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Distribution and ecology of *Pseudo-nitzschia* species (Bacillariophyceae) in surface waters of the Weddell Sea (Antarctica)

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Abstract The distribution of six *Pseudo-nitzschia* species and their relationship with environmental conditions were studied for the first time in a vast zone of the Weddell Sea (∼61–77°S, Antarctica). Both qualitative and quantitative phytoplankton samples, collected during summer 2004, were examined using light and scanning electron microscopy. Phytoplankton abundance and composition showed great variability along our study area. Diatoms were the most conspicuous phytoplankton group in the northern area while small flagellates were generally dominant in the southern stations. The genus *Pseudo-nitzschia* was broadly distributed and significantly contributed to total diatom densities. A marked contrast in *Pseudo-nitzschia* species distribution was observed in three main zones divided by the Weddell Front (WF) and the Antarctic Slope Front (ASF). *P. subcurvata* and *P. turgiduloides* were the most abundant species in the neritic Weddell Sea zone, south of the ASF, mainly near the ice-edge in shallower waters and in conditions of long photoperiod. In contrast, *P. prolongatoides* and *P. lineola* dominated north of the ASF; the first was associated with deeper and nutrient-rich waters whereas the latter showed a weak relation with environmental variables examined. Finally, *P. turgidula* and *P. heimii* were mostly observed in the Weddell–Scotia Confluence Zone in the warmest and far from ice covered waters, north of the WF. A brief morphological *Pseudo-nitzschia* species description is given in the Appendix, including morphometrics and pictures.

Keywords Antarctica · Diatoms · Phytoplankton distribution · *Pseudo-nitzschia* · Weddell Sea

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Introduction

Pseudo-nitzschia Peragallo is a marine diatom genus widespread in all oceans of the world. It comprises about 30 recognized species almost all exclusively planktonic and, many of them, regular bloom-producers (Fryxell and Hasle 2003; Quiroga 2006). Studies focusing on this genus have globally increased since the discovery that several of the species are implicated in domoic acid (DA) outbreaks and can be responsible for amnesic shellfish poisoning (ASP) in sea birds, marine mammals and humans (Bates 2000; Fehling et al. 2004). The description of new species

and the growing number of reports on the occurrence of *Pseudo-nitzschia* spp. in the last years are good examples of this situation (e.g. Lundholm and Moestrup 2002; Lundholm et al. 2002, 2003, 2006; Kaczmarska et al. 2005; Hernández-Becerril and Díaz-Almeyda 2006; Almandoz et al. 2007). Likewise, recent experimental and observational studies in several regions of the world have shown the importance of a variety of factors, such as salinity (Thessen et al. 2005), nutrient' concentrations (Caroppo et al. 2005), pH (Lundholm et al. 2004) and photoperiod (Fehling et al. 2005, 2006) in determining *Pseudo-nitzschia* spp. growth and distribution.

Pseudo-nitzschia species have been recurrently observed in the Antarctic region (Hasle 1964, 1965) and particularly in the Weddell Sea. Previous studies showed that the genus *Pseudo-nitzschia* is a conspicuous component in phytoplankton assemblages and one of the most frequently dominating diatom genera (Estrada and Delgado 1990; Kang and Fryxell 1993). However, the identification to species has been overlooked in these works that were dealing with general phytoplankton distribution (e.g. Estrada and Delgado 1990; Bianchi et al. 1992) or has been limited to the recognition of groups of morphologically similar species during enumerations (Hasle 1965; Schloss and Estrada 1994; Kang et al. 2001). Furthermore, since most of these studies were conducted only in space-limited areas, the *Pseudo-nitzschia* distribution in the Weddell Sea is still poorly understood. In this region, the phytoplankton distribution is mainly determined by ice cover dynamics (Garibotti et al. 2005; Krell et al. 2005), iron concentration (Holm-Hansen et al. 2004), water mass distribution (Mura et al. 1995; Kang et al. 2001) and the occurrence of fronts (Estrada and Delgado 1990; Krell et al. 2005). However, there is much controversy about the relevance of each of these factors in regulating individual phytoplankton species abundance and distribution. Consequently, more species-specific studies are needed for a better understanding of environmental controls on key algae (Boyd 2002).

In this work, we study in detail the occurrence and distribution of six *Pseudo-nitzschia* species analyzing biological samples collected in the frame of a wider research program, which aims at assessing the role of plankton communities in the sea–air fluxes of CO_2 in the SW Atlantic Ocean (Balestrini et al. 2000; Schloss et al. 2007). Data were collected on board the Argentinean icebreaker "Almirante Irizar" on a transect carried out in the Weddell Sea, from about 61° to 77°S. The goal of this study is to gather further insight into the distribution and abundance of *Pseudo-nitzschia* species across surface waters of the Weddell Sea. In particular, we focus our attention to relate the observed distribution patterns to vertical thermal structure and environmental factors, such as ice cover, bathymetry, surface temperature, salinity,

nutrients and photoperiod. Additionally, a brief morphological *Pseudo-nitzschia* species description is given in the Appendix, including morphometrics and pictures.

Materials and methods

Field sampling

Sampling was carried out between 30 January and 6 February 2004 on board the icebreaker "Almirante Irizar", along a series of 39 stations located between the proximities of the South Orkney Islands (60°54′S) and the Argentinean station "Belgrano 2" (77°39′S) in the Southern Weddell Sea (Fig. 1; Table 1). Sampling procedures for water collection and chemical and biological analyses were the same as in Schloss et al. (2007) and Almandoz et al. (2007). Seawater was obtained from a continuous pumping system powered by a screw pump placed at 9 m depth on the ship's exterior (see Poisson et al. 1993 and Balestrini et al. 2000 for details). Microscopic in situ observations of the water samples showed that the pumping system did not break phytoplanktonic organisms.

At each station, both qualitative and quantitative samples were taken for phytoplankton analyses. Qualitative samples were collected by filtering seawater from the continuous system through a 20 μm mesh net, whereas
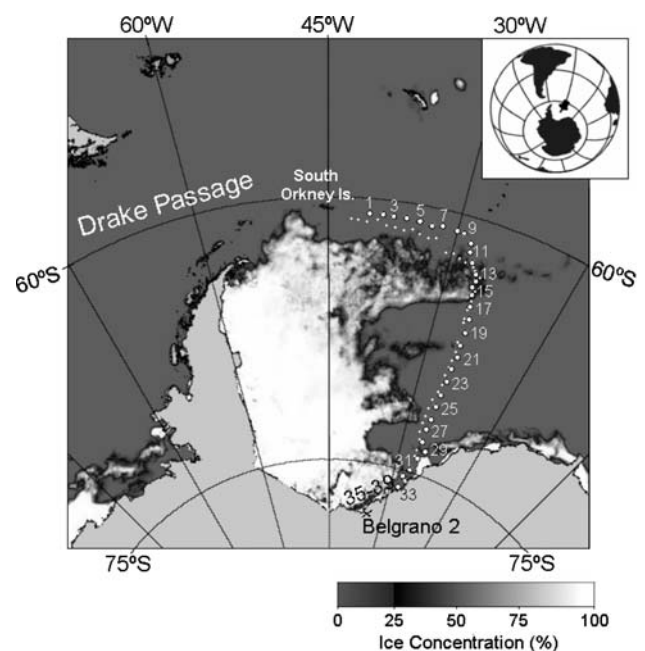
Fig. 1 Map of the study area showing the location of sampling stations (*circles*), XBT sections (*crosses*) and ice concentration (calculated from AMSR-E data) in the Weddell Sea during the sampling period

Table 1 Location of surface sampling stations carried out in the Weddell Sea during summer 2004

Station	Latitude	Longitude	Station	Latitude	Longitude
1	60°54.04	40°09.99	21	67°47.12	25°09.66
2	60°51.13	38°51.61	22	68°33.31	25°23.19
3	60°53.91	37°27.50	23	69°19.69	25°24.51
4	60°55.30	36°05.06	24	70°05.32	25°38.26
5	60°58.35	34°31.00	25	70°50.47	25°43.68
6	61°01.85	33°02.38	26	71°36.89	25°49.03
7	61°00.33	31°53.12	27	72°21.30	26°00.20
8	60°59.88	30°04.79	28	73°03.10	25°58.63
9	61°04.53	29°15.45	29	73°35.16	25°32.02
10	61°29.91	28°13.99	30	74°05.44	25°58.56
11	61°54.80	27°58.34	31	74°46.08	26°37.31
12	62°29.36	27°19.74	32	75°20.09	27°48.57
13	63°00.89	26°29.50	33	76°01.13	28°01.02
14	63°20.11	26°12.67	34	76°27.34	30°07.60
15	63°43.15	26°23.68	35	76°31.92	30°32.88
16	64°10.85	26°09.13	36	76°38.20	31°10.87
17	64°49.58	25°47.38	37	76°47.16	32°33.79
18	65°33.42	25°22.47	38	77°15.74	34°00.60
19	66°18.70	25°13.88	39	77°39.33	35°00.75
20	67°06.26	25°22.79	–	–	–

quantitative samples were collected in 250-ml bottles. All samples were fixed with Lugol's iodine solution and kept in dark conditions at room temperature until analysis. For chlorophyll *a* determination, 2–4 l of seawater were filtered onto GF/F filters and frozen at –20°C until analysis. Ninety percent acetone pigment extracts were read in a Beckman DU 650 spectrophotometer, and corrected for phaeopigments. Concentrations were calculated following Strickland and Parsons (1972).

Vertical thermal structure

Data from 36 bathythermographs (XBT) were used to study the relation between the surface biological parameters and large-scale water mass distribution and thermal front positions. Vertical profiles of temperature (up to 800 m) were collected from 7 to 11 February 2004, sailing back north from "Belgrano 2" to South Orkney Islands. XBT casts and biological sampling were performed on similar tracks (see Fig. 1) with a maximum time lag of 11 days. This time lag may be considered smaller than the typical time of variability of large scale thermal fronts which undergo some meridional displacements and change their intensity on seasonal time scale (Artamonov et al. 2004).

Environmental data

Surface (9 m) water temperature and salinity were measured continuously with Sea-Bird SB sensors. Duplicate samples for nitrate, nitrite, phosphate and silicate were taken from the continuous seawater pumping system, filtered through Whatman GF/F filters, and kept frozen (–20°C) until analysis. Nitrate, nitrite and silicate were measured with an automatic analyzer (Autoanalyzer Technicon II$^{®}$), while phosphate was determined manually, following the method described in Strickland and Parsons (1972).

Data on the light regime were obtained from http://www.webcalculator.co.uk/environmental/daycalc, using the location (latitude and longitude) and date (Julian day) of the sampling stations.

Daily sea ice concentration maps were derived from the advance microwave scanning radiometer (AMSR-E), a passive-microwave radiometer installed aboard the Aqua satellite. The maps were produced with a resolution of 6.25×6.25 km by the Institute of Environmental Physics of the University of Bremen (Germany). The sea-ice concentration was calculated using the ARTIST Sea-Ice (ASI) algorithm (Kaleschke et al. 2001). In order to analyze the influence of the ice-edge proximity on the phytoplankton distribution, the distance (in km) between the sampled stations and the 80% sea-ice concentration isoline was obtained from the sea-ice concentration maps.

Microscopic analysis

Qualitative samples were observed by light microscopy (LM) both in water mounts and in oxidized material mounted on Naphrax, and were additionally examined by scanning electron microscopy (SEM) for comprehensive morphological analysis. Subsamples were taken and washed with distilled water several times for desalinization. Centrifugation at 2,500 rpm was performed for 45 min, to ensure pelleting of the very light frustules. The organic material was then removed according to Hasle and Fryxell (1970). Observations were made with a phase contrast Wild M20 microscope (equipped with an attached camera) and a Jeol JSM-6360 LV (SEM).

Cells were enumerated with an Iroscope SI-PH inverted microscope according to the procedures described by Utermöhl (1958), and cell density was obtained after Andersen and Throndsen (2003). Of each sample, 50 or 100 ml of water were settled for 24 or 48 h, respectively, in a composite sedimentation chamber whose bottom was subsequently observed with phase-contrast at 400× magnification. The organisms were counted in two stages; cells

were enumerated in random fields until to observe at least 100 cells of the most frequent taxon (i.e. most diatoms were identified to species level whereas many phytoflagellates were identified to class level), to estimate general phytoplankton composition. In addition, and in order to obtain an acceptable error of *Pseudo-nitzschia* species abundance, at least 100 valves of the dominant species were counted in random fields or in one or two strips of the chamber, depending on the cell concentration. The whole chamber bottom was scanned either when it was not possible to reach 100 cells of the dominant species or when the less frequent species could not be detected. Empty cells were distinguished and not included in the results. Since flagellates generally lose their flagella by the addition of fixatives, unidentified phytoflagellates and round-shaped organisms with or without flagella were included in a single group as "flagellates" and classified according to their size.

Data analysis

Canonical correspondence analysis (CCA) was used to examine the relationship between species composition and the different environmental variables (Ter Braak 1986; Ter Braak and Verdonschot 1995). Associated Monte Carlo Permutation test (999 unrestricted permutations, $P \leq 0.05$) was used to assess the overall significance of the ordination and the significance of the first axis. Abundance data were transformed taking square roots, to prevent a few high values from unduly influencing the analysis (Ter Braak 1986). Because of missing environmental data, stations 13 and 22 were excluded from the analysis, which was performed using the software CANOCO 4.5 (Ter Braak and Šmilauer 2002).

Results

Physical, chemical and biological characteristics of the studied area

The major water mass in the upper 1,000 m of the Weddell Sea is the warm deep water (WDW). This water mass is relatively warm and salty (subsurface temperature maximum in Fig. 2), with low O_2 content and high nutrient concentrations. In the surface layers and above the WDW lies the fresher and colder Antarctic surface water (ASW) that in the southernmost stations is characterized by temperatures near to freezing point (see Figs. 2, 3b). The temperature minimum at the base of the ASW is characteristic of the winter water (WW) that lies approximately at 100 m depth, which may be considered as a proxy of the winter mixed layer depth. The general circulation in the Weddell Sea is dominated by a large cyclonic gyre whose clockwise water flow is amplified in the outer limbs (e.g. Fahrbach et al. 1994) that are defined by the Weddell Front (WF) and the Antarctic Slope Front (ASF). The WF marks the northern limit of waters, characteristic of the Weddell Sea interior and the southern limit of the Weddell Scotia Confluence Zone (WSCZ). The hydrological properties of the WF largely change with longitude since WSCZ is characterized by strong mixing events (e.g. Whitworth et al. 1994; Brandon et al. 2004). In the eastern flank of the Plateau of the South Orkney Islands, the WF may be identified as the region near 60–62°S where the subsurface maximum of temperature does not reach 0.5°C (Heywood and King 2002). Heywood et al. (2004) have shown that east of the South Orkney Islands, the WF meanders in a rather complex path, closely following the 2,000–2,500 m isobaths of the South Orkney Islands shelf. In this area, the quasi-zonal cruise track does not allow for an orthogonal

Fig. 2 Vertical temperature section across the eastern Weddell Sea compiled from XBT profiles. The approximate surface position of the Weddell Front (*WF*) and Antarctic Slope Front (*ASF*) are shown (see text for details). *Vertical thin lines* represent the XBT casts
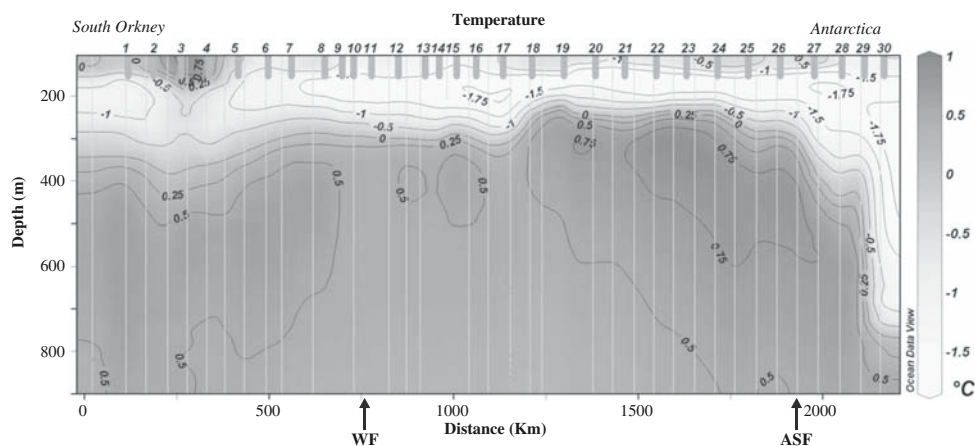
intersection of the WF. Consequently, mainly based on the results of Heywood and King (2002) and Heywood et al. (2004), the WF may be only approximately located between Sts 9 and 11. In the southern limb, the Antarctic Slope Front (ASF) defines the boundary between the relatively cold waters filling the Antarctic continental shelf and the warmer and more saline waters farther offshore (Heywood et al. 2004). The ASF is located between station 26 and 27 (Fig. 2) and is identified by a subsurface temperature gradient between WDW and a thickened layer of ASW (Whitworth et al. 1998). Frontal zones are characterized by stronger surface and subsurface currents and may act as barriers for the spreading of biota.

The collected temperature profiles, together with other published results are used to identify in the study area (see Fig. 2) the three main zones: (1) the Weddell–Scotia Confluence Zone, north of the WF (WSCZ, Sts 1–9), (2) the oceanic Weddell Sea zone (Sts 10–26) and (3) the neritic Weddell Sea zone (Sts 27–39).

The sampled area was mostly ice-free during navigation except for two zones (Sts 15–16 and 30–39) in the proximity to the ice-border, where free floating pack ice was present (Figs. 1, 3a). Surface temperatures and salinities varied between 0.7 and –1.5°C and from 32.62 to 34.01 psu, respectively, with a general decreasing and increasing trend superimposed on high wavelength variability (Fig. 3b). The bottom depths exceed 4,000 m in open waters decreasing to <500 m in the southern area over the shelf (Fig. 3c). Nutrient concentrations were high throughout the studied area (Fig. 3d–f), showing partial depletions mainly in a few northern stations and near the ASF. Photoperiod increased gradually southwards, from days with 17 h of light and 7 h of dark to days with 24 h of continuous light south of 73°S.

Chl-a concentration and total phytoplankton abundance showed higher mean values in the WSCZ and in the neritic Weddell Sea zone, whereas the lowest values were observed in the oceanic Weddell Sea area (Table 2; Fig. 4a). Chl-a concentrations ranged from 0.2 to 8.1 mg m^{-3}, with a mean of 2.0 ± 2.1 mg m^{-3}. The highest values were found at stations 5–7 (6.2–6.6 mg m^{-3}) and at station 27 (8.1 mg m^{-3}) and were associated with diatom and small flagellate (≤5 μm) blooms, respectively (Fig. 4). Total phytoplankton abundance ranged between 7.1 × 10^4 and 6.2 × 10^6 cells l^{-1} (Fig. 4a). Diatoms and small flagellates (≤5 μm) were the two main phytoplankton groups contributing to total cell abundance. Dinoflagellates, prasinophytes, silicoflagellates, flagellates (6–15 μm) and
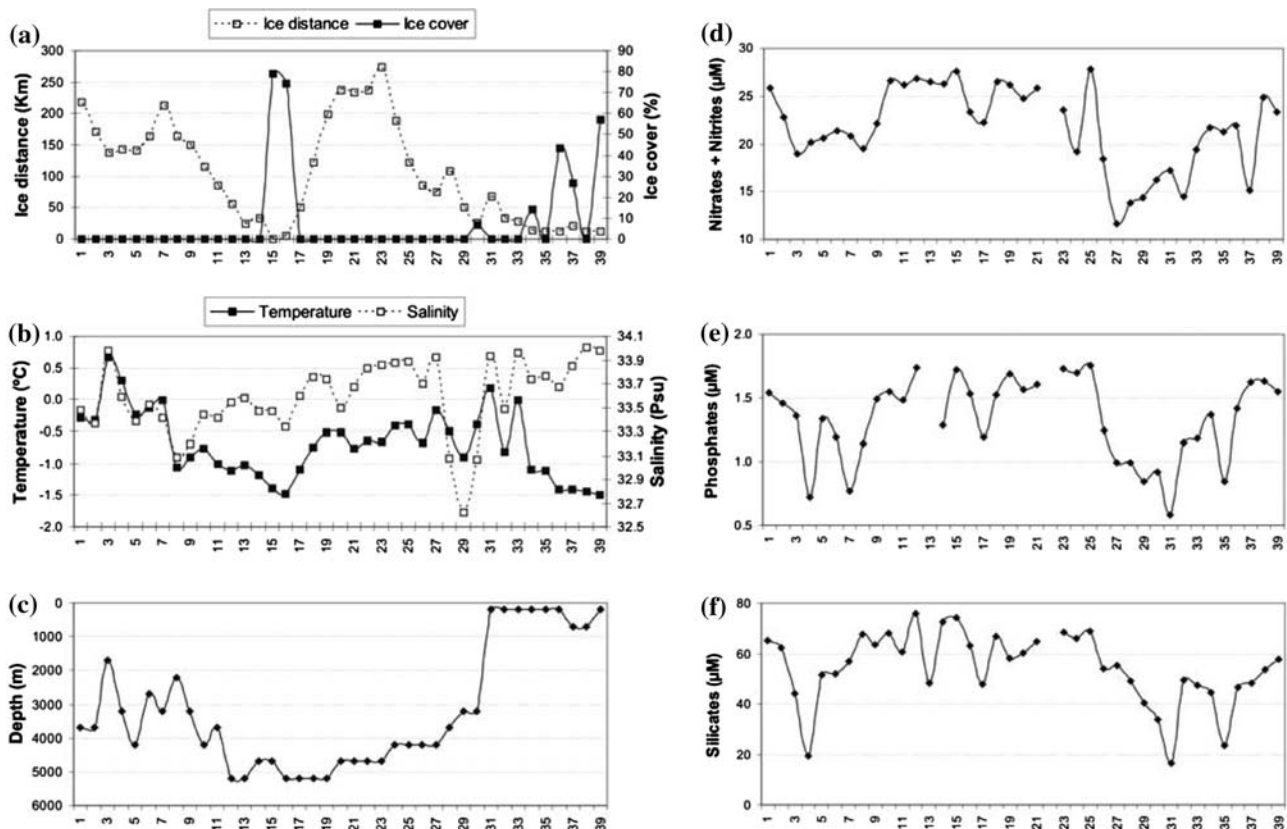
Fig. 3 **a** Ice cover percentage and distance between the sampled stations and the 80% sea-ice concentration isoline; **b** surface distribution of temperature and salinity; **c** depths; and surface concentrations of nitrates + nitrites (**d**), phosphates (**e**) and silicates (**f**), along the study area

Table 2 Average ± standard deviation of values of chlorophyll *a* concentration (chl *a*), total phytoplankton, diatoms and flagellates (≤5 μm) abundance, percent contribution of *Pseudo-nitzschia* to total diatoms densities (% Pseudo contribution) and percent contribution of *P. prolongatoides* (PP) plus *P. lineola* (PL) and *P. subcurvata* (PS) plus *P. turgiduloides* (PT) to total *Pseudo-nitzschia* densities in distinct regions within the study area

Zone	Chl-*a* (mg m⁻³)	Total Phytoplankton (×10⁵cells l⁻¹)	Diatoms (×10⁵cells l⁻¹)	Flagellates (≤5 μm) (×10⁵cells l⁻¹)	% Pseudo contribution	PP + PL (%)	PS + PT (%)
WSCZ (Sts 1–9)	3.5 ± 2.3	12.6 ± 4.5	8.8 ± 3.9	2.6 ± 0.9	42.9 ± 15.0	92.0 ± 9.7	6.9 ± 8.8
Oceanic WZ (Sts 10–26)	0.5 ± 0.3	5.1 ± 4.7	1.8 ± 1.2	2.5 ± 3.6	4.8 ± 4.8	90.1 ± 9.1	9.7 ± 9.2
Neritic WZ (Sts 27–39)	2.7 ± 2.1	19.4 ± 16,3	4.8 ± 4.0	13.5 ± 15.8	3.0 ± 2.1	24.2 ± 15.5	75.8 ± 15.5

Regions were differentiated based on collected temperature profiles. These comprise the Weddell Scotia Confluence Zone (WSCZ), and the Oceanic and Neritic Weddell Zones (Oceanic and Neritic WZ, respectively)

cryptophytes were also found, but in much lower concentrations (Fig. 4c). Diatom densities ranged from 1.8×10^4 (St 11) to 1.3×10^6 cells l⁻¹ (St 7), and their contribution to total phytoplankton abundance varied among the above defined zones. In the northern, central and southern zones diatoms dominated in 100, 47 and 23% of the stations, respectively (Fig. 4b, c). The genera *Fragilariopsis* (especially *F. cylindrus* (Grun.) Krieger and *F. curta* (V.H.) Hustedt), *Pseudo-nitzschia* (see later) and *Chaetoceros* (mainly *C. bulbosus* (Ehr.) Heiden and *C. neglectus* Karsten) were the most prominent among diatoms. Small flagellate (≤5 μm) abundance ranged from 3.7×10^4 (St 11) to 6.0×10^6 cells l⁻¹ (St 27) but, contrasting with diatoms, their relative abundance increased from north to south dominating in 0, 53 and 77% of stations in the northern, central and southern zone, respectively (Fig. 4b, c). The peak at station 27 was due to the high abundance of *Phaeocystis antarctica* Karsten which was also widespread along the study area.

Pseudo-nitzschia density distribution

The genus *Pseudo-nitzschia* was present in all samples analyzed with densities ranging from 2.2×10^2 to 7.5×10^5 cells l⁻¹ ($\bar{x} = 1.05 \pm 2.06 \times 10^5$cells l⁻¹). The highest abundances ($>10^5$ cells l⁻¹) were observed to the north of the WF (Sts 1–9), while densities notably diminished to the south (Sts 10–39) (Fig. 5a). Average *Pseudo-nitzschia* contribution to total diatoms densities was 13 ± 18%, reaching higher proportions (up to 71% in St 4) in the northern stations (Fig. 5a; Table 2). The high abundances in the northern zone were mainly related to a bloom of *P. prolongatoides* (Hasle) Hasle (up to 7.2×10^5 cells l⁻¹) observed approximately between Sts 4 and 8 (Fig. 5). The rest of the species showed peak abundances near an order of lower magnitude (Table 3).

Pseudo-nitzschia heimii Manguin and *P. turgidula* (Hust.) Hasle were mainly confined north of the WF while *P. prolongatoides*, *P. subcurvata* (Hasle) Fryxell,

P. lineola (Cleve) Hasle and *P. turgiduloides* (Hasle) Hasle were present in the entire area of study (Fig. 5b). A separation into two main regimes was evident: one dominated by *P. prolongatoides* and *P. lineola* to the north of the ASF, and other dominated by *P. subcurvata* and *P. turgiduloides* to the south of the ASF (Table 2; Fig. 5b).

Pseudo-nitzschia species distribution and environmental conditions

CCA was used to relate the distribution of *Pseudo-nitzschia* species to environmental variables. The Eigenvalues for axes 1 (0.2) and 2 (0.04) explained 69% of the cumulative variance in the species data. The associated permutation test showed that CCA axes 1 and all canonical axes explained a significant amount of variation in the species data ($P < 0.05$).

The ordination diagrams showing CCA results are presented in Fig. 6. Stations and species are shown separately (Fig. 6a, b) to avoid overlapping of points. Positions of the stations on the biplot reflect their species composition and association to the environmental factors (represented by arrows). Different symbols were used to discriminate groups of stations in which different *Pseudo-nitzschia* species dominated (Fig. 6a). Likewise, Fig. 6b shows the distributions of the species with regards to the different environmental variables (see below). The distance between the symbols in the diagram reflects the dissimilarity in the distribution of the relative abundance of those species across the samples. The species symbols can be projected perpendicularly onto the line overlaying the arrow of a particular environmental variable, to approximate the optima of individual species with respect to values of that environmental variable (Ter Braak and Šmilauer 2002).

Based on the intersect correlations, daylength, ice-distance and ice cover were more strongly related to axis 1, whereas temperature, depth and phosphates dominated axis 2. Stations in the coastalmost areas (Sts 30–39 on the right of the diagram) in which *P. subcurvata* and *P.*

Fig. 4 Phytoplankton biomass, abundance and general composition along the studied area. **a** Chlorophyll *a* (Chl-*a*) concentration and total phytoplankton abundance distributions. **b** Cell abundance of diatoms and small flagellates (≤5 μm) along the study area. **c** Relative abundances of the main phytoplankton groups identified along transect
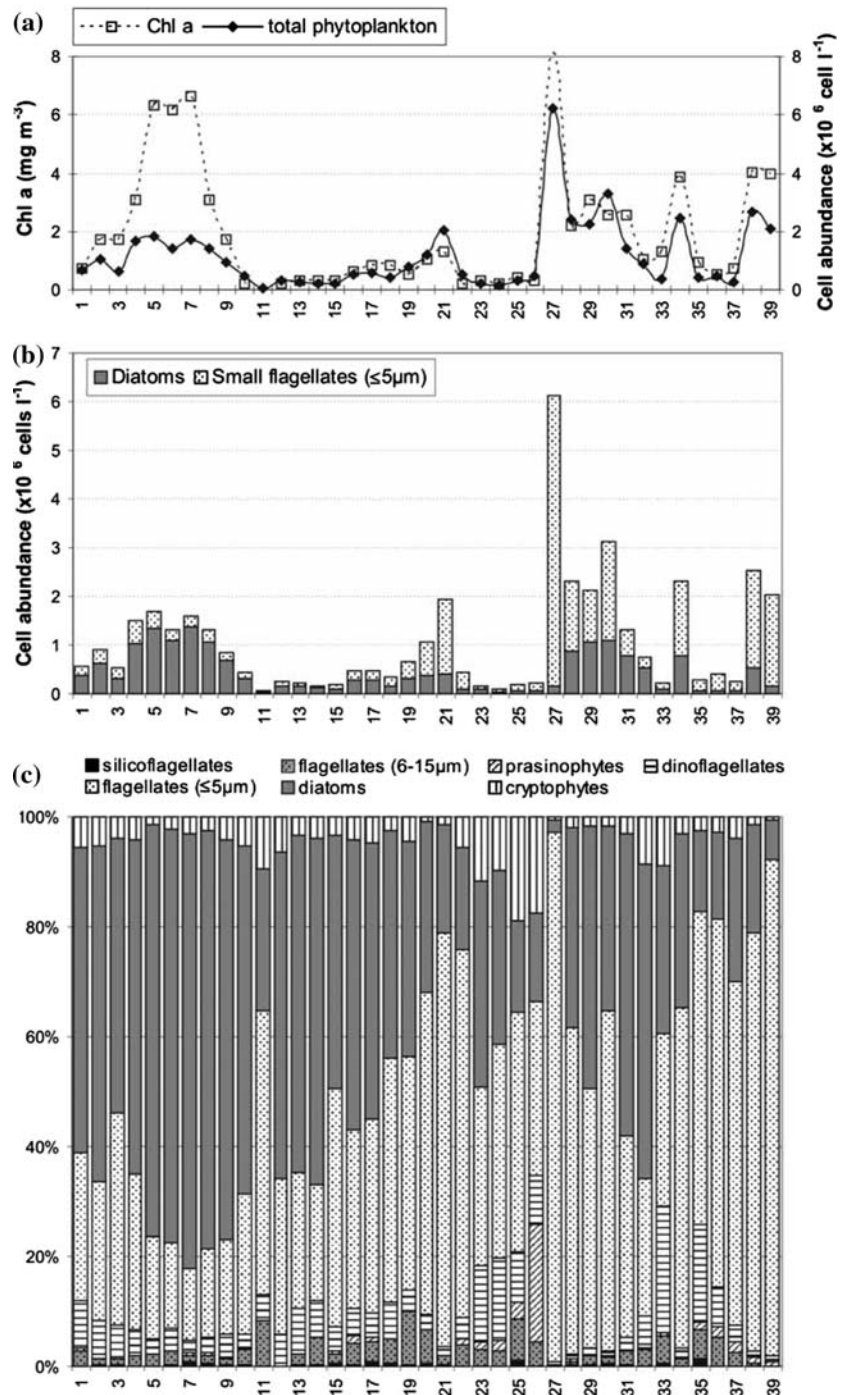

turgiduloides were especially abundant, appear separated from the others and are mainly associated with long photoperiods, heavy ice cover and high salinities (Fig. 6). On the other hand, oceanic stations dominated by *P. prolongatoides* and *P. lineola*, were largely associated with high distances to ice, deeper topographies and nutrient-rich waters, although *P. lineola* showed a weak relation with environmental variables examined. An additional division can be made between Sts 1–8 and the rest of the stations (see the top-left panel of the diagram). These stations correspond to the northernmost sampling sites which were associated with relatively warmer and ice-free waters and in which *P. turgidula* and *P. heimii* were mainly observed.

Discussion and summary

The genus *Pseudo-nitzschia* has been the focus of attention of numerous investigations in the last 20 years. However, just a few studies about this genus have been carried out in
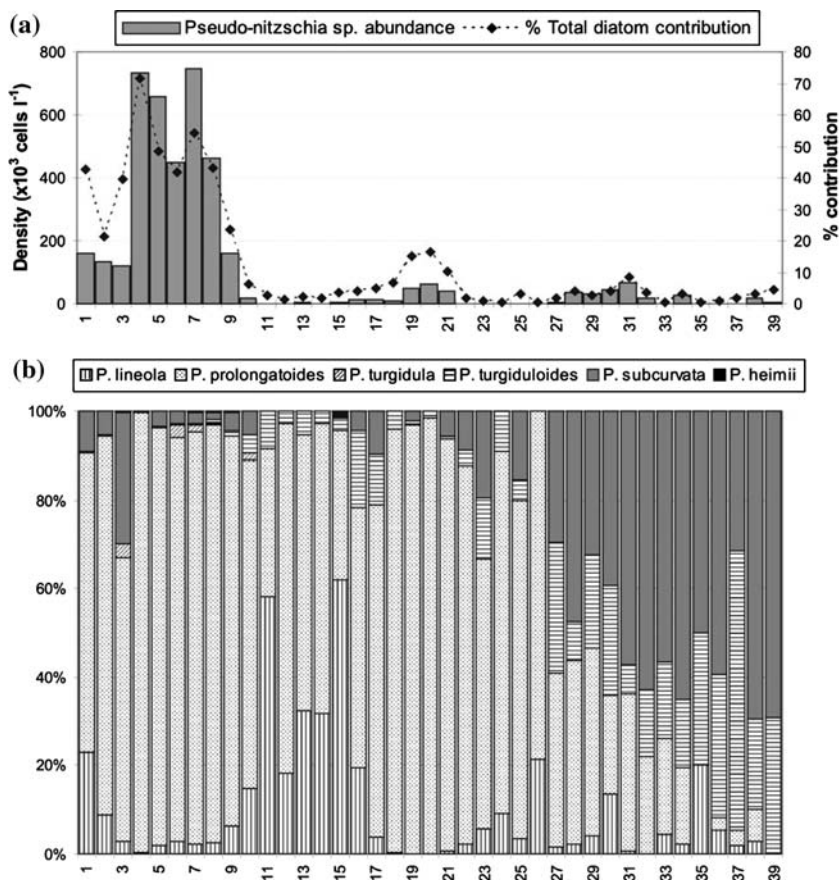
Table 3 Environmental conditions recorded during peak abundances of *Pseudo-nitzschia* species in the Weddell Sea

Species	Highest density (cells l^{-1})	Station	Temperature (°C)	Salinity (Psu)	$NO_2^- + NO_3^-$ (µm)	PO_4^{3-} (µm)	SiO_3^{2-} (µm)
P. heimii	1.28×10^3	7	–0.02	33.41	20.85	0.77	56.77
P. lineola	3.66×10^4	1	–0.28	33.48	25.87	1.54	64.95
P. prolongatoides	7.25×10^5	4	0.31	33.59	20.19	0.72	19.18
P. subcurvata	3.84×10^4	31	0.18	34.12	17.20	0.58	16.33
P. turgidula	1.23×10^4	6	–0.14	33.52	21.32	1.19	52.05
P. turgiduloides	1.13×10^4	30	–0.39	33.07	16.22	0.92	33.77

Fig. 6 Canonical
correspondence analysis (*CCA*)
ordination diagram showing the
relationship between **a**
environmental variables
(*arrows*) and stations (1–39),
in which *P. prolongatoides*
(*square*), *P. subcurvata* (*circle*),
P. lineola (*cross*) and *P.
turgiduloides* (*up-triangle*) were
the most abundant *Pseudo-
nitzschia* species; and **b**
environmental variables and
Pseudo-nitzschia species
distribution
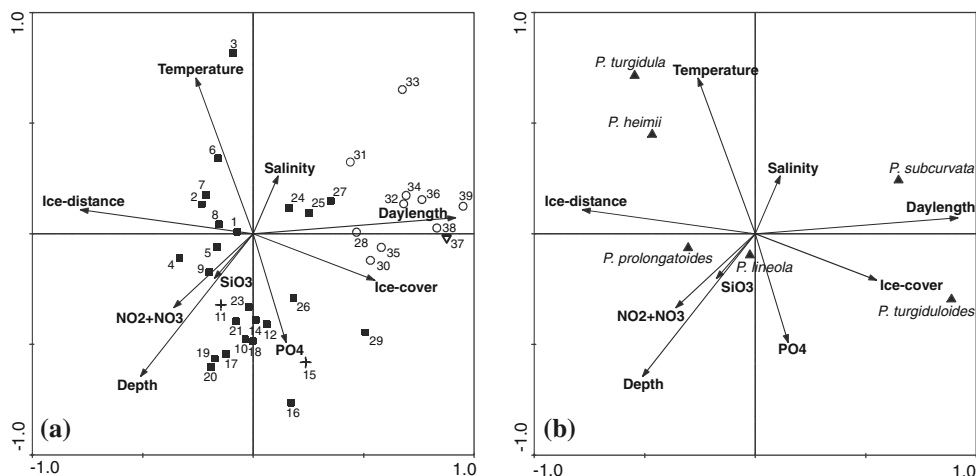
the Antarctic region, and this one is the first attempt to elucidate their species-specific summer distribution in a vast zone of the Weddell Sea by means of the analysis of biological, physical and chemical data. The analysis of vertical profiles of temperature allowed us to define the water masses in the area, as well as the main thermal frontal structures in the Weddell Sea that separate the area of study in three regions with different biological characteristics. In fact, phytoplankton abundance and composition showed great variability along the study area. The highest Chl *a* concentrations were found in the northern and southern parts of the transect, whereas the central region showed lower values. A similar pattern of phytoplankton biomass distribution showing a contrast between poor open waters and richer neritic or frontal areas has been previously reported for a comparable summer transect along the Weddell Sea (Estrada and Delgado 1990). Diatoms were the most conspicuous phytoplankton group in the northern area while small flagellates were generally dominant in south of the ASF. These results are consistent with the general scheme proposed by Smetacek et al. (1990) which postulates that flagellates are the typical representatives of phytoplankton in Antarctic waters while large diatoms occasionally bloom in special areas. Furthermore, this idea is largely supported by the results of other authors in several regions of the Weddell Sea (Estrada and Delgado 1990; Nöthig et al. 1991; Bianchi et al. 1992; Kang and Fryxell 1993; Schloss and Estrada 1994; Kang et al. 2001; Krell et al. 2005). Among the most abundant genera, the genus *Phaeocystis* (included in the group of the flagellates), several pennate diatoms of the genera *Fragilariopsis*, *Pseudo-nitzschia* and *Nitzschia*, and centric diatoms such as *Chaetoceros* and *Thalassiosira*, have been recurrently found (Estrada and Delgado 1990; Nöthig et al. 1991; Bianchi et al. 1992; Kang and Fryxell 1993; Kang et al. 2001; Krell et al. 2005).

The most conspicuous peaks of Chl *a* were observed north of the WF and south of the ASF, where two qualitatively different blooms were observed. To the north of the WF, high Chl *a* concentrations (>6 mg m^{-3}) were associated with a phytoplankton assemblage dominated by diatoms and a partial depletion of nutrients, suggesting an early stage of the bloom. This stage could be related to the intermediate distance to the ice-edge (≈ 100–200 km), which stabilizes the water column and favors diatom blooms. In contrast, south of the ASF the alternate high (i.e. Sts 34, 38–39) and low (i.e. Sts 35–37) Chl *a* values together with nutrient consumption and a phytoplankton assemblage mostly dominated by flagellates, but where diatoms were also numerically important, suggest an advanced bloom stage. The higher ice-cover and the proximity to the ice-edge in this area suggest the start of refreezing, typical of the end of the growth season.

Data analysis shows that the genus *Pseudo-nitzschia* is broadly distributed in the Weddell Sea and contributes significantly to total diatom densities. However, in spite of more than 30 species described for this genus, its species richness in Antarctic waters seems to be low (Hasle and Medlin 1990). We report the presence of six species in the Weddell Sea: *P. heimii*, *P. lineola*, *P. prolongatoides*, *P. subcurvata*, *P. turgidula* and *P. turgiduloides*. Three of them, *P. prolongatoides*, *P. subcurvata* and *P. turgiduloides*, have been described as endemic for Antarctica (Hasle and Syvertsen 1997) while the other three, although cosmopolitan (Hasle and Syvertsen 1997), are commonly found well represented in southern cold water regions (Hasle 1964, 1965; Ferrario and Licea 2006).

P. prolongatoides was the most abundant *Pseudo-nitzschia* species in 67% of all samples examined and it was observed in bloom conditions at the WSCZ, reaching densities up to 7.2×10^5 cells l^{-1} and representing more than 70% of total diatom densities. High cell concentrations of *P. prolongatoides* of up to 2.5×10^5 and 1.4×10^5 cells l^{-1} have been previously observed in open waters of the northwestern Weddell Sea (Kang and Fryxell 1993) and in the Indian sector of the Southern Ocean, to the south of the Polar Front (Kopczynska et al. 1986), suggesting that it is a common phytoplankton component in the Antarctic region. The other common species, in order of observed relative dominance, were *P. subcurvata* (26%), *P. lineola* (5%) and *P. turgiduloides* (3%).

The study of the distribution of *Pseudo-nitzschia* species in three areas of the Weddell Sea characterized by different physical conditions has shown that (1) *P. subcurvata* and *P. turgiduloides* are the most abundant species south of the ASF; (2) *P. prolongatoides* and *P. lineola* dominate north of the ASF; and (3) *P. turgidula* and *P. heimii* are observed mostly north of WF in the WSCZ. A direct comparison of our results is difficult due to lack of similar investigations in the Weddell Sea. However, our findings are in general agreement with the results of Hasle (1964, 1965), who studied the distribution of this genus in the Pacific sector of the Southern Ocean. She found that *P. prolongatoides* was apparently more widespread than *P. subcurvata* and also observed great abundances of *P. subcurvata* and *P. turgiduloides* far south in her study area. Moreover, in the same work (Hasle 1965) it was pointed out that the *P. heimii* distribution pattern is probably more or less similar to that of *P. turgidula* together with the absence of both species in the samples collected far south in the Antarctic Zone. Conversely, high concentrations of *P. heimii* and *P. turgidula* have been mentioned in northern Antarctic waters of the Drake Passage (Ferrario and Licea 2006). All this suggests that the WF acts as barrier (Sokolov and Rintoul 2002; Acha et al. 2004) for phytoplankton distribution (Kopczynska et al. 1986) and that the

presence of these two species only in the northern Antarctic waters could be a general pattern in the entire Southern Ocean.

The separation of *Pseudo-nitzschia* distributions in the three main zones divided by the location of the WF and ASF reflects ecological differences among them. CCA shows that *P. subcurvata* and *P. turgiduloides* were observed mainly near the ice-edge in shallower waters and in conditions of long photoperiod; *P. prolongatoides* was associated with deeper and nutrient-rich waters, while *P. turgidula* and *P. heimii* were observed mostly in the warmest and far from ice waters to north of the WF. Conversely, *P. lineola* was close to the center in the ordination diagram, which denotes that it is poorly related to the axes and suggests that its variability could be driven by factors not considered in the analysis. The main variables that explained a significant fraction of the total variation in the *Pseudo-nitzschia* specific composition were bathymetry, proximity to the ice-edge, photoperiod and temperature. This is not surprising, because several studies have also documented changes in phytoplankton assemblages along these gradients (Estrada and Delgado 1990; Nöthig et al. 1991; Bianchi et al. 1992; Kang et al. 2001; Krell et al. 2005). For example, bathymetry is well known to be an important factor affecting phytoplankton distribution (Holm-Hansen et al. 2005), and an apparent distinction among *Pseudo-nitzschia* species preference for neritic and oceanic waters has been previously observed (Hasle 1965). The major importance of the ice melting on phytoplankton composition has been also frequently reported for the Southern Ocean (e.g. Ferreyra et al. 2005; Garibotti et al. 2005; Krell et al. 2005). Ice melting, which normally occurs during spring/summer, induces the stabilization of the water column, triggering the development of phytoplankton blooms. Moreover, it releases ice algae to the water, providing a seeding effect (inoculation) of cryophilic species (Garrison et al. 1987). In this sense, Hasle (1964) observed great abundances of *P. subcurvata* far south in the Pacific Antarctic Zone, and suggested that this could be related to a preference for neritic conditions or the proximity to the ice-border. In addition, with the exception of *P. turgidula*, all the *Pseudo-nitzschia* species found during this study have been observed living in the ice (Hegseth and Von Quillfeldt 2002). On the other hand, Fehling et al. (2005) suggested that photoperiod is a potentially important factor influencing the species composition, timing, density and toxicity of *Pseudo-nitzschia* blooms, based on laboratory experiments. They found that a rise of 9 h in the photoperiod (from 9 h light:15 h dark to 18 h light:6 h dark) influenced the growth of *P. delicatissima* and *P. seriata*. Moreover, photoperiod was the most significant environmental variable accounting for the variation of *Pseudo-nitzschia* distribution in Scottish waters (Fehling et al. 2006).

Despite these clear patterns of *Pseudo-nitzschia* distribution in the Weddell Sea as evidenced by this study, there is still to be established whether this corresponds to a stable pattern or to an exceptional one taking place during the study period. Consequently, further studies are needed to ascertain whether the distributional patterns suggested here are determined by the spatial heterogeneity along the transect or are they reflecting different stages of the phytoplankton succession found in these areas during sampling. *Pseudo-nitzschia* species shifts during seasonal progression and inter-annual variability have been evidenced from other studies in non-polar regions (Villac 1996; Caroppo et al. 2005; Kaczmarska et al. 2007).

Nowadays, ten species of the genus *Pseudo-nitzschia* are considered as potential domoic acid (DA) producers and the number of DA events is increasing worldwide (Bates 2000; Fryxell and Hasle 2003). Massive mortalities of high-level organisms in the food chain, like mammals and sea birds, have been attributed to the trophic transfer of DA by the predation of vectors that consume the toxic phytoplankton species and concentrate the toxin. Mussels, crabs, fishes and krill, the latest a fundamental member in Antarctic marine ecosystems, are among the most common vectors in the transfer of DA in other regions of the world (see review in Bates and Trainer 2006). Curiously, and as far as we could ascertain, there are no records of DA production by Antarctic clones of *Pseudo-nitzschia*. From the species found through this survey, only *P. turgidula* has tested positive for DA production from field and cultures studies in New Zealand (Rhodes et al. 1996), although there may have been some uncertainty about the identification of this species (Fryxell and Hasle 2003). Conversely, clones of *P. subcurvata*, *P. turgiduloides* and *P. lineola* isolated from Antarctica tested negative (Fryxell et al. 1991; Kang et al. 1993), whereas there are no available information about DA production studies on *P. prolongatoides* and *P. heimii*. Therefore, the question about the potential toxicity of Antarctic *Pseudo-nitzschia* is still open to future research.

Appendix: *Pseudo-nitzschia*'s diagnostic characteristics

The morphology of the *Pseudo-nitzschia* species observed during the present study fitted well with the classical descriptions provided by Hasle (1964, 1965) and more recent reviews (Hasle and Syvertsen 1997; Ferrario and Licea 2006). Nevertheless, some of the specific morphometric data recorded here allow widening of published measurements (Table 4). As it is well known, a detailed morphological analysis using electron microscopy is essential for reliable *Pseudo-nitzschia* species identification. However, particularly during this study, the cell outline and its symmetry, together with the shape of the cell ends and the colony type formation were useful and consistent features allowing species differentiation during light microscope qualitative observations and enumerations.

Pseudo-nitzschia heimii Manguin (Fig. 7m–p)

Cells are lanceolate, 79–102 μm long and 5.2–5.7 μm wide, with round broad ends and central interspace. Striae (19–22 in 10 μm) are perforated by two rows of poroids (4–7 in 1 μm) and are more densely spaced than the fibulae (12–16 in 10 μm).

Pseudo-nitzschia lineola (Cleve) Hasle (Fig. 7e–h)

Cells are linear, 41–106 μm long and 2.1–2.7 μm wide, with acute ends and central interspace. Striae (22–28 in 10 μm)

are usually uniseriate but in some specimens one or both valve ends presented striae with two rows of poroids (4–6 in 1 μm). Fibulae are less dense than striae (11–18 in 10 μm).

Pseudo-nitzschia prolongatoides (Hasle) Hasle (Fig. 7q–t)

Cells are lanceolate, expanded in the middle part, 20–85 μm long and 1.5–2.6 μm wide, with rostrate ends and central interspace. Striae (29–33 in 10 μm) with two to three rows of poroids (10–13 in 1 μm) and 16–21 fibulae in 10 μm. It was commonly observed in star-like colonies of four cells and also in typical stepped chains of two cells.

Pseudo-nitzschia subcurvata (Hasle) Fryxell (Fig. 7u–x)

Cells are curved, expanded in the middle part, with one side sharp or slightly concave and the other side convex, and attenuated towards acute ends, 48–86 μm long and 1.3–1.8 μm wide. Without central interspace. Striae (43–55 in 10 μm) with one row of poroids (6–8 in 1 μm). Fibulae irregularly spaced (12–22 in 10 μm). Mostly solitary, chains of two cells were rarely observed.
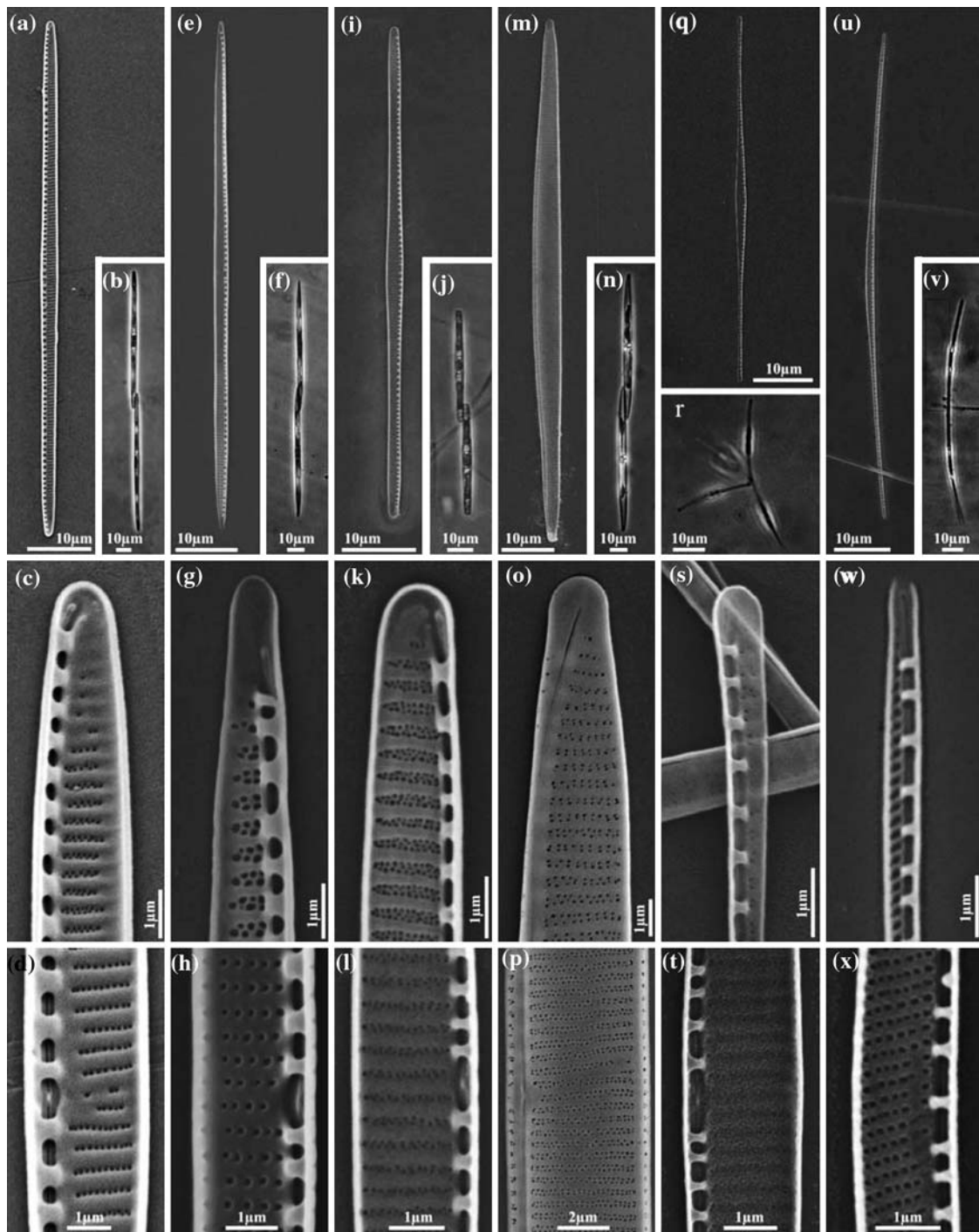
Pseudo-nitzschia turgidula (Hust.) Hasle (Fig. 7i–l)

Cells are lanceolate to almost rhombic–lanceolate, 41–79 μm long and 2.3–2.5 μm wide, with broad round ends and central interspace. Striae (24–28 in 10 μm) with generally two rows of poroids (7–9 in 1 μm) but some specimens with an incomplete third row. Fibulae homogenously distributed (15–18 in 10 μm). In girdle view, cells present conspicuous truncate ends.

Table 4 Morphometric summary of the *Pseudo-nitzschia* species observed in the Weddell Sea

Species	Length (μm)	Width (μm)	CI	Fibulae (in 10 μm)	Striae (in 10 μm)	Rows of poroids	Poroids (in 1 μm)
P. heimii	79–102	5.2–5.7	Yes	12–16	19–22	2	4–7
Hasle and Syvertsen (1997)	67–120	4–6	Yes	11–16	19–26	2	–
P. lineola	41–106	2.1–2.7	Yes	11–18	22–28	1–2	4–6
Hasle and Syvertsen (1997)	56–112	1.8–2.7	Yes	11–16	22–28	1–2	–
P. prolongatoides	20–85	1,5–2.6	Yes	16–21	29–33	2–3	10–13
Hasle and Syvertsen (1997)	20–70	0.5–2.5	Yes	15–18	30–35	2–3	–
P. subcurvata	48–86	1.3–1.8	No	12–22	43–55	1	6–8
Hasle and Syvertsen (1997)	47–113	1.5–2.5	No	12–18	44–49	1	–
P. turgidula	41–79	2.3–2.5	Yes	15–18	24–28	2 (3)	7–9
Hasle and Syvertsen (1997)	30–80	2.5–3.5	Yes	13–18	23–28	2	–
P. turgiduloides	81–126	2–2.9	Yes	10–14	18–24	1–2	7–10
Hasle and Syvertsen (1997)	63–126	1.2–2.7	Yes	10–13	17–21	–	–

Data in Hasle and Syvertsen (1997) are added for comparative purposes. *CI* central interspace

Fig. 7 Light (*LM*) and scanning electron (*SEM*) micrographs of *Pseudo-nitzschia* species reported in the Weddell Sea, showing the *valve shape*, apical and central part details (SEM) and colonies (LM). **a–d** *P. turgiduloides*, **e–h** *P. lineola*, **i–l** *P. turgidula*, **m–p** *P. heimii*, **q–t** *P. prolongatoides*, **u–x** *P. subcurvata*

Pseudo-nitzschia turgiduloides (Hasle) Hasle (Fig. 7a–d)

Cells are lanceolate, expanded in the middle, 81–126 µm long and 2–2.9 µm wide, with broad round ends and central interspace. Striae (18–24 in 10 µm) with one or two rows of poroids (7–10 in 1 µm). Fibulae homogenously distributed (10–14 in 10 µm). In girdle view, cells with truncate ends.

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