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海洋浮游纤毛虫在世界海区的时空分布*

于 莹[1,2] 张武昌[1**] 丰美萍[1,2] 李海波[1,2] 赵 苑[1] 肖 天[1]
([1]中国科学院海洋研究所海洋生态与环境科学重点实验室, 山东青岛 266071; [2]中国科学院大学, 北京 100049)

摘 要 作为微型浮游动物的重要组成部分,海洋浮游纤毛虫是连接微食物环和经典食物链的重要中介,在海洋浮游生态系统物质循环和能量流动中发挥重要的作用。从20世纪60年代至今,关于纤毛虫丰度和生物量的分布已经积累了大量的资料,目前纤毛虫丰度和生物量分布的研究大部分集中在温带海区,热带和极地海区的研究尚少。本文概述了世界海区纤毛虫丰度和生物量的水平分布、垂直分布特点及周年变化规律。纤毛虫丰度和生物量一般在饵料丰富、生产力较高的海区较高;纤毛虫倾向分布在水体的中上层;纤毛虫的丰度和生物量一年之内呈现双峰型或单峰型,纤毛虫群落的粒级组成一般春季较大,夏季较小,砂壳纤毛虫丰度占纤毛虫丰度的比例一般在夏季或秋季较高。

关键词 浮游纤毛虫; 丰度; 生物量; 水平分布; 垂直分布; 周年变化

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Spatiotemporal distribution patterns of planktonic ciliates in the world sea areas.

YU Ying[1,2], ZHANG Wu-chang[1**], FENG Mei-ping[1,2], LI Hai-bo[1,2], ZHAO Yuan[1], XIAO Tian[1] ([1] *Key Laboratory of Marine Ecology and Environmental Sciences*, *Institute of Oceanology*, *Chinese Academy of Sciences*, *Qingdao* 266071, *Shandong*, *China*; [2] *University of Chinese Academy of Sciences*, *Beijing* 100049, *China*). *Chinese Journal of Ecology*, 2013, **32**(4): 1045-1053.

Abstract: As an important component of microzooplankton, marine planktonic ciliates are the key link between the microbial food web and classical food chain, playing an important role in the material cycling and energy flow in marine planktonic ecosystems. Since the 1960s, studies on the marine ciliate abundance and biomass in the sea areas of the world, especially in the temperate regions, have been performed extensively. In this paper, the horizontal distribution, vertical distribution, and annual variation patterns of the abundance and biomass of marine planktonic ciliates in the world sea areas were summarized. Generally, ciliates tend to distribute in the middle and upper water layers, their abundance and biomass are higher in the sea areas with more diet supply and higher primary production and showed a bimodal or unimodal pattern in a year, larger ciliates are more prevalent in spring than in summer, and the contribution of tintinnid to the total ciliate abundance was higher in summer or autumn.

Key words: planktonic ciliates; abundance; biomass; horizontal distribution; vertical distribution; annual variation.

海洋浮游纤毛虫(以下简称纤毛虫)是一类广泛存在的、营浮游生活的纤毛虫,主要隶属于旋毛纲(Spirotrichea Bütschli, 1889)下的寡毛亚纲(Oligotrichia Bütschli, 1887/1889)及环毛亚纲(Choreotrichia Small & Lynn, 1985)(Lynn, 2008),包括无壳纤毛虫及砂壳纤毛虫2大类。纤毛虫是微型浮游动物的重要组成部分,主要摄食 pico-和 nano-级浮游生物,同时又被中型浮游动物和鱼类幼体所摄食,因此是连接微食物环和经典食物链的重要中介(Azam *et al.*, 1983; Pierce & Turner, 1992)。纤毛虫粒径较小,相对于中型浮游动物有较快的生长率、摄食率及代谢率(Fenchel, 1974),因此对环境变化的响应更为迅速,在海洋浮游生态系统的物质循环和能量流动中发挥重要的作用。

20世纪60年代以来,在世界各海区逐渐开展

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**通讯作者 E-mail: wuchangzhang@163.com
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了微型浮游动物(包括纤毛虫)的丰度和生物量分布的研究(张武昌等, 2001)。1983年"微食物环(microbial loop)"的概念提出之后,关于微型浮游动物生态学的研究大量涌现,积累了很多纤毛虫丰度和生物量分布的资料。中国研究者从20世纪90年代开始关注纤毛虫生态学,目前已经在渤海、黄海、东海、南海进行了调查(张武昌等, 2009)。张武昌等(2001)总结了世界各海区纤毛虫丰度和生物量的数值范围。本文概述200 m以浅的真光层中纤毛虫丰度和生物量的水平分布、垂直分布特点及周年变化规律。

1 研究海区

纤毛虫丰度和生物量时空分布的研究遍布世界各海区,从温带、热带到两极,从近岸到大洋,但大部分研究集中在温带近岸海区,如欧洲沿岸(地中海、波罗的海)、北美大西洋沿岸及亚洲太平洋沿岸,热带和极地海区和大洋的研究尚少(图1、图2、图3)。

2 纤毛虫丰度和生物量的水平分布

2.1 分布特点

纤毛虫丰度和生物量一般在饵料丰富、生产力高的海区较高。在温带海湾及河口区,一般表现为近岸高于远岸。如西北太平洋的Hiroshima Bay(Kamiyama *et al.*, 2003)及胶州湾(Chen & Yang, 2009),纤毛虫丰度在湾内比湾外高。如东北大西洋的Po River河口(Revelante *et al.*, 1985)和Rhone River河口(Christaki *et al.*, 2009),河口内的纤毛虫丰度高于河口外。热带海区如印度洋西北部,纤毛虫的丰度和生物量在生产力高的海区较高,在寡营养海区较低(Leakey *et al.*, 1996)。极地海区如Weddell Sea冰区,纤毛虫丰度在Chl-a浓度较高的冰缘海区较高(Kivi & Kuosa, 1994)。

在河口区,砂壳纤毛虫往往表现出相反的水平分布模式,趋于分布在远岸(向海一侧),如东北大西洋的Nervión River河口区,砂壳纤毛虫主要分布在河口外侧(Urrutxurtu *et al.*, 2003; Urrutxurtu, 2004)。

2.2 季节变化

在同一海区不同的季节,纤毛虫丰度的水平分布可能呈现不同的特点。如东海冬季和春季,纤毛虫丰度从内陆架向外陆架逐渐增加;夏季,纤毛虫丰度在长江羽状锋区较高;秋季,纤毛虫丰度在陆架中部较高(Chiang *et al.*, 2003)。在西北大西洋的Irminger Sea,纤毛虫丰度冬季在调查海区南部较高,春季在西北部较高,夏季在北部较高(Montagnes *et al.*, 2010)。

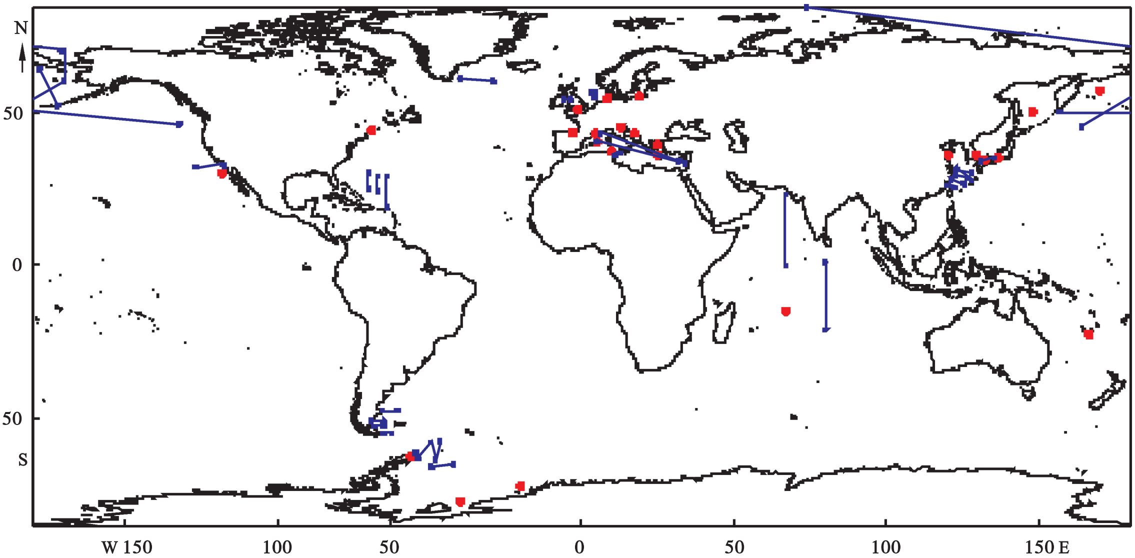

图1 纤毛虫丰度和生物量水平分布的研究海区分布示意图

Fig. 1 Global distribution of studies about horizontal distribution of ciliate abundance and biomass

(Beers & Stewart, 1967, 1969; Taniguchi, 1984; Revelante *et al.*, 1985; Sorokin *et al.*, 1985, 1996; Sanders, 1987; Nothig *et al.*, 1991; Buck *et al.*, 1992; Leakey *et al.*, 1992, 1996; Nielsen *et al.*, 1993; Kamiyama, 1994; Kivi & Kuosa, 1994; Uye *et al.*, 1996, 2000; Sherr *et al.*, 1997; Tillmann & Hesse, 1998; Witek, 1998; Dolan *et al.*, 1999, 2002, 2006; Montagnes *et al.*, 1999, 2010; Pitta & Giannakourou, 2000; Pitta *et al.*, 2001; Sorokin & Sorokin, 2002; Chiang *et al.*, 2003; Iriarte *et al.*, 2003; Kamiyama *et al.*, 2003; Ota & Taniguchi, 2003; Urrutxurtu *et al.*, 2003; Urrutxurtu, 2004; Kim *et al.*, 2007; Vidjak *et al.*, 2007; Hlaili *et al.*, 2008; Chen & Yang, 2009; Christaki *et al.*, 2009; Andersen *et al.*, 2011; Hannachi *et al.*, 2011; Santoferrara *et al.*, 2011)。

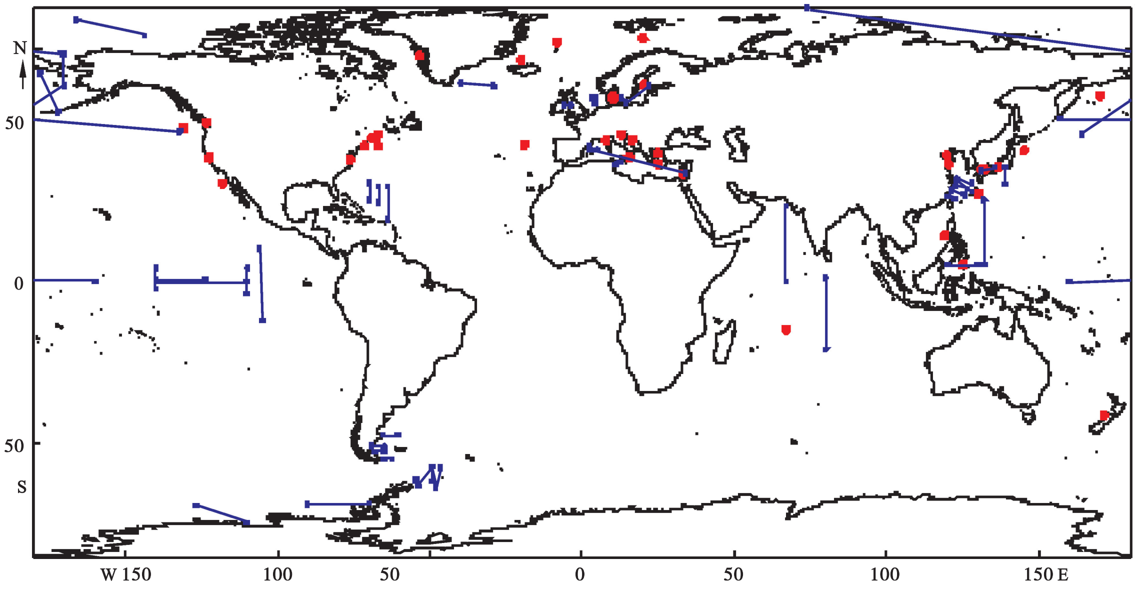

图 2　纤毛虫丰度和生物量垂直分布的研究海区分布示意图

Fig. 2　Global distribution of studies about vertical distribution of ciliate abundance and biomass

(Beers & Stewart, 1969, 1971; Taniguchi, 1977, 1984; Takahashi & Hoskins, 1978; Endo *et al.* , 1983; Revelante & Gilmartin, 1983; Revelante *et al.* , 1985; Sorokin *et al.* , 1985, 1996; Middlebrook *et al.* 1987; Sanders, 1987; Verity, 1987; Stoecker *et al.* , 1989; Dolan & Coats, 1990, 1991; Fenchel *et al.* , 1990; Putt, 1990; Simengando *et al.* , 1992; Alder & Boltovskoy, 1993; Nielsen *et al.* , 1993; Kivi & Kuosa, 1994; Dolan & Marrase, 1995; James & Hall, 1995; Leakey *et al.* , 1996; Uye *et al.* , 1996, 1998, 2000; Crawford & Lindholm, 1997; Sherr *et al.* , 1997, 2003; Levinsen *et al.* , 1999; Montagnes *et al.* , 1999, 2010; 张武昌和王荣, 2000; Perez, *et al.* 2000; Pitta & Giannakourou, 2000; Bojanić, *et al.* 2001; Pitta *et al.* , 2001; Chiang *et al.* , 2003; Kamiyama *et al.* , 2003; Mouritsen & Richardson, 2003; Ota & Taniguchi, 2003; Setala & Kivi, 2003; Karayanni *et al.* , 2005; Rollwagen-Bollens *et al.* , 2006; Gómez, 2007; Tanaka *et al.* , 2007; Chen & Yang, 2009; Sitran *et al.* , 2009; Andersen *et al.* , 2011; Hannachi *et al.* , 2011; Santoferrara *et al.* , 2011; Taylor *et al.* , 2011; Tsai *et al.* , 2011; Wickham *et al.* , 2011)。

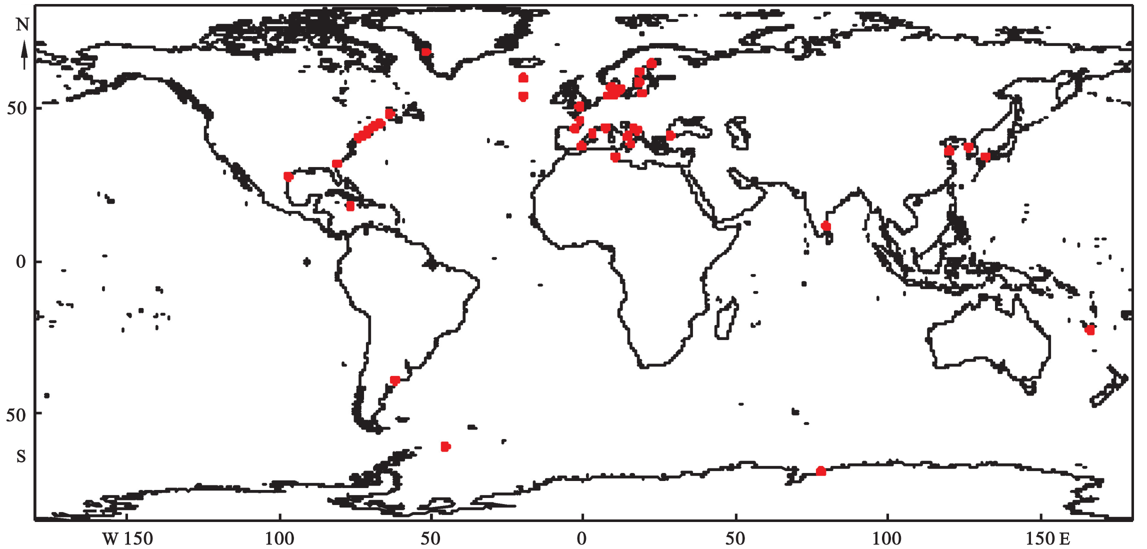

图 3　纤毛虫丰度和生物量周年变化的研究海区分布示意图

Fig. 3　Global distribution of studies about annual variation of ciliate abundance and biomass

(Zeitschel, 1967; Gold & Morales, 1975; Rassoulzadegan, 1977; Hargraves, 1981; Smetacek, 1981; Capriulo & Carpenter, 1983; Verity, 1986, 1987; Andersen & Sorensen, 1986; Middlebrook *et al.* 1987; Revelante & Gilmartin, 1987; Sanders, 1987; Montagnes *et al.* , 1988; Lynn *et al.* , 1991; Leakey *et al.* , 1992, 1993,1994; Buskey, 1993; Bernard & Rassouladegan, 1994; Kamiyama, 1994; Nielsen & Kiorboe, 1994; Kamiyama & Tsujino, 1996; Grey *et al.* , 1997; Tamigneaux *et al.* , 1997; Vaque *et al.* , 1997; Witek, 1998; Levinsen *et al.* , 2000; Bojanić *et al.* 2001 ,2005; Bojanić, 2001; Gilabert, 2001; Modigh, 2001; Godhantaraman, 2002; Levinsen & Nielsen, 2002; Modigh & Castaldo, 2002; Gómez & Gorsky, 2003; Urrutxurtu *et al.* , 2003; Balkis, 2004; Johansson *et al.* , 2004; Urrutxurtu, 2004; Dolan *et al.* , 2006; Samuelsson *et al.* , 2006; Vidjak *et al.* , 2007; Dupuy *et al.* , 2007; Yang *et al.* , 2008; Pettigrosso & Popovich, 2009; Sitran *et al.* , 2009; Kchaou *et al.* , 2009; Solić *et al.* , 2010; Verity & Borkman, 2010; 于莹等, 2011 ;Jiang *et al.* , 2011; Bojanić *et al.* , 2012; Loder *et al.* , 2012)。

3 纤毛虫丰度和生物量的垂直分布

3.1 分布特点

大部分深水海区,纤毛虫主要分布在水体的中上层,经常在表层或次表层出现丰度和生物量的高值。温带海区如东北大西洋的 Irish Sea(采样水深为 100 m 以浅),纤毛虫丰度在水体上层较高,随水深递减(Montagnes *et al.*,1999)。热带海区如印度洋西北部(采样水深为 200 m 以浅),纤毛虫主要分布在水体的上层(Leakey *et al.*, 1996)。极地海区的资料在南极(如 Kivi & Kuosa, 1994)和北极(如 Sherr *et al.*,2003)都有报道,如 Weddell Sea(采样水深为 80 m 以浅),纤毛虫丰度在 40 m 以上水体较高(Kivi & Kuosa, 1994);在北极 Chukchi Sea 及 Bering Sea(采样水深为 160 m 以浅),无壳纤毛虫主要分布在 50 m 以上水层,砂壳纤毛虫主要分布在表层(Taniguchi, 1984)。

在一些近岸浅水海区,如东北大西洋的 Aarhus Bay(水深为 16 m)(Mouritsen & Richardson, 2003)及东北太平洋的 San Francisco Estuary(水深为 10 m)(Rollwagen-Bollens *et al.*, 2006),纤毛虫在水体中的垂直分布通常较均匀。

有些海区纤毛虫趋向分布在水体底层,但这类情况并不多见。如东北大西洋的 Gulf of Hammamet(采样水深为 600 m 以浅),纤毛虫丰度和生物量从表层到底层增加(Hannachi *et al.*, 2011)。

3.2 季节变化

在不同的季节,水体呈现不同的理化特性,如层化现象的发生、缺氧的形成等,纤毛虫在水体中的垂直分布可能会随之发生变化,在不同的季节呈现不同的分布特点。如东北大西洋 Adriatic Sea 的寡营养海区,水体层化时期纤毛虫生物量在密度跃层以上较高;水体混合时期纤毛虫的垂直分布较均匀(Revelante *et al.*, 1985)。在西北大西洋的 Chesapeake Bay,春季底部缺氧形成之前,纤毛虫丰度在底层较大;夏季缺氧形成后,纤毛虫主要分布在水体上层(Dolan & Coats, 1991)。

4 纤毛虫丰度和生物量的周年变化

4.1 丰度和生物量

大多数海区纤毛虫的丰度和生物量呈现双峰型,一般在春季、夏季或春季、秋季达到峰值,冬季往往较低。这类情况主要出现在温带海区,如西北大西洋的 Gulf of Maine(Montagnes *et al.*, 1988)及东北大西洋的 Southampton 近岸(Leakey *et al.*, 1992),纤毛虫的丰度和生物量均出现春季和夏季 2 个峰值。东北大西洋的 Kattegat 纤毛虫丰度呈现春季和秋季 2 个峰值(Nielsen & Kiorboe, 1994)。东北大西洋的 Kiel Bight 纤毛虫生物量呈现春季和秋季 2 个峰值(Smetacek, 1981)。

一些海区纤毛虫的丰度和生物量呈现单峰型,但不同海区出现峰值的时间没有统一的规律,可能在春季、夏季或者秋季达到峰值,冬季往往较低。这类情况在温带、热带及极地海区均有报道,温带海区如东北大西洋的 Baltic Sea,纤毛虫生物量在春季出现峰值(Johansson *et al.*, 2004)。热带海区如印度东南沿岸河口区,砂壳纤毛虫丰度和生物量均在夏季达到峰值(Godhantaraman, 2002)。极地海区如南极 Borge Bay(Leakey *et al.*, 1994)和 Ellis Fjord(Grey *et al.*, 1997),纤毛虫丰度夏季较高,冬季较低。

4.2 群落结构

纤毛虫群落的粒级组成一般春季较大,夏季较小,如 Gulf of Maine(Montagnes *et al.*, 1988),及东北大西洋的 Gdansk Basin(Witek, 1998)。也有一些海区呈现相反的趋势,如 Southampton 近岸(Leakey *et al.*, 1992)和东北大西洋的 Kaštela Bay(Bojanić, 2001; Bojanić *et al.*, 2001),纤毛虫粒级夏季较大。

砂壳纤毛虫种类数一般在夏季或秋季最多。如西北大西洋的 Narragansett Bay(Hargraves, 1981)和 Hiroshima Bay(Kamiyama *et al.*, 1996),砂壳纤毛虫种类数夏季最多;Baltic Sea(Johansson *et al.*, 2004)及 Kaštela Bay(Bojanić *et al.*, 2005),砂壳纤毛虫种类数在秋季最多。

砂壳纤毛虫丰度一般在温度较高的季节较高,尤其是在近岸海区的夏季或者秋季,砂壳纤毛虫丰度可能会超过无壳纤毛虫丰度占优势(Leakey *et al.*, 1994)。如砂壳纤毛虫丰度占纤毛虫总丰度的比例在夏季最高(57%)(于莹等, 2011)。

5 纤毛虫丰度和生物量时空分布的影响因素

纤毛虫丰度和生物量的时空分布可能受非生物因子和生物因子 2 大类因素的影响。非生物因子主要包括温度、盐度等;生物因子主要包括饵料(如浮游植物、鞭毛虫、腰鞭毛虫、细菌及蓝细菌等)和摄食者(如桡足类等后生动物)。

温度可能影响纤毛虫丰度的季节变化,而盐度可能影响纤毛虫的地理分布(Kršinić, 1980)。在 Nervión River 河口区,砂壳纤毛虫丰度与温度正相关,在温度较高的季节丰度较高;砂壳纤毛虫趋向分布在河口的向海一侧,这可能是受盐度和浊度的共同影响(Urrutxurtu, 2004)。

纤毛虫丰度和生物量的周年变化及空间分布模式通常与浮游植物(Chl-a)、细菌等饵料的周年变化及空间分布模式吻合,两者之间常常表现出明显的正相关,这可能是由于纤毛虫与浮游植物、细菌等之间存在较为紧密的摄食和被摄食的营养关系(Montagnes *et al.*, 2010)。如南极 Signy Island 近岸海区,纤毛虫丰度和生物量的季节变化与 Chl-a 浓度及细菌的生物量相吻合(Leakey *et al.*, 1994)。Hiroshima Bay 湾内较高的纤毛虫丰度与较高的 Chl-a 浓度相对应 (Kamiyama, 1994)。在 Kaštela Bay,纤毛虫与浮游植物及细菌的垂直分布吻合,均趋向于分布在水体的上层 (Bojanić *et al.*, 2001)。

除了饵料,后生动物的摄食对纤毛虫丰度和生物量的影响可能也较大。如 Kaštela Bay,饵料及后生动物的摄食可能共同影响纤毛虫丰度的周年变化(Bojanić *et al.*, 2001)。在北极 Disko Bay 纤毛虫生物量随浮游植物在次表层出现最大值,其原因可能与饵料及桡足类的摄食有关(Levinsen *et al.*, 1999)。

6　存在的问题及展望

目前关于纤毛虫丰度和生物量时空分布的资料在世界各海区均有报道,但大部分研究集中在温带海区,热带和极地海区的研究尚不充分。随着海洋调查项目的日益增多,海洋调查技术的进一步提高,向热带和极地海区的深入探索应该是未来需要加强的方向之一。

纤毛虫丰度和生物量的变化可能受温度、盐度、饵料及摄食者等影响,但由于这些影响因素大都通过相关性分析得到,其结果只在一定程度上说明纤毛虫与环境因子间的变化关系(Sanders, 1987),要进一步了解影响纤毛虫丰度和生物量变化的内在机制,还需要通过开展相关的培养、摄食实验进行验证。

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作者简介　于　莹,女,1986 年生,博士研究生,主要从事海洋浮游动物生态学。E-mail: yuyingxlf001@163.com
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