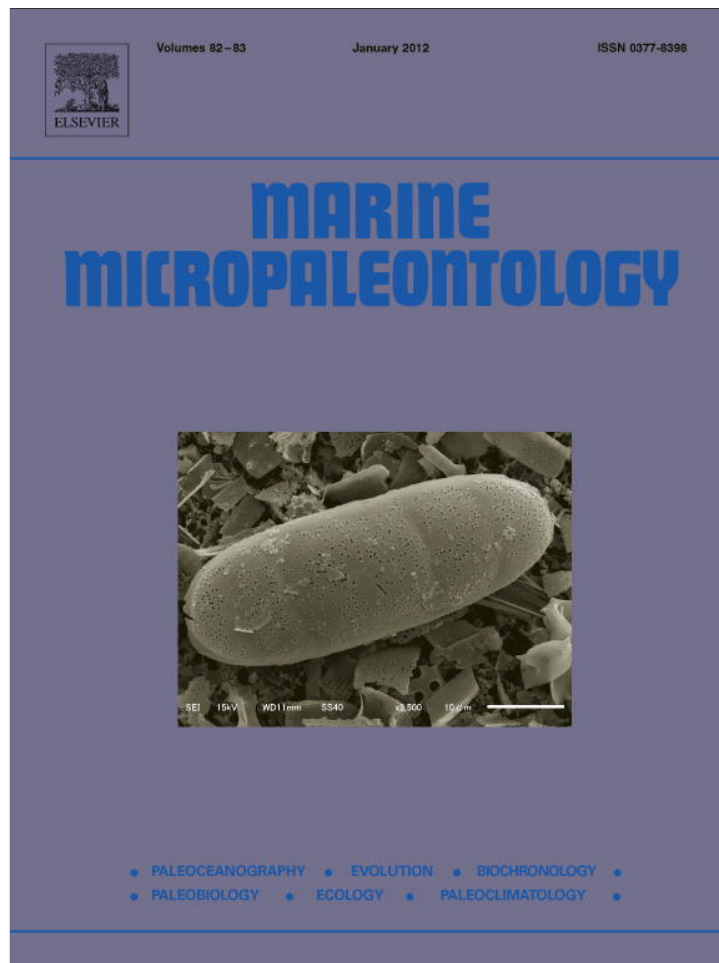


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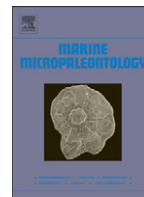
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Average process length variation of the marine dinoflagellate cyst *Operculodinium centrocarpum* in the tropical and Southern Hemisphere Oceans: Assessing its potential as a palaeosalinity proxy

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ABSTRACT

The study investigates the morphological variability of the dinoflagellate cyst *Operculodinium centrocarpum* (resting cyst of *Protoceratium reticulatum*) in core-top samples distributed over the Southern Hemisphere and the tropics in relation to sea-surface temperature (SST) and sea-surface salinity (SSS) at the corresponding sites. The process lengths show a moderate inverse relationship to summer SST (sSST) ($R^2 = 0.44$) and sSSS/sSST ($R^2 = 0.4$), however, lateral transport of cysts probably produced noise in the plots. After excluding tropical and Southern Hemisphere sites considered to have been affected by long distance lateral transport, the relationship between process length and density follows the equation $sD = 0.8422x + 1016.9$ ($R^2 = 0.55$) with a *Root Mean Square Error* = 0.63 kg m^{-3} , while the negative correlation with sSST increases up to $R^2 = 0.79$. Next to salinity, this study thus highlights the importance of a second factor, temperature, affecting process length in the tropics and the Southern Hemisphere oceans.

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1. Introduction

Abrupt climate changes during the last glacial cycle have been linked to the thermohaline circulation (THC) mode shifts (Broecker et al., 1985; 1990; Rahmstorf, 2002). The circulation mode depends on density variations in the area of North Atlantic Deep Water (NADW) formation (Broecker et al., 1990). Surface density changes in the North Atlantic are caused by a varying supply of high saline equatorial water and by the amount of fresh water input from melting high-latitude ice caps. It has been demonstrated that the strength of the THC is also influenced by changes in SSS in the tropical Atlantic (Stocker and Wright, 1991; Rahmstorf, 1996; Schmittner and Clement, 2002; Schmidt et al., 2004) and even related with density variations of Antarctic Intermediate Water regulated by the fresh-water input in the Southern Ocean (Weaver et al., 2003). Determining

past salinity changes of ocean surface waters therefore is essential for understanding past climate variations.

Different methods have been proposed to quantify past salinity changes, for example, the dinoflagellate cyst based transfer function approaches (de Vernal et al., 1993; 1994), $\delta^{18}\text{O}$ of foraminifer shells in combination with an independent estimate of SST (e.g., Duplessy et al., 1991; Rostek et al., 1993; Wang et al., 1995; Lamy et al., 2002; Nürnberg and Groeneveld, 2006; De Schepper et al., 2009), foraminiferal Ba/Ca (Weldeab et al., 2007), alkenones (e.g., Blanz et al., 2005) and δD in long-chain ($\text{C}_{25}\text{--}\text{C}_{37}$) n-alkanes (e.g., Schouten et al., 2006; van der Meer et al., 2007; 2008). However, most of the aforementioned methods have to deal with large uncertainties in the reconstructed values (e.g., Rohling and Bigg, 1998; Schmidt, 1999; Rohling, 2000; Bendle et al., 2005; Nürnberg and Groeneveld, 2006; Telford, 2006). The absence of an unequivocal approach points to the need of further investigation into reliable palaeosalinity proxies.

A number of studies have demonstrated an environmentally controlled morphological variability of certain dinoflagellate cysts. A positive relation between variable process lengths of *Lingulodinium*

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machaerophorum – the resting cyst of *Lingulodinium polyedrum* – and salinity was first noted in the Black Sea by Wall et al. (1973). Cysts bearing short processes have been associated with low salinity near-coastal and estuarine environments (Nehring, 1994; Dale, 1996; Nehring, 1997; Ellegaard, 1998) and were used semi-quantitatively in the Black Sea (Dale, 1996; Mudie et al., 2001; Marret et al., 2009), the Baltic Sea (Dale, 1996; Brenner, 2005; Head, 2007) and the Limfjord (NW Denmark) (Ellegaard, 2000), and for down-core salinity reconstructions in the SW Black Sea (Verleye et al., 2009) and the Cariaco Basin (Mertens et al., 2009a). Culture experiments by Hallett (1999) showed a relationship between the average process lengths of *L. machaerophorum* and both salinity (positive) and temperature (negative), which was later confirmed by Mertens et al. (2009b) after analysing 144 globally distributed core-top samples. Several other dinoflagellate cyst species also have been recorded bearing shorter processes with reduced salinity conditions. These species include *Operculodinium centrocarpum* (resting cyst of *Protoceratium reticulatum*) (e.g., Nehring, 1994; Dale, 1996; Nehring, 1997; Ellegaard, 1998), cysts of *Pentapharsodinium dalei* (Nehring, 1994; 1997) and several *Spiniferites* species (Wall et al., 1973; Gundersen, 1988; Dale, 1996; Lewis et al., 1999; Ellegaard et al., 2002). Because of its cosmopolitan occurrence (Wall et al., 1977; Marret and Zonneveld, 2003) and its biostratigraphical range down to the Eocene (Head, 1996), *O. centrocarpum* seems to be the most suitable cyst for determining past SSS changes. So far, this species has been semi-quantitatively related to fluctuations in SSS by de Vernal et al. (1989), Dale (1996), Ellegaard (2000), Brenner (2005) and Head (2007), and for down-core summer SSS reconstructions in Limfjord (Mertens et al., 2010). Similar to the studies of Hallett (1999) and Mertens et al. (2009b) for *L. machaerophorum*, the average process lengths of *O. centrocarpum* in a late Quaternary down-core record in the SE Pacific suggested a relationship with both salinity (positive) and temperature (negative) (Verleye and Louwye, 2010a).

This study aims to elucidate the relationship between temperature and salinity variations and the average process lengths of

O. centrocarpum, in order to assess its potential as a proxy for past environmental changes in terms of salinity, temperature or density. For that purpose, process lengths in 83 Southern Hemisphere core-top samples were measured and coupled to modern instrumental temperature and salinity data in the surface waters to suggest a possible relationship.

2. Material and methods

2.1. Location, preparation and microscopic analyses of core-top samples

A total of 114 core-top samples were analysed for biometric measurements of *O. centrocarpum* cysts from New Zealand (Sun and McMinn, 1994; McMinn and Wells, 1997), Tasmania (Dale, unpublished), South Australia (Dale, pers. comm.), Indian Ocean (Abidi, 1997; Young, 2005), South and equatorial Atlantic (Rau et al., 2006; Dale, pers. comm.; Zonneveld, pers. comm.), and the SE Pacific (Verleye and Louwye, 2010b) (Fig. 1; Table 1). As far as available, sedimentation rates between 4 cm kyr⁻¹ (McMinn and Wells, 1997) and 300 cm kyr⁻¹ (offshore Chile; Lamy et al., 2004; Kaiser et al., 2005; Lamy et al., 2007) are observed at the studied sites. All surface samples may therefore be at least of Holocene age, if not modern. It is thus assumed here that the environmental conditions affecting the morphological variability of the cysts are similar to recent environmental conditions.

The palynological methods used to extract cysts from the sediment all involved treatments with cold hydrochloric (HCl) and hydrofluoric (HF) acids, followed by sieving and/or sonication.

O. centrocarpum measurements in samples from Abidi (1997), Verleye and Louwye (2010b), Dale (pers. comm.) and Zonneveld (pers. comm.) were performed using a Zeiss Axiomager.1A and Zeiss Axioskop2 light microscopes, both equipped with a AxioCam MRc5 digital camera and 100× oil immersion objectives. The biometric analyses of the samples from Sun and McMinn (1994), McMinn and Wells (1997) and Rau et al. (2006) were made using an Olympus

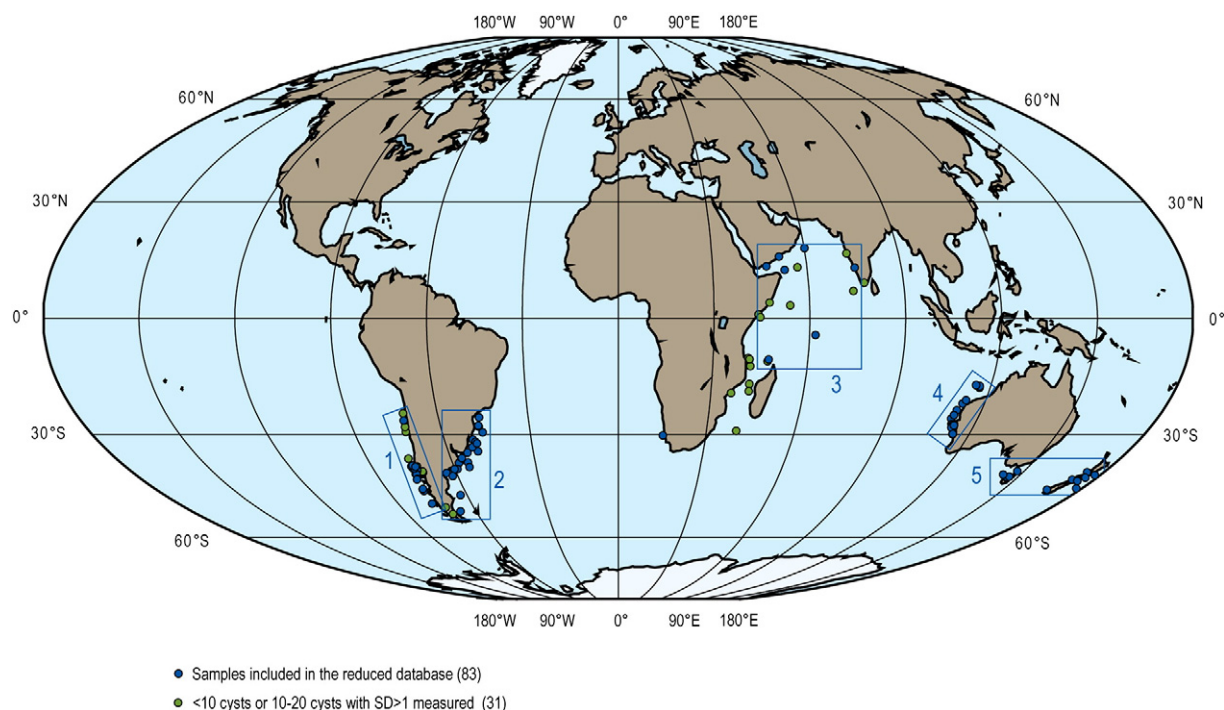


Fig. 1. Locations of the 114 studied core-top sites. Blue dots: samples included into the reduced database in which enough cysts were measured to give reproducible results. Green dots: not included into the reduced database, not enough cysts measured to be reproducible. The numbers on the chart refer to different regions: (1) SE Pacific Ocean; (2) SW Atlantic Ocean; (3) West Indian Ocean; (4) East Indian Ocean (NW Australia); (5) New Zealand and Tasmania (South Australia). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

BH-2 light microscope, equipped with a Color View II (Cell F Software Imaging System) and 100× oil immersion objectives. The East Indian Ocean core-top samples (Young, 2005) were analysed using an Olympus BH-2 microscope with 100× oil immersion objectives. All photomicrographs were made using a Zeiss AxioImager.A1 light microscope equipped with an AxioCam MRC5 digital camera (AxioVision 4.6 software) and Zeiss EC Plan-NEOFLUAR 100× oil immersion objectives (Plate 1). Measurements were made by T.J. Verleye, K.N. Mertens and M.D. Young (Table 1). The length of each process was measured from the middle of the process base to the process tip (Plate 2, figs. 11 and 12). Fragments representing less than half of a cyst were not measured, nor were cysts with mostly broken processes (Plate 2, fig. 8). For each cyst, the three longest processes parallel to the focal plane of the light microscope were measured. Three reasons can be advanced for choosing the three longest processes (Mertens et al., 2009b). Firstly, the longest processes reflect unobstructed growth during cyst formation. Secondly, the accuracy of the proxy increases since the longest processes document the largest variation. Thirdly, only a restricted number of processes are measurable or are parallel to the focal plane of the light microscope, which makes it imperative to follow a consistent approach.

When less than 10 cysts per sample were available for measurement, the sample was excluded from the database because the results are considered not reproducible. When between 10 and 20 cysts were measured, samples were excluded if the standard deviation was $> 1 \mu\text{m}$, and included when the standard deviation was $< 1 \mu\text{m}$. We consider this cut-off value of $1 \mu\text{m}$ as acceptable, because values were then comparable to other samples where more processes were measured. Samples in which more than 20 cysts/sample were measured were included in our dataset, and resulted in a reduced dataset of 83 samples (Fig. 2; Table 1). Measuring 20 cysts or more yields reproducible results according to Verleye and Louwye (2010b), who compared two independent measurements (on different cysts) in an *ad random* chosen sample.

Cyst body diameters were measured in 41 of the 83 samples. Thirty-three samples were measured by T.J. Verleye and 8 by K.N. Mertens. The central body diameter could not be measured on each specimen because cysts were sometimes severely crumpled or torn (Plate 2, figs. 4–7). Because considerable deformation of the cyst body may have occurred prior to measuring, prudence is recommended while interpreting these data.

2.2. Salinity and temperature data

The biometric measurements on *O. centrocarpum* cysts were compared with the recent seasonal and annual sea-surface temperature (SST), sea-surface salinity (SSS), SSS/SST ratio and sea-surface water density. The oceanographical parameters were obtained using the gridded one-degree World Ocean Atlas 2009 (NODC, 2009) and the Ocean Data View software (Schlitzer, 2010). Annual SST from the dataset (see Section 3.2) ranges between 8 and 29 °C ($\Delta 21$ °C), while SST during summer (sSST) varies between 10 and 29 °C ($\Delta 19$ °C) (Locarnini et al., 2010). The SSS variations are less prominent, annually ranging from 32.4 to 36.2 psu ($\Delta 3.8$ psu) and from 31.7 to 36.4 psu ($\Delta 4.7$ psu) during summer (January–March for the Southern Hemisphere sites) (Antonov et al., 2010).

3. Results

3.1. Process length variation in core-top samples

In the reduced database, a total of 9,936 *O. centrocarpum* processes length measurements gave an average of 8.8 μm , with a standard deviation of 1.7 μm , and a range from 3.2 to 16.3 μm . The 2th and 98th percentiles correspond with a process length of 5.5 μm and 12.4 μm , respectively. The observed range is comparable to the ranges

reported by Wall and Dale (1968) for Atlantic specimens (6 to 16 μm), Reid (1974) for coastal cysts from the British Isles (7 to 14 μm) and Mertens et al. (2010) for Baltic specimens (0.5 to 13.5 μm). The distribution is slightly skewed to the right (0.18) due to tailing at the right side of the size-frequency curve, and approaches a mesokurtic distribution with a kurtosis of -0.07 (Fig. 3a). The recorded morphotypes were similar to those described by Matsuoka et al. (1997), Nehring (1997), Ellegaard (2000), Head (2007) and Mertens et al. (2010). No cysts lacking processes such as those recorded in the Baltic Sea (Mertens et al., 2010) were observed in the core-top samples.

The cyst body diameters of 1587 specimens were measured, which resulted in an average 40 μm with a standard deviation of 5.2 μm . The cyst body sizes range from 26 to 61 μm . This large range may be explained through compression or tearing of the cyst. When ignoring the 2% largest and smallest cysts, the size range is almost halved from 35 μm to 21 μm , corresponding to cyst body sizes between 31 μm (2th percentile) and 52 μm (98th percentile). This range is comparable to *O. centrocarpum* cyst body measurements by Nehring (1997) for the German coast (31–44 μm), Reid (1974) for the British coast (33–46 μm), Matsuoka (1990) for the Pacific (28–50 μm) and Mertens et al. (2010) for the Baltic Sea (23–62 μm). The size-frequency curve is skewed to the right (0.50). This is most likely caused by mechanical deformation of the cysts often resulting in larger cyst diameters (Fig. 3b). The histogram has a positive kurtosis of 0.34, assuming a rather leptokurtic distribution.

3.2. Regional correlations between parameters

In the SE Pacific, a significant positive relationship is observed between the average process length and summer SSS/summer SST (sSSS/sSST) ($R^2 = 0.74$) and summer density ($R^2 = 0.73$), while a negative relationship is recorded with summer SST (sSST) ($R^2 = 0.65$) (Table 2). No significant relationship is observed with summer SSS (sSSS). The SW Atlantic data show a positive relationship with both sSSS ($R^2 = 0.76$) and sSST ($R^2 = 0.51$) (Table 2). Regional data from the East and West Indian Ocean and from Australia and New Zealand show no significant relationship between process length variation and sSSS, sSST, sSSS/sSST and summer density.

3.3. Correlation between environmental parameters and process length from all Southern Hemisphere and tropical sites

The combination of the Southern Hemisphere and tropical sites into one database results in a moderate relationship between process length and sSST ($R^2 = 0.44$) and sSSS/sSST ($R^2 = 0.4$) (Fig. 4a and c). A weak relationship is observed with sSSS ($R^2 = 0.26$) and summer density ($R^2 = 0.24$) (Fig. 4b and d). The body diameter of the cysts shows a moderate relationship with the recorded process lengths of $R^2 = 0.50$, but shows no relationship at all with any of the environmental parameters of interest ($R^2 = 0.03$ for sSSS and $R^2 = 0$ for sSST, sSSS/sSST and summer density) (Table 3).

4. Discussion

4.1. Transport and preservation

Dinoflagellate cysts may be transported over long distances away from the original environment where they were formed, by moving water masses and shedding of sediment from the continental margins. This could seriously challenge the validity of assuming a direct relationship between cysts in bottom sediments and prevailing environmental conditions in the immediately overlying surface waters, particularly at deeper water oceanic sites (Dale and Dale, 1992; Dale, 1996). It is therefore important to consider the extent to which this may have affected the samples used here. The reduced

Table 1
An overview of the reduced dataset, including their geographical position, the abundances of *O. centrocarpum*, the sample providers, the biometric results and the environmental parameters of interest.

ID	Station/slide	Sampling gear*	Lat.	Long.	Depth (m)	%Ocen	Reference	Process length (µm)	Stdev	Body diameter (µm)	Stdev	Cysts measured	Measurer**	sSST (0 m)	sSSS (0 m)	sSSS/sSST (0 m)	sDensity (0 m)
1	89K	BC	-11.73	47.43	3800	10.2	Abidi (1997)	7.90	0.83	36.0	4.4	12	T	28.7	34.9	1.22	1022.09
2	900939	BC	-5.57	61.63	3860	1.5	Abidi (1997)	6.86	0.63	34.8	3.3	25	T	28.6	34.9	1.22	1022.10
3	85682	BC	10.88	52.38	3092	0.6	Abidi (1997)	7.21	1.00	35.3	4.8	20	T	23.7	35.5	1.50	1024.15
4	77195	BC	11.50	74.53	1426	7.0	Abidi (1997)	7.25	0.90	35.6	3.6	42	T	27.7	34.5	1.25	1022.15
5	76136	BC	11.87	46.82	1649	1.3	Abidi (1997)	7.10	0.85	35.2	3.1	40	T	29.3	36.4	1.24	1023.04
6	14107	BC	11.85	46.75	1608	1.4	Abidi (1997)	7.13	1.03	35.1	2.8	22	T	29.3	36.4	1.24	1023.05
7	14105	BC	14.30	51.00	2120	0.9	Abidi (1997)	6.85	0.71	34.1	3.5	19	T	27.2	36.0	1.32	1023.41
8	3488	BC	16.52	59.53	2120	1.7	Abidi (1997)	7.29	0.85	37.0	2.7	10	T	25.8	36.0	1.40	1023.89
9	AR10(1)	GC	-38.33	-57.05	81	89.0	Dale (pers. comm.)	8.79	1.09	39.4	3.8	50	T	17.6	33.1	1.88	1023.88
10	AR11(2)	GC	-38.93	-57.92	66	92.0	Dale (pers. comm.)	8.57	1.18	40.3	4.4	50	T	17.3	33.3	1.92	1024.11
11	AR18(1)	GC	-40.65	-59.42	84	32.0	Dale (pers. comm.)	8.63	1.37	43.8	2.1	25	T	17.1	33.3	1.95	1024.21
12	AR26(1)	GC	-40.65	-60.45	59	14.0	Dale (pers. comm.)	8.73	1.09	41.0	3.3	50	T	17.9	33.2	1.85	1023.92
13	AR28(1)	GC	-41.72	-64.05	102	90.0	Dale (pers. comm.)	8.98	1.13	40.3	3.4	50	T	20.0	33.9	1.69	1023.90
14	AR31(1)	GC	-42.60	-62.27	82	78.0	Dale (pers. comm.)	8.88	0.87	41.0	3.8	50	T	17.3	33.5	1.94	1024.30
15	AR36(1)	GC	-48.13	-63.18	137	80.0	Dale (pers. comm.)	8.56	1.11	41.4	3.8	45	T	12.1	33.6	2.78	1025.47
16	AR39(1)	GC	-52.93	-67.32	73	23.0	Dale (pers. comm.)	9.19	1.55	37.7	3.8	50	T	10.2	33.0	3.23	1025.36
17	AR4(1)	GC	-36.10	-53.52	140	80.0	Dale (pers. comm.)	8.72	1.31	43.4	4.4	50	T	21.3	33.0	1.55	1022.88
18	AR7(1)	GC	-37.55	-56.20	73	92.0	Dale (pers. comm.)	8.55	1.16	42.6	3.3	50	T	18.8	31.7	1.68	1022.57
19	NZ1(1)	SS	-43.62	172.75	-	59.0	Dale (pers. comm.)	9.97	1.24	40.3	4.7	50	T	14.9	34.5	2.31	1025.62
20	NZ10(2)	SS	-41.50	174.73	-	50.0	Dale (pers. comm.)	9.62	1.06	40.4	3.0	50	T	16.9	34.9	2.07	1025.46
21	NZ6(2+3)	SS	-46.53	168.45	-	56.0	Dale (pers. comm.)	9.69	1.10	40.0	3.4	50	T	12.8	34.6	2.70	1026.11
22	TA1(2)	GC	-43.12	147.05	21	82.0	Dale (pers. comm.)	9.05	1.05	39.3	4.5	50	T	16.5	35.1	2.13	1025.74
23	TA2(1)	GC	-43.00	147.12	14	87.0	Dale (pers. comm.)	8.98	0.91	38.9	3.2	50	T	16.5	35.1	2.13	1025.74
24	TA3(2)	GC	-42.72	147.37	8	82.0	Dale (pers. comm.)	8.70	0.98	38.4	2.6	50	T	16.7	35.2	2.11	1025.77
25	TA6(2)	GC	-41.22	148.28	8	50.0	Dale (pers. comm.)	9.01	0.91	38.7	3.8	50	T	17.6	35.4	2.01	1025.66
26	6202-4	MC	-29.08	-47.17	1493	83.3	Zonneveld (pers. comm.)	10.09	1.80	45.6	4.5	50	K	25.6	36.3	1.42	1024.17
27	6223-3	MC	-35.73	-49.68	4280	55.9	Zonneveld (pers. comm.)	9.65	1.45	39.1	4.3	50	K	22.6	35.3	1.56	1024.30
28	Geo86201	MC	-26.67	-46.43	473	74.5	Zonneveld (pers. comm.)	9.89	1.33	-	-	50	T	26.0	35.8	1.38	1023.65
29	Geo86203	MC	-28.83	-47.30	1001	83.3	Zonneveld (pers. comm.)	9.87	1.35	45.4	5.9	50	T	25.9	36.3	1.40	1024.03
30	Geo86207	MC	-30.63	-46.32	3202	84.0	Zonneveld (pers. comm.)	10.11	1.42	45.3	6.4	50	T	24.8	36.4	1.47	1024.45
31	Geo86211	MC	-32.50	-50.25	654	80.3	Zonneveld (pers. comm.)	9.81	1.15	42.8	4.1	50	T	24.3	34.6	1.42	1023.23
32	Geo86213	MC	-33.17	-49.57	1494	77.6	Zonneveld (pers. comm.)	9.63	1.22	45.1	4.4	21	T	23.8	35.3	1.49	1023.97
33	Geo86216	MC	-34.62	-51.23	2032	71.7	Zonneveld (pers. comm.)	9.23	1.42	43.2	5.1	50	T	23.1	34.4	1.49	1023.41
34	Geo86221	MC	-33.55	-49.22	3038	80.6	Zonneveld (pers. comm.)	9.56	1.53	46.7	4.8	50	T	23.7	35.5	1.50	1024.10
35	Geo86311	MC	-38.82	-54.63	996	78.5	Zonneveld (pers. comm.)	9.55	1.14	44.0	4.5	50	T	18.5	33.3	1.81	1023.89
36	Geo86317	MC	-40.08	-54.60	3115	16.9	Zonneveld (pers. comm.)	9.46	1.15	41.5	4.9	50	T	17.2	33.9	1.96	1024.58
37	MD962084 10 cm	PC	-31.45	15.31	1084	N/A	Rau et al. (2006)	9.97	1.44	41.5	5.4	50	K	19.1	35.3	1.84	1025.18
38	F749	Dredge	-44.02	175.43	1427	33.3	Sun and McMinn (1994)	9.01	1.48	36.3	3.1	50	K	15.1	34.6	2.29	1025.64
39	G133	Dredge	-43.08	176.75	393	49.3	Sun and McMinn (1994)	9.11	1.49	37.1	4.3	50	K	16.0	34.8	2.17	1025.58
40	H551	GC	-46.12	179.15	3632	20.5	Sun and McMinn (1994)	9.01	1.46	35.4	3.5	50	K	13.8	34.4	2.48	1025.72
41	J1007	GC	-42.33	179.00	2276	26.0	Sun and McMinn (1994)	9.07	1.27	37.2	3.5	50	K	17.1	35.0	2.05	1025.50
42	S036-75L 0-2 cm	PC	-42.18	144.37	1085	11.5	McMinn and Wells (1997)	9.12	1.64	36.5	4.2	41	K	15.0	34.9	2.33	1025.89
43	ODP1232 (1,2)	PC	-39.88	-75.90	4075	2.3	Verleye and Louwye (2010b)	9.62	1.31	-	-	20	T	16.6	33.6	2.03	1024.58
44	ODP1233	PC	-41.00	-74.45	844	1.2	Verleye and Louwye (2010b)	9.30	1.64	-	-	30	T	15.6	33.4	2.14	1024.61
45	FD75-3-04 (2)	GC	-27.47	-71.93	6154	25.6	Verleye and Louwye (2010b)	9.22	1.52	-	-	33	T	19.3	34.6	1.79	1024.63
46	M8011-4 (2,3)	PC	-42.11	-75.59	3847	7.3	Verleye and Louwye (2010b)	9.63	1.63	-	-	48	T	15.5	33.4	2.16	1024.63
47	M8011-5	GC	-42.07	-75.45	3854	3.3	Verleye and Louwye (2010b)	9.67	1.62	-	-	50	T	15.5	33.4	2.16	1024.62
48	M8011-7	PC	-42.07	-75.74	3819	2.6	Verleye and Louwye (2010b)	9.33	1.29	-	-	50	T	15.5	33.4	2.15	1024.63
49	M8011-8 (2)	PC	-42.04	-75.81	3810	2.9	Verleye and Louwye (2010b)	9.57	1.31	-	-	50	T	15.6	33.4	2.15	1024.63
50	M8011-9	PC	-41.97	-75.68	3819	7.1	Verleye and Louwye (2010b)	9.77	1.51	-	-	49	T	15.6	33.4	2.14	1024.63
51	M8011-10 (2)	GC	-42.08	-75.54	3850	4.6	Verleye and Louwye (2010b)	9.57	1.65	-	-	50	T	15.5	33.4	2.16	1024.63
52	M8011-11	GC	-40.48	-75.24	4101	4.2	Verleye and Louwye (2010b)	9.77	1.65	-	-	50	T	16.1	33.5	2.08	1024.61
53	M8011-12	PC	-40.50	-75.15	4137	2.3	Verleye and Louwye (2010b)	9.36	1.19	-	-	46	T	16.1	33.5	2.09	1024.61
54	M8011-13 (2,3)	PC	-39.66	-75.17	4413	2.6	Verleye and Louwye (2010b)	8.82	1.54	-	-	20	T	16.4	33.6	2.05	1024.58

Table 1 (continued)

55	M8011-15	GC	-39.67	-75.25	4219	1.6	Verleye and Louwyte (2010b)	9.01	1.56	-	-	50	T	16.4	33.6	2.04	1024.58
56	RR9702A-01	MC	-50.65	-76.96	3964	8.2	Verleye and Louwyte (2010b)	11.18	1.51	-	-	45	T	10.8	33.5	3.09	1025.62
57	RR9702A-06	MC	-46.88	-76.60	3298	7.8	Verleye and Louwyte (2010b)	10.25	1.74	-	-	50	T	13.2	33.3	2.52	1025.06
58	RR9702A-08	MC	-46.35	-76.67	3014	2.6	Verleye and Louwyte (2010b)	10.21	1.46	-	-	50	T	13.4	33.3	2.49	1024.99
59	RR9702A-10	MC	-46.32	-76.54	2879	3.9	Verleye and Louwyte (2010b)	9.86	1.44	-	-	50	T	13.4	33.3	2.49	1024.98
60	RR9702A-12	MC	-43.42	-76.25	3523	5.6	Verleye and Louwyte (2010b)	9.35	1.60	-	-	34	T	14.9	33.2	2.23	1024.63
61	RR9702A-14	MC	-43.54	-76.48	3471	6.2	Verleye and Louwyte (2010b)	9.93	1.62	-	-	34	T	14.9	33.2	2.23	1024.65
62	RR9702A-20 (2)	MC	-39.97	-74.47	1055	1.0	Verleye and Louwyte (2010b)	9.26	2.03	-	-	21	T	16.1	33.5	2.09	1024.61
63	FR10/95 - GC-27	GC	-30.50	114.28	843	32.6	Young (2005)	7.64	0.89	-	-	50	M	22.5	35.7	1.59	1024.60
64	FR10/95-GC-24	GC	-28.75	113.06	1577	39.0	Young (2005)	7.27	0.86	-	-	50	M	23.1	35.6	1.54	1024.38
65	FR2/96-GC-7	GC	-26.98	111.34	3090	50.0	Young (2005)	7.48	0.65	-	-	50	M	23.6	35.5	1.50	1024.13
66	FR10/95-GC-20	GC	-24.74	111.83	841	35.8	Young (2005)	6.73	0.84	-	-	48	M	24.9	35.3	1.42	1023.60
67	FR2/96-GC-6	GC	-28.42	112.29	3575	39.4	Young (2005)	5.98	0.80	-	-	41	M	23.0	35.6	1.55	1024.39
68	FR10/95-GC-23	GC	-28.75	112.78	2470	31.7	Young (2005)	6.93	0.89	-	-	39	M	23.1	35.6	1.54	1024.39
69	FR2/96-GC-3	GC	-29.30	112.94	3343	39.8	Young (2005)	6.89	0.85	-	-	39	M	22.6	35.7	1.58	1024.55
70	FR10/95-GC-26	GC	-29.24	113.56	1738	36.9	Young (2005)	6.72	1.05	-	-	38	M	22.7	35.7	1.57	1024.53
71	FR2/96-GC-5	GC	-28.39	113.16	735	29.7	Young (2005)	6.89	1.21	-	-	38	M	23.2	35.6	1.54	1024.36
72	FR2/96-GC-1	GC	-31.11	114.55	2530	34.0	Young (2005)	7.50	0.88	-	-	36	M	22.0	35.7	1.62	1024.75
73	FR2/96-GC-4	GC	-28.72	113.39	936	33.7	Young (2005)	6.40	0.89	-	-	33	M	23.2	35.6	1.54	1024.36
74	FR2/96-GC-2	GC	-29.35	112.95	3370	31.0	Young (2005)	6.64	0.81	-	-	31	M	22.6	35.7	1.58	1024.55
75	FR10/95-GC-25	GC	-28.73	113.37	1010	29.7	Young (2005)	6.72	0.78	-	-	30	M	23.2	35.6	1.54	1024.36
76	FR2/96-GC-29	GC	-18.96	116.39	344	24.7	Young (2005)	7.11	1.15	-	-	23	M	28.5	35.0	1.23	1022.24
77	FR10/95-GC-18	GC	-22.99	112.83	1055	22.7	Young (2005)	7.03	0.98	-	-	22	M	25.7	35.2	1.37	1023.26
78	FR2/96-GC-28	GC	-18.80	116.34	502	19.2	Young (2005)	6.81	0.47	-	-	19	M	28.5	35.0	1.23	1022.22
79	FR10/95-GC-29	GC	-30.99	114.59	1220	26.1	Young (2005)	7.58	0.68	-	-	18	M	22.2	35.7	1.61	1024.69
80	FR10/95-GC-17	GC	-22.13	113.50	1093	16.0	Young (2005)	6.39	0.60	-	-	15	M	26.7	35.1	1.32	1022.92
81	FR10/95-GC-21	GC	-26.00	111.63	982	9.5	Young (2005)	7.76	0.94	-	-	15	M	24.1	35.4	1.47	1023.93
82	FR2/96-GC-27	GC	-18.56	116.27	1024	12.5	Young (2005)	7.14	0.60	-	-	13	M	28.5	35.0	1.23	1022.22
83	FR10/95-GC-12	GC	-18.25	114.99	2034	19.0	Young (2005)	7.54	0.71	-	-	12	M	28.2	35.0	1.24	1022.28

*BC, Box Core; GC, Gravity Core; MC, Multicore; PC, Piston Core; SS, Sediment Sucker.

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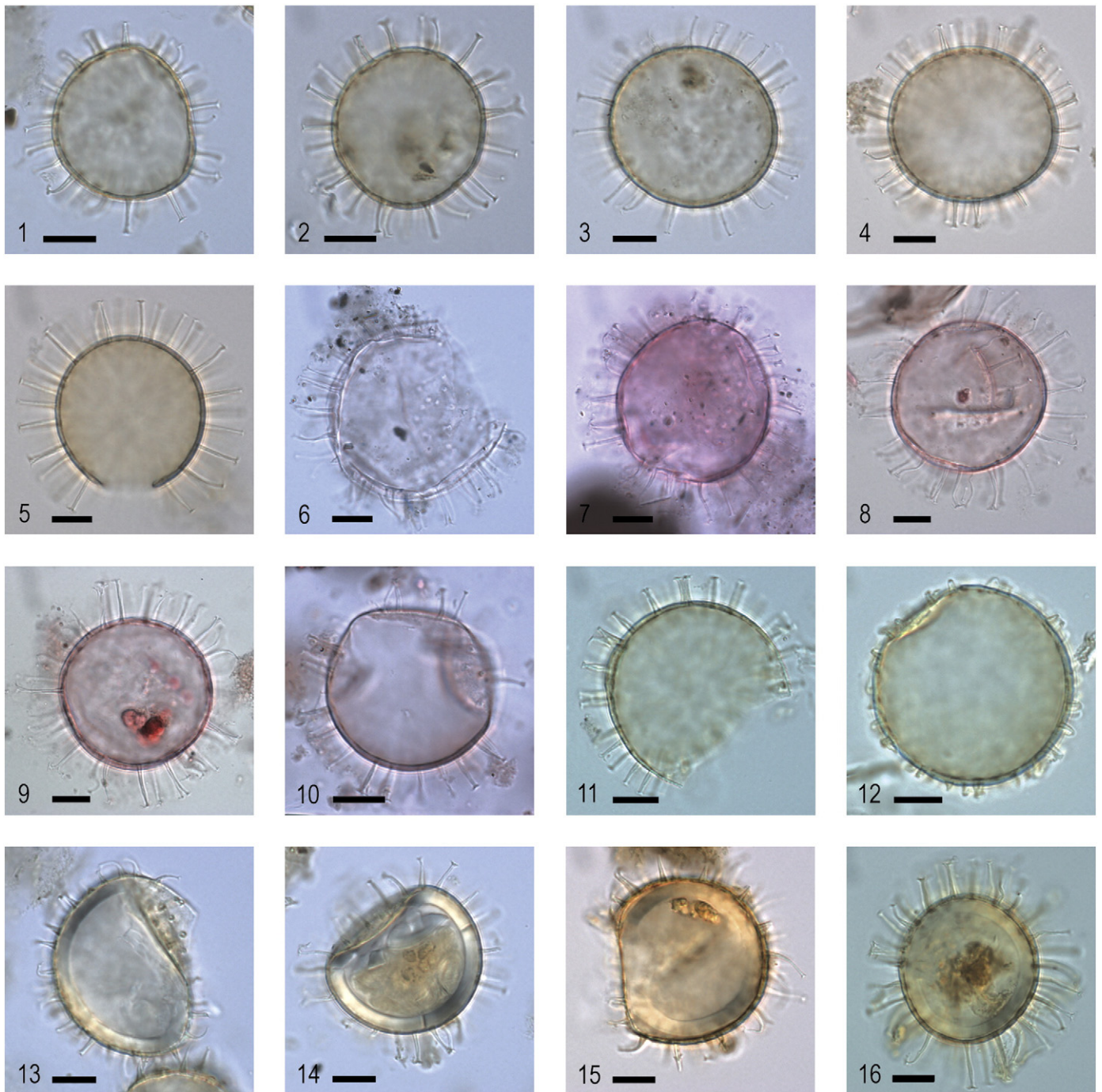


Plate 1. Photomicrographs of the morphological variation of *O. centrocarpum* cysts from recent sediments of the Southern Hemisphere and fossil sediments from ODP 1233, offshore Chile (41°S). Process lengths vary from rather short (10–12), over average (1–4) to long (5–9). (1) cyst from the Argentine Continental Shelf, slide AR26(1), England Finder reference (EF) N37/3; (2) cyst from the Argentine Continental Shelf, slide AR39(1), EF K44/0; (3) cyst from the coast of New Zealand, slide NZ10(2), EF E40/0; (4) cyst from the coast of Tasmania, slide TA2(1), EF P36/2; (5) cyst from the Chilean Fjord area, slide CHILE6(1), EF N38/3; (6) cyst from offshore Chile, slide RR9702A-01, EF T40/0; (7) cyst from offshore Chile, slide RR9702A-06, EF T36/3; (8) cyst from down-core ODP 1233 (14.4 cal ka BP), slide 1233 C-3H-2 42–44 20.72 mcd, EF W22/4; (9) cyst from down-core ODP 1233 (14.4 cal ka BP), slide 1233 C-3H-2 42–44 20.72 mcd, EF N42/0; (10) cyst from the West Indian Ocean, slide 76136, EF O32/0; (11) cyst from the coast of New Zealand, slide NZ10/3, EF K/39-2; (12) cyst from the coast of New Zealand, slide NZ10/3, EF O37/0; (13) cyst with cell content from the Argentine Continental Shelf, slide AR26(1), EF N37/0; (14) cyst with cell content from the Argentine Continental Shelf, slide AR26(1), EF O40/0; (15) cyst with cell content and the remains of red bodies from the Argentine Continental Shelf, slide AR10(1), EF G41/1; (16) cyst with cell content and the remains of red bodies from the Argentine Continental Shelf, slide AR28(1), O40/4. The scale-bars represent 10 μ m.

database contains samples from the SE Pacific, the SW and SE Atlantic, the East and West Indian Ocean, from offshore New Zealand and from the Tasmanian coast (Fig. 2).

Verleye and Louwe (2010b) observed a good fit between cyst assemblages and the oceanographical boundaries in the SE Pacific (25–53°S) (Fig. 2), and therefore assume only negligible lateral transport along the Chilean coast. This is in agreement with data from Ingle

et al. (1980) and Shaffer et al. (1999; 2004), who demonstrate that SE Pacific currents below 300 m water depth move very slowly. Also the Gunther Undercurrent at a water depth of 100 to 300 m diminishes in strength south of 33°S (Lamy et al., 2001).

The SW Atlantic samples are located on the Argentine Continental Shelf and near the continental slope which marks the western border of the Argentine Basin (26–53°S) (Fig. 2). This region has complex

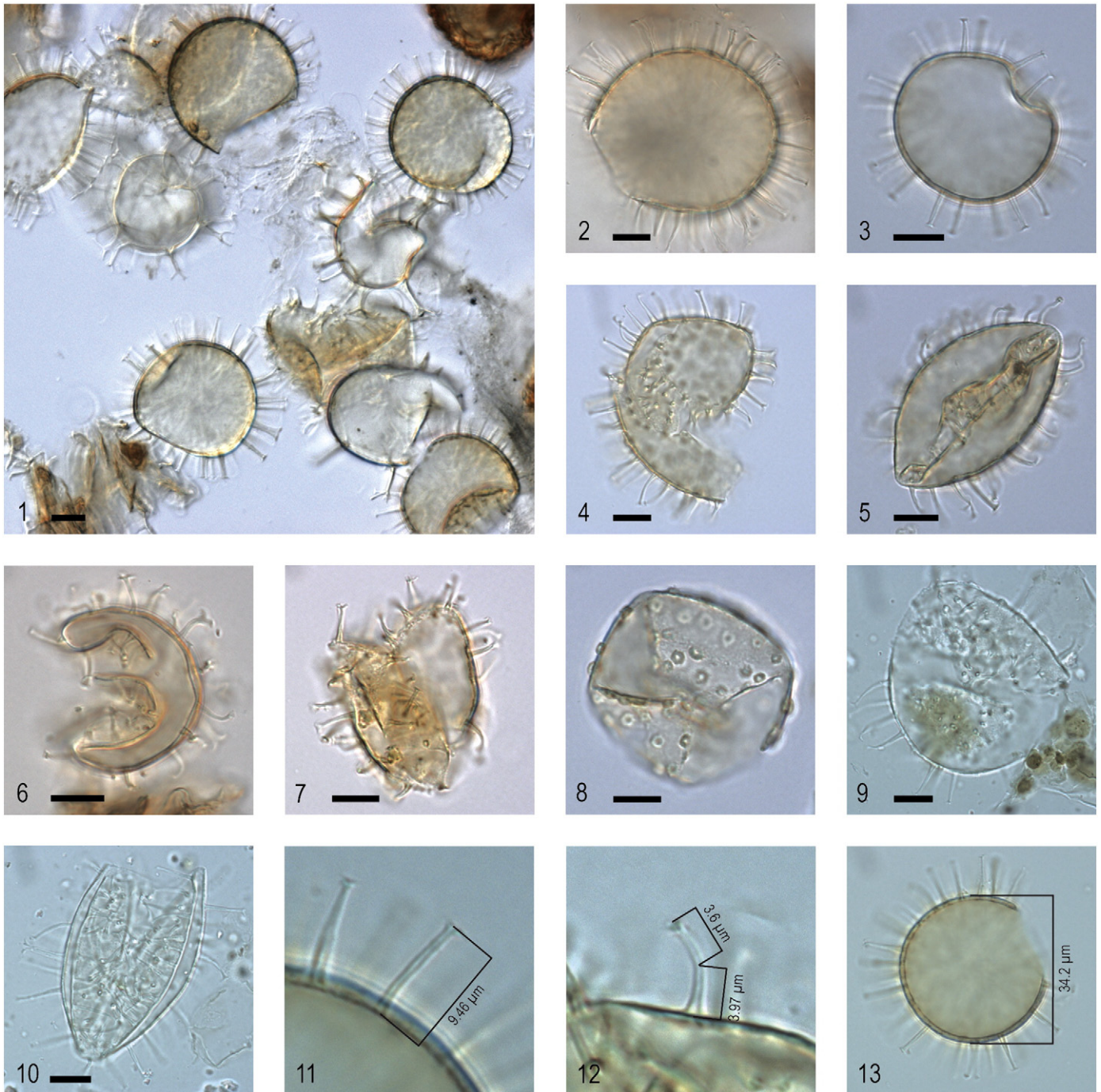


Plate 2. Photomicrographs of *O. centrocarpum* cysts from recent sediments of the Southern Hemisphere. (1) high concentration of *O. centrocarpum* cysts with interspersed *Spiniferites* cysts in coastal sediments of New Zealand, slide NZ10(2), EF F41/4; (2) cysts with large central body diameter from the coastal sediments of New Zealand, slide NZ1(1), EF H38/0–3; (3) cyst with small central body diameter from the coast of New Zealand, slide NZ10(2), EF E35/0–1; (4–7) broken and deformed cysts; (4) broken cyst from the Argentine Continental Shelf, slide AR28(1), EF K42/1; (5) deformed cyst from the Argentine Continental Shelf, slide AR4(1), EF L40/1; (6) compressed cyst from the Chilean Fjord area, slide CHILE20(1), EF P41/1; (7) crumpled cyst from the Argentine Continental Shelf, slide AR31(1), EF (?); (8) malformed cyst from the Argentine Continental Shelf, slide AR39(1), EF H44/0; (9) cyst from offshore South Africa, slide PS2230-1, EF M43/4; (10) cyst from offshore South Africa, slide PS2230-1, EF H41/4; (11–13) measurement procedures; (11) straight processes are measured as the distance between the middle of the process base and the tip; (12) curved processes are measured in two steps, with both measurements converging at the point of inflection; (13) the cyst body diameter is measured as the distance between the outer membranes of two opposite parts of the cyst wall.

oceanographic and ecological characteristics due to the bathymetry, changes in coastline bearing, variable wind strength and directions, large seasonal input of continental run-off and locally generated cells of high salinity (Lucas et al., 2005). The latter may cause slight deviations between the *in situ* salinities and the salinity estimations made by the one-degree gridded World Ocean Atlas 2009. The shallow sample locations of Dale (pers. comm.) (59 to 140 m) limit the duration of particle sinking based on the findings by Zonneveld et

al. (2010), who investigated the sinking rates of organic walled dinoflagellate cysts offshore NW Africa and recorded sinking rates of $>274 \text{ m day}^{-1}$ at average. Rapid vertical transport through the water column is facilitated by agglomeration and flocculation in the presence of other structureless organic matter (such as marine snow) or, to a lesser degree, by a downward transport in fecal pellets (Silver and Alldredge, 1981; Mudie, 1996). This prevents lateral transport over long-distances, but short-distance coast-ocean transport of cysts cannot

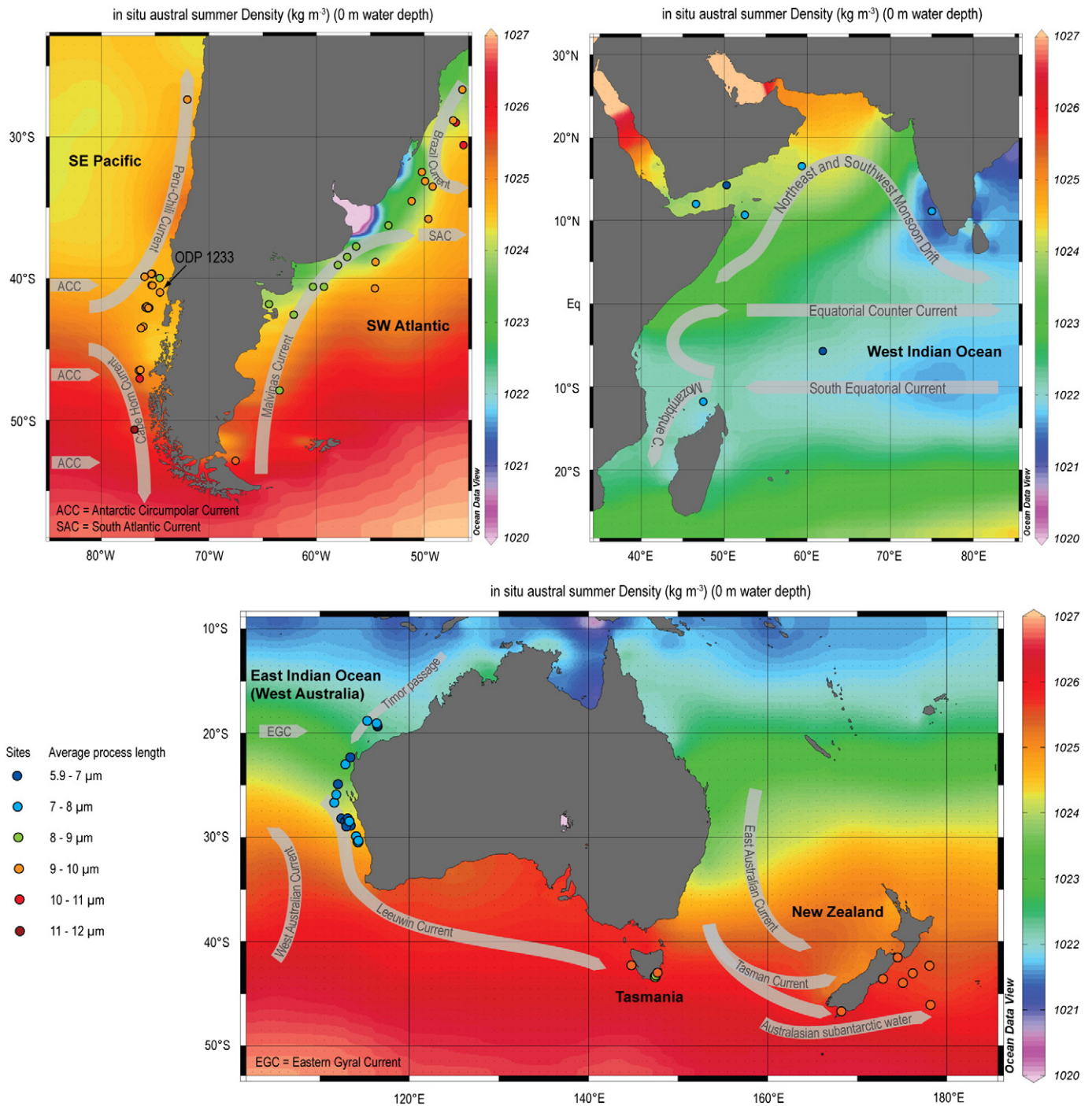


Fig. 2. Geographical position of the samples included in the reduced database together with the main surface currents. The colour of the dots represents the measured average process length of *O. centrocarpum* at the respective sites. The austral summer sea-surface density values are based on the gridded one-degree World Ocean Atlas 2009 (NODC, 2009) and charts are made using the Ocean Data View software (Schlitzer, 2010). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

be excluded. In contrast, the samples located on the continental slope adjacent to the Argentine Basin (~500 to 4300 m water depth; Zonneveld, pers. comm.) may have been significantly transported from the south according to the findings of Lange (1985) and Mollenhauer et al. (2006).

Abidi (1997) suggests that no long-distance lateral transport of dinoflagellate cysts in the West Indian Ocean occurred (Fig. 2). A two-fold reason is advanced for this by the work of Abidi (1997). Firstly, a good match is observed between oceanographic boundaries and the recorded cyst assemblages. Secondly, the biogeographic distributions of dinoflagellate cyst taxa and foraminifer taxa are very similar.

Additionally, Zonneveld and Brummer (2000) found no indication of significant lateral transport of cysts in the NW Arabian Sea.

Offshore NW Australia (East Indian Ocean), the strength and direction of sea-surface currents are variable and are determined by the monsoonal winds (Fig. 2). The hydrography of the area is further complicated by several deeper water masses all flowing in different directions (e.g., Tomczak and Godfrey, 1994; Wijffels et al., 1996). However, Gingele et al. (2001) found no irrefutable evidence for lateral suspended matter transport from the Timor Passage along the path of the northern branch of the Leeuwin Current (NW Australia). But further southward, a poleward transport of clay minerals was observed along

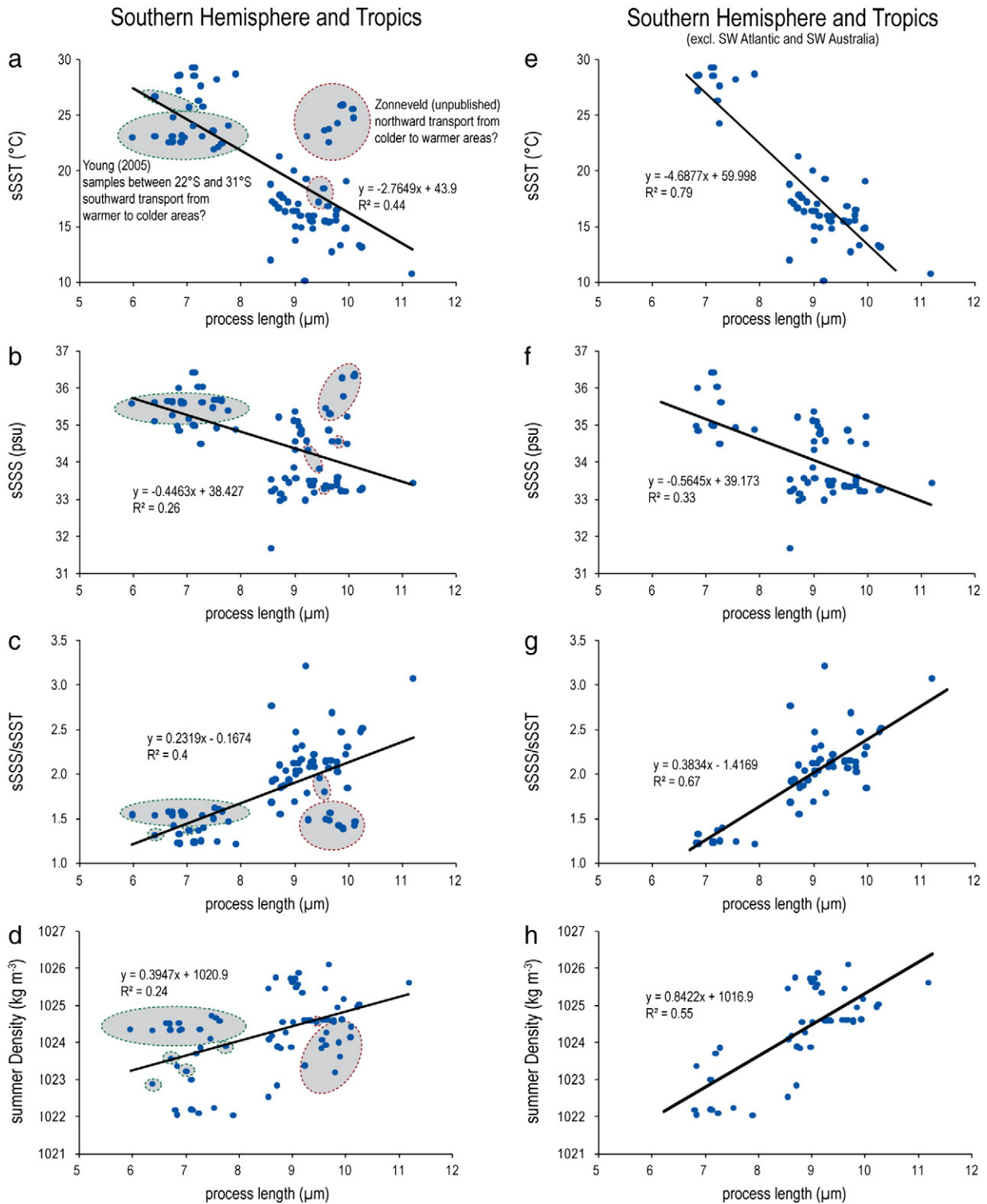


Fig. 4. Scatter plots for the Southern Hemisphere and the Tropics. (a) Process length versus sSST; (b) process length versus sSSS; (c) process length versus sSSS/sSST; (d) process length versus summer density. On the plots a–d, samples considered to be affected by long-distance lateral transport are encircled in pale grey. The red dashed lines encircle the samples located at the border of the Argentine Basin (northward transport), while the green dashed lines ring the samples located offshore West Australia (22–31°S) (southward transport). The scatter plots (e) to (h) show the data without samples considered to be affected by long distance lateral transport. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

offshore West Sweden (Godhe et al., 2001), at point Barrow offshore Alaska (Bursa, 1963), several Norwegian fjords (Braarud and Bursa, 1939; Braarud et al., 1974; Braarud, 1976; Aasen et al., 2005), local waters around Woods Hole (USA) (Wall and Dale, 1968), the North Atlantic and the North Sea (Reid, 1978), in Okkirai Bay (Northern

Japan) (Koike et al., 2006), the Salton Sea (California) (Reifel et al., 2002) and the Strait of Georgia (British Columbia, Canada) (Cassis, 2005; Pospelova et al., 2010).

As in Mertens et al. (2010) and based on the aforementioned observations, it is reasonable to assume that the process length

Table 3

Relationship between process length and body diameter variability and sSST, sSSS, sSSS/sSST and summer density on global scale.

	Global dataset correlations									
	sSST (°C)		sSSS (psu)		sSSS/sSST		summer Density (kg m ⁻³)		Process length (µm)	
	Δ	R ²	Δ	R ²	Δ	R ²	Δ	R ²	R ²	
Process length (µm) (83)	19.0	0.44	4.7	0.26	2.0	0.40	4.0	0.24	/	
Body diameter (µm) (41)	19.0	0.00	4.7	0.03	2.0	0.00	4.0	0.00	0.50	

variability of *O. centrocarpum* cysts reflects changing sea-surface conditions during the summer months of the respective hemisphere, and our data support this.

4.2.2. Morphological variation of *O. centrocarpum* cysts in the tropics and the Southern Hemisphere

Firstly, we consider the average process length variability on a regional scale to determine its relationship with sSSS and sSST. For the SE Pacific, lateral transport of cysts is considered to be limited (Verleye and Louwye, 2010b), and process lengths of *O. centrocarpum* are thus expected to reflect immediate surface water conditions as calculated by the World Ocean Atlas 2009. The SE Pacific samples exhibit a significant negative relationship between process lengths and sSST ($R^2=0.65$), and a positive correlation between process lengths and sSSS/sSST ($R^2=0.74$) and summer density ($R^2=0.73$). In contrast to earlier studies, no relationship is recorded with sSSS ($R^2=0.09$), which may be caused by the limited sSSS range ($\Delta 1.4$ psu). The observed significant relationship with summer density supports the similar conclusions of Mertens et al. (2010). In contrast, no relationship with summer density ($R^2=0$) but a significant correlation with sSSS ($R^2=0.76$) was recorded offshore Argentina. This may be related with a northward transport of cysts near the continental slope along a constant salinity gradient but a latitudinal increasing SST gradient, in turn influencing sea surface water density. When considering only the shallow samples from the continental shelf (Dale, pers. comm.), no significant relationship was observed with any of the environmental parameters. The cyst signal could however be slightly biased by local hydrographical effects such as slight increases in salinity (Lucas et al., 2005) which are not considered by the World Ocean Atlas 2009. The high numbers of broken cysts recorded in sample AR36(1) may be indicative for relatively short-distance coast-ocean transport. This could also explain the relatively short process lengths at this site (8.6 µm), since salinity decreases towards the coast because of river water discharges (a.o. Deseado River). When excluding sample AR36(1), the regional correlations between process lengths as recorded in samples from the continental shelf and sSSS/sSST and summer density increase from $R^2=0.16$ to 0.46 and from $R^2=0.12$ to 0.48, respectively. The relation with sSSS and sSST however show only limited increases from $R^2=0.08$ to 0.17 and from $R^2=0.08$ to 0.33, respectively.

Except for the SE Pacific and the SW Atlantic, no relationship was observed on a regional scale between the process length and sSSS, sSST, sSSS/sSST and summer density (Table 2). For the West Indian Ocean, New Zealand and South Australian sites, this may be caused by the narrow sSSS and sSST ranges recorded in the respective regions (Table 1). Some samples from the West Indian Ocean originate from the Arabian Sea where intense upwelling occurs, so local hydrographical variability could have affected process length. The East Indian sites do cover a considerable sSST range of 6.6 °C, but neither show a relationship between process length and the environmental parameters (Table 2). For the sites located offshore NW Australia between 22 and 31°S, the cysts may be transported in a poleward direction by the Leeuwin Current, approaching the West Australian coast in this area (Fig. 2). This is in agreement with the findings of Gingele et al. (2001) who observed transport of clay minerals towards higher latitudes offshore West Australia. Therefore, the sSST in the area of cyst deposition may be somewhat cooler compared with the sSST in the area of cyst

formation due to poleward transport of the cysts. SSS remains rather constant along Western Australia. Assuming a positive relationship with summer density as demonstrated for the SE Pacific, process lengths may slightly underestimate the immediate surface water density values (Fig. 2), and thus considerably distort regional trends.

In a further attempt to gain better insight into the environmental factors controlling process length variation of *O. centrocarpum* cysts, we combined the regional data to produce a Southern Hemisphere database which extends the sSSS and sSST ranges up to 4.7 psu and 19 °C, respectively. A moderate relationship is then observed between process length variability and sSST ($R^2=0.44$; negative) and sSSS/sSST ($R^2=0.4$; positive) (Fig. 4a and c). Lateral transport as previously suggested most likely produces noise on the scatter plots, and therefore affected to a certain extent the relationship between process length variability and sSSS and sSST (Fig. 4a–d). Both the SW Australian (22–31°S) (Young, 2005) and the oceanic SW Atlantic (Zonneveld, pers. comm.) data deviate from the other sites in a way which corresponds with the expected direction of transport, i.e., towards cooler water offshore SW Australia and towards warmer water for the SW Atlantic deep sea sites (Fig. 4a). The weak negative relationship with sSSS ($R^2=0.26$) is misleading because sSSS is positively correlated with sSST ($R^2=0.46$) and the variation in sSSS is limited compared to the changes in sSST (Fig. 4a and b). A positive relationship with sSSS as observed in many other studies (de Vernal et al., 1989; Dale, 1996; Ellegaard, 2000; Brenner, 2005; Head, 2007; Mertens et al., 2010) and a negative relationship with sSST as demonstrated here suggest that summer density may play a crucial role in determining process length variations, as observed in the SE Pacific. Taking into account the possible effects of long distance lateral transport, the SW Australian data most likely originates from slightly lower density environments (warmer water) compared to their current position in the plot, while the opposite holds for the SW Atlantic deep sea data (Fig. 4d). Correcting for this might improve the correlation between process length variability and summer density (Fig. 4d). When excluding the SW Australian and SW Atlantic samples, the negative correlation with sSST increases up to $R^2=0.79$ (Fig. 4e). The positive correlation between process length variability and summer density increases up to $R^2=0.55$ (Fig. 4h), while the correlation with sSSS/sSST increases up to $R^2=0.67$ (Fig. 4g).

4.2.3. sSSS/sSST versus summer density

The good correlation between process length variability and the sSSS/sSST ratio could point towards a causal relationship between both parameters. This ratio however faces serious problems with temperatures approaching zero in polar regions where the species also is reportedly present. A limited shift in SST from 0.2 to 0.1 °C immediately doubles the ratio, which can increase above 300 in the high latitudes and should correspond with process lengths of >800 µm according to the linear regression formula. In the (sub)tropical, temperate and sub-polar regions however, no such drastic shifts in the ratio occur, and confirms the positive and negative relationship with sSSS and sSST, respectively. These observations suggest that this relation to process length is probably an artefact, and the relation to density is more likely, as already suggested by Mertens et al. (2010). When excluding the sites considered to be affected by long distance lateral transport (SW Atlantic, SW Australia), the relationship between process length (x) and summer density (sD) follows

the equation $sD = 0.8422x + 1016.9$ ($R^2 = 0.55$) with a Root Mean Square Error (RMSE) = 0.63 kg m^{-3} (Fig. 4h). The lower correlation between process length variability and density compared to the Baltic–Kattegat–Skagerrak data could be the result of the restricted density range of the studied sites ($\Delta 4 \text{ kg m}^{-3}$). The relationship is also clearly less steep compared to the relationship observed in the Baltic–Kattegat–Skagerrak estuarine system (Mertens et al., 2010), which is expressed through the equation $sD = 3.3745x + 998.42$ ($R^2 = 0.82$). Further research is therefore required to investigate whether both geographical separated populations have the same genetic affinities and to analyse what causes the distinct morphological adaptations associated with changes in density. However, despite this problem, regional quantitative density reconstruction should be possible using regional *O. centrocarpum* process length calibration formula.

5. Conclusions

The study gives a better insight into the main determining factors influencing process length variability in cysts of *Protoceratium reticulatum* (= *O. centrocarpum*) in the tropics and the Southern Hemisphere. A moderate negative relationship with sSST ($R^2 = 0.44$) is observed, which increases up to $R^2 = 0.79$ after excluding samples considered to be affected by long distance lateral transport. No obvious relationship with sSSS is observed due to its restricted range in this study. Both the relationship with temperature and salinity (as observed in earlier studies) suggest density play a major role in determining process length variability of *O. centrocarpum*. A positive relationship with summer density has been observed after excluding samples considered to be affected by long distance meridional transport, through the equation $sD = 0.8422x + 1016.9$ ($R^2 = 0.55$) with a RMSE = 0.63 kg m^{-3} . The different relationship between process length and density in the Southern Hemisphere compared to the Baltic–Kattegat–Skagerrak estuarine system (Mertens et al., 2010) requires further study and makes it difficult to construct a global database of process length variability but points towards a rather regional application of the proxy. The core-top database must also be further extended in the tropics and the Southern Hemisphere to include a broader range of sSST and sSSS, in order to improve our understanding of the possible effects of density on process length variability, preferably with shallower water sites less susceptible to long-distance cyst transport. Nevertheless, it seems likely that in many parts of the ocean the main value of process length as a palaeosalinity proxy will be in conjunction with other proxies providing estimates of SST, rather than a direct palaeosalinity proxy as first envisioned.

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References

Aasen, J., Samdal, I.A., Miles, C.O., Dahl, E., Briggs, L.R., Aune, T., 2005. Yessotoxins in Norwegian blue mussels (*Mytilus edulis*): uptake from *Protoceratium reticulatum*, metabolism and depuration. *Toxicon* 45, 265–272.

- Abidi, N., 1997. Les Kystes de dinoflagelles marqueurs de l'environnement océanique: repartition actuelle dans l'océan Indien occidental et application a deux sequences sédimentaires du Canal de Mozambique. PhD Thesis, Université Pierre et Marie Curie (Paris VI), p. 183.
- Antonov, J.I., Seidov, D., Boyer, T.P., Locarnini, R.A., Mishonov, A.V., Garcia, H.E., 2010. World ocean atlas 2009: salinity. In: Levitus, S. (Ed.), NOAA Atlas NESDIS 69, Volume 2. U.S. Government Printing Office, Washington, D.C. 184 p.
- Bendle, J., Rosell-Melé, A., Ziveri, P., 2005. Variability of unusual distributions of alkenones in the surface waters of the Nordic seas. *Paleoceanography* 20, PA2001. doi:10.1029/2004PA001025.
- Blanz, T., Emeis, K.-C., Siegel, H., 2005. Controls on alkenone unsaturation ratios along the salinity gradient between the open ocean and the Baltic Sea. *Geochimica et Cosmochimica Acta* 69, 3589–3600.
- Braarud, T., 1976. The natural history of the Hardangerfjord. 12. The ecology of taxonomic groups and species of phytoplankton related to their distribution patterns in a fjord area. *Sarsia* 60, 41–62.
- Braarud, T., Bursa, A., 1939. The phytoplankton of the Oslo Fjord 1933–1934. *Hvalrådets Skrifter, Scientific Results of Marine Biological Research* 19, 1–49.
- Braarud, T., Föyn Hovsfang, B., Hjelmfoss, P., Överland, A.-K., 1974. The natural history of the Hardangerfjord. 10. The phytoplankton in 1955–56. The quantitative phytoplankton cycle in the fjord waters and in the offshore coastal waters. *Sarsia* 55, 63–98.
- Brenner, W.W., 2005. Holocene environmental history of the Gotland Basin (Baltic Sea) – a micropalaeontological model. *Palaeogeography, Palaeoclimatology, Palaeoecology* 220, 227–241.
- Broecker, W.S., Peteet, D.M., Rind, D., 1985. Does the ocean–atmosphere system have more than one stable mode of operation? *Nature* 315, 21–26.
- Broecker, W.S., Bond, G., Klas, M., Bonani, G., Wolfli, W., 1990. A salt oscillator in the glacial Atlantic? The concept. *Paleoceanography* 5, 469–478.
- Bursa, A., 1963. Phytoplankton in coastal waters of the Arctic Ocean at Point Barrow, Alaska. *Arctic* 16, 239–262.
- Cassid, D., 2005. The effect of harmful algae on the summer mortality of juvenile Pacific oysters (*Crassostrea gigas*). MSc Thesis, University of British Columbia, Canada, p. 73.
- Dale, B., 1996. Dinoflagellate cyst ecology: modeling and geological applications. In: Jansoni, J., McGregor, D.C. (Eds.), *Palynology: Principles and Applications*, vol. 3. AASP Foundation, Dallas, TX, pp. 1249–1275.
- Dale, A.L., Dale, B., 1992. Dinoflagellate contributions to the sediment flux of the Nordic Seas. In: Honjo, S. (Ed.), *Ocean Biocoenosis Series 5. Woods Hole Oceanographic Institution Press*, Woods Hole, pp. 45–76.
- De Schepper, S., Head, M.J., Groenewald, J., 2009. North Atlantic current variability through marine isotope stage M2 (circa 3.3 Ma) during the mid-Pliocene. *Paleoceanography* 24, PA4206. doi:10.1029/2008PA001725.
- de Vernal, A., Goyette, C., Rodrigues, C.G., 1989. Contribution palynostratigraphique (dinokystes, pollen et spores) à la connaissance de la Mer Champlain: coupe de Saint-Césaire, Québec. *Canadian Journal for Earth Sciences* 26, 2450–2464.
- de Vernal, A., Rochon, A., Hillaire-Marcel, C., Turon, J.L., Guiot, J., 1993. Quantitative reconstruction of sea-surface conditions, seasonal extent of sea-ice cover and melt-water discharges in high latitude marine environments from dinoflagellate cyst assemblages. In: Peltier, W.R. (Ed.), *Ice in the Climate System. NATO ASI Series I, Springer-Verlag*, Berlin, pp. 611–621.
- de Vernal, A., Turon, J.-L., Guiot, J., 1994. Dinoflagellate cyst distribution in high-latitude environments and quantitative reconstruction of sea-surface temperature, salinity and seasonality. *Canadian Journal of Earth Sciences* 31, 48–62.
- Duplessy, J.-C., Labeyrie, J., Juillet-Leclerc, A., Maitre, F., Duprat, J., Sarinthein, M., 1991. Surface salinity reconstruction of the North Atlantic Ocean during the Last Glacial Maximum. *Oceanologica Acta* 14, 311–324.
- Ellegaard, M., 1998. Dinoflagellate cysts from Danish marine sediments – with emphasis on *Gymnodinium catenatum*-like cysts. PhD Thesis, University of Copenhagen.
- Ellegaard, M., 2000. Variations in dinoflagellate cyst morphology under conditions of changing salinity during the last 2000 years in the Limfjord, Denmark. *Review of Palaeobotany and Palynology* 109, 65–81.
- Ellegaard, M., Lewis, J., Harding, I., 2002. Cyst-theca relationship, life cycle, and effects of temperature and salinity on the cyst morphology of *Gonyaulax baltica* sp. nov. (Dinophyceae) from the Baltic Sea area. *Journal of Phycology* 38, 775–789.
- Fenner, J., Di Stefano, A., 2004. Late Quaternary oceanic fronts along Chatham Rise indicated by phytoplankton assemblages, and refined calcareous nannofossil stratigraphy for the mid-latitude SW Pacific. *Marine Geology* 205, 59–86.
- Gingele, F.X., De Deckker, P., Hillenbrand, C.-D., 2001. Clay mineral distribution in surface sediments between Indonesia and NW Australia – source and transport by ocean currents. *Marine Geology* 179, 135–146.
- Godhe, A., Norén, F., Kuylenstierna, M., Ekberg, C., Karlson, B., 2001. Relationship between planktonic dinoflagellate abundance, cysts recovered in sediment traps and environmental factors in the Gullmar Fjord, Sweden. *Journal of Plankton Research* 23, 923–938.
- Grindley, J.R., Nel, E., 1968. Mussel poisoning and shellfish mortality on the west coast of Africa. *South African Journal of Sciences* 64, 420–422.
- Grindley, J.R., Nel, E., 1970. Red water and mussel poisoning at Elands Bay, December 1966. *Fisheries Bulletin South Africa* 6, 36–55.
- Gundersen, N., 1988. En palynologisk undersøkelse av dinoflagellatcyster langs en synkende salinitetsgradient i recente sedimenter fra Østersjø-området. Cand. Scient. Dissertation. Geologisk Institutt, Universitetet i Oslo, Norway, p. 96.
- Hallett, R.I., 1999. Consequences of environmental change on the growth and morphology of *Lingulodinium polyedrum* (Dinophyceae) in culture. Ph.D. thesis, University of Westminster, p. 109.
- Head, M.J., 1996. Modern dinoflagellate cysts and their biological affinities. In: Jansoni, J., McGregor, D.C. (Eds.), *Palynology: principles and applications: American Association of Stratigraphic Palynologists Foundation*, vol. 3, pp. 1197–1248.

- Head, M.J., 2007. Last interglacial (Eemian) hydrographic conditions in the southwestern Baltic Sea based on dinoflagellate cysts from Tistinge Kline, Denmark. *Geological Magazine* 144, 987–1013.
- Ingle, J.C., Keller, G., Kolpack, R.L., 1980. Benthic foraminiferal biofacies, sediments and water masses of the southern Peru–Chile Trench area, southeastern Pacific Ocean. *Micropaleontology* 26, 113–150.
- Kaiser, J., Lamy, F., Hebbeln, D., 2005. A 70-kyr sea surface temperature record off southern Chile (Ocean Drilling Program Site 1233). *Paleoceanography* 20. doi:10.1029/2005PA001146.
- Koike, K., Horie, Y., Suzuki, T., Kobiyama, A., Kurihara, K., Takagi, K., Kaga, S.N., Oshima, Y., 2006. *Protoceratium reticulatum* in northern Japan: environmental factors associated with seasonal occurrence and related contamination of yessotoxin in scallops. *Journal of Plankton Research* 28, 103–112.
- Kokinos, J.P., Anderson, D.M., 1995. Morphological development of resting cysts in cultures of the marine dinoflagellate *Lingulodinium polyedrum* (= *L. machaerophorum*). *Palynology* 19, 143–166.
- Lamy, F., Hebbeln, D., Röhl, U., Wefer, G., 2001. Holocene rainfall variability in southern Chile: a marine record of latitudinal shifts of the Southern Westerlies. *Earth and Planetary Science Letters* 185, 369–382.
- Lamy, F., Rühlemann, C., Hebbeln, D., Wefer, G., 2002. High- and low-latitude climate control on the position of the southern Peru–Chile current during the Holocene. *Paleoceanography* 17. doi:10.1029/2001PA000727.
- Lamy, F., Kaiser, J., Ninnemann, U., Hebbeln, D., Arz, H., Stoner, J., 2004. Antarctic timing of surface water changes off Chile and Patagonian ice sheet response. *Science* 304, 1959–1962.
- Lamy, F., Kaiser, J., Arz, H.W., Hebbeln, D., Ninnemann, U., Timm, O., Timmermann, A., Toggweiler, J.R., 2007. Modulation of the bipolar seesaw in the Southeast Pacific during Termination 1. *Earth and Planetary Science Letters* 259, 400–413.
- Lange, C.B., 1985. Spatial and seasonal variations of diatom assemblages off the Argentine coast (South Western Atlantic). *Oceanologica Acta* 8, 361–368.
- Lewis, J., Rochon, A., Harding, L., 1999. Preliminary observations of cyst-theca relationships in *Spiniferites ramosus* and *Spiniferites membranaceus* (Dinophyceae). *Grana* 38, 113–124.
- Locarnini, R.A., Mishonov, A.V., Antonov, J.I., Boyer, T.P., Garcia, H.E., 2010. World ocean atlas 2009: temperature. In: Levitus, S. (Ed.), NOAA Atlas NESDIS 68, Volume 1. U.S. Government Printing Office, Washington, D.C, p. 184.
- Lucas, A.J., Guerrero, R.A., Mianzán, H.W., Marcelo Acha, E., Lasta, C.A., 2005. Coastal oceanographic regimes of the Northern Argentine Continental Shelf (34–43°S). *Estuarine, Coastal and Shelf Science* 65, 405–420.
- Marret, F., Zonneveld, K.A.F., 2003. Atlas of modern organic-walled dinoflagellate cyst distribution. *Review of Palaeobotany and Palynology* 125, 1–200.
- Marret, F., Mudie, P., Aksu, A., Hiscott, R.N., 2009. A Holocene dinocyst of a two-step transformation of the Neoeuxinian brackish water lake into the Black Sea. *Quaternary International* 197, 72–86.
- Matsuoka, K., 1990. *Protoceratium reticulatum* (Claparède and Lachmann) Bütschli. In: Fukuyo, Y., Takano, H., Chihara, M., Matsuoka, K. (Eds.), *Red Tide Organisms in Japan – an Illustrated Taxonomic Guide*. Uchida-Roukakuho, Tokyo, pp. 110–111.
- Matsuoka, K., McMinn, A., Wrenn, J., 1997. Restudy of the holotype of *Operculodinium centrocarpum* (Deflandre and Cookson) Wall (Dinophyceae) from the Miocene of Australia, and the taxonomy of related species. *Palynology* 21, 19–33.
- McMinn, A., Wells, P., 1997. Use of dinoflagellate cysts to determine changing Quaternary sea-surface temperature in southern Australia. *Marine Micropaleontology* 29, 407–422.
- Mertens, K.N., González, C., Delusina, I., Louwye, S., 2009a. 30 000 years of productivity and salinity variations in the late Quaternary Cariaco Basin revealed by dinoflagellate cysts. *Boreas* 38, 647–662.
- Mertens, K.N., Ribeiro, S., Bouimetarhan, I., Caner, H., Combourieu Nebout, N., Dale, B., De Vernal, A., Ellegaard, M., Filipova, M., Godhe, A., Goubert, E., Grøsfjeld, K., Holzwarth, U., Kotthoff, U., Leroy, S.A.G., Londeix, L., Marret, F., Matsuoka, K., Mudie, P.J., Naudts, L., Peña-Manjarrez, J.L., Persson, A., Popescu, S.-M., Pospelova, V., Sangiorgi, F., van der Meer, M.T.J., Vink, A., Zonneveld, K.A.F., Vercauteren, D., Vlassenbroeck, J., Louwye, S., 2009b. Process length variation in cysts of a dinoflagellate, *Lingulodinium machaerophorum*, in surface sediments: investigating its potential as salinity proxy. *Marine Micropaleontology* 70, 54–69.
- Mertens, K.N., Dale, B., Ellegaard, M., Jansson, I.-M., Godhe, A., Kremp, A., Louwye, S., 2010. Process length variation in cysts of the dinoflagellate *Protoceratium reticulatum*, from surface sediments of the Baltic–Kattegat–Skagerrak estuarine system: a regional salinity proxy. *Boreas*. doi:10.1111/j.1502-3885.2010.00193.x.
- Mollenhauer, G., McManus, J.F., Benthien, A., Müller, P.J., Eglinton, T.I., 2006. Rapid lateral particle transport in the Argentine Basin: molecular ¹³C and ²³⁰Th_{XS} evidence. *Deep-Sea Research Part I* 53, 1224–1243.
- Montresor, M., Zingone, A., Sarno, D., 1998. Dinoflagellate cyst production at a coastal Mediterranean site. *Journal of Plankton Research* 20, 2291–2312.
- Mudie, P.J., 1996. Fecal pellets. Pellets of dinoflagellate-eating zooplankton. In: Jansonius, J., McGregor, D.C. (Eds.), *Palynology: principles and applications*. American Association of Stratigraphic Palynologists, 3, pp. 1087–1089.
- Mudie, P.J., Aksu, A.E., Yasar, D., 2001. Late Quaternary dinoflagellate cysts from the Black, Marmara and Aegean Sea: variations in assemblages, morphology and paleosalinity. *Marine Micropaleontology* 43, 155–178.
- Nehring, S., 1994. Spatial distribution of dinoflagellate resting cysts in recent sediments of Kiel Bight, Germany (Baltic Sea). *Ophelia* 39 (2), 137–158.
- Nehring, S., 1997. Dinoflagellate resting cysts from recent German coastal sediments. *Botanica Marina* 40, 307–324.
- NODC, 2009. World Ocean Atlas 2009, CD-ROM's Data Set. National Oceanographic Data Center, Silver Spring, MD.
- Nürnberg, D., Groeneveld, J., 2006. Pleistocene variability of the subtropical convergence at East Tasman Plateau: evidence from planktonic foraminiferal Mg/Ca (ODP Site 1172A). *Geochemistry, Geophysics, Geosystems* 7, Q04P11. doi:10.1029/2005GC000984.
- Pitcher, G.C., Joyce, L., 2009. Dinoflagellate cyst production on the southern Namaqua shelf of the Benguela upwelling system. *Journal of Plankton Research* 31, 865–875.
- Pospelova, V., Esenkulova, S., Johannessen, S.C., O'Brein, M.C., Macdonald, R.W., 2010. Organic-walled dinoflagellate cyst production, composition and flux from 1996 to 1998 in the central Strait of Georgia (BC, Canada): a sediment trap study. *Marine Micropaleontology* 75, 17–37.
- Rahmstorf, S., 1996. On the freshwater forcing and transport of the Atlantic thermohaline circulation. *Climate Dynamics* 12, 799–811.
- Rahmstorf, S., 2002. Ocean circulation and climate during the past 120,000 years. *Nature* 419, 207–214.
- Rau, A., Rogers, J., Chen, M.-T., 2006. Late Quaternary palaeoceanographic record in giant piston cores off South Africa, possibly including evidence of neotectonism. *Quaternary International* 148, 65–77.
- Reid, P.C., 1974. Gonyaulacacean dinoflagellate cysts from the British Isles. *Nova Hedwigia* 25, 579–637.
- Reid, P.C., 1978. Dinoflagellate cysts in the plankton. *New Phytologist* 80, 219–229.
- Reifel, K.M., McCoy, M.P., Rocke, T.E., Tiffany, M.A., Hurlbert, S.H., Faulkner, D.J., 2002. Possible importance of algal toxins in the Salton Sea, California. *Hydrobiologia* 473, 275–292.
- Reinecke, P., 1967. A dinoflagellate causing a red tide at Elands Bay, Cape Province, in December 1966. *The Journal of South African Botany* 33, 157–160.
- Rohling, E.J., 2000. Paleosalinity: confidence limits and future applications. *Marine Geology* 163, 1–11.
- Rohling, E.J., Bigg, G.R., 1998. Paleosalinity and $\delta^{18}\text{O}$: a critical assessment. *Journal of Geophysical Research* 103, 1307–1318.
- Rossi, S., Fiorillo, I., 2010. Biochemical features of a *Protoceratium reticulatum* red tide in Chipana Bay (Northern Chile) in summer conditions. *Scientia Marina* 74, 633–642.
- Rostek, F., Ruhland, G., Bassinot, F.C., Müller, P.J., Labeyrie, L.D., Lancelot, Y., Bard, E., 1993. Reconstructing sea surface temperature and salinity using $\delta^{18}\text{O}$ and alkenone records. *Nature* 364, 319–321.
- Schlitzer, R., 2010. Ocean Data View. Available at <http://odv.awi.de>. (accessed 01.11.10).
- Schmidt, G.A., 1999. Error analysis of paleosalinity calculation. *Paleoceanography* 14, 422–429.
- Schmidt, M.W., Spero, H.J., Lea, D.W., 2004. Links between salinity variation in the Caribbean and North Atlantic thermohaline circulation. *Nature* 428, 160–163.
- Schmittner, A., Clement, A.C., 2002. Sensitivity of the thermohaline circulation to tropical and high latitude freshwater forcing during the last glacial–interglacial cycle. *Paleoceanography* 17. doi:10.1029/2000PA000591.
- Schouten, S., Ossebaer, J., Schreiber, K., Kienhuis, M.V.M., Langer, G., Benthien, A., Bijma, J., 2006. The effect of temperature, salinity and growth rate on the stable hydrogen isotopic composition of long chain alkenones produced by *Emiliania huxleyi* and *Gephyrocapsa oceanica*. *Biogeosciences* 3, 113–119.
- Seguel, M., Tocornal, M.A., Sfeir, A., 2005. Floraciones algales nocivas en los canales y fiordos del sur de Chile. *Ciencia y Tecnología del Mar* 28, 5–13.
- Shaffer, G., Hormazabal, S., Pizarro, O., Salinas, S., 1999. Seasonal and interannual variability of currents and temperature off central Chile. *Journal of Geophysical Research* 104 (29), 29951–29961.
- Shaffer, G., Hormazabal, S., Pizarro, O., Ramos, M., 2004. Circulation and variability in the Chile Basin. *Deep Sea Research, Part I* 51 (10), 1367–1386. doi:10.1016/j.dsr.2004.05.006.
- Silver, M.W., Alldredge, A.L., 1981. Bathypelagic marine snow: deep-sea algal and detrital community. *Journal of Marine Research* 39, 501–530.
- Stocker, T.F., Wright, D.G., 1991. Rapid transitions of the ocean's deep circulation induced by changes in surface water fluxes. *Nature* 351, 729–732.
- Sun, X., McMinn, A., 1994. Recent dinoflagellate cysts from the Chatham Rise, Southern Ocean, East of New Zealand. *Palynology* 18, 41–53.
- Telford, R.J., 2006. Limitations of dinoflagellate cyst transfer functions. *Quaternary Science Reviews* 25, 1375–1382.
- Tomczak, M., Godfrey, J.S., 1994. *Regional Oceanography: an Introduction*. Pergamon Press, Oxford. 442 p.
- van der Meer, M.T.J., Baas, M., Rijpstra, W.I.C., Marino, G., Rohling, E.J., Sinninghe Damsté, J.S., Schouten, S., 2007. Hydrogen isotopic compositions of long-chain alkenones record freshwater flooding of the Eastern Mediterranean at the onset of sapropel deposition. *Earth and Planetary Science Letters* 262, 594–600.
- van der Meer, M.T.J., Sangiorgi, F., Baas, M., Brinkhuis, H., Sinninghe-Damsté, J.S., Schouten, S., 2008. Molecular isotopic and dinoflagellate evidence for Late Holocene freshening of the Black Sea. *Earth and Planetary Science Letters* 267, 426–434.
- Verleye, T.J., Louwye, S., 2010a. Late Quaternary environmental changes and latitudinal shifts of the Antarctic Circumpolar Current as recorded by dinoflagellate cysts from offshore Chile (41°S). *Quaternary Science Reviews* 29, 1025–1039.
- Verleye, T.J., Louwye, S., 2010b. Recent geographical distribution of organic-walled dinoflagellate cysts in the southeast Pacific (25–53°S) and their relation to the prevailing hydrographical conditions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 298, 319–340.
- Verleye, T.J., Mertens, K.N., Louwye, S., Arz, H.W., 2009. Holocene salinity changes in the southwestern Black Sea: a reconstruction based on dinoflagellate cysts. *Palynology* 33, 77–100.
- Wall, D., Dale, B., 1968. Modern dinoflagellate cysts and evolution of the Peridinales. *Micropaleontology* 14, 265–304.
- Wall, D., Dale, B., Harada, K., 1973. Descriptions of new fossil dinoflagellates from the late Quaternary of the Black Sea. *Micropaleontology* 19, 18–31.

- Wall, D., Dale, B., Lohman, G.P., Smith, W.K., 1977. The environmental and climate distribution of dinoflagellate cysts in modern marine environments from regions in the North and South Atlantic Ocean and adjacent seas. *Marine Micropaleontology* 2, 121–200.
- Wang, L., Sarnthein, M., Duplessy, J.C., Erlenkeuser, H., Jung, S., Pfaumann, U., 1995. Paleo sea surface salinities in the low-latitude Atlantic: the $\delta^{18}\text{O}$ record of *Globigerinoides ruber* (White). *Paleoceanography* 10, 749–761.
- Weaver, A.J., Saenko, O.A., Clark, P.U., Mitrovica, J.X., 2003. Meltwater pulse 1A from Antarctica as a trigger of the Bølling-Allerød warm interval. *Science* 299, 1709–1713.
- Weldeab, S., Lea, D.W., Schneider, R.R., Andersen, N., 2007. 155,000 years of West African monsoon and ocean thermal evolution. *Science* 316, 1303–1307.
- Wijffels, S.E., Hautala, S., Meyers, G., Morawitz, W., The, W.O.C.E., 1996. Indonesian throughflow repeat hydrography sections: I10 and IR6. *International WOCE Newsletter* 24, 25–28.
- Young, M.D., 2005. The distribution and organic- and calcareous-walled dinoflagellate cysts from the Eastern Indian Ocean; A proxy for late Quaternary palaeoceanographic reconstructions. Unpublished PhD Thesis. The Australian National University.
- Zingone, A., Siano, R., D'Alelio, D., Sarno, D., 2006. Potentially toxic and harmful microalgae from coastal waters of the Campania region (Tyrrhenian Sea, Mediterranean Sea). *Harmful Algae* 5, 321–337.
- Zonneveld, K.A.F., Brummer, G.-J.A., 2000. (Palaeo-)ecological significance, transport and preservation of organic-walled dinoflagellate cysts in the Somali Basin, NW Arabian Sea. *Deep-Sea Research Part II* 47, 2229–2256.
- Zonneveld, K.A.F., Susek, E., Fischer, G., 2010. Seasonal variability of the organic-walled dinoflagellate cyst production in the coastal upwelling region off Cape Blanc (Mauritania): a five-year survey. *Journal of Phycology* 46, 202–215.