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A survey of ciliates at the long-term sampling station "Helgoland Roads", North Sea

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Abstract This study presents a new checklist of ciliates at the long-term sampling station Helgoland Roads. The work is based on a microzooplankton monitoring programme from January 2007 to June 2009 and a ciliate monitoring programme from June 2010 to May 2012. The checklist includes 89 ciliate taxa from 46 different genera. The total abundance of the ciliate community at Helgoland Roads ranged between 0.14 and 67.7×10^3 cells L^{-1} with a distinct peak in June. The total carbon biomass ranged between 0.2 and 234.6 µg C L^{-1}. The ciliate community showed a clear temporal succession pattern during the monitoring periods. The present study is not only the first detailed and updated list of ciliates at Helgoland Roads, but also provides information on seasonality, i.e. the temporal variation of species composition, abundance and carbon biomass as well as information on the biogeographic distribution of dominant ciliates in comparison with other relevant studies.

Keywords Plankton · North Sea · Seasonality · Biogeographic distribution · Helgoland Reede

Introduction

It is recognized that microzooplankton plays an important role in the microbial food web: on one hand as dominant grazers of phytoplankton and on the other hand as an important link from the microbial loop to higher trophic levels (Azam et al. 1983; Sherr and Sherr 1987; Vargas et al. 2007, 2008; Löder et al. 2012). Ciliates make up a substantial proportion in terms of numbers as well as biomass and thus play a crucial role in microzooplankton communities (Finlay et al. 1979, 1988; Pratt and Cairns 1985; Edwards and Burkill 1995). Ciliates are commonly referred to as a taxonomic group with multiple ecological functions in the marine food web (Lynn 2008). They are primary grazers on pico- and nanoplankton within the size range of 0.2–20 µm, and meanwhile, they also serve as important food source for metazoans, such as copepods (Gifford 1991; Pierce and Turner 1992; Legendre and Rassouldezgan 1995; Xu et al. 2008; Löder et al. 2011). Some ciliates that harbour algal endosymbionts or plastids from ingested algal prey are mixotrophic and function as primary producers (Laval-Peuto et al. 1986; Stoecker et al. 1987). Some ciliates live as epibionts, and some parasitic ciliates are pathogenic to aquatic organisms, such as sea urchin and fish (Song et al. 2003). Ciliates also play a significant role in regulating bacterial populations (Song et al. 2009) and regenerating nutrients (Dolan 1997). They are commonly used as bioindicators on water quality since they can be sensitive to marine pollution due to their short generation time and delicate membranes (Caspers and Karbe 1967; Sládeček 1973; Song et al. 2009; Xu et al. 2011).

Marine research has a long tradition at Helgoland resulting in a unique data set of over 50 years long of comprehensive physical, chemical and biological data of the North Sea with a work-daily resolution (Franke et al. 2004; Greve et al. 2004; Wiltshire and Dürselen 2004; Wiltshire and Manly 2004). Although ciliates have received much attention over the last decades, no ciliate

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taxa had been recorded in the routine programme at Helgoland Roads before 1999. By 2007, some ciliates (*Myrinecta rubra*, *Laboea strobila* and *Mesodinium pulex*) were recorded routinely (www.pangaea.de). As a part of the assessment of the necessity for monitoring microzooplankton at Helgoland Roads, Löder et al. (2012) investigated the microzooplankton from January 2007 to June 2009, in which 62 ciliate taxa were recorded. Following upon this monitoring programme, a 2-year ciliate monitoring programme was established at Helgoland Roads in order to investigate the species composition and seasonality of the ciliate community in more detail and with higher frequency to gain more ecological information on this important functional group. During this period, the former checklist was supplemented with 27 additional ciliate taxa.

This study was aimed at providing the first detailed ciliate checklist at Helgoland Roads. This is crucial not only to obtain an idea of the ciliate diversity which was previously missing in the Helgoland Roads time series, but also to provide a basic reference for future surveys on microzooplankton communities in the North Sea where the ciliated protozoa have not been well studied and the existing documentations are out of date. In addition, the temporal distributions of dominant ciliate taxa are provided in this study to provide a good basis for further taxonomical and ecological studies in this marine region. The seasonal variation of the ciliate community in terms of species composition, abundance and carbon biomass is discussed and compared with relevant studies from other marine regions as well to enlighten the worldwide distributional patterns of dominant ciliate taxa recorded at Helgoland Roads.

Materials and methods

Helgoland Roads is located in the German Bight and is subject to both coastal influences and marine influences from the open North Sea (Wiltshire et al. 2010). The annual average temperature and salinity are 10.4 °C (max 18.5 °C, min 2.0 °C) and 32.0 (max 34.3, min 28.4), respectively (www.pangaea.de). Surface water samples were taken at 7:30 in the morning at Helgoland Roads (54°11.30′N; 7°54.00′E) once a week from January 2007 until June 2009 (first monitoring period, Löder et al. 2012) and twice a week from June 2010 until May 2012 (second monitoring period). About 250 ml of water sample was fixed with acid Lugol's solution (final concentration 2 %) immediately and stored in cold and dark conditions. Despite some drawbacks (e.g. obstruction on subsequent silver impregnation), acid Lugol's solution was used over other methods to ensure comparability over many years because all Helgoland Roads samples are fixed in it and have been so far

nearly 80 years. Moreover, acid Lugol's solution causes much less cell losses than other fixatives (Stoecker et al. 1994).

Triplicate 50 mL subsamples (the second monitoring period) were settled using Utermöhl chambers (Utermöhl 1958) for at least 24 h to enhance the opportunity of recording rare species and to reduce the counting biases. The whole chamber was counted at 200-fold magnification under an inverted microscope (Zeiss Axiovert 135). Of each taxon recorded, images were taken and used for subsequent biovolume estimations as well as the documentation and assignment of rare species. The biovolume of each taxon was calculated according to the geometric models described by Hillebrand et al. (1999) after the measurement of the linear dimension of each taxon with the open source software "ImageJ". The average biovolume (at least 20 individuals for normal taxa and all individuals for rare taxa) was converted into carbon using the conversion factor (0.19 pg C μm^{-3}) given by Putt and Stoecker (1989) according to the Lugol's concentration used in this study. Carbon concentrations (μg C L^{-1}) in this study are referred to as biomass or carbon biomass. All samples were processed within 6 months. Additionally, concentrated samples from 20 to 80 μm mesh size plankton nets were collected twice a week and examined under a light microscope in the laboratory for live observations of ciliates in order to obtain more morphological features for the identification.

All ciliate taxa observed and identified were listed. Due to difficulties that can occur with the identification of ciliates after fixation with acid Lugol's solution, some ciliates were only identified to genus level or put into different size groups or morphotypes (e.g. for some taxa in the complex genus *Strombidium* and scuticociliates). Most of the ciliate taxa in this study were identified mainly according to Montagnes (2003) for typical planktonic ciliates and Carey (1992) and Song et al. (2009) for periphytic and benthic ciliates. The identification of tintinnids was based on Kofoid and Campbell (1929, 1939). Local documentations for the German North Sea on ciliate fauna were also referred to, such as Hartwig (1973), Küsters (1974) and Maeda and Carey (1985). In this study, we applied the taxonomic systematics of Lynn (2008). Mixotrophy of the ciliates was not observed in the laboratory and thus is not actively differentiated to in this study. However, all ciliates except *Mesodinium rubrum* and *Mesodinium major* were considered heterotrophic. Johansson et al. (2004) have shown that all mixotrophic ciliates have phagotrophic capabilities. *M. rubrum* was recorded as mixotrophic, because recent studies have shown that it has phagotrophic capabilities (Park et al. 2007). *M. major* was recorded as phototrophic according to recent study by Garcia-Cuetos et al. (2012).

Results and discussion

Taxonomic composition and temporal variation

The taxonomic checklist of the ciliate community at Helgoland Roads is presented in Table 1. During the two monitoring periods, 89 ciliate taxa, representing 46 different genera, were identified. In terms of diversity, the order Strombidiida was the most diverse group, accounting for 26 % of the total taxa number, followed by Tintinnida and Choreotrichida, accounting for 16 and 12 % respectively of the total taxa numbers. Throughout the whole monitoring period, the abundance exhibited an obvious temporal variation with generally high values in spring and summer, low values in autumn and winter and a distinct peak in June (maximum abundance 6.77×10^4 cells L^{-1}, Fig. 1). This was mainly due to the bloom of two photosynthesis-performing ciliates *M. rubrum* and *M. major* (Fig. 2c, d) which were responsible for 83 % of the peak in terms of cell numbers. The temporal variation of carbon biomass showed a similar pattern to that of abundance with a distinct peak in June (maximum value 234.58 µg C L^{-1}, Fig. 1).

In terms of carbon biomass, the order Strombidiida played the most important role during the monitoring, accounting for 51 and 42 % of the carbon biomass respectively in the first and second monitoring period. *M. rubrum* and *M. major* became more dominant in the second monitoring and together were responsible for nearly 40 % of carbon biomass (23 % in the first monitoring), followed by Choreotrichida (7 and 10 % respectively in the first and second monitoring) and Haptorida (6 and 2 % respectively in the first and second monitoring). Tintinnida and Prorodontida played a smaller role (2–4 %). Other ciliate groups were of negligible importance from a biomass perspective, accounting for less than 1 % of the carbon biomass for both monitoring periods.

Although the ciliate community was slightly variable every year with respect to species composition, abundance and carbon biomass, it exhibited a clear temporal succession pattern during the monitoring. Strombidiida normally dominated the ciliate community from March to May when ciliate abundance rapidly increased due to their quick response to enhanced food availability (Löder et al. 2012). *M. rubrum* and *M. major* became dominant since late spring and were the major contributors to the peak in June. After this distinct peak, they gradually decreased and continued to dominate the ciliate community together with aloricate oligotrichs and choreotrichs during the summer months when the ciliate community demonstrated a higher diversity (number of observed taxa: 70 in summer, 60 in spring, 64 in autumn and 44 in winter) as most of the rare ciliate taxa occurred during this time period. In autumn, *Tiarina fusus* and some tintinnids were present in the water

column and contributed to the ciliate community. In winter, the ciliate community showed very low values in terms of both taxa number and abundance as well as carbon biomass.

Because of the importance of the Helgoland Time series in the international context (see Wiltshire et al. 2010, www.pangaea.de and ICES data banks) and the lack of information on microzooplankton at Helgoland and indeed in general when compared with other planktonic groups, detailed information on different ciliate groups is provided here below.

Typically planktonic ciliate groups

Aloricate oligotrichs and choreotrichs have been extensively studied over the recent decades in many different marine ecosystems, and they are broadly distributed all over the world (Lynn and Montagnes 1991; Pierce and Turner 1992; Garrison et al. 2005). They play an important role in microbial food webs (Gifford 1991; Pierce and Turner 1992; Liu et al. 2005) and dominate the marine microzooplankton communities episodically (Agatha 2011). Aloricate oligotrichs and choreotrichs represent the most important groups at Helgoland Roads. Their abundance increased intensively from March onwards due to their quick response to enhanced food availability and remained at a high level until late summer. They dominated the microzooplankton community together with *M. rubrum* and *M. major* during the spring bloom when heterotrophic dinoflagellates were still present in low numbers (Löder et al. 2012). Among them, the order Strombidiida was more diverse (23 taxa vs. 11 taxa) and abundant than the order Choreotrichida. Within the order Strombidiida, medium-sized species ranging between 30 and 60 µm (<50,000 µm³ cell volume) were normally quite abundant and comprised a main part of the total carbon biomass, e.g. *Strombidium* cf. *acutum*, *S.* cf. *emergens* (Fig. 2b), *S.* cf. *epidemum*, *S.* cf. *stylifer*, *S.* cf. *sulcatum*, *S.* cf. *tressum* and *Tontonia gracillima* (Fig. 2a). Large-sized species over 60 µm (>50,000 µm³ cell volume) contributed considerably to the carbon biomass, though most of them were less abundant than medium-sized species with the exception of *L. strobila* (Fig. 2l) and *Strombidium capitatum*.

Within the order Choreotrichida, *Lohmanniella oviformis* (Fig. 2j) normally occurred in spring and summer with maxima of around 2.0×10^3 cells L^{-1}. *Strobilidium* sp. 1 (15 µm), whose maximum abundance was more than 1.0×10^4 cells L^{-1}, normally occurred from late spring to autumn and was very abundant in summer. Other species in the order Choreotrichida were not so abundant over the year with an abundance ranging between 10 and 500 cells L^{-1}, such as *Pelagostrobilidium* cf. *neptunii* (Fig. 2e) and *Strombidinopsis* sp. (Fig. 2h).

Table 1 Revised ciliate checklist: seasonality as well as maximum abundance, the mean biovolume and mean carbon content of each taxon according to the results of both monitoring programmes and occurrence frequency of each taxon according to the results of the second monitoring

Ciliates	Observed seasonality	Occurrence frequency (%)[a]	Maximum (cells L^{-1})	Month with maxima	Biovolume (μm^3 cell^{-1})	Carbon (pg cell^{-1})
Order Strombidiida						
Cyrtostrombidium sp.1 70 μm	Jan–Dec	7	480	Apr	9,845	1,871
Cyrtostrombidium sp.2 160 μm	Apr–Jan	3	80	Oct	170,893	32,470
Laboea strobila	Jan–Nov	57	2,240	Mar	91,865	17,454
Strombidium capitatum	Jan–Oct	23	1,120	Apr	99,785	18,959
Strombidium cf. acutum	Jan–Dec	8	3,020	Apr	43,563	8,277
Strombidium cf. conicum	Mar–Sep	16	360	May	24,877	4,727
Strombidium cf. emergens	Jan–Nov	41	2,727	Jun	35,923	6,825
Strombidium cf. epidemum	Jan–Dec	77	24,840	Apr	6,465	1,228
Strombidium cf. lynii	Jan–Dec	39	487	Aug	36,968	7,024
Strombidium siculum	May–Sep	6	73	Jul	11,375	2,161
Strombidium cf. stylifer	Jan–Dec	78	2,480	May	7,296	1,386
Strombidium cf. sulcatum	Jan–Oct	59	8,213	May	8,862	1,684
Strombidium cf. tressum	Mar–Sep	22	2,640	Apr	9,694	1,842
Strombidium sp.1 20 μm	Jan–Dec	71	4,987	Jun	4,977	946
Strombidium sp.2 25 μm	Feb–Sep	14	1,680	Jul	2,463	468
Strombidium sp.3 30 μm a	Jan–Dec	12	540	Apr	5,893	1,120
Strombidium sp.4 30 μm b	Sep–May	3	200	May/Oct	4,157	790
Strombidium sp.5 35 μm	Jan–Dec	28	580	Aug	8,244	1,566
Strombidium sp.6 50 μm	Jan–Sep	11	367	Jul	9,390	1,784
Strombidium sp.7 60 μm	Jan–Dec	22	1,200	Jul	19,294	3,666
Strombidium sp.8 100 μm	Jan–Dec	11	267	May	105,853	20,112
Tontonia gracillima	Jan–Dec	74	3,740	Aug	25,089	4,767
Tontonia sp.	Jan–Dec	17	2,553	Jul	3,886	738
Order Choreotrichida						
Leegaardiella cf. ovalis	Jan–Dec	36	380	Feb	5,594	1,063
Leegaardiella cf. sol	Jan–Dec	20	780	Apr	22,301	4,237
Lohmanniella oviformis	Nov–Aug	42	2,753	Jun	4,725	898
Pelagostrobilidium cf. neptunii	Jan–Nov	40	407	Jul	54,726	10,398
Rimostrombidium cf. sphaericum	Jul–???	<1	40	Jul	74,475	14,150
Rimostrombidium cf. spiralis	Jan–Dec	22	207	Oct	18,578	3,530
Rimostrombidium sp.	Jan–Nov	12	1,120	May	100,779	19,148
Strobilidium sp.1 15 μm	Jan–Nov	44	10,160	Aug	1,061	202
Strobilidium sp.2 45 μm	Apr–Aug	13	970	Jun	38,186	7,255
Strombidinopsis sp.1 90 μm	Jul–Apr	10	40	Mar/Oct	94,898	18,031
Strombidinopsis sp.2 120 μm	Jul–Dec	11	333	Jul	103,546	19,674
Order Cyclotrichiida						
Askenasia regina	May–Oct	9	380	Oct	172,422	32,760
Askenasia sp.	Apr–Sep	1	60	Jun	269,492	51,203
Askenasia stellaris	May–Sep	14	473	May	50,965	9,683
Mesodinium cf. pupula	May–Mar	6	680	Aug	4,102	779
Mesodinium major	Jan–Dec	90	52,640	Jun	21,637	4,111
Mesodinium pulex	Jan–Dec	20	1,600	Aug	2,258	429
Mesodinium rubrum	Jan–Dec	100	31,760	Jun	2,356	448

Table 1 continued

Ciliates	Observed seasonality	Occurrence frequency (%)[a]	Maximum (cells L^{-1})	Month with maxima	Biovolume (μm^3 cell^{-1})	Carbon (pg cell^{-1})
Order Tintinnida						
Acanthostomella sp.[b]						
Eutintinnus sp.1 30 μm	May–Oct	14	240	Oct	4,169	792
Eutintinnus sp.2 60 μm	Aug–Oct	4	120	Aug	32,695	6,212
Favella ehrenbergii	Jul–Oct	11	327	Sep	100,917	19,174
Salpingella sp.	Oct–Jan	8	260	Nov	1,953	371
Stenosemella cf. *pacifica*	Sep–Jun	27	6,440	May	10,722	2,037
Tintinnid sp.1 30 μm	Jan–Dec	14	1,800	Jun	1,496	284
Tintinnid sp.2 70 μm	Sep–Dec	1	40	Sep	58,219	11,062
Tintinnidium cf. *balechi*	Jan–Dec	29	1,360	Jan	4,114	782
Tintinnopsis bütschlii	Aug–Sep	4	707	Sep	27,253	5,178
Tintinnopsis cf. *cylindrical*	Jul–Oct	5	47	Aug	23,842	4,530
Tintinnopsis cf. *parvula*	Mar–Jan	33	940	Jul	4,279	813
Tintinnopsis cf. *radix*	Aug–Oct	3	80	Oct	27,489	5,223
Tintinnopsis sp.	Jan–Jul	10	40	Jun	34,653	6,584
Order Euplotida						
Aspidisca sp.	Apr–Nov	1	13	Nov	18,368	3,490
Diophrys cf. *appendiculata*	Feb–Oct	3	13	Jul	13,225	2,513
Euplotes cf. *trisulcatus*	Apr–Dec	18	353	Jul	7,561	1,437
Order Urostylida						
Holosticha sp.	Jan–Dec	20	627	Sep	3,388	644
Metaurostylopsis cf. *salina*	Nov–???	2	53	Nov	4,349	826
Thigmokeronopsis cf. *stoecki*	Aug–???	1	20	Aug	7,307	1,388
Order Sporadotrichida						
Tachysoma cf. *dragescoi*	Mar–Dec	10	93	May	3,739	710
Order Heterotrichida						
Condylostentor sp.	Aug–Sep	2	7	Aug/Sep	32,399	6,156
Condylostoma sp.	Mar–???	<1	7	Mar	38,916	7,394
Order Pleurostomatida						
Litonotus sp.	Aug–Nov	3	13	Sep	3,582	681
Loxophyllum sp.	Jul–Nov	2	27	Nov	893	170
Order Dysteriida						
Dysteria sp.	Jan–Dec	13	747	Nov	1,926	366
Hartmannula cf. *derouxi*	Apr–May	2	10	Apr	12,537	2,382
Order Chlamydodontida						
Chlamydonella cf. *derouxi*	Jan–Nov	9	87	Apr	1,543	293
Order Endogenida						
Acineta cf. *compressa*	Apr–Aug	3	60	Aug	35,298	6,707
Acineta sp.	May–Jul	2	13	Jul	27,560	5,236
Order Exogenida						
Ephelota sp.	Apr–May	2	7	Apr/May	50,772	9,647
Order Sessilida						
Cothurnia sp.	Nov–???	<1	7	Nov	1,779	338
Vorticella sp.	Jan–Dec	3	620	May	6,729	1,278
Order Haptorida						
Chaenea cf. *vorax*	May–???	2	7	May	38,040	7,228
Cyclotrichium sp.	Mar–Oct	12	380	Apr	595,288	113,105

Table 1 continued

Ciliates	Observed seasonality	Occurrence frequency (%)[a]	Maximum (cells L^{-1})	Month with maxima	Biovolume (μm^3 cell^{-1})	Carbon (pg cell^{-1})
Didinium gargantuan	Apr–Sep	7	87	Aug	68,770	13,066
Lacrymaria sp.	Jan–Dec	8	20	Mar	35,881	6,817
Spathidium sp.	Mar–Nov	1	500	Jun	5,864	1,114
Order Prorodontida						
Balanion comatum 15 μm	Mar–Jan	23	4,426	Jun	443	84
Balanion comatum 25 μm	Jan–Nov	32	1,880	Jun	2,356	448
Holophrya cf. *caspica*	May–Aug	2	13	May/Aug	69,133	13,135
Holophrya cf. *vorax*	Aug–Oct	8	80	Aug	92,074	17,494
Placus sp.	Apr–Nov	27	273	Aug	8,954	1,701
Tiarina fusus	Jun–Dec	22	1,687	Sep	7,561	1,437
Miscellaneous						
Aloricate oligotrichs < 10 μm	Jan–Dec	29	3,080	Jun	347	66
Aloricate oligotrichs < 15 μm	Jan–Dec	55	19,360	Jun	805	153
Scuticociliates 10–30 μm	Jan–Dec	55	3,980	Sep	1,595	303
Scuticociliates 30–50 μm	Jan–Dec	41	1,320	Aug	17,641	3,352

[a] Occurrence frequency (%) = the percentage of total occurrence times within 198 samples during the present monitoring

[b] There was no information on the abundance and seasonality for this species because only an empty lorica was recorded during the monitoring

Nano-sized aloricate oligotrichs (5–15 μm), which were too small to identify even at an order level, predominated numerically mainly in summer with maxima of up to more than 1.9×10^4 cells L^{-1}. Together with other tiny ciliates, such as *Strombidium* sp. 1 (20 μm), *Strobilidium* sp. 1 (15 μm), *L. oviformis* (Fig. 2j), *Leegaardiella* cf. *ovalis* and *Balanion comatum* (Fig. 2i), nano-sized ciliates probably play an essential role at Helgoland Roads by feeding on bacteria and picophytoplankton which are too small to be used by larger ciliates (Sorokin et al. 1996; Zingel et al. 2007).

Seven ciliate taxa were documented in the order Cyclotrichiida during the monitoring. In the previous monitoring, *M. rubrum* and *M. major* were recorded as two different size groups of *M. rubra* as also in many other studies (e.g. Montagnes and Lynn 1989; Rychert 2004). In the second monitoring, according to the recent study by Garcia-Cuetos et al. (2012), the smaller one (15 μm) was assigned to the species *M. rubrum* and the larger one (35 μm) was assigned to the species *M. major*. They have been recorded in all oceans of the world from polar regions to equatorial latitudes (Edwards and Burkill 1995; Sorokin et al. 1996; Pérez et al. 2000; Mironova et al. 2009; Wickham et al. 2011; Löder et al. 2012), and they are the most abundant and frequent ciliates at Helgoland Roads. *M. rubrum* (Fig. 2c) usually reached its maximum abundance in spring time (3.18×10^4 cells L^{-1} and 14.2 μg C L^{-1}), followed by a bloom of *M. major* (Fig. 2d) in June (5.26×10^4 cells L^{-1} and 216.4 μg C L^{-1}). Montagnes and Lynn (1989) reported

that the larger form occurred at colder times of the year and the smaller form occurred at warmer times. Garcia-Cuetos et al. (2012) mentioned that *M. rubrum* was abundant in the summer and early autumn and *M. major* was mainly found in the winter and early spring in Danish waters. However, such segregation cannot be confirmed by our results from Helgoland Roads. The "Medusa" form of *M. major* observed by Garcia-Cuetos et al. (2012) was found in autumn and winter time at Helgoland Roads during the second monitoring period. In addition, some reproductive individuals of both species observed further confirmed the separation of these two similar photosynthesis-performing ciliates.

Mesodinium pulex was one of the three ciliates recorded during the regular phytoplankton monitoring at Helgoland Roads. This organism has been reported from freshwater, brackish and marine waters (Song et al. 2009). Our monitoring results showed that it was less abundant (maximum value 100 cells L^{-1}) in the second monitoring compared to the period 2007–2009 with maximum abundance 1.6×10^3 cells L^{-1}.

The primarily planktonic genus *Askenasia* was another group recorded in the order Cyclotrichiida at Helgoland Roads. It has been documented in many marine ecosystems, such as the Atlantic Ocean, the Pacific Ocean, the North Sea and the English Channel (Earland and Montagnes 2002). *Askenasia stellaris* that was inaccurately identified as *Mesodinium* sp. in the first monitoring mainly occurred from May to September with a maximum
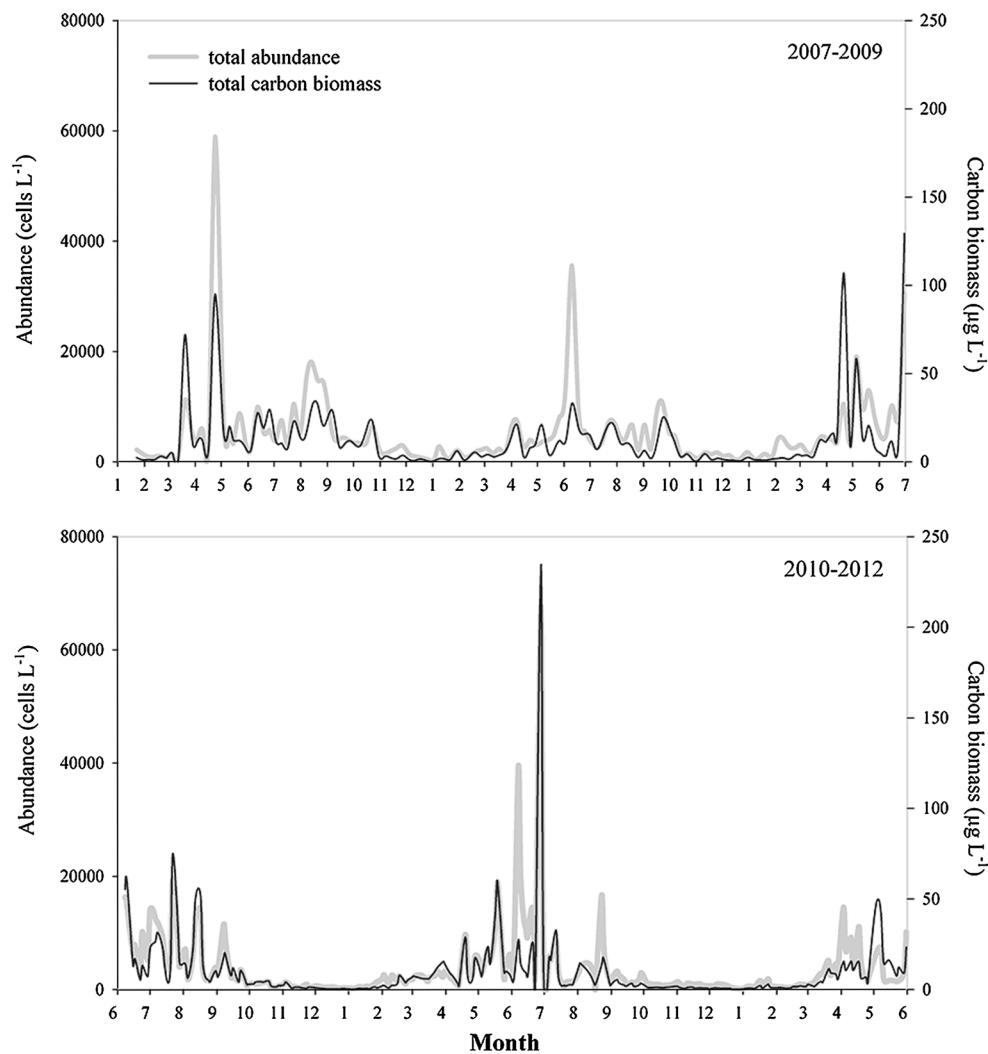
Fig. 1 The total abundance and carbon biomass of the ciliate community at Helgoland Roads during the first and second monitoring periods

abundance of about 470 cells L^{-1} at Helgoland. It was recorded in the plankton of coastal waters in some studies, such as the Finnish Gulf (Leegaard 1920), the North Sea near Hamburg (Kahl 1931), the Alligator Harbor, Florida (Borror 1963), and the Kandalaksha Gulf, White Sea (Burkovsky 1970).

Askenasia regina was previously found mainly in the upper water column with low abundances (Earland and Montagnes 2002). It occurred in the surface samples at the same time period as *A. stellaris* at Helgoland Roads. It can be easily differentiated from the latter due to its larger size. An unknown *Askenasia* sp. was recorded in the monitoring. It rarely occurred in spring and summer and was very conspicuous due to its large size (50–100 μm in diameter) and broad hemispherical body shape. It remains to be identified to species level.

Tintinnid ciliates are a ubiquitous component of the microzooplankton community in marine ecosystems

(Gavrilova and Dolan 2007). During the monitoring, 14 tintinnid taxa from 7 different genera were recorded. According to Pierce and Turner (1993), these tintinnids belong to two different distributional types: cosmopolitan tintinnids (*Acanthostomella*, *Eutintinnus* and *Salpingella*) and neritic tintinnids (*Favella*, *Stenosemella*, *Tintinnopsis* and *Tintinnidium*). As in many other coastal regions (e.g. Dolan and Marassé 1995; Sitran et al. 2009), tintinnids were generally a minor group in terms of abundance and carbon biomass at Helgoland Roads. They made up only about 3 % of the total carbon biomass of the ciliate community. *Tintinnidium* cf. *balechi* (Fig. 2n), *Stenosemella* cf. *pacifica* (Fig. 2k) and *Tintinnopsis* cf. *parvula* were comparatively abundant among these tintinnids, and they were dominant species during late autumn and winter when the ciliate abundance was very low.

Tintinnidium cf. *balechi* has very long and thin collar membranelles (20–35 μm), and its contractile stalk is
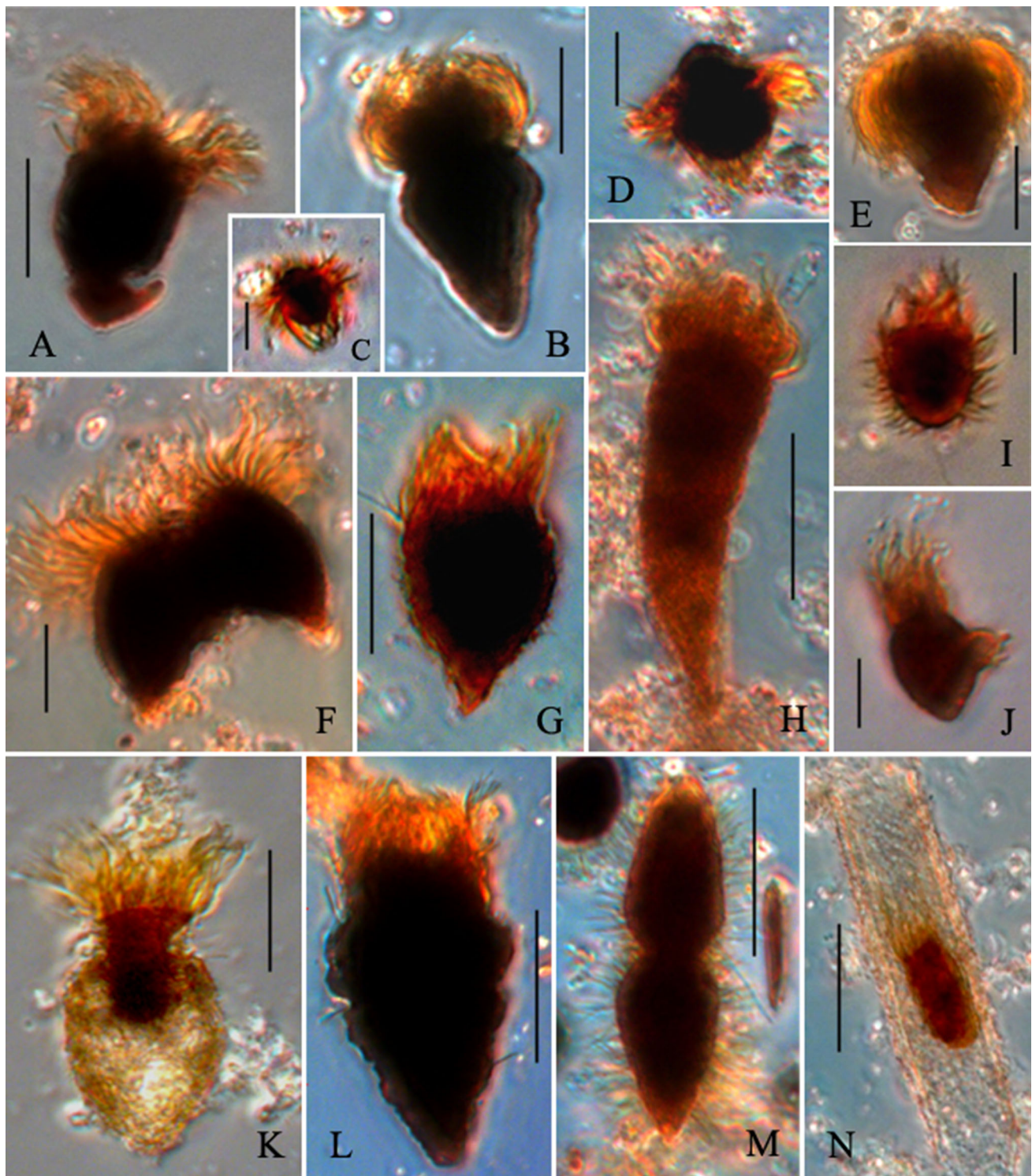
Fig. 2 Some dominant ciliates at Helgoland Roads (Lugol's fixed specimens). **a** *Tontonia gracillima*; **b** *Strombidium* cf. *emergens*; **c** *Mesodinium rubrum*; **d** *Mesodinium major*; **e** *Pelagostrobilidium* cf. *neptunii*; **f** *Rimostrombidium* sp.; **g** *Strombidium* cf. *lynii*; **h** *Strombidinopsis* sp.; **i** *Balanion comatum*; **j** *Lohmanniella oviformis*; **k** *Stenosemella* cf. *pacifica*; **l** *Laboea strobila*; **m** *Tiarina fusus*; **n** *Tintinnidium* cf. *balechi*. *Scale bars* = 20 μm (**a, b, d–g, k**); 10 μm (**c, i, j**); 30 μm (**h, l–n**)

attached to the wall of its lorica. In our samples, the lorica of this species covered a wide range from 50 μm (broken lorica) to 150 μm (complete lorica) due to its fragility. This

organism usually appeared in autumn and remained until early summer with high abundances (maximum value 1.36×10^3 cells L^{-1}) from November to January.

Stenosemella cf. *pacifica* is a widely distributed tintinnid, which has been recorded in the North Atlantic (Agatha and Tsai 2008), the Gulf of Mexico (Balech 1968), the Yellow Sea (Xu and Song 2005), the North Pacific (Kofoid and Campbell 1929, 1939) and the South Pacific (Burns 1983). According to our observations, its lorica was about 40–60 μm long and was composed of an agglomerated bowl and a short unobvious hyaline collar that sometimes was covered by an agglomerated second collar (as described in Agatha and Tsai 2008). It often occurred from late autumn until early spring at Helgoland Roads with an abundance normally varying between 20 and 150 cells L^{-1}. In the spring of 2009 and the winter of 2011, its abundance reached much higher values than during other time periods and the maximum abundances were up to 6.44×10^3 and 1.04×10^3 cells L^{-1}, respectively.

Tintinnopsis cf. *parvula* has a cosmopolitan distribution in marine and brackish coastal waters and occurs from the Arctic to trophic areas (Agatha 2010). Its lorica was about 40–65 μm long in our samples and composed of an agglomerated bowl and a narrow collar. It occurred infrequently throughout the year at Helgoland Roads with a maximum abundance of about 940 cells L^{-1}. It can be difficult to distinguish *Tintinnopsis* cf. *parvula* from *Stenosemella* cf. *pacifica* because they sometimes coexisted, and their lorica have similar sizes and morphology. However, upon careful observation, *Stenosemella* cf. *pacifica* can be distinguished from *Tintinnopsis* cf. *parvula* due to its wider size (35–45 vs. 20–30 μm) and the agglomerated second collar.

Tintinnopsis bütschlii (Fig. 3n) was first recorded at Helgoland Roads during the second monitoring. It is very easy to be distinguished from other tintinnids due to its obvious outward expansion of the lorica opening. It occurred only in August and September 2010 with a maximum abundance of 700 cells L^{-1}, but it did not appear in any of the other samples. The large tintinnid *Favella ehrenbergii*, which has been recorded in many marine regions, such as the Black Sea (Gavrilova and Dolan 2007), the Baltic Sea (Mironova et al. 2009) and the Yellow Sea (Xu et al. 2011), normally occurred in July and disappeared in October at Helgoland Roads. It was usually present in low abundances ranging between 10 and 50 cells L^{-1}, though sometimes its abundance reached more than 100 cells L^{-1}, and its maximum abundance recorded was 330 cells L^{-1}. *Salpingella* sp. was a small tintinnid that mainly occurred in autumn with an abundance varying between 10 and 260 cells L^{-1}. Two different *Eutintinnus* species with cell lengths of about 30 and 60 μm respectively were recorded. Both species showed very low abundances (less than 50 cells L^{-1}). *Tintinnopsis* cf. *radix* and *Tintinnopsis* cf. *cylindrica* were identified as

the same species in the first monitoring. Though they had a similar shape, the lorica of *Tintinnopsis* cf. *cylindrica* (120–180 μm) was much smaller than that of *Tintinnopsis* cf. *radix* (250–300 μm). In addition, we recorded an empty lorica of *Acanthostomella* sp. only once during the monitoring.

Typically periphytic and benthic ciliates

Besides the typically planktonic groups mentioned above, another 32 ciliate taxa from 11 different orders were recorded during the monitoring. Most of them were rare species and occurred at very low abundances and frequencies at Helgoland Roads, such as *Diophrys* cf. *appendiculata* (Fig. 3a) and *Aspidisca* sp. from the order Euplotida, *Metaurostylopsis* cf. *salina* (Fig. 3m) and *Thigmokeronopsis* cf. *stoecki* (Fig. 3i) from the order Urostylida, *Condylostoma* sp. and *Condylostentor* sp. from the order Heterotrichida, *Litonotus* sp. (Fig. 3d) and *Loxophyllum* sp. from the order Pleurostomatida, *Hartmannula* cf. *derouxi* (Fig. 3b) from the order Dysteriida, *Chlamydonella* cf. *derouxi* from the order Chlamydodontida, *Acineta* cf. *compressa* (Fig. 3g) and *Acineta* sp. from the order Endogenida, *Ephelota* sp. from the order Exogenida, *Cothurnia* sp. (Fig. 3c) from the order Sessilida, *Cyclotrichium* sp., *Didinium gargantua* (Fig. 3j), *Spathidium* sp., *Lacrymaria* sp. (Fig. 3l) and *Chaenea* cf. *vorax* (Fig. 3h) from the order Haptorida, *Holophrya* cf. *caspica* (Fig. 3k) and *H.* cf. *vorax* from the order Prorodontida.

Meanwhile, some rare species occasionally occurred at high abundances and possibly played an important role during some periods of the year, such as *Euplotes* cf. *trisulcatus* which mainly occurred in spring and summer and was comparatively more abundant in 2010 with a maximum abundance about 350 cells L^{-1}. *Holosticha* sp. was merely present in summer and also more abundant in 2010 than in other monitoring years with a maximum abundance of more than 600 cells L^{-1}. *Dysteria* sp. (Fig. 3F) was first recorded in November 2010 at Helgoland Roads, and its maximum abundance was up to 750 cells L^{-1}. *Vorticella* sp. which is a typical sessile ciliate was frequently recorded in the first monitoring with a maximum abundance of 620 cells L^{-1}. In the second monitoring, it was only recorded five times altogether, within which it was abundant at two times in November 2011 with abundances of 200 and 287 cells L^{-1}, respectively.

Balanion comatum (Fig. 2i), which is a nano-sized ciliate with cell lengths ranging from 10 to 25 μm, normally occurred from spring until the end of autumn with maxima often in May and June. Its maximum abundance was nearly 5.70×10^3 cells L^{-1} during the first monitoring period
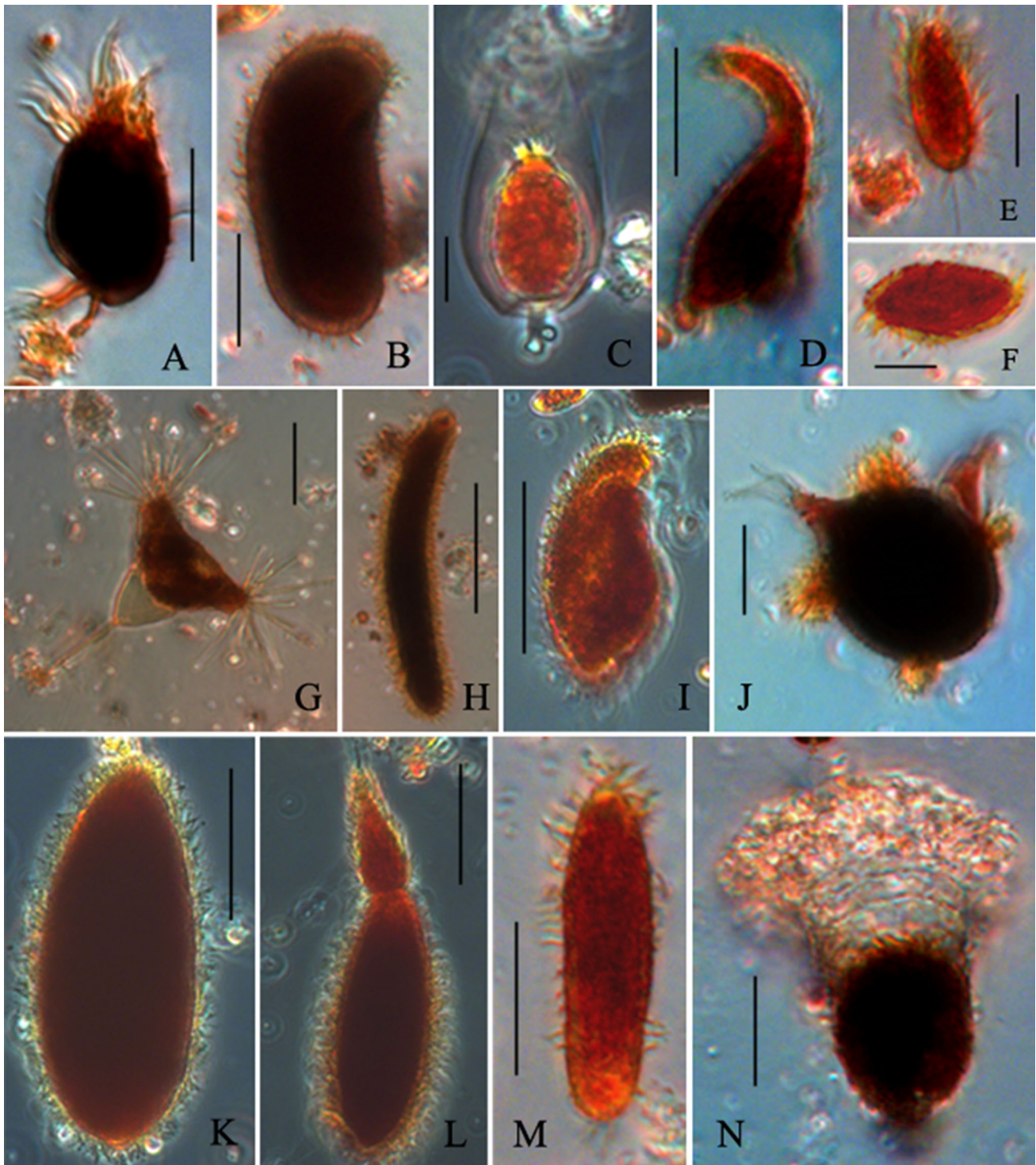
Fig. 3 Some rare ciliates at Helgoland Roads (Lugol's fixed specimens). **a** *Diophrys* cf. *appendiculata*; **b** *Hartmannula* cf. *derouxi*; C *Cothurnia* sp.; **d** *Litonotus* sp.; **e** *Uronema* cf. *marinum*; **f** *Dysteria* sp.; **g** *Acineta* cf. *compressa*; **h** *Chaenea* cf. *vorax*; **i** *Thigmokeronopsis* cf. *stoecki*; **j** *Didinium gargantua*; **k** *Holophrya* cf. *caspica*; **l** *Lacrymaria* sp.; **m** *Metaurostylopsis* cf. *salina*; **n** *Tintinnopsis bütschlii*. *Scale bars* = 20 μm (**a, b, d, j, m, n**); 10 μm (**c, e, f**); 40 μm (**g–i, k, l**)

and 2.30×10^3 cells L^{-1} during the second monitoring period. *T. fusus* (Fig. 2m) was one of the dominant ciliates at Helgoland Roads during late summer and autumn with maximum abundances of 1.52×10^3 cells L^{-1} in the first monitoring period and 1.69×10^3 cells L^{-1} in the second monitoring period.

Scuticociliates at Helgoland Roads were simply divided into two different size groups during the monitoring due to the difficulties in identifying this complex ciliate group. *Uronema* cf. *marinum* (Fig. 3e) and *Pleuronema* cf. *coronatum* were two commonly recorded scuticociliate species. *Uronema* cf. *marinum* normally occurred at low numbers. However, its abundance was extremely high (3.98×10^3 cells L^{-1}), and several conjugation individuals were observed at one time in September 2010. It is known that scuticociliates mainly feed on bacteria (Song et al. 2009), so that they may play a certain role in transferring energy from picoplankton to higher trophic levels together with other nano-sized ciliates.

Although these typically periphytic and benthic ciliates occurred at low abundances and frequencies in the water column, they probably play a minor but rather specific role in the ciliate community as they are known for their significant contribution to the stability of the community structure in disturbed or polluted natural systems (Caspers and Karbe 1967; Sládeček 1973; Xu et al. 2011).

Comparison with other marine regions

This study presents the first detailed checklist of the ciliate community at Helgoland Roads, the North Sea. This is important because to date, little is known about the potential role these organisms might play in this marine region (Wiltshire et al. 2010). Comparing these new results with other marine regions shows that in terms of diversity, the number (89 taxa) recorded in this study is similar to those of many other marine areas, such as the Yellow Sea (78 species in coastal waters of Incheon, Korea, Xu et al. 2011) and the Bellingshausen and Amundsen Seas, west of the Antarctic Peninsula (70 species, Wickham et al. 2011). In the Irminger Sea, Montagnes et al. (2010) recorded around 80 ciliate morphotypes with strombidiids (26 taxa) and tintinnids (16 taxa) being the highest in terms of taxa number, which is quite similar to that found in this study. However, Mironova et al. (2009) reported about 160 typically planktonic ciliates in a review paper on the planktonic ciliates of the Baltic Sea, which is probably due to the comprehensive long-term studies on the ciliate fauna overall in the Baltic Sea and also its diverse water bodies with different salinities and nutrient loads.

In terms of species composition, the ciliate community at Helgoland Roads was dominated by aloricate oligotrichs and choreotrichs, mainly *Strombidium* spp., *Strobilidium* spp., *Tontonia* spp. and *L. strobila*, which are typical of many coastal and oceanic waters including the Irish Sea (Edwards and Burkill 1995), the southern North Sea (Steif 1988), the Baltic Sea (Mironova et al. 2009), the Irminger Sea (Montagnes et al. 2010), the Bering Sea and North Pacific (Sorokin et al. 1996). As in many other coastal

waters, *M. rubrum* and *M. major* are very important components of the ciliate community at Helgoland Roads. Similarly, on the northwest shelf of the Bering Sea, up to 30–40 % of the ciliate community was comprised of *M. rubrum* (probably the mixture of *M. rubrum* and *M. major*, Sorokin et al. 1996). In the Bornholm Basin (the southern part of the central Baltic Sea), they dominated the microzooplankton communities in spring and early summer with a biomass 200–300 μg C L^{-1} (Mironova et al. 2009). However, in Jiaozhou Bay, in the Yellow Sea, both *Mesodinium species* were not documented during a 1-year biweekly investigation on ciliate community at 5 stations (Jiang et al. 2011). In the Irminger Basin of the North Atlantic, Montagnes et al. (2008) recorded relatively low abundances ($0–5 \times 10^3$ cells L^{-1}) compared with that found in coastal areas. In the deep Bering Sea, they were rare, comprising only 3–6 % of the total ciliate abundance (Sorokin et al. 1996).

Although tintinnids were not as abundant as aloricate oligotrichs and *Mesodinium* spp. at Helgoland Roads, they were the group with the second highest diversity and 14 tintinnids were recorded in this study. Similarly, Graziano (1989) reported a total of 17 tintinnids in a study on the annual cycle of tintinnids off the Isle of Man. However, tintinnids exhibit a much higher diversity in some other marine areas compared to Helgoland Roads. In the Yellow Sea, Xu et al. (2011) reported 30 tintinnid taxa in the coastal waters of Incheon, and Jiang et al. (2011) reported 23 tintinnids accounting for 22 % of the total abundance and 15 % of the carbon biomass of the ciliate community in Jiaozhou Bay. A high species richness of tintinnids was often reported for the Mediterranean, such as 67 species in the Gulf of Milazzo (Sitran et al. 2009) and 57 species in a 4-year study in the Gulf of Naples (Modigh and Castaldo 2002). The dominance of tintinnids in the ciliate assemblage was also reported in some other locations, such as the Laizhou Bay, Bohai Sea (Zhang and Wang 2000) and the northern Hiroshima Bay, the Seto Inland Sea (Kamiyama 1994). Suzuki and Taniguchi (1998) speculated that tintinnids might be more adaptive to eutrophic environments than other ciliates, although the ecological processes were not clear.

The total abundance and carbon biomass of the ciliate community at Helgoland Roads ranged between $0.14–67.7 \times 10^3$ cells L^{-1} and $0.2–234.6$ μg C L^{-1}, respectively (Fig. 1), which are similar to the values from the Baltic Sea where ciliate abundance ranged between $0.17–88 \times 10^3$ cells L^{-1} in the southern Baltic Sea and the biomass ranged from 13 to 300 μg C L^{-1} in the Bornholm Basin (Mironova et al. 2009). However, the ciliate community at Helgoland Roads exhibited a wider range compared to many other temperate marine waters (Bojanić et al. 2005; Montagnes et al. 2010; Jiang et al. 2011) in

terms of both abundance and carbon biomass, although the mean values were quite similar. For example, the maximum abundance at Helgoland Roads (67.7×10^3 cells L^{-1}) is higher than the value reported from the Irish Sea where 24×10^3 cells L^{-1} were found in early June (Edwards and Burkill 1995). In the Yellow Sea, a distinct peak with 29.54×10^3 cells L^{-1} was recorded in August (Jiang et al. 2011). Such differences might result from the spatial and temporal resolution of the sampling in these studies, or the hydrological features and some other environmental factors of these marine areas.

The ciliate blooms at Helgoland Roads normally occurred in spring and summer and mainly consisted of photosynthesis-performing ciliates *M. rubrum* and *M. major* as well as some aloricate oligotrich ciliates. Vertical distribution of *M. rubrum* has been investigated in some studies, which reported that this ciliate appears to be most abundant in the upper layers, especially under bloom conditions (Fenchel 1968; McManus and Fuhrman 1986). Aloricate oligotrich ciliates can respond rapidly to the enhanced food availability (Löder et al. 2012) and exhibit high growth rates when abundant prey populations are available (Montagnes 1996). Many aloricate oligotrich ciliates are mixotrophic (Stoecker et al. 1987), such as *S. capitatum* and *L. strobila*, and can conduct vertical migration to get optimal nutrient and light conditions or avoid predation by predators (McManus and Fuhrman 1986; Pérez et al. 2000; Lynn 2008). In addition, ciliates probably exist in small patches in the plankton (Montagnes 1996), which might be an explanation of the fact that the ciliate abundance could vary dramatically during the monitoring.

Comparing the species composition of the ciliate communities between different marine regions is difficult partly due to the different methods used in the studies. In our case for reasons outlined in the methods above, we used acid Lugol's solution. The fixation of ciliates in plankton samples with Lugol's solution is sometimes criticized because it may sometimes not provide enough species-specific features in several taxa (e.g. *Strombidium* spp. and *Strobilidium* spp.) resulting in difficulties in identification below genus level (Agatha 2011). However, each method has its flaws. The traditional fixative, formalin, which may allow the observation of chlorophyll fluorescence to estimate the trophic status of ciliates, can erode the more fragile ciliates and thus cause severe loss of cells (Stoecker et al. 1989, 1994). Another fixative Bouin's solution, which can yield similar cell counts with acid Lugol's solution and causes less cell shrinkage, is much more toxic than Lugol's solution. Other methods like protargol staining, however, are not feasible to carry out in a routine monitoring programme. In spite of such different methods, it is interesting that the species composition of the ciliate communities at Helgoland Roads and many other marine regions are quite similar to each other. This is most likely due to the fact that the majority of ciliates are cosmopolitans.

One specific feature of the ciliate community at Helgoland Roads is the presence of a large number of typically periphytic and benthic ciliates in the community, which is probably related to the shallow water depth of the North Sea around Helgoland (5–10 m). These ciliates were normally very rare, and some even only occurred once all through the year. These taxa occurred in the water column due to some reasons, such as disturbance by storms or stratification (Hausmann et al. 2007). These rare ciliate taxa are hard to find in a low-frequency monitoring programme and thus were absent in the first monitoring programme with only one sample per week. Furthermore, some ciliate taxa have similar morphological features, and it is very difficult to distinguish them from each other, especially after having been fixed by acid Lugol's solution. Thus, they were probably misidentified as other taxa or grouped in one taxon as "Euplotes spp." in the first monitoring period. Some ciliates with obviously distinctive morphological features, such as *Tintinnopsis bütschlii* and *Tontonia* sp., are, however, potentially newcomers to the ciliate community at Helgoland Roads as they could not have been ignored if they were present in the water samples. *Tintinnopsis bütschlii* was often recorded in warm waters, such as the Yellow Sea (Xu and Song 2005), the South China Sea (Tan et al. 2010) and the Aegean Sea (Durmus et al. 2011). Its occurrence at Helgoland Roads may be associated with the warming trend in this region, or may result from ballast water, which need to be monitored in future. Unfortunately, we could not prove this hypothesis due to the lack of data on the ciliate community at Helgoland Roads before the two monitoring periods. This highlights the importance of conducting such monitoring programmes on a continuous and regular basis, especially at a long-term sampling station like Helgoland Roads.

Nevertheless, although there are some inevitable deficiencies as in all studies, we have added substantially to our knowledge of ciliates at Helgoland Roads and presented here a detailed checklist as well as the information on the abundance, carbon biomass and seasonality of dominant ciliate taxa of the ciliate community in the southern North Sea. This study has already laid the cornerstone and provided North Sea researchers with a long-needed basic reference for investigations on the biogeography of ciliates.

Perspectives on future ciliate monitoring

Eighty-nine ciliate taxa were recorded in total, and this number is in line with most marine regions studied in the literatures. However, we still believe that the diversity of

the ciliate community at Helgoland Roads was underestimated as some ciliate taxa had to be put into different size groups or morphotypes due to the methodological limitations described above. An example is Scuticociliates, which were simply divided into two different size groups in the monitoring, are very likely to include more taxa based on our live observations. The complex genus *Strombidium* is also possibly more diverse than presented here. Doherty et al. ([2007](#)) investigated the ciliate diversity within the subclasses Choreotrichia and Oligotrichia in coastal northwest Atlantic waters using molecular and morphological methods and found that the estimates of diversity based on molecular method were much higher for oligotrich ciliates, especially in the genus *Strombidium* which was 2 to 3 times higher than the number of distinct morphospecies observed microscopically. In recent years, molecular methods have been applied to the study of protist diversity in many different ecosystems and have revealed a large protist diversity, suggesting a large fraction of eukaryotic microbial communities remain to be discovered (Moreira and López-García [2002](#); Šlapeta et al. [2005](#)). In spite of some inherent limitations, molecular methods are being advanced and can reveal cryptic species and genetic diversity hidden beneath morphological homogeneity (McManus and Katz [2009](#)). Therefore, detailed investigations into the ecology of ciliates in the North Sea should be underpinned by combining morphological observations with molecular methods to gain a more precise evaluation on the diversity of ciliates, especially in aloricate oligotrichs and nano-sized ciliates (Doherty et al. [2007](#)). These are the most productive and numerous part of the ciliate community at Helgoland Roads. Unfortunately, they are studied to a lesser extent than larger ciliates which have been potentially over-represented due to obvious methodological advantages.

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