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渤海湾浮游纤毛虫丰度和生物量的周年变化

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摘要:为了解渤海湾浮游纤毛虫丰度、生物量和种类组成的周年变化,于 2019 年 7 月—2020 年 6 月在渤海湾一个站位进行每月 1 次共 12 个航次浮游纤毛虫样品的采集。样品按照 Utermöhl 方法进行分析,通过倒置显微镜镜检,计算纤毛虫的丰度和生物量。无壳纤毛虫和砂壳纤毛虫出现峰值的时间不同,无壳纤毛虫丰度和生物量均在 4 月和 8 月呈现双峰值,砂壳纤毛虫丰度和生物量均在 7 月出现单峰值。周年砂壳纤毛虫丰度占纤毛虫总丰度的比例平均为(28.6±32.6)%,5—7 月较高,均超过 50%。共鉴定砂壳纤毛虫 6 属 21 种,其中拟铃虫属(*Tintinnopsis*)种类最多,6—8 月砂壳纤毛虫种类数最高。砂壳纤毛虫种类组成呈现明显的周年变化,温度是驱动砂壳纤毛虫群落周年变化的主要环境因子。砂壳纤毛虫群落 Shannon 指数的平均值为 0.95±0.78,Pielou 指数的平均值为 0.52±0.34,均在 6—8 月较高。除无壳纤毛虫外,砂壳纤毛虫丰度、纤毛虫总丰度和砂壳纤毛虫丰度占纤毛虫总丰度的比例均与温度、Chl a 浓度呈显著的正相关,与盐度呈显著的负相关。

关键词:浮游纤毛虫;丰度;生物量;周年变化;渤海湾

Annual variation of abundance and biomass of planktonic ciliates in the Bohai Bay, China

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Abstract: To understand annual variation of abundance and biomass of planktonic ciliates in the Bohai Bay, ciliates were sampled monthly at a fixed station from July 2019 to June 2020. A 1-L sample of surface water was collected with a 2.5 L Niskin water sampler and fixed in 1% acid Lugol's iodine solution. Water samples were pre-concentrated using the Utermöhl method and observed under an Olympus IX71 inverted microscope at 100× or 400 ×magnification. The dimensions of the ciliates were measured and the cell volume of each species was estimated using appropriate geometric shapes. The carbon: volume ratio used to calculate biomass was 0.19 pg C/μm^3. Aloricate ciliates were divided into three classes according to the

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size of cell volume. The classification of tintinnids was based on taxonomic literature. The average abundance of aloricate ciliates was (1382±1929) ind/L, ranging from 137 ind/L to 6748 ind/L. The average biomass of aloricate ciliates was (2.29±3.05) μg C/L, ranging from 0.09 μg C/L to 10.83 μg C/L. The average tintinnid abundance was (946±2384) ind/L, ranging from 0 ind/L to 8440 ind/L. The average tintinnid biomass was (3.86±11.57) μg C/L, ranging from 0.00 μg C/L to 40.57 μg C/L. The average abundance of total ciliates was (2328±2735) ind/L, ranging from 143 ind/L to 8577 ind/L. The average biomass of total ciliates was (6.15±11.35) μg C/L, ranging from 0.09 μg C/L to 41.02 μg C/L. Both abundance and biomass of aloricate ciliates and tintinnids showed strong annual variations throughout the year. Two peaks of aloricate ciliates were observed in April and August, respectively. Tintinnid abundance and biomass peaked in July. Tintinnids occupied (28.6±32.6)% of total ciliate abundance, being higher (>50%) from May to July. Twenty one tintinnid species were identified, 13 of which were in genus *Tintinnopsis*. The dominant species were *Leprotintinnus simplex*, *Leprotintinnus nordqvisti* and *Tintinnidium primitivum*. Species number of tintinnids showed higher level from June to August. Species composition of tintinnids exhibited obvious annual variation, and temperature was the main environmental factor driving the annual variation of tintinnid community. The average value of the Shannon index and Pielou index of tintinnid community were 0.95±0.78 and 0.52±0.34, respectively. Both Shannon index and Pielou index of tintinnid community were higher from June to August. There were not significant relationships between aloricate ciliate abundance and environmental factors. Tintinnid abundance, total ciliate abundance, and the percentage of tintinnids to total ciliate abundance were significantly positively correlated with temperature and Chl a concentration, while negatively correlated with salinity.

Key Words: planktonic ciliate; abundance; biomass; annual variation; Bohai Bay

作为海洋微食物网的重要组成类群[1—2],浮游纤毛虫粒径较小(5—200 μm),主要包括营浮游生活的无壳寡毛类纤毛虫和砂壳纤毛虫两大类,分别隶属于纤毛门(Ciliophora Doflein),旋毛纲(Spirotrichea Bütschli)下的寡毛亚纲(Oligotrichia Bütschli)及环毛亚纲(Choreotrichia Small & Lynn)[3]。

温带近岸海区的浮游纤毛虫丰度和生物量呈现明显的季节波动,一年之中往往呈现双峰值,一般在春季和夏季[4]或春季和秋季[5]达到高峰。无壳纤毛虫通常在浮游纤毛虫中占绝对优势,砂壳纤毛虫占浮游纤毛虫丰度的比例一般<10%[6—7],砂壳纤毛虫偶尔在温度较高的夏季或秋季超过无壳纤毛虫丰度占优势[8—10]。

渤海湾位于渤海西部,面积约为 $1.47\times10^4 km^2$,平均水深 12.5 m,海水交换能力弱,是一个典型的半封闭性浅水海湾。于莹等[11—12]对渤海湾浮游纤毛虫丰度和种类的季节变化有过调查,但没有完整的周年变化资料。本研究于 2019 年 7 月—2020 年 6 月在渤海湾天津近岸海域进行浮游纤毛虫丰度和生物量的周年调查,为渤海湾浮游生态系统研究提供基础数据和参考资料。

1　材料和方法

2019 年 7 月—2020 年 6 月在渤海湾固定站位(117°59′E,39°02′N,水深 9—12 m,图 1)进行每月 1 次(2019 年 7 月 22 日、8 月 23 日、9 月 23 日、10 月 21 日、11 月 25 日、12 月 23 日、2020 年 1 月 16 日、2 月 24 日、3 月 20 日、4 月 19 日、5 月 25 日及 6 月 22 日)共 12 个航次纤毛虫样品的采集。

用 YSI Professional Plus 便携式水质分析仪测定表层海水的温度和盐度。采集表层水样 500 mL,用 GF/F 滤膜过滤,滤膜置于-20℃冰箱保存。滤膜带回实验室用 90%丙酮低温(0 ℃)萃取 24 h 后,用分光光度计测量叶绿素 *a*(Chl a)浓度。

采集表层水样 1 L,用 Lugol′s 液固定(终浓度 1%)。样品分析按照 Utermöhl 方法[13]进行,自然沉淀至少 48 h,虹吸后剩余约 150 mL,于阴凉处保存。取 16 mL 放于沉降杯内,在 Olympus IX71 倒置显微镜下 100 倍或 400 倍镜检,记录无壳纤毛虫和砂壳纤毛虫(不计空壳)的个数。测量纤毛虫虫体的体长、体宽等,按最接近的几何形状(如柱体、球体和锥体)计算体积。生物量由体积乘转换系数($0.19\ pg\ C/\mu m^3$)[14]得来,砂壳纤毛虫

体积直接按照肉体体积计算。

按照纤毛虫细胞体积的大小将无壳纤毛虫分成3种粒级:小型无壳纤毛虫(ACI, 10^3—10^4 μm^3)、中型无壳纤毛虫(ACII, 10^4—10^5 μm^3)及大型无壳纤毛虫(ACIII, >10^5 μm^3)[15]。砂壳纤毛虫根据文献[16]鉴定到种,按照砂壳纤毛虫种类出现的季节规律,将砂壳纤毛虫分为周年出现种、冬季种、春季种、夏季种及秋季种五大类[17]。

根据徐兆礼等[18]的公式计算优势度(Y),Y>0.02时,该种为优势种。砂壳纤毛虫群落的多样性采用Shannon指数(H')[19],均匀度采用Pielou指数(J)[20]。

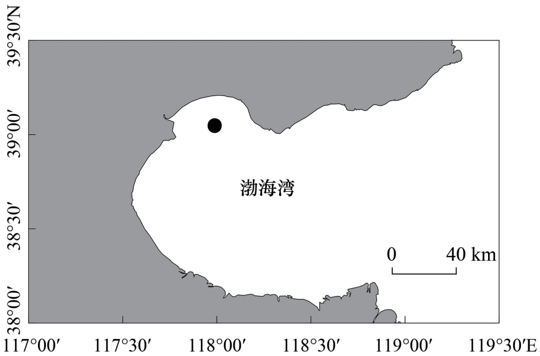

图1 采样站位图

Fig.1 Location of the sampling station

采用R语言的vegan程序包进行砂壳纤毛虫群落结构和环境因子的Mantel检验,经过9999次排列得到统计结果,置信度设为95%;采用SPSS 20.0进行纤毛虫丰度和生物量与环境因子的相关性分析,运用Pearson相关分析方法,置信度设为95%。

2 结果

2.1 环境因子

表层海水温度、盐度和Chl a浓度呈现明显的周年变化。年平均温度为(14.15±9.79) ℃(平均值±标准差,下同),1月最低(2.35 ℃),7月最高(29.60 ℃);年平均盐度为31.53±0.44,夏秋季较低,其中7月最低(30.76);年平均Chl a浓度为(3.67±4.19) μg/L,一年之中出现两个峰值,分别在3月(5.53 μg/L)和7月(15.29 μg/L,图2)。

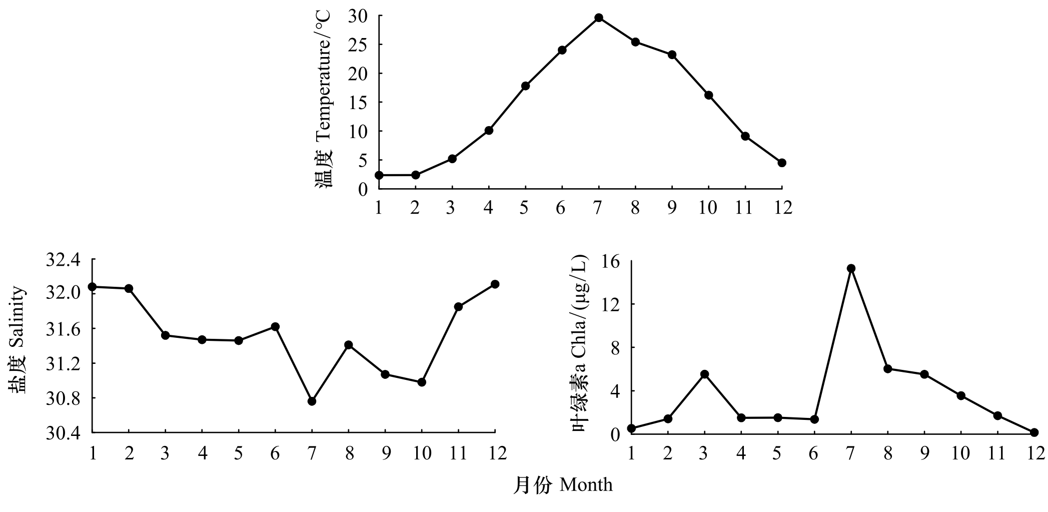

图2 温度、盐度及Chl a浓度的周年变化

Fig.2 Annual variation of water temperature, salinity and Chl a concentration

2.2 纤毛虫丰度和生物量

无壳纤毛虫年平均丰度为(1382±1929)个/L(137—6748 个/L),年平均生物量为(2.29±3.05) μg C/L(0.09—10.83 μg C/L),丰度和生物量均在4月和8月呈现双峰值;砂壳纤毛虫年平均丰度为(946±2384) 个/L(0—8440 个/L),年平均生物量为(3.86±11.57) μg C/L(0.00—40.57 μg C/L),丰度和生物量均在7月出现最高值;总纤毛虫年平均丰度为(2328±2735) 个/L(143—8577 个/L),年平均生物量为(6.15±

11.35) μg C/L(0.09—41.02 μg C/L),丰度和生物量均在 4 月和 7 月呈现双峰值(图 3)。

砂壳纤毛虫占纤毛虫总丰度的比例平均为(28.6±32.6)%,5—7 月较高,占比均超过 50%,其中 7 月最高(98.4%)。

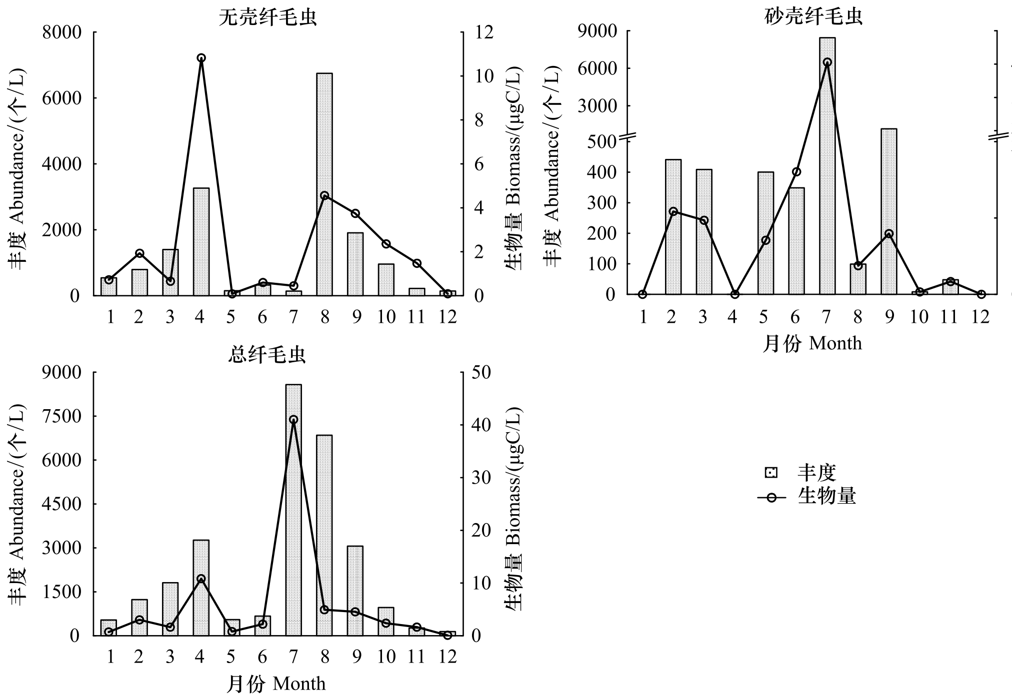

图 3　无壳纤毛虫、砂壳纤毛虫及总纤毛虫丰度和生物量的周年变化

Fig.3　Annual variation of abundance and biomass of aloricate ciliates, tintinnids and total ciliates

2.3　无壳纤毛虫粒级结构

无壳纤毛虫粒级结构没有呈现明显的季节规律。ACI 在无壳纤毛虫丰度中占绝对优势,占无壳纤毛虫丰度的比例平均为(76.7±25.1)%;ACII 占无壳纤毛虫丰度的比例平均为(20.6±25.2)%;ACIII 占无壳纤毛虫丰度的比例最小,平均值为(2.7±4.9)%(图 4)。

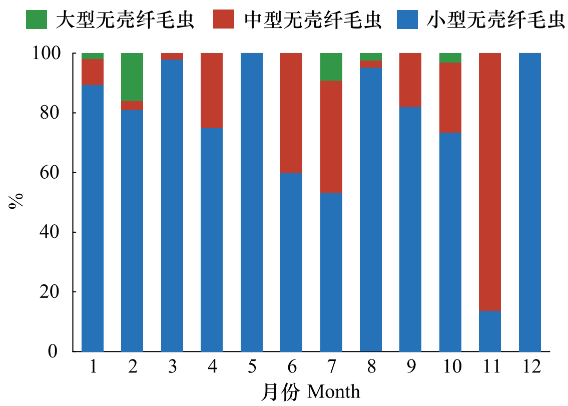

图 4　无壳纤毛虫粒级组成的周年变化

Fig.4　Annual variation of size classes of aloricate ciliates

2.4　砂壳纤毛虫群落

2.4.1　种类组成

共鉴定砂壳纤毛虫 6 属 21 种(表 1),其中拟铃虫属(*Tintinnopsis*)种类最多(13 种)。优势种为简单薄铃虫(*Leprotintinnus simplex*, Y = 0.08)、诺氏薄铃虫(*Leprotintinnus nordqvisti*, Y = 0.04)和原始筒壳虫(*Tintinnidium primitivum*, Y=0.03)。砂壳纤毛虫种类数在 6—8 月较高,7 月最高(10 种)。

丰度较高(丰度占砂壳纤毛虫总丰度的比例>2%)的种类有 10 种,为简单薄铃虫(36.9%)、诺氏薄铃虫(19.5%)、原始筒壳虫(11.0%)、直颈拟铃虫(*Tintinnopsis directa*, 8.2%)、寇氏拟铃虫(*Tintinnopsis kofoidi*, 7.0%)、波罗的拟铃虫(*Tintinnopsis baltica*, 3.2%)、罗氏拟铃虫(*Tintinnopsis lohmanni*, 2.8%)、根状拟铃虫(*Tintinnopsis radix*, 2.8%)、布氏拟铃虫(*Tintinnopsis butschlii*, 2.6%)及三亚类杯虫(*Metacylis sanyahensis*, 2.0%)。其中,寇氏拟铃虫只在温度较低(2.4—5.2℃)的冬季出现,是冬季种。波罗的拟铃虫只在温度为

17.8℃的春季出现,是春季种。原始筒壳虫在春季和夏季均有发现,在夏季(>23.2℃)丰度较高;三亚类杯虫、布氏拟铃虫、罗氏拟铃虫、根状拟铃虫、诺氏薄铃虫、简单薄铃虫及直颈拟铃虫只在温度较高(>23.2℃)的夏季出现,是夏季种(图 5)。

2.4.2 群落结构

砂壳纤毛虫种类组成周年变化明显,不同种群出现季节更替。2、3 月寇氏拟铃虫占优,5 月波罗的拟铃虫占优,6 月三亚类杯虫占优,7 月简单薄铃虫、诺氏薄铃虫及直颈拟铃虫丰度较高,8 月长形旋口虫(*Helicostomella longa*)及原始筒壳虫丰度较高,9 月原始筒壳虫占优,10 月卡拉直克拟铃虫(*Tintinnopsis karajacensis*)占比 100%,11 月筒状拟铃虫(*Tintinnopsis tubulosoides*)及爱氏网纹虫(*Favella ehrenbergii*)占优(图 6)。Mantel 检验表明,驱动砂壳纤毛虫群落周年变化的主要环境因子是温度,次要因子是盐度(表 2)。

砂壳纤毛虫群落 Shannon 指数的平均值为 0.95±0.78,在 6—8 月较高,7 月最高(2.11);Pielou 指数的平均值为 0.52±0.34,在 6—8 月及 12 月较高,12 月最高(1.00)。

表 1 渤海湾砂壳纤毛虫种类

Table 1 Species list of tintinnids in the Bohai Bay

物种名 Species	最大丰度 Maximum abundance/(个/L)	出现的月份 Occurrence month	口径范围 Lorica oral diameter/μm
爱氏网纹虫 *Favella ehrenbergii*	22	11	64—68
巴拿马网纹虫 *F. panamensis*	79	7	>80
长形旋口虫 *Helicostomella longa*	43	8	20—24
诺氏薄铃虫 *Leprotintinnus nordqvisti*	2568	7△,8,9	40—44
简单薄铃虫 *L. simplex*	4780	7△,8,9	52—56
卵形类杯虫 *Metacylis oviformis*	56	6	32—36
三亚类杯虫* *M. sanyahensis*	224	6	48—52
原始筒壳虫 *Tintinnidium primitivum*	984	5,7,8,9△	28—32
波罗的拟铃虫 *Tintinnopsis baltica*	413	5	32—36
巴西拟铃虫 *T. brasiliensis*	56	5	40—44
布氏拟铃虫 *T. butschlii*	375	6,7△	76—80
直颈拟铃虫 *T. directa*	1067	7	40—44
卡拉直克拟铃虫 *T. karajacensis*	119	7△,10	36—40
寇氏拟铃虫 *T. kofoidi*	485	2△,3	32—36
罗氏拟铃虫 *T. lohmanni*	336	6,7△	44—48
矮小拟铃虫 *T. nana*	21	8	20—24
根状拟铃虫 *T. radix*	316	6,7△	44—48
圆锥拟铃虫 *T. rapa*	42	3	20—24
斯氏拟铃虫 *T. schotti*	14	7,8△	>80
妥肯丁拟铃虫 *T. tocantinensis*	40	7	24—28
筒状拟铃虫 *T. tubulosoides*	26	2,3,11△	32—36

*:渤海的新纪录种;△:最大丰度出现的月

表 2 砂壳纤毛虫群落结构(用 Bray-Curtis 相异度测量)和环境因子的 Mantel 检验

Table 2 Mantel test between tintinnid community (measured as Bray-Curtis dissimilarity) and environmental factors

环境因子 Environmental factor	群落距离 Community distance	
	P	*R*
温度 Temperature/℃	<0.001	0.39
盐度 Salinity	0.045	0.13
Chl a 浓度 Chl a concentration/(μg/L)	0.863	-0.09

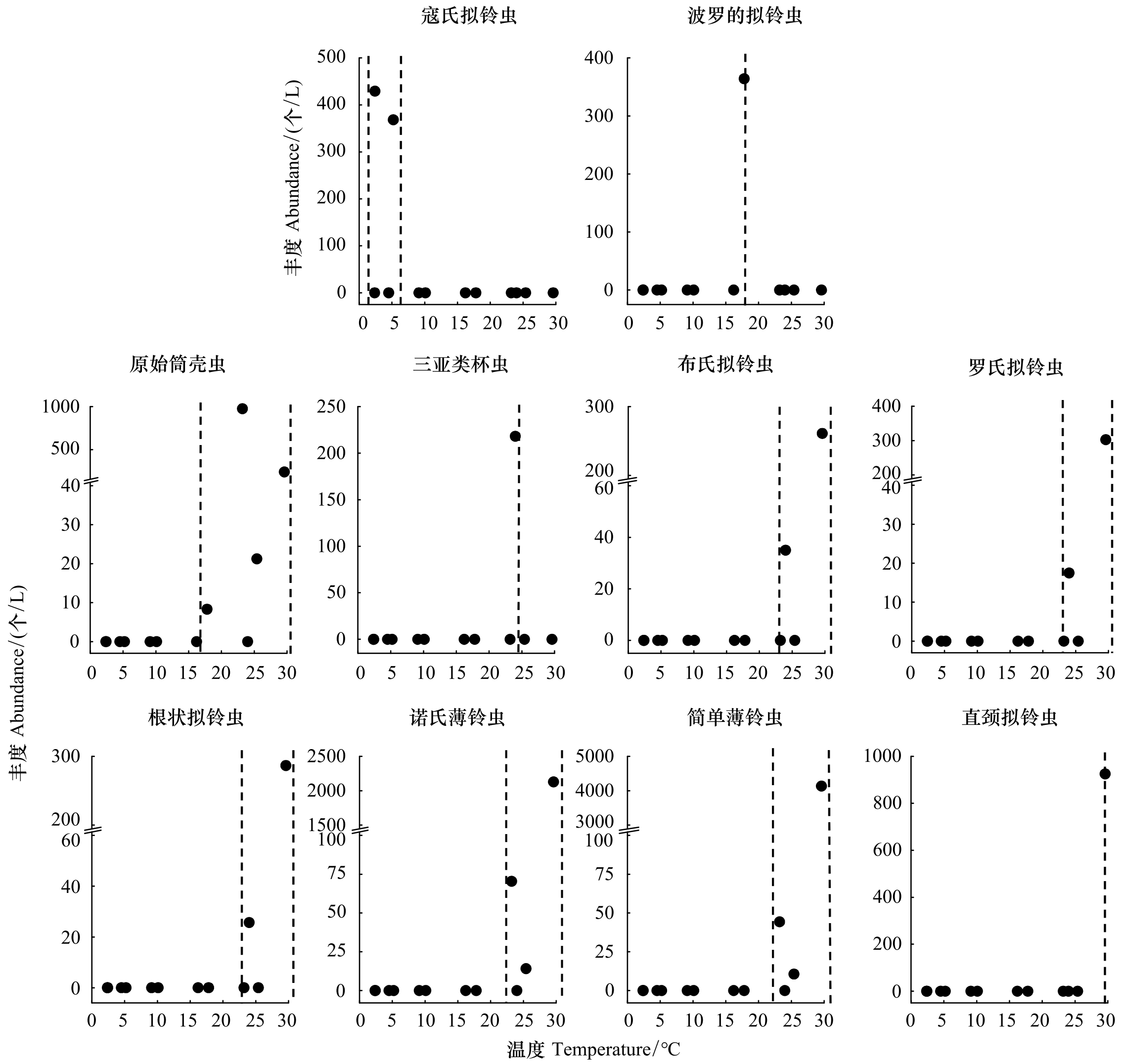

图 5　丰度较高砂壳纤毛虫种类出现的温度范围

Fig.5　Temperature range in which abundant tintinnids occurred

2.5　纤毛虫与环境因子相关性分析

无壳纤毛虫丰度与温度、盐度和 Chl a 浓度均没有明显相关性。砂壳纤毛虫丰度、纤毛虫总丰度及砂壳纤毛虫占纤毛虫总丰度的比例均与温度呈极显著的正相关;砂壳纤毛虫丰度和纤毛虫总丰度均与盐度呈极显著的负相关,砂壳纤毛虫占纤毛虫总丰度的比例与盐度呈显著的负相关;砂壳纤毛虫丰度、纤毛虫总丰度及砂壳纤毛虫占纤毛虫总丰度的比例均与 Chl a 浓度呈极显著的正相关(表 3)。

3　讨论

近年来,多数研究主要关注纤毛虫丰度、种类组成与环境因子的关系[21—23]及物理过程如水团等对纤毛虫丰度分布的影响[24—27],只有少数研究关注纤毛虫群落组成长时间序列的变化[28—29]。本文在渤海湾近岸海区开展纤毛虫丰度和种类组成的周年调查,补充渤海湾纤毛虫长时间序列的数据。

与其它海区相比,本次调查中纤毛虫丰度和生物量均处在已有文献的范围之内(0—145000 个/L,0—400 μg C/L)[30];与之前渤海湾的研究[11—12]相比,本次调查中无壳纤毛虫丰度相差不大,砂壳纤毛虫丰度明显较高;与獐子岛海区[31]、胶州湾[9]周年资料对比(表 4),渤海湾纤毛虫丰度较低,砂壳纤毛虫丰度占纤毛虫总丰度的比例稍高。

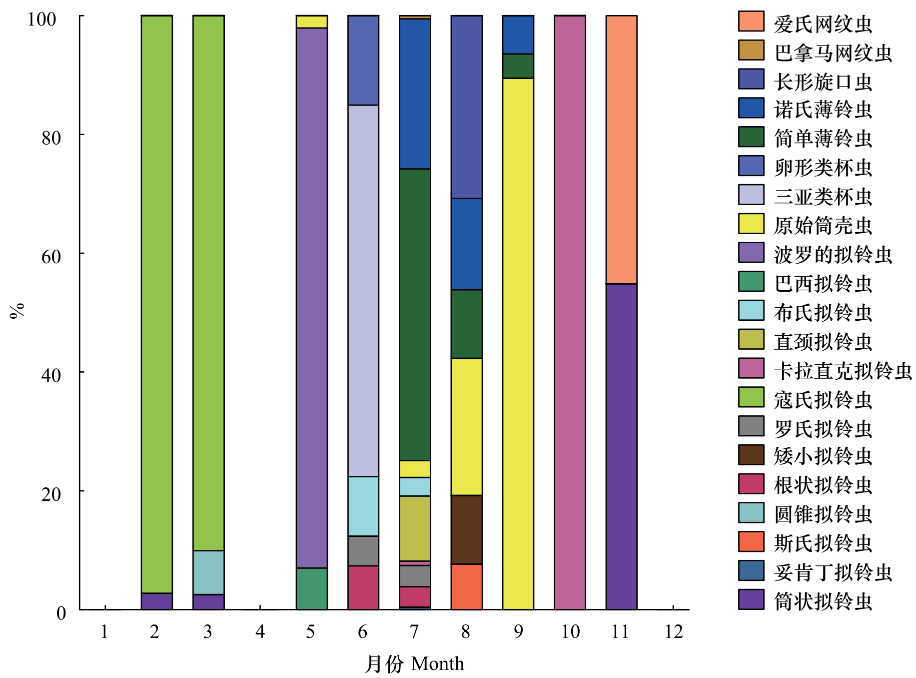

图 6 砂壳纤毛虫种类组成的周年变化

Fig.6 Annual variation of species composition of tintinnids

表 3 纤毛虫丰度及砂壳纤毛虫占纤毛虫总丰度的比例与温度、盐度及 Chl a 浓度的相关性分析

Table 3 Correlation between ciliate abundance, and percentage of tintinnids to total ciliate abundance and water temperature, salinity and Chl a concentration

	温度 Temperature/℃	盐度 Salinity	Chl a 浓度 Chl a concentration/(μg/L)
无壳纤毛虫丰度 Aloricate ciliate abundance/(个/L)	0.261	−0.168	0.126
砂壳纤毛虫丰度 Tintinnid abundance/(个/L)	0.526 **	−0.577 **	0.878 **
纤毛虫总丰度 Total ciliate abundance/(个/L)	0.636 **	−0.614 **	0.840 **
砂壳纤毛虫丰度比例 Percentage of tintinnids to total ciliate abundance/%	0.549 **	−0.438 *	0.565 **

*:差异显著($P<0.05$);**:差异极显著($P<0.01$)

表 4 我国海区浮游纤毛虫群落的周年变化数据

Table 4 Annual studies of planktonic ciliate communities in China seas

海区 Region	采样时间 Date	纤毛虫丰度 Abundance/ (个/L)	纤毛虫生物量 Biomass/ (μg C/L)	砂壳纤毛虫 种类数 Species number	砂壳纤毛虫 丰度比例 Percentage/%	文献 Source
莱州湾	2011-05—2011-11; 2012-03—2012-04	0—318 *	—	26	—	[32]
獐子岛	2009-07—2010-06	166—26625	0.05—38.29	23	6.6	[31]
胶州湾	2007-01—2007-12	41—31077	0.06—99.37	38	25	[9]
渤海湾	2019-07—2020-06	143—8577	0.09—41.02	21	28.6	本研究

*:砂壳纤毛虫丰度

3.1 纤毛虫丰度和生物量的周年变化

本研究中纤毛虫丰度和生物量分别在春季和夏季出现峰值,表现出典型的温带近岸海区的周年变化规

律。温带近岸海区如 Gdansk Basin[33]、Kaštela Bay[34]、胶州湾[9]等,纤毛虫丰度和生物量通常在春、夏季或者春、秋季呈现双峰型,这可能与饵料水平(Chl a 浓度)的周年变化密切相关。与多数研究类似[35—37],渤海湾纤毛虫丰度和生物量与 Chl a 浓度呈极显著的正相关,其两个峰值与 Chl a 浓度的峰值基本吻合,稍有滞后,这说明上行控制在渤海湾纤毛虫丰度和生物量周年变化中扮演重要的角色。

渤海湾无壳纤毛虫和砂壳纤毛虫出现峰值的时间存在较大差异,这可能是由于无壳纤毛虫和砂壳纤毛虫在不同营养条件下的竞争力不同导致的。砂壳纤毛虫摄食的饵料粒级较大(多为 nano 级浮游植物),且由于肉体外具壳需要的饵料更多,因此在寡营养条件下(pico 级浮游植物占优)生长能力较低[38];在较高饵料条件下(nano 级浮游植物占优),砂壳纤毛虫具有更高的竞争力,丰度往往较高,有时会超过无壳纤毛虫在丰度上占优势[39]。本研究中 7 月砂壳纤毛虫丰度高达 8440 个/L,远超无壳纤毛虫占绝对优势,这可能与 7 月较高水平的饵料条件(用 Chl a 浓度指示)有关。

3.2　砂壳纤毛虫种类

渤海湾砂壳纤毛虫各种类只在某些月份出现,不同种群更替有序,砂壳纤毛虫群落组成呈现明显的周年变化。与莱州湾的研究结果[32]不同,本次渤海湾调查中只记录了冬季种、春季种及夏季种,没有发现周年出现种。

本研究中大部分砂壳纤毛虫丰度都偏向在温度较高的夏季较高,值得注意的两种砂壳纤毛虫——波罗的拟铃虫和寇氏拟铃虫,其偏好的水温较低(低于 18℃)。波罗的拟铃虫只在水温为 17.8 ℃的 5 月出现,其他月没有记录,这说明波罗的拟铃虫偏好温度适中的环境,在温度较高或较低时不适合生长[40]。寇氏拟铃虫只在温度低于 5.2 ℃的 2、3 月出现,是一种喜低温的砂壳纤毛虫,这与胶州湾的研究结果[41]不同,胶州湾寇氏拟铃虫一般在温度为 5—15 ℃时丰度较高。这种差异可能是由于本研究采样站位单一的局限性导致,需要在今后积累更大范围的样品来得出更准确的结论。喜低温砂壳纤毛虫种类的出现可以作为冷水团的指示种,在浮游纤毛虫与物理过程的耦合关系研究中发挥重要的指示作用。

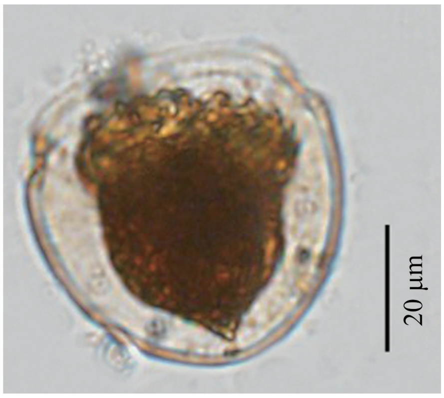

图 7　三亚类杯虫显微照片

Fig.7　Micrograph of *Metacylis sanyahensis*

3.3　渤海的新纪录种——三亚类杯虫

本研究在渤海首次纪录到三亚类杯虫(图 7),该种类为南方种[42],一般在我国近岸 36°N 以南海区有发现,如胶州湾[42]、东海[43—44]及南海近岸[45—46],本研究第一次在我国 36°N 以北海区纪录到三亚类杯虫,且与其它海区相比,渤海湾三亚类杯虫个体稍大(表 5)。

表 5　我国海区的三亚类杯虫

Table 5　*Metacylis sanyahensis* in China seas

海区 Region	壳长 Lorica length/μm	口径 Lorica oral diameter/μm	最大丰度 Maximum abundance/(个/L)	出现的月份 Occurrence month	水温 Temperature/℃	文献 References
胶州湾	28	48	—	8	—	[42]
东海	24—26	22—24	1	12	19.4	[43]
东海	41—43	40—42	39	8	27.0	[44]
海南岛	38—42.5	38—40	—	—	—	[45]
南海	30—32	22—24	181	8	28.3	[46]
渤海湾	48—49	46—48	224	6	24.0	本研究

现有资料表明,三亚类杯虫在我国海区丰度不高,出现频率也较低,一般趋向分布在温度较高的夏季,在其它季节很少观测到。作为喜高温的南方种,三亚类杯虫北移,在渤海湾出现,可能与全球变暖有关,可以作为暖水团的指示种在微型浮游动物与水团的耦合关系研究中发挥重要的指示作用。

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