海洋纤毛虫——巨大拟阿脑虫的实验生态学研究 Ⅳ. 捕食竞争对种群生长的影响

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摘要：作为系列研究的第四部分，就捕食竞争、食物等因素与海洋纤毛虫——巨大拟阿脑虫（纤毛门，盾纤目）种群生长的关系进行了探讨。结果显示，单独或混合培养的纤毛虫对细菌生长均有很强的抑制作用。在竞争者存在时，巨大拟阿脑虫和扇形游仆虫的种群生长均受到了不同程度的制约而维持较为稳定的共存状态。实验表明，盾纤类纤毛虫作为高效的食菌者对于维持一个健康的养殖环境具有积极意义。

关键词：巨大拟阿脑虫；竞争；种群生长；细菌

On experimental ecology of the marine ciliate *Paranophrys magna* Ⅳ: effects of competition on population growth

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Abstract: The scuticociliate *Paranophrys magna* Borror, 1972 is commonly found in a variety of marine waters, especially in mariculture biotope. The effects of different initial population density, temperature, salinity and pH on the population growth have been studied using experimental methods in previous reports. As the fourth part of this series, the present paper deals with the effects of the competitor (a hypotrichous ciliate) and food on the population growth of *Paranophrys magna*.

The experiment was divided into four treatments: 1) the medium without any ciliate as a control; 2) the medium inoculated with *Paranophrys magna* as *Paranophrys*-treatment; 3) with *Euplotes vannus* as *Euplotes*-treatment and 4) the medium inoculated with both *Paranophrys magna* and *Euplotes vannus* (as mixing－treatment). Each treatment was carried out as three independent replicates. All work was performed in room temperature with initial density of 30 ind./ml of ciliates. During experiments, the density of cells was recorded periodically with counting slide, while the density of bacteria was assessed with the globulimeter. According to the formula $\ln Nt=\ln N+rt$, the increasing rate of populations was calculated with regression analysis based on the method of least square.

In control treatment, the population growth turned into exponential growth phase in a few hours due to high temperature and concentrations of organic materials. During equilibrium phase the density of bacteria remained 1.02×10^{8} ind./ml. The medium turned turbid as the density of bacteria was amplified.

In *Paranophrys*-treatment, the natural rate of population growth of ciliates was significantly lower than that of bacteria due to shortage of food from 0 to 1 day. As the density of bacteria increased, the maximum density of ciliates reached 2.97×10^{4} ind./ml and the natural rate of population growth remained 3.22 ± 0.046/d after one day. With the increasing of density of ciliates, the growth of bacteria was

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inhibited by ciliates and the density decreased to 6.42×10^7 ind./ml. After the growth of ciliates came into equilibrium phase, the density of bacteria leveled off steadily at a lower value as 2/3 of that in control treatment.

In *Euplotes*-treatment, the interrelation of growth between ciliates and bacteria was similar to that in *Paranophrys*-treatment, however, the density of *Euplotes vannus* decreased to a lower value as 1/10 of that of *Paranophrys magna*, the maximum value reached 2328 ind./ml and the natural rate of population growth remained 1.57 ± 0.002/d. In the same way as in *Paranophrys*-treatment, the growth of bacteria was also inhibited by ciliates.

In mixing－treatment, the growth of the two species of ciliates developed into the exponential growth phase after 24 hours. During this phase the increasing of density of *Paranophrys magna* lasted for 1 day, then the maximum density reached 900ind./ml and the natural rate of population growth remained 1.79 ± 0.021/d, while the growth of *Euplotes vannus* lasted for 1.5 about days, then the maximum density reached 1175ind./ml and the natural rate of population growth increased to 2.10 ± 0.046/d. It was obvious that the density of *Euplotes vannus* remained higher than that of *Paranophrys magna* in this treatment.

It was revealed that there was a difference between mixing culture and non mixing culture on the population growth of the two ciliates. The maximum density of the former was only about 3% of that in the latter (870 vs. 29679 ind./ml) and the natural rate of population growth decreased to about 1/2 during exponential growth phase, while the population growth of *Euplotes vannus* was inhibited at a lower degree. The natural rates of population growth of the two species ciliates were different among all the treatments (*Paranophrys* with single culture > *Euplotes* with mixing culture > *Paranophrys* with mixing culture > *Euplotes* with single culture). Compared with control, the population growth of bacteria were inhibited in different degree in other three treatments (mixing-treatment > *Paranophrys*-treatment > *Euplotes*-treatment).

The results also indicate that the population growth of both ciliated protozoa, *Paranophrys magna* and *Euplotes vannus*, were inhibited by the competition and that their densities dropped to a steady and lower level when two species were cultured together. The maximum population density and the natural rate of increase during the exponential phase in *Paranophrys magna* was only 870 ind./ml, 1.79 ind./ml when mixed with *Euplotes vannus* while the values were 29670 ind./ml, 3.22 ind./ml when cultured alone. The results support the viewpoint that there is a negative correlativity between size and increasing rate of population in ciliate protozoa (Fenchel, 1968).

The growth of bacteria was inhibited strongly when ciliates were cultured either individually or mixed. The density of bacteria dropped sharply at beginning of exponential growth and decreased finally to a lower level during experiments. As effective predators, ciliates used might be very helpful for maintaining the quality of aquiculture waters.

Key words: *Paranophrys magna*; competition; population growth; bacteria
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盾纤类纤毛虫是广泛生存于各类水环境、尤其在富营养化水体中常见多发的原生动物。该类纤毛虫个体较小且普遍以细菌和有机碎屑为食,同时又常常被大型纤毛虫及其他微型浮游动物所摄食,因而在初级生产力向较高营养级传递的过程中起着重要的枢纽作用[1]。人们还发现,盾纤类的少数种类可兼性寄生在海水养殖体内,而引起宿主的死亡[2,3]。

迄今为止,国内外对该类纤毛虫的研究多限于形态分类学描述和一些有关摄食习性等方面的研

究[illegible],对其种群动力学及生态学功能的了解仍不多,有关该类纤毛虫在水体内尤其是高密度的集约化养殖(含育苗)水体中的功能与作用则在争议之中(但通常被归入危害类群中),而作为食菌者,他们对养殖环境的贡献作用无疑被忽视了。因此,探讨其个体及种群生态学对于评估盾纤类纤毛虫在水域生态系中的作用是十分必要的。

本研究所涉之巨大拟阿脑虫是一在海水及富营养的养殖水体中较常见的盾纤类纤毛虫。在本系列研究的前三部分中探讨了初始种群密度及食物、温度、盐度及pH值等环境因子对其种群生长的影响以及纤毛虫对环境胁迫的应答反应等问题。作为系列研究的第四部分,本文就捕食竞争者(扇形游仆虫)、食物与其种群生长的关系进行了探讨。

1 材料与方法

1.1 纤毛虫种群的维持及驯化培养 实验用纤毛虫(巨大拟阿脑虫,*Paranophrys magna* Borror,1972,以下简称拟阿脑虫)于1998年5月采自青岛郊区一育蟹池,盐度20。虫体分离后在室温下以煮沸消毒海水(盐度20)为培养液建立纯培养,米粒繁殖的细菌为饵料。

将拟阿脑虫接种于高盐度海水培养液中,以缓慢过渡方式进行驯化,使其在盐度约为30的培养液中正常生长繁殖。

用于与拟阿脑虫共试验的扇形游仆虫(*Euplotes vannus*,以下简称游仆虫)采自青岛近郊一对虾育苗场,盐度29,维持培养方法及条件同前。

1.2 培养液 培养用海水经煮沸消毒后用滤纸过滤,盐度29。50ml海水中加入15滴25g/L的牛肉浸膏悬液作为细菌培养基,作为纤毛虫生长繁殖的饵料。

1.3 实验方案 实验共设4组:①空白对照组(培养液中无纤毛虫);②拟阿脑虫实验组(培养液+拟阿脑虫);③游仆虫实验组(培养液+游仆虫);④混合培养实验组(培养液+拟阿脑虫+游仆虫)。各实验组中纤毛虫的初始密度均为30 ind./ml,定期用计数板和血球计数板测定纤毛虫及细菌的种群密度;每组分别设3个平行,室温(22~24℃)培养。

1.4 纤毛虫种群自然增长率的计算方法 根据公式 $\ln Nt=\ln No+rt$(Nt为经过时间t后的种群密度,No为种群初始密度),增长率以最小二乘法回归分析得出,以时间为横坐标,因变量是纤毛虫密度(个体/ml)的自然对数,其斜率即种群自然增长率r[3]。

2 结果

空白组细菌的生长情况见图1。由于培养基有机质浓度及培养温度较高以至种群生长在数小时之内便迅速进入了指数增长期,平衡期细菌密度约为 1.02×10^8 ind./ml。

一个可明显观察到的现象是,在3个实验组培养过程中,细菌的大量繁殖使培养液首先由清澈变得浑浊。随着纤毛虫的活动和摄食,培养液从纤毛虫种群指数增长期的末期(约1d后)开始逐渐出现絮状沉淀而重新变得清澈起来。

拟阿脑虫实验组中纤毛虫及细菌的数量变化见图2,图中显示了前者对后者的明确影响。从其种群生长曲线可以明显分为3个时期:①停滞期 在培养0~1d之内,由于其饵料不足,种群生长明显低于细菌生长;②指数增长期 随着细菌密度的增加,纤毛虫食物逐渐丰足,纤毛虫种群在经历了1d的停滞期之后,迅速生长繁殖起来,最大种群密度高达 2.97×10^4 ind./ml,拟阿脑虫在这一时期的种群自然增长率为 3.22 ± 0.046/d;随着纤毛虫数量的增加,对细菌的摄食强度加大,使细菌的生长与对照组相比,尚在指数增长期就被抑制,最大密度仅为 6.42×10^7ind./ml,相当于对照组不足2/3的数量(图3);③平衡期 纤毛虫种群进入

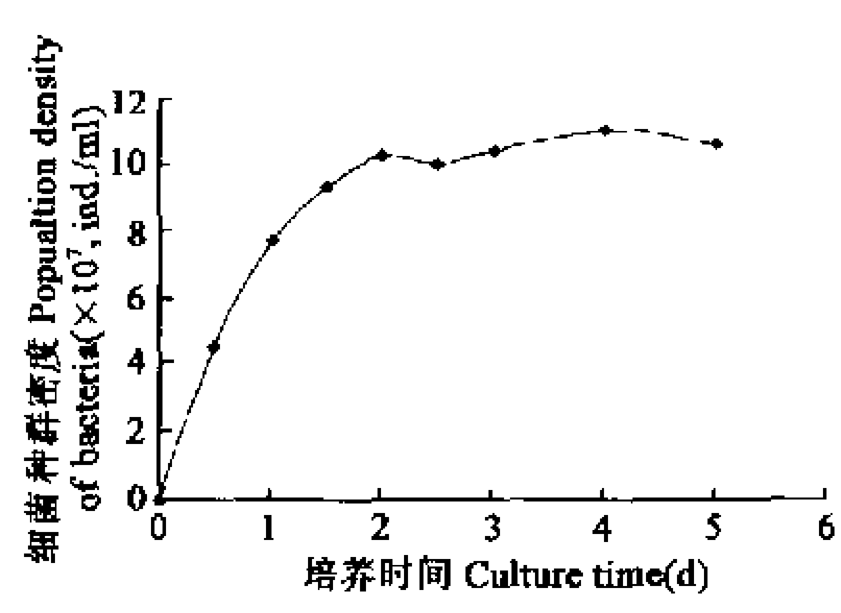

图1 空白对照组细菌的生长曲线

Fig.1 Growth curve of bacteria in control group

平衡期后，对细菌的摄食强度稳定，细菌的数量也相继稳定下来。

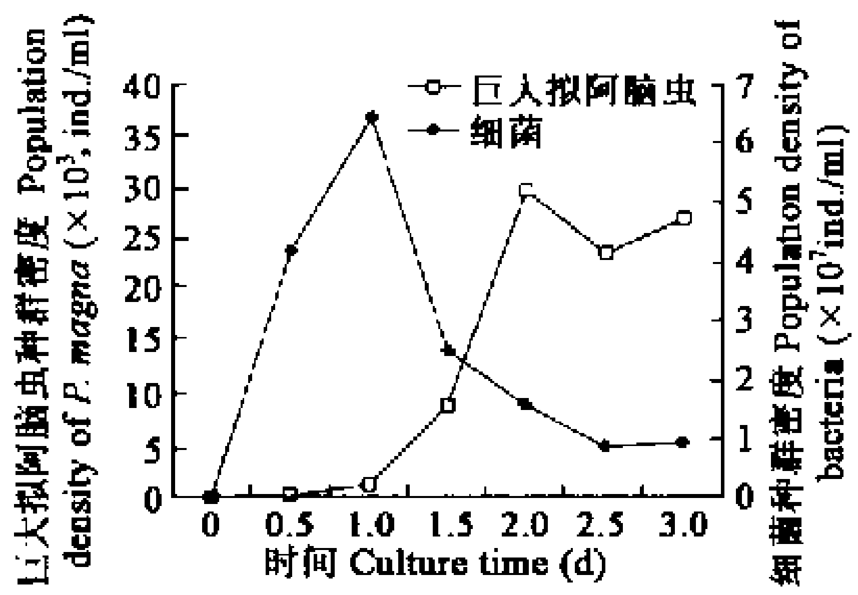

图2 拟阿脑虫实验组中纤毛虫和细菌的生长曲线

Fig. 2 Growth curve of ciliate and bacteria in experimental group of *P. magna*

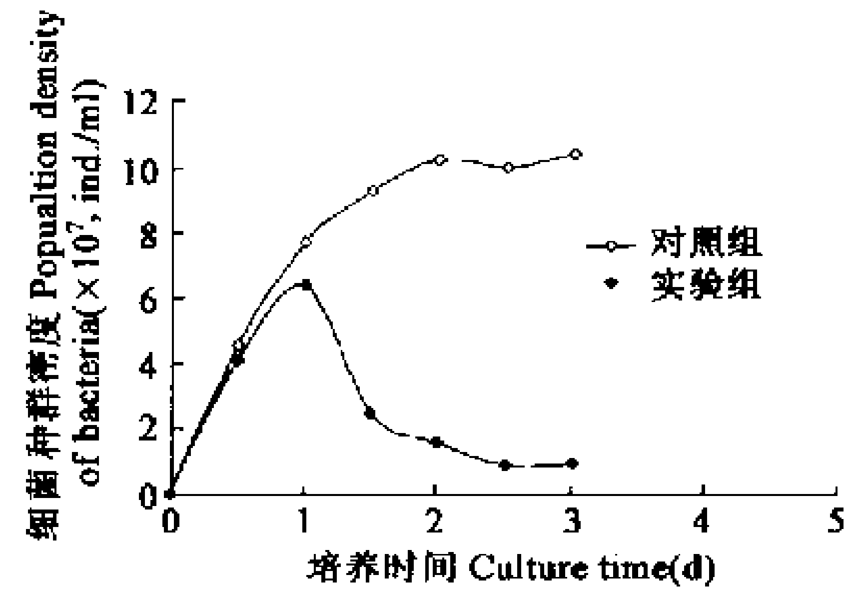

图3 拟阿脑虫实验组与空白组细菌数量的变化比较

Fig. 3 Comparison of bacteria growth between experimental and control group

游仆虫实验组中，纤毛虫及细菌数量变化见图4，两者的关系与前组类似，但游仆虫的个体数量仅为拟阿脑虫的约1/10，最大种群密度为2328 ind. /ml，种群自然增长率为1.57±0.002/d。该实验组中对细菌种群生长的抑制（图5）与拟阿脑虫实验组（图3）也十分相似。

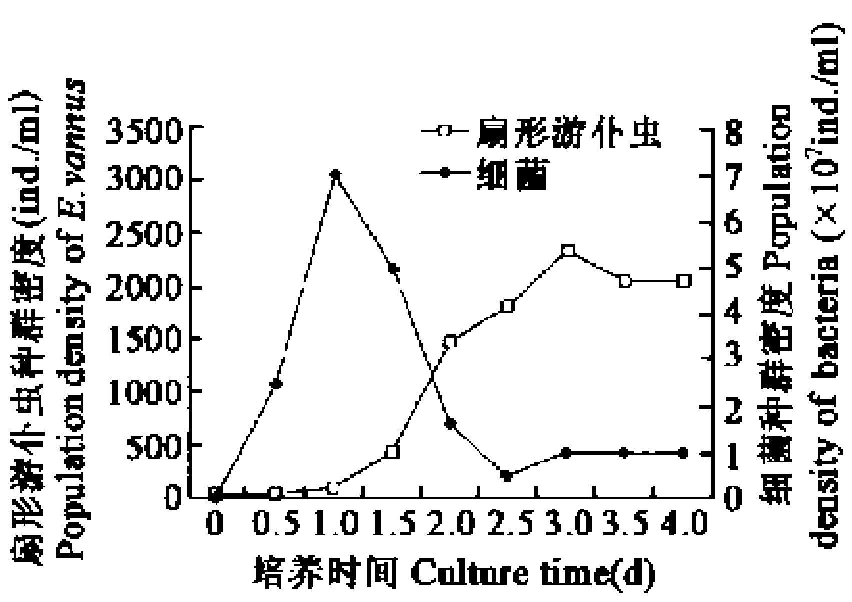

图4 游仆虫实验组中纤毛虫和细菌的生长曲线

Fig. 4 Growth curve of ciliate and bacteria in experimental group of *E. vannus*

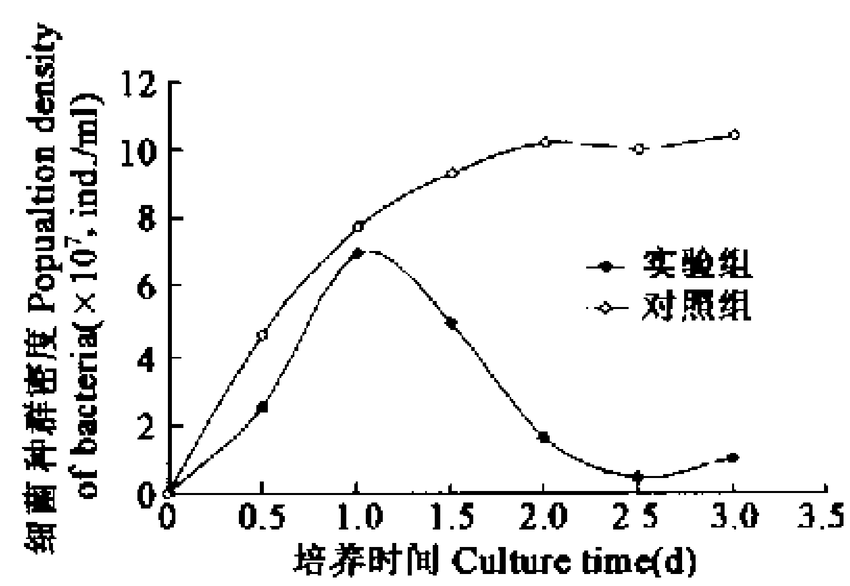

图5 游仆虫实验组与空白组细菌数量的变化比较

Fig. 5 Comparison of bacteria growth between experimental group of *E. vannus* and control group

图6及图7显示了混合培养实验组内各纤毛虫及细菌的数量变化，两种纤毛虫均在1d之后进入指数增长期，拟阿脑虫种群在指数增长期持续了1d，最大种群密度约为900ind. /ml，种群自然增长率为1.79±0.021/d；游仆虫种群则持续了1.5d，最大种群密度约为1175ind. /ml，种群自然增长率为2.10±0.046/d。此组实验还显示，游仆虫密度始终大于拟阿脑虫。

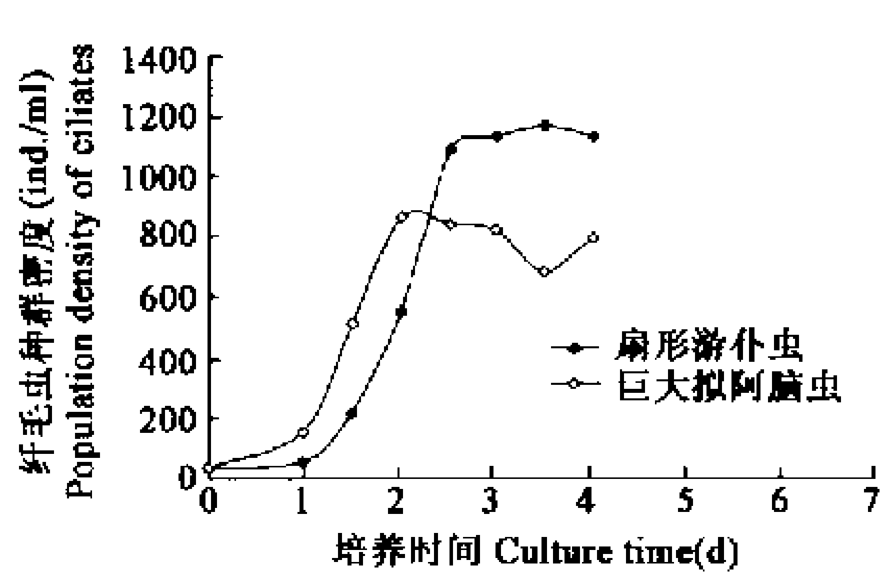

图6 混合培养实验组中纤毛虫的生长曲线

Fig. 6 Growth curve of ciliates in experimental group of mixed culture

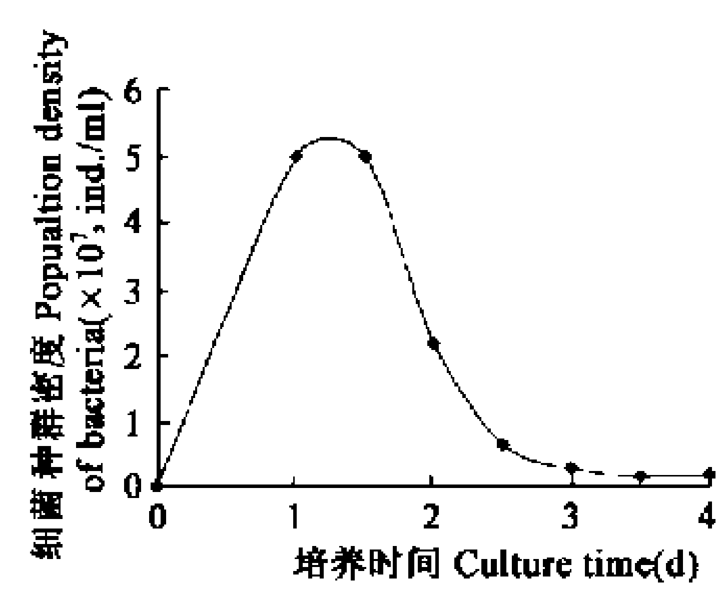

图7 混合培养实验组中细菌的生长曲线

Fig. 7 Growth curve of bacteria in experimental group of mixed culture

图 8 和图 9 分别显示了混合培养组中拟阿脑虫和游仆虫种群生长情况同单独培养时的差异。前者的最大种群密度仅为单独培养时的约 3%(870ind./ml:29670 ind./ml),指数增长期的种群自然增长率也比单独培养时下降了近一半(1.79/d:3.22/d);相对而言游仆虫的种群生长受抑制的程度较小。

同对照组相比,3 个实验组中细菌的数量均受到不同程度的抑制(图 10),其中在混合培养组中受抑制程度最大,依次为拟阿脑虫和游仆虫实验组。

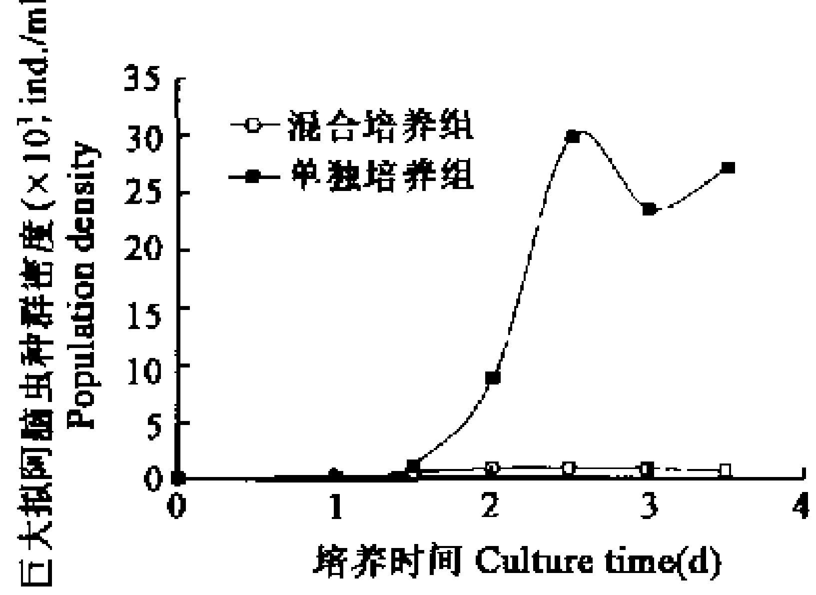

图 8　拟阿脑虫实验组与混合培养组中拟阿脑虫的种群生长比较

Fig. 8　Comparison of growth between experimental group(only *P. magna*)and the group with two species

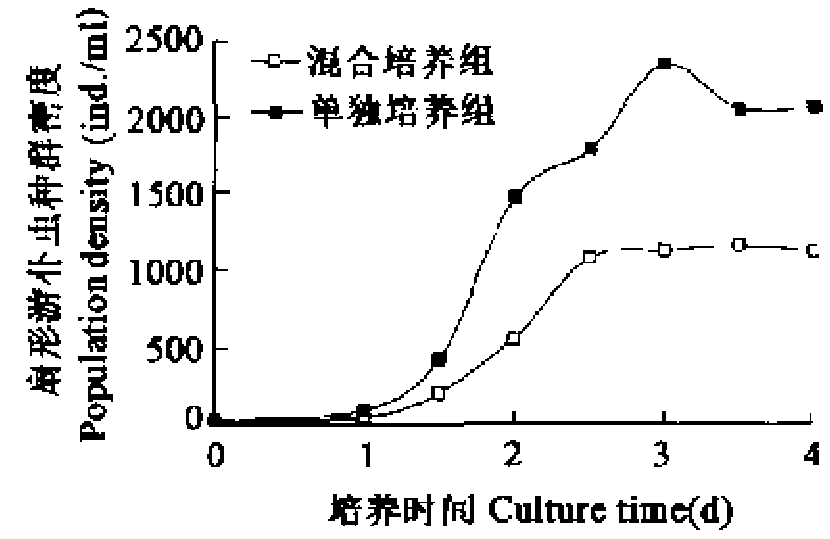

图 9　游仆虫实验组与混合培养组中游仆虫的种群生长比较

Fig. 9　Comparison of *E. vannus* growth between experimental group(only *E. Vannus*)and group with two species

在不同实验组中两种纤毛虫的种群自然增长率的比较见图 11,大小依次为:单独培养的拟阿脑虫(3.22±0.046/d)>混合培养组中的游仆虫(2.10±0.046/d)>混合培养组的拟阿脑虫(1.79±0.021/d)>单独培养的游仆虫(1.57±0.002/d)。

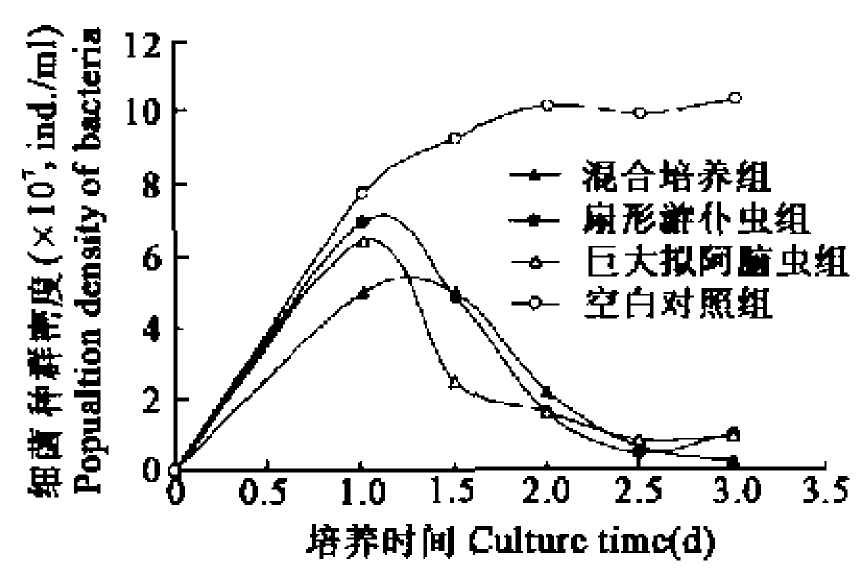

图 10　4 个实验组中细菌种群生长的比较

Fig. 10　Comparison of population growth of bacteria among four experimental groups

3　讨论

已有研究表明,纤毛虫在水环境中是细菌最有效的摄食者之一[1,3,10],纤毛虫与异养鞭毛虫等原生动物一起通过取食细菌将初级生产力向较高营养级传递。在污水处理系统中也是利用了纤毛虫对细菌的摄食习性来达到净化污水的目的,同时对细菌的捕食又可防止细菌种群的老化,从而更有利于提高降解速度[10]。在海水养殖环境中,通常为大家所接受的观点是,一定数量的微生物存在是无害的,但当细菌数量过大时,则必须加以控制。在生产实践中,这一人为控制表现为在对"危险"阈值的主观认定后而(盲目地!)予以大剂量的抗生素使用。但近年来许多实践又表明,在未经人工干涉的小的闭合环境中(如对虾育苗水体内),特定类群的纤毛虫(食菌者)的出现往往标志着水体向良好的健康状况转化,而且这种良好的水况往往可以构成一有益而稳定的状态。

由于盾纤类大多是嗜污性的,极易在富营养水体中发展成优势类群,因此长期以来一直被笼统地视为养殖或育苗环境中的危害类群。但近年来的研究表明,除极少数兼性寄生种外,绝大多数盾纤类对养殖动物并无明显的"危害"。而作为食菌者,盾纤类本身是高效率的食菌者,其在多污水体中的繁盛自身是由于水体过富的后发性结果而非导致水体恶化的原因。换言之,食菌类纤毛虫(包括盾纤类)更可能是促进和维持(而非破坏)水体健康的有益因子。

在本研究中,3 个实验组都清楚地表明了这两种纤毛虫对细菌大量繁殖的有效抑制作用,由于纤毛虫的摄食,使细菌数量在指数生长期开始不久便急剧下降,而最终维持在一个较低的水平。

本文研究结果支持 Fenchel 的报道,即纤毛虫的体积与种群增长率呈负相关关系[11]。本实验所用游仆虫的虫体为 80～140×52～76μm,拟阿脑虫的体积较小,大小约为 46～100×14～42μm,在单独培养时,拟阿脑虫的种群自然增长率比游仆虫的要高得多。

本实验同时还揭示了纤毛虫种间的竞争关系。扇形游仆虫在海水生态系中是一较易大量发生的常见种类,在与巨大拟阿脑虫的混合培养中,它作为后者的食物竞争者而逐渐占据了优势。从图 8 和图 11 可以看出,拟阿脑虫种群的生长同单独培养时相比,受到了很大的抑制,种群自然增长率甚至不及体积比它大许多的游仆虫,在种群数量上与单独培养时的情况相比更是有大幅的下降。

在混合培养实验组中,巨大拟阿脑虫的种群生长虽然受到很大抑制,但因体积小,繁殖速度较快,故种群自然增长率仍比扇形游仆虫单独培养时为高。

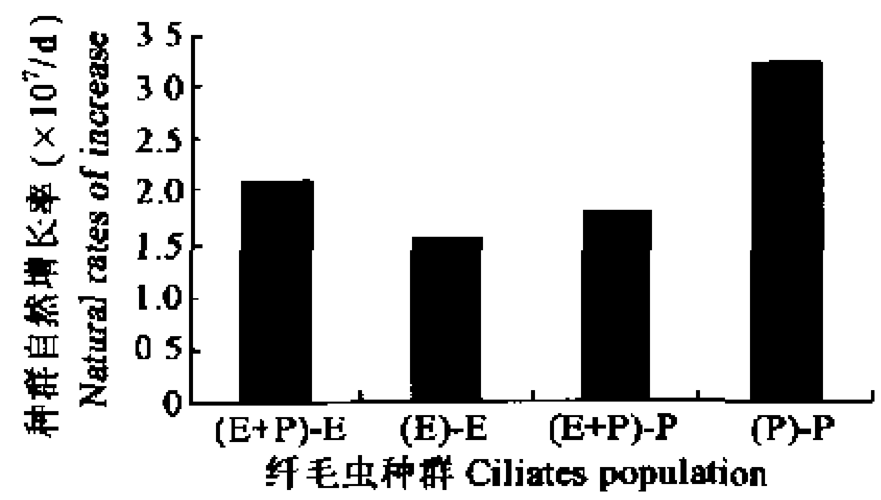

图 11 不同纤毛虫种群的种群自然增长率

Fig. 11 Natural rates of increase of different ciliate populations

(E+P)-E:混合培养组的游仆虫种群 Population of *E. vannus* in mixed culture;(E)-E:单独培养的游仆虫种群 Ciliate population in experimental group of *E. vannus*;(E+P)-P:混合培养组的拟阿脑虫种群 Population of *P. magna* in mixed culture;(P)-P:单独培养的拟阿脑虫种群 Ciliate population in experimental group of *P. magna*

由图 11 结果显示,扇形游仆虫在竞争者存在的情况下种群自然增长率竞争比单独培养时还高,从竞争抑制这一角度来看似乎不合理,但由图 9 可看出,游仆虫在单独培养时种群指数增长期持续了约 36h,在有拟阿脑虫存在的情况下仅仅持续了 24h,因此前者单独培养时在种群数量上远大于混合培养组(2328ind./ml>1175ind./ml),可见对有限饵料的竞争对纤毛虫的抑制影响是很明显的。作者认为对于游仆虫在竞争者存在的情况下种群自然增长率比单独培养时高的这一现象,可以视作纤毛虫在索饵竞争条件下的一种"适者生存"的策略。但目前还无法明了为何此现象在巨大拟阿脑虫没有出现。可能的解释是(1)不同种类纤毛虫的摄食速率有差异,巨大拟阿脑虫的摄食速率可能小于扇形游仆虫,因而在竞争中逐渐失去优势;(2)在匍底生活的游仆虫存在时,拟阿脑虫主要是以悬游在水体中的形式存在,而细菌主要丛集在底质上,饵料的相对匮乏限制了拟阿脑虫的繁殖速度。但是,这些假设还有待于进一步的证据来验证。

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