有代表性的种群组成的样本和环境参数, 所以桡足类是进化生态学中生活史策略研究的理想材料, 其研究成果必将促进进化生态学和桡足类生物学的发展。

References:

[1] Grice G D and Gibson V R. Resting eggs in *Pontella meadi* (Copepoda: Calanoida). *Journal of the Fisheries Research Board of Canada*, 1975, **34**: 410～412.

© 1994-2006 China Academic Journal Electronic Publishing House. All rights reserved.　http://www.cnki.net

[2] Hairston N G and De Stasio B T. Rate of evolution slowed by a dormant propagule pool. *Nature*, 1988, **336**: 239～242.

[3] Williams-Howze J. Dormancy in the free-living copepod orders Cyclopoida, Calanoida, and Harpacticoida. *Oceanography and Marine Biology: an Annual Review*, 1997, **35**: 257～321.

[4] Murray M M and Marcus N H. Survival and diapause egg production of the copepod Centropages hamatus raised on dinoflagellate diets. *Journal of Experimental Marine Biology and Ecology*, 2002, **270**: 39～56.

[5] Danks H V. Insect dormancy: an ecological perspective. *Biological Survey of Canada Mongraph*. Series No. 1. Ottawa, Canada, 1987. 1～439.

[6] Marcus N H, Lutz R, Burnett W, *et al*. Age, viability, and vertical distribution of zooplankton resting eggs from an anoxic basin: Evidence of an egg bank. *Limnology and Oceanography*, 1994, **39**: 497～506.

[7] Hairston N G, Van Brunt R, Kearns C M, *et al*. Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology*, 1995, **76**: 1706～1711.

[8] Hind A, Gurney W S, Heath C M, *et al*. Overwintering strategies in *Calanus finmarchicus*. *Marine Ecology Progress Series*, 2000, **193**: 95～107.

[9] Maria C B, William F L, Janet W R, *et al*. Diapause in copepods (Crustacean) from ephemeral habits with different hydroperiod in Everglades National Park (Florida, U. S. A.). *Hydrobiologia*, 2001, **453/454**: 295～308.

[10] Hairston N G and Caceres C. Distribution of crustacean diapause: micro- and macroevolutionary pattern and process. *Hydrobiologia*, 1996, **320**: 27～44.

[11] Elgmork K. A bottom resting stage in the planktonic freshwater copepod *Cyclops scutifer* (Sars). Oikos, 1962, **13**: 306～310.

[12] Wierzbicka M. On the resting stage and mode of life of some species of Cyclopoida. *Polskie Archiw vn Hydroiologii*, 1962, **10**: 216～229.

[13] Papinska K. The effect of fish predation on Cyclops life cycle. *Hydrobiologia*, 1988, **167**: 449～453.

[14] Elgmork K. Seasonal occurrence of *Cyclops strenuous strenuous* in relation to environment in small water bodies in southern Norway. *Folia Limnologica Scandinavica*, 1959, **11**: 1～196.

[15] Sarvala J. Benthic resting periods of pelagic cyclopoids in an oligotrophic lake. *Holarctic Ecology*, 1979, **2**: 88～100.

[16] Elgmork K. Dynamics of zooplankton communities in some small inundated ponds. *Folia Limnologica Scandinavica*, 1964, **12**: 1～83.

[17] Maier G. Coexistence of the predatory cyclopoids *Acanthocyclops robustus* (Sars) and Mesocyclops leuckarti (Claus) in a small eutrophic lake. *Hydrobiologia*, 1990, **198**: 185～203.

[18] Santella L and Ianora A. Fertilization envelops in diapause eggs of *Pontella mediterranea* (Crustacean, Copepoda). *Molecular Reproduction and Development*, 1992, **33**: 463～469.

[19] Kasahara S, Uye S, Onbe T. Calanoida copepod eggs in sea-bottom muds. *Marine Biology*, 1974, **26**: 167～171.

[20] Marcus N H. Calanoid copepod, cladoceran, and rotifer eggs in sea-bottom sediments of northern California coastal waters. *Marine Biology*, 1990, **123**: 459～465.

[21] Lindley J A. Distribution of overwintering calanoid copepod eggs in sea-bed sediments around southern Britain. *Marine Biology*, 1990, **104**: 209～217.

[22] Uye S. Resting egg production as a life history strategy of marine planktonic copepods. *Bulletin of Marine Science*, 1985, **37**: 440～449.

[23] Blades-Eckelbarger P I and Marcus N H. The origin of cortical vesicles and their role in egg envelope formation in the "spiny" eggs of a calanoid copepod, *Centropages velificatus*. *Biological Bulletin*, 1992, **182**: 41～52.

[24] Marcus N H. Recruitment of copepod nauplii into the plankton: importance of genetic variation. *Bulletin of Marine Science*, 1984, **37**: 684～690.

[25] Sullivan B K and McManus L T. Factors controlling seasonal succession of the copepods *Acartia hudsonica* and *A. tonsa* in Narragansett Bay, Rhode Island: temperature and resting egg production. *Marine Ecology Progress Series*, 1986, **28**: 121～128.

[26] Belmonte G and Puce M. Morphological aspects of subitaneous and resting eggs from *Acartia josephinae* (Calanoida). *Hydrobiologia*, 1994, **292/293**: 131～135.

[27] Uye S, Yoshiya M, Ueda K, *et al*. The effects of organic sea-bottom pollution on survivability of resting eggs of neritic calanoids. *Crustacean* (suppl.), 1984, **7**: 391～403.

[28] Uye S. Development of neritic copepods *Acartia clausi* and *A. steuri* Ⅰ. some environmental factors affecting egg development and the nature of resting eggs. *Bulletin of the Plankton Society of Japan*, 1980, **27**: 1～9.

[29] Viitasalo M. Calanoid resting eggs in the Baltic Sea: implications for the population dynamics Acartia bifilosa (Copepoda). *Marine Biology*, 1992, **114**: 397～405.

[30] Peterson W T, Kimmerer W. Processes controlling recruitment of the marine calanoid copepod *Temora longicornis* in Long Island Sound:

© 1994-2006 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

egg production, egg mortality, and cohort survival rates. *Limnology and Oceanography*, 1994, **39**: 1594～1605.

[31] Conver R J. Comparative life histories in the genera Calanus and Neocalanus in high latitudes of the northern Hemisphere. *Hydrobiologia*, 1988, **67/168**: 127～142.

[32] Ohman M D, Drits A V, Elizabeth C M, *et al*. Differential dormancy of co-occurring copepods. *Deep Sea Research Part II*, 1998, **45**: 1709～1740.

[33] Kosobokova K N. Reproduction of the calanoid copepod *Calanus propinquus* in the southern Weddell Sea, Antarctica: observations in laboratory. *Hydrobiologia*, 1994, **292/293**: 219～227.

[34] Colebrook J M. Continuous plankton records: overwintering and annual fluctuations in the abundance of zooplanktokton. *Marine Biology*, 1982, **84**: 261～265.

[35] Norrbin M F. Seasonal patterns in gonad maturation sex ration and size in some small, high-latitude copepods: implications for overwintering tactics. *Journal of Plankton Research*, 1994, **16**(2): 115～131.

[36] Miller C B and Clemons M J. Revised life history analysis for large frazing copepods in the subarctic Pacific Ocean. *Progress in Oceanography*, 1989, **20**: 293～313.

[37] Omori M. Calanus cristatus and submergence of the Oyashio water. *Deep-Sea Research*, 1967, **14**: 525～532.

[38] Hairston N G, Walton W, Li K. The causes and consequences of sex-specific mortality in a freshwater copeod. *Limnology and Oceanography*, 1983, **28**: 935～947.

[39] Walton W E. Factors regulating the reproductive phenology of *Onychodiaptomus birgei* (Copepods: Calanoida). *Limnology and Oceanography*, 1985, **30**: 167～179.

[40] Hairston N G and Van Brunt R. Diapause dynamics of two diaptomid copepod secies in a large lake. *Hydrobiologia*, 1994, **292/293**: 209～218.

[41] Raera O and Tonolli V. Body size and number of eggs in dipaptomids, as related to water renewal in mountain lakes. *Limnology and Oceanography*, 1956, **1**: 118～122.

[42] Watras C J. Subitaneous and resting eggs of copepods: relative rates of clutch production by *Diaptomus leptopus*. *Canadian Journal of Fisheries and Aquatic Sciences*, 1986, **37**: 1579～1581.

[43] Gehrs C W and Martin B D. Production of resting eggs by *Diaptomus clavipes* Schacht (Copepoda, Calanoida). *American Midland Naturalist*, 1974, **91**: 487～489.

[44] Comita G W. The seasonal zooplankton cycles, production and transformation of energy in Severson Lake, Minnesota. *Archiv fur Hydrobiologe*, 1972, **70**: 14～66.

[45] De Stasio B T. The role of dormancy and emergence patterns in the dynamics of a freshwater zooplankton community. *Limnology and Oceanography*, 1990, **35**: 1079～1090.

[46] Moghraby A I A study on diapause of zooplankton in a tropical river——the Blue Nile. *Freshwater Biology*, 1977, **7**: 201～212.

[47] Hada A, Uye S, Onbe T. The seasonal life cycle of Sinocalanus tenellus (Copepoda: Calanoida) in a brackish-water pond. *Bulletin of the Plankton Society of Japan*, 1986, **33**: 29～41.

[48] Ranade M R. Observations on the resistance of Tigriopus fulvus (Fischer) to changes in temperature and salinity. *Journal of the Marine Biological Association of the United Kingdom*, 1957, **36**: 115～119.

[49] Damgaard D M and Devenport J. Salinity tolerance, salinity preference and temperature tolerance in the high-shore harpacticoid copepod *Tigriopus brevicornis*. *Marine Biology*, 1994, **118**: 443～449.

[50] Venable D L and Lawlor. Delayed germination and dispersal in desert annuals: Escape in space and time. *Oecologia*, 1980, **46**: 272～282.

[51] Levin S A, Cohen D, Hastings A. Dispersal strategies in patchy environments. *Theoretial Population Biology*, 1984, **26**: 165～191.

[52] Templeton A R and Levin D A. Evolutionary consequences of seed pool. *The American Naturalist*, 1979, **114**: 232～249.

© 1994-2006 China Academic Journal Electronic Publishing House. All rights reserved.　http://www.cnki.net