GEOSCIENCES

A review on the diversity and distribution of athecate dinoflagellates in South Atlantic and in the Atlantic sector of the Southern Ocean: Research insights and gaps

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Abstract: This review summarizes the state of knowledge on athecate dinoflagellates occurring within the South Atlantic Ocean and Atlantic sector of the Southern Ocean. We compiled data from 105 articles and selected 33 addressing any aspect of athecate dinoflagellate studies. Our aim is to discuss the patterns in athecate dinoflagellate distribution by building a thorough species list and an occurrence map based on species recorded in coastal and oceanic waters. We found 69 species totaling 141 occurrences in the entire South Atlantic Ocean basin. Contradicting global trends, most species distributed throughout this region are subtropical. We linked this trend to a higher local effort in dinoflagellate research instead of higher biodiversity, especially when compared to usual hotspots in biodiversity attributed to tropical oceans. The Subantarctic and Antarctic regions had a low number of occurrences, with 12 and 5, respectively. Except for the occurrence of *Gyrodinium lachryma* in the Antarctic Zone, all records are unique, poorly described and never recorded again for species such as *Gymnodinium baccatum* and *Gymnodinium antarcticum*. This demonstrates that the state of knowledge regarding athecate dinoflagellates in the South Atlantic and especially in the Antarctic region is still limited due to a lack of directed investigation.

Key words: Antarctic, ecology, distribution, review.

INTRODUCTION

Dinoflagellates are a eukaryotic and almost entirely marine (83%) phytoplankton group (Goméz 2012) composed of autotrophic/mixotrophic or heterotrophic life forms at the same proportions (Taylor et al. 2008). The diversity of the group is estimated at more than 2,300 known species (Goméz 2005).

Historically, major dinoflagellate taxonomic divisions have been defined according to specific morphological features (Reñé et al. 2015). The lack of a theca, i.e., the hard membrane-bound cell wall formed by cellulose, is the general criterion for grouping certain dinoflagellates species within the athecate dinoflagellates.

Athecate forms include several genera of organisms occupying a wide range of habitats and trophic modes, most of which are free-living, such as *Cochlodinium*, *Amphidinium*, *Gyrodinium*, and the highly diverse *Gymnodinium*, which accounts for 297 species (Thessen et al. 2012). Some species belonging to the genera *Karenia*, *Cochlodinium*, *Gymnodinium* and *Gyrodinium* can also cause extensive blooms, and some species, such as *Karenia mikimotoi*, *Karenia brevis* and *Gymnodinium catenatum*, are potentially toxic to marine ecosystems and even

humans (Botes et al. 2003, Proença et al. 2001). In addition, athecate dinoflagellates account for approximately 25% of the total diversity of dinoflagellates worldwide, but their occurrence, distribution and most of their members are still poorly understood (Gómez 2007, Thessen et al. 2012).

Recently, interest in athecate dinoflagellates has been increasing worldwide primarily due to research indicating the gross underestimation of the group's diversity due to doubtful identifications coupled with a lack of molecular data (Reñé et al. 2015, Le Bescot et al. 2016, Ibarbalz et al. 2019). Potentially toxic species blooming in the coastal waters of the United States (Stumpf et al. 2022), China Sea (Liu et al. 2020), and Northern Europe (Karlson et al. 2021) have also raised research interest in the group. Previous researchers identified key factors driving the apparent low diversity of athecate dinoflagellates in some regions. Reasons for this scenario include the high frequency of species recorded only once or poorly described, known as "oncers" (Thessen et al. 2012); the minute size of the nanoplankton size fraction; and the use of inadequate methodology for athecate dinoflagellate enumeration/identification (Goméz 2012). Seeking to clarify the factors driving athecate dinoflagellate diversity, distribution and ecology, research efforts have already been made in the North Pacific (Gómez 2007), Mediterranean Sea (Reñé et al. 2015), New Zealand (De Salas et al. 2003, Haywood et al. 2004) and Japan (Benico et al. 2020). In contrast, for the South Atlantic Ocean, including the Atlantic Sector of the Southern Ocean, to date, only a few efforts have been focused on athecate dinoflagellates (Akselman 1985, 1986, Proença et al. 2001). Moreover, a large part of the species listed in those studies were either demonstrated to be different forms of the same species or were reallocated to other genera by more recent studies (Gómez et al. 2015, Goméz 2018).

Several aspects of athecate dinoflagellate-related knowledge, such as occurrence, ecological traits and diversity patterns, are still open subjects in the South Atlantic Ocean and Antarctic Sector. Furthermore, the knowledge about which species occur in these regions and their contribution to phytoplankton communities is still limited. To address this issue, we review and summarize the current state of knowledge regarding athecate dinoflagellate distribution in the entire South Atlantic Ocean and Atlantic sector of Southern Ocean, discussing some regional trends in species occurrence and ecological traits. We also compare scientific production in the last 60 years concerning free-living and non-aberrant athecate dinoflagellates, which maintain typical dinoflagellate characteristics, i.e., transversal flagellum and condensed chromosomes for at least one stage of their life cycle (Gómez et al. 2010). Dinoflagellates from coastal and oceanic waters were investigated, and records from the first recorded species to 2021 were discussed. Species recorded in estuarine and epicontinental waters were not included. To improve the understanding of diversity patterns, we created an occurrence map to illustrate the species listed herein while discussing differences related to major climatic zones and limitations on species records compared to other ocean basins.

MATERIALS AND METHODS

The primary search was conducted on open online repositories such as Scopus and Web of Science for any study that mentioned "phytoplankton" or "dinoflagellates" in the Antarctic and South Atlantic waters. Since most of the studies, species lists or books regarding

athecate dinoflagellates are not available in Scopus and Web of Science, we resorted through institutional repositories, books and paper research materials to better compile species occurrence data. We consulted species records from specific references, ecological studies and original records of 105 articles. Within this database, we sorted articles containing species-level identification of athecate dinoflagellates and recovered 33 references. All species were cross-referenced with the list of living dinoflagellates (Goméz 2005). The current taxonomy classification was checked on the AlgaeBase webpage (Guiry & Guiry 2022). Species occurrence was classified according to four climatic zones: Tropical, Subtropical,

Subantarctic and Antarctic. Classification was attributed either based upon the designation according to the original publication or allocated to a zone by matching the coordinates presented in the publication (if applicable) to a biogeographic division (Longhurst 2010). Species without a known location were excluded from this review. Additionally, we also included the synonym used in the original description/record (if applicable), temperature/salinity (if present), depth range, abundance, environment (coastal/oceanic) and trophic mode (see Table II and Figure 1). The species trophic mode was assigned according to the presence/absence of plastids either in 1) the original description of the species or 2) specific literature mentioning
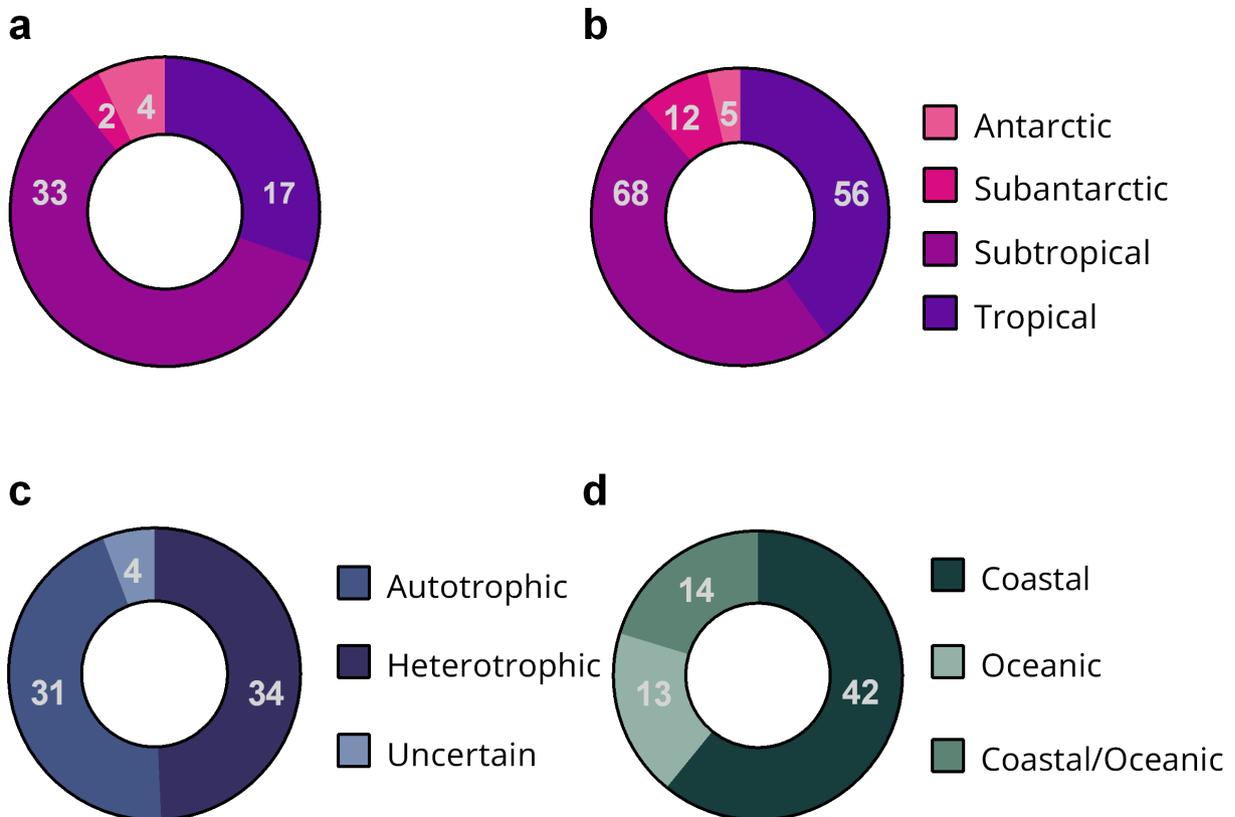

Figure 1. Metrics of the athecate dinoflagellate species investigated during the review. Letters indicate (a) number of species registered exclusively in one determined zone (56 out of 69), (b) number of records (occurrence/points of distribution) of all species per zone, (c) trophic mode of all species recorded in this review and (d) type of environment of all species recorded in this review.

feeding patterns. We excluded up to 50 records (Supplementary Material - Table SI) because 1) they were found in lagoons, 2) they were recorded in Brazil but belong to the North Atlantic portion, 3) they were Antarctic species but not of the Atlantic Sector and 4) the origin of the specimen or description was uncertain.

RESULTS AND DISCUSSION
Tropical Zone

Diversity is usually high in tropical zones, which translates to a higher presence of rare species or species that were recorded only once. Although we found a high number of exclusively tropical species recorded (17) (Figure 1a), they accounted for 56 out of 141 occurrences (Figure 1b, 2) and were mostly recorded in the northwesternmost South Atlantic Ocean, confined to waters with temperature ranges between 15 and 30 °C. In this region, a large portion of the coastal species described by Wood (1966) are associated with the Amazon River plume. The presence of benthic *Amphidinium klebsii* and *Amphidinium turbo* (Table I) in the area was related to bottom resuspension, primarily due to the Amazon River overflow and the unstable nature of bottom material such as silt.

As with most of the records and descriptions we found, the species occurring in the Amazon region were only recorded once by a single author (see Table I). In that case, Wood (1966) reported that the presence of autotrophic organisms such as *Gymnodinium galeaeforme* and *Gymnodinium marinum* in deeper layers (>100 m) is probably related to the high turbulence and turbidity at the site under the influence of continental waters. The author pointed out that the heterogeneity of the area and the high turbidity of the surrounding waters do not have a great effect even on autotrophic species that rely on sunlight to survive. Since *G. galeaeforme*

and *G. marinum* are abundant in the Amazon zone, other unknown factors may influence athecate dinoflagellate occurrence in this region.

Since stratification is a key factor for dinoflagellate occurrence (Smayda 2002), the salinity front formed by the Amazon River plume flowing offshore could favor the abundance of athecate dinoflagellates, while turbidity is not high enough to become light-limiting. Even so, more precise discussions are not possible because of the lack of further research conducted in this area.

In the region around 22°S, stratification controls dinoflagellate succession (Werlang et al. 2020). Coastal athecate dinoflagellates were observed during the spring in Brazilian waters. *Levanderina fissa* and *Pseliodinium fusus* (=*Gymnodinium fusus*) are linked to high salinity (35.7–34.5) and high temperature (21.9–23 °C), as is *Balechina gracilis* (Table II). During spring, temperature-induced stratification starts to confine phytoplankton to a shallower mixed layer, which tends to cause nutrient starvation and culminates in low abundances between 0–9.52×10^2 cells L^{-1} for both *P. fusus* and *L. fissa* (Werlang et al. 2020). *Gyrodinium falcatum* (Table I) also inhabits these waters, but in its case, low abundance (0–9.52×10^2 cells L^{-1}) was linked to the lack of prey, usually diatoms that do not thrive in highly stratified environments.

A low abundance of heterotrophic athecate dinoflagellates was noted by Cesar-Ribeiro et al. (2020) in oligotrophic oceanic waters such as the South Atlantic Tropical region. In these environments, heterotrophic species such as *Gyrodinium britannia*, *Gyrodinium spirale* and *Gyrodinium striatissimum* have no advantage because there is no prey available. Instead, smaller autotrophic species such as *Torodinium robustum* or possibly mixotrophic species such as several *Gymnodinium* species (see Table I) can be distributed in this location due to highly

Table I. Species list with accepted name (species), synonyms (if the case in the original description), location (climatic zone), and references.

	Species	Synonym	Location	Reference
	Akashiwo			
1	*Akashiwo sanguinea*	*Gymnodinium cf. splendens,Gymnodinium sanguineum*	Tropical/ Subtropical/ Subantarctic	Akselman 1985; Mendéz 1993; Pitcher & Calder 2000; Tenembaum et al. 2007; Gonçalves-Araujo et al. 2012; Guinder et al. 2020
	Amphidinium			
2	*Amphidinium crassum*	*Amphidinium phaecysticola*	Subantarctic/ Subtropical	Elbrächter 1979; Guinder et al. 2020
3	*Amphidinium klebsii*	*Amphidinium klebsi*	Tropical	Wood 1966
4	*Amphidinium turbo*		Tropical	Wood 1966
5	*Amphidinium sphenoides*		Tropical	Gonçalves-Araujo et al. 2012; Cesar-Ribeiro et al. 2020
	Balechina			
6	*Balechina gracilis*	*Gymnodinium amphora, Gymnodinium situla, Gyrodinium cuneatum, Gymnodinium gracile*	Subtropical	Elbrächter 1979; Marangoni et al. 2001; Gómez et al. 2015
	Brachidinium			
7	*Brachidinium capitatum*	*Brachydinium capitatum*	Tropical	Tenembaum et al. 2007
	Cochlodinium			
8	*Cochlodinium pulchellum*		Subtropical	Elbrächter 1979
9	*Cochlodinium semistriatum*		Subtropical	Elbrächter 1979
10	*Cochlodinium strangulatum*		Subtropical	Gómez et al. 2017
	Cucumeridinium			
11	*Cucumeridinium coeruleum*	*Balechina cf. marianae, Gymnodinium costatum, Gymnodinium coeruleum*	Tropical/ Subantarctic	Wood 1966; Balech 1979; Tenembaum et al. 2007
12	*Cucumeridinium lira*	*Gymnodinium lira, Gymnodinium lyra*	Subtropical	Gómez et al. 2015; Cesar-Ribeiro et al. 2020
	Dissodinium			
13	*Dissodinium pseudolunula*		Subtropical	Elbrächter 1979
	Erythropsidinium			
14	*Erythropsidinium agile*	*Erythropsis agilis*	Subtropical	Elbrächter 1979
	Gymnodinium			
15	*Gymnodinium agiliforme*		Subantarctic	Balech 1979
16	*Gymnodinium antarcticum*	*Gymnodinium frigidum*	Antarctic	Balech & El-Sayed 1965
17	*Gymnodinium baccatum*		Antarctic	Balech & El-Sayed 1965

Table I. Continuation.

18	*Gymnodinium bonaerense*		Subtropical	Akselman 1985
19	*Gymnodinium catenatum*		Subtropical	Balech & El-Sayed 1965; Pitcher & Matthews 1996; Proença et al. 2001
20	*Gymnodinium filum*		Tropical/ Subantarctic	Gonçalves-Araujo et al. 2012
21	*Gymnodinium flavum*		Tropical/ Antarctic/ Subantarctic	Wood 1966; Balech 1976
22	*Gymnodinium galeaeforme*	*Gymnodinium galaeforme* (orthographic mistake)	Tropical	Wood 1966
23	*Gymnodinium gelbum*		Tropical	Wood 1966
24	*Gymnodinium grammaticum*		Subtropical	Wood 1966; Elbrächter 1979
25	*Gymnodinium katodiniforme*		Subtropical	Elbrächter 1979
26	*Gymnodinium marinum*		Tropical	Wood 1966
27	*Gymnodinium mirabile*		Tropical	Wood 1966
28	*Gymnodinium multistriatum*		Tropical	Wood 1966
29	*Gymnodinium patagonicum*		Subtropical/ Subantarctic	Balech 1971
30	*Gymnodinium punctatum*		Tropical	Wood 1966
31	*Gymnodinium scopulosum*		Tropical	Wood 1966
	Gyrodinium			
32	*Gyrodinium britannia*	*Spirodinium spirale*	Subtropical	Elbrächter 1979
33	*Gyrodinium corallinum*		Subtropical	Marangoni et al. 2001
34	*Gyrodinium fissoides*		Subtropical	Elbrächter 1979
35	*Gyrodinium fusiforme*		Subantarctic/ Subtropical	Gonçalves-Araujo et al. 2012; Cesar-Ribeiro et al. 2020
36	Gyrodinium fusus		Subantarctic	Negri et al. 1992; Antacli et al. 2018
37	*Gyrodinium glaciale*		Antarctic	Balech 1976
38	Gyrodinium lachryma		Antarctic	Balech & El-Sayed 1965; 1971; 1973; 1976; Baylón et al. 2019; Garcia et al. 2020
39	Gyrodinium maculatum		Subtropical	Elbrächter 1979
40	Gyrodinium nasutum		Tropical	Wood 1966
41	*Gyrodinium obtusum*		Subtropical	Elbrächter 1979
42	*Gyrodinium ochraceum*		Subtropical/ Tropical	Wood 1966; Elbrächter 1979;
43	*Gyrodinium prunus*		Tropical	Wood 1966

Table I. Continuation.

44	*Gyrodinium spirale*		Tropical/ Subtropical/ Subantarctic	Elbrächter 1979; Marangoni et al. 2001; Antacli et al. 2018; Cesar-Ribeiro et al. 2020; Guinder et al. 2020
45	*Gyrodinium striatissimum*	*Gymnodinium striatissimum*	Subtropical	Elbrächter 1979
46	*Gyrodinium zeta*		Subtropical	Stephen & Hockey 2007
	Karenia			
47	*Karenia bicuneiformis*		Subtropical	Botes et al. 2003
48	*Karenia cristata*		Subtropical	Botes et al. 2003
49	*Karenia mikimotoi*	*Gymnodinium cf. mikimotoi*	Subtropical	Stephen & Hockey 2007
	Karlodinium			
50	*Karlodinium elegans*		Subtropical	Fabro & Almandoz 2021
51	*Karlodinium veneficum*	*Gymnodinium cf. aureolum, Gymnodinium galatheanum*	Subantarctic/ Tropical	Braarud 1957; Negri et al. 1992; Carreto et al. 1995
	Kirithra			
52	*Kirithra asteri*		Subtropical	Boutrup et al. 2017
	Lebouridinium			
53	*Lebouridinium glaucum*	*Katodinium glaucum*	Subtropical	Elbrächter 1979
	Levanderina			
54	*Levanderina fissa*		Tropical	Werlang et al. 2020
	Nematodinium			
55	*Nematodinium torpedo*		Subtropical/ Tropical	Wood 1966; Elbrächter 1979
	Polykrikos			
56	*Polykrikos schwartzii*		Subtropical	Pitcher & Calder 2000; Marangoni et al. 2001; Antacli et al. 2018; Cesar-Ribeiro et al. 2020
	Protodinium			
57	*Protodinium simplicius*		Subtropical	Elbrächter 1979
58	*Protodinium simplex*	*Gymnodinium simplex*	Tropical	Wood 1966
	Pseliodinium			
59	*Pseliodinium fusus*	*Gyrodinium falcatum, Gymnodinium fusus, Pseliodinium vaubanni* (orthographic mistake)	Tropical/ Subtropical	Elbrächter 1979; Tenembaum et al. 2007; Werlang et al. 2020
	Sclerodinium			
60	*Sclerodinium calyptroglyphe*	*Gymnodinium calyptroglyphe*	Subtropical	Elbrächter 1979; Marangoni et al. 2001

Table I. Continuation.

	Takayama			
61	*Takayama helix*		Subtropical	De Salas et al. 2003
	Torodinium			
62	*Torodinium robustum*		Subantarctic/ Tropical/ Subtropical	Negri et al. 1992; Brandini & Fernandes 1996; Gonçalves-Araujo et al. 2012; Antacli et al. 2018; Cesar-Ribeiro et al. 2020; Guinder et al. 2020; Werlang et al. 2020
63	*Torodinium teredo*		Subtropical	Elbrächter 1979
	Warnowia			
64	*Warnowia cf. polyphemus*		Tropical	Tenembaum et al. 2007
65	*Warnowia pulchra*		Subtropical	Akselman 1986
66	*Warnowia purpurata*		Subtropical	Elbrächter 1979
67	*Warnowia purpurescens*		Subtropical	Elbrächter 1979
68	*Warnowia rubescens*		Subtropical	Akselman 1986
69	*Warnowia violescens*		Tropical	Wood 1966

adapted behavior related solely to nutritional mode (Cesar-Ribeiro et al. 2020). In this case, even low abundances of other *Gymnodinium* species (Table I) can be present in oceanic waters linked to three water masses, namely, the South Atlantic Central Water (SACW), Subtropical Mode Water 18 (STMW18) and Atlantic Tropical Water (TW), all of which are of oligotrophic nature (Cesar-Ribeiro et al. 2020). The occurrence of athecate autotrophic dinoflagellates such as *Amphidinium sphenoides* is positively correlated with temperatures between 12–18 °C typical of the STMW18 but not with salinity (35.03–35.80). This observation reinforces local temperature as a defining factor for a few species of dinoflagellates, at least in oceanic environments, although a large part of dinoflagellates is theorized to be cosmopolitan (Taylor et al. 2008).

On the southeastern side of the South Atlantic Ocean, there is only one major oceanographic feature where athecate dinoflagellates have been recorded: the Benguela Current Upwelling System. The northern region of that current, located in the tropical South Atlantic, is notably undersampled compared to the southern region (Barlow et al. 2018). As in most of the studies comprising dinoflagellates, attention is usually directed to bloom-forming species (Gómez et al. 2017), which are more concentrated in the southern part of the system, which accounts for the majority of species records in the region (6 out of 7).

The only record in the northern region: *Karlodinium veneficum* (=*Gymnodinium galatheanum*; Table I) is associated with at least one bloom related to the later (stratified) phase of the upwelling front in the Northern Benguela upwelling system. Little is known about this record made by Braarud (1957) or the factors behind the bloom spotted by researchers that allowed for the description of that species. The only information regards deleterious effects to local fauna and human activities where the blooms occurred, similar to the ones reported in the Subtropical Zone where *K. veneficum* caused

deleterious effects and water discolorations in the Uruguay and Argentine waters (Negri et al. 1992, Carreto et al. 1995).

Subtropical Zone

Subtropical waters maintain a high abundance of dinoflagellates (Fernandes & Brandini 1999, Gonçalves-Araujo et al. 2012) and account for most of the recorded species (33) and species occurrences (68) (Figure 1a, b) in the South Atlantic Ocean. The effect of the discrepancy in data availability is also noted when comparing coastal and oceanic records: most of the species (42) are recorded for coastal environments, while similar proportions of dinoflagellates can be found in either oceanic (13) waters or both environments (14) (Figure 1d). *Karlodinium elegans*, *Protodinium simplicius* and *Cucumeridinium lira* are examples of species that can be found in both oceanic and coastal environments (Table II). In that case, they are always rare, even if they occur in the usually nutrient-rich coastal waters. For example, *K. elegans* was reported by Fabro & Almandoz (2021) as comprising only 0.2% of the total community in Argentinian waters.

In contrast, the nutrient-rich Subtropical Shelf Water (STSW) and Plata Plume Water (PPW) define the occurrence of several dinoflagellates in the Subtropical Zone where most of the species recorded are found (Figure 1a, b, figure 2). The PPW is indicated to be responsible for the advection of low-salinity waters and, consequently, works as a primary driver of high abundances of *Akashiwo sanguinea* and *Gymnodinium catenatum* in Argentinian coastal waters (Carreto et al. 1995) and Brazil (Proença et al. 2001). *A. sanguinea* bloom events occur in at least two locations on the Uruguay coast (Negri et al. 1992, Méndez et al. 1993). Red tides were observed in Piriapolis beach (18 × 10^6 cells L^{-1}) and Punta del Este (44 × 10^3 cells L^{-1}), extending northward to Brazilian waters (Méndez et al. 1993). Although known to be cosmopolitan and occur in Brazilian waters as well (Islabão et al. 2017, Werlang et al. 2020), there are no reports of red tides or bloom events caused by *A. sanguinea* in the South Atlantic Ocean outside of the Subtropical Zone between Uruguay and Argentina. Conversely, *Gymnodinium catenatum* was recorded by Balech (1964) at 37–38°S in the coastal region of Argentina close to Mar del Plata (Table I, II, Figure 2). Species occurrence was conditioned by the intrusion of warm waters from the Brazil Current (BC) (Table II) on the Argentinian Continental Shelf. Later, Méndez & Carreto (2018) raised the hypothesis of southward transportation of field populations of *G. catenatum* causing blooms and toxic events in Argentina and Uruguay only.

Other autotrophic species, such as *Torodinium robustum* and *Torodinium teredo*, were also reported in the same area, probably also taking advantage of nutrient enrichment to proliferate. Even though *T. robustum* and *T. teredo* (Table I) are not reported to cause blooms, they seem to accompany flora during major bloom events and occur in low abundance, probably outcompeted by the other bloom-forming species. Since cold, enriched and low-salinity waters (~33) contribute to *Akashiwo sanguinea* and *Gymnodinium catenatum* blooms in southern Brazil (Proença et al. 2001), Uruguay (Méndez et al. 1993) and Argentina (Carreto et al. 1995), local cold conditions play a central role in species outbreaks and can indicate an adaptation of Brazilian strains to colder waters or the presence of cryptic species, as reported in blooms in the North Atlantic (Hallegraeff et al. 2012).

Low water temperature (7–8 °C) and salinity between 33.4 and 33.6 have a great influence on the chlorophyll-*a* signal (6–10 μg L^{-1}) of *Karlodinium veneficum* in the Argentinian

Table II. Environmental variables, trophic mode and methodology used to study the athecate dinoflagellates. LM= Light Microscopy, TEM= Transmission Electron Microscopy, SEM= Scanning Electron Microscopy, SSU rDNA= Small Subunit of ribosomal DNA, LSU rDNA= Large Subunit of ribosomal DNA, A= Autotrophic, H= Heterotrophic, U= Uncertain. Abundance was expressed either in cells L $^{-1}$ or categories such as abundant, moderate, rare and very rare. N.S = Not Specified, *Use of fixatives. This information can be found in the references listed in Table I.

	Species	Temp. (°C)/ Sal.	Deep Range (m)	Abundance (cells L^{-1})	Environment	Methods	Description	Micrographs	Trophic Mode
	Akashiwo								
1	*Akashiwo sanguinea*	16–17	surface	9.0×10^2–18×10^6	Coastal	LM*	No	No	A
	Amphidinium								
2	*Amphidinium crassum*	17.1–17.3	0–100	N. S	Coastal	LM*	No	No	H
3	*Amphidinium klebsii*	15–25	0–80	moderate	Coastal/ Oceanic	LM*	No	No	A
4	*Amphidinium turbo*	15–30	0–120	abundant	Coastal/ Oceanic	LM*	No	No	A
5	*Amphidinium sphenoides*	12–18/ 35.03–35.80	surface	N. S	Oceanic	LM*	No	No	A
	Balechina								
6	*Balechina gracilis*	23	surface	N. S	Coastal	LM/ SEM/ SSU rDNA	Yes	No	H
	Brachidinium								
7	*Brachidinium capitatum*	N. S	N. S	N. S	Coastal	LM*	No	No	U
	Cochlodinium								
8	*Cochlodinium pulchellum*	16.3–16.6	0–25	N. S	Coastal	LM*	Yes	No	H
9	*Cochlodinium semistriatum*	16.7	0–50	N. S	Coastal	LM*	Yes	No	H
10	*Cochlodinium strangulatum*	N. S	N. S	N. S	Coastal	LM/ SEM/ LSU rRNA	Yes	Yes	H
	Cucumeridinium								
11	*Cucumeridinium coeruleum*	20–25	surface	very rare	Oceanic	LM*	No	No	A
12	*Cucumeridinium lira*	N. S	N. S	N. S	Coastal/ Oceanic	LM*/ SEM/ SSU rDNA	Yes	Yes	H
	Dissodinium								
13	*Dissodinium pseudolunula*	16.3–16.7	surface	N. S	Coastal	LM*	Yes	No	H
	Erythropsidinium								
14	*Erythropsidinium agile*	16.6–16.7	surface	N. S	Coastal	LM*	Yes	No	U
	Gymnodinium								
15	*Gymnodinium agiliforme*	10.7–12	0–100	rare	Oceanic	LM*	Yes	No	A
16	*Gymnodinium antarcticum*	N. S	0–100	abundant	Coastal	LM*	Yes	No	A
17	*Gymnodinium baccatum*	N. S	0–100	abundant	Oceanic	LM*	Yes	No	A
18	*Gymnodinium bonaerense*	11–17/ 23.6–33.7	0–8	0–5.15×10^4	Oceanic	LM*	No	No	A
19	*Gymnodinium catenatum*	16.8–17.6	surface	N. S	Coastal	LM*	Yes	Yes	A
20	*Gymnodinium filum*	8.1–18.8	N. S	0-4.0×10^1	Oceanic	LM*	No	No	U
21	*Gymnodinium flavum*	15–20	40–120	rare	Oceanic	LM*	No	No	A

Table II. Continuation.

22	*Gymnodinium galeaeforme*	15–25	40–160	moderate	Coastal/ Oceanic	LM*	No	No	A
23	*Gymnodinium gelbum*	18.5–30	100–200	abundant	Coastal/ Oceanic	LM*	Yes	No	A
24	*Gymnodinium grammaticum*	15–30	0–120	moderate-abundant	Oceanic	LM*	No	No	A
25	*Gymnodinium katodiniforme*	18.2	100–200	N. S	Coastal	LM*	Yes	No	H
26	*Gymnodinium marinum*	10–25	0–100	moderate-abundant	Coastal/ Oceanic	LM*	No	No	A
27	*Gymnodinium mirabile*	20–25	0-100	moderate-abundant	Oceanic	LM*	No	No	A
28	*Gymnodinium multistriatum*	15–25	20–1000	moderate	Coastal/ Oceanic	LM*	No	No	A
29	*Gymnodinium patagonicum*	5/ 34.11–34.13	surface	rare	Oceanic	LM*	Yes	No	A
30	*Gymnodinium punctatum*	15–20	70	rare	Oceanic	LM*	No	No	A
31	*Gymnodinium scopulosum*	20–25	surface	rare	Oceanic	LM*	No	No	A
	Gyrodinium								
32	*Gyrodinium britannia*	17.1	surface	N. S	Coastal	LM*	No	No	H
33	*Gyrodinium corallinum*	N. S	N. S	N. S	Coastal	LM*	No	No	H
34	*Gyrodinium fissoides*	16.7	0–50	N. S	Coastal	LM*	Yes	No	H
35	*Gyrodinium fusiforme*	8.1–18.8/ 33.85–35.98	surface	0–3.2× 10^3	Oceanic	LM*	No	No	H
36	*Gyrodinium fusus*	9.5–13.5/ 32.4–33.4	N. S	N. S	Coastal	LM*	No	No	H
37	*Gyrodinium glaciale*	N. S	N. S	N. S	Coastal/ Oceanic	LM*	Yes	No	H
38	*Gyrodinium lachryma*	6.29	0–100	rare	Coastal	LM*	Yes	No	H
39	*Gyrodinium maculatum*	16.7	0–50	N. S	Coastal	LM*	Yes	No	H
40	*Gyrodinium nasutum*	10–30	10–1000	rare	Coastal/ Oceanic	LM*	Yes	No	H
41	*Gyrodinium obtusum*	16.7–17.1	100–200	N. S	Coastal	LM*	Yes	No	H
42	*Gyrodinium ochraceum*	16.7–18.1	100–200	N. S	Coastal	LM*	Yes	No	H
43	*Gyrodinium prunus*	10–30	120	rare	Coastal/ Oceanic	LM*	Yes	No	H
44	*Gyrodinium spirale*	18.2	200–100	N. S	Coastal	LM*	Yes	No	H
45	*Gyrodinium striatissimum*	16.3–18.7	N. S	N. S	Coastal	LM*	Yes	No	H
46	*Gyrodinium zeta*	N. S	N. S	N. S	Coastal	LM*	No	No	H
	Karenia								
47	*Karenia bicuneiformis*	N. S	surface	0.5× 10^6	Coastal	LM/ SEM/ LSU (28S) rDNA, HPLC	Yes	Yes	A
48	*Karenia cristata*	N. S	surface	N. S	Coastal	LM/ SEM/ LSU (28S) rDNA, HPLC	Yes	Yes	A

Table II. Continuation.

49	*Karenia mikimotoi*	N. S	surface	N. S	Coastal	LM/ SEM/ LSU (28S) rDNA, HPLC	Yes	Yes	A
	Karlodinium								
50	*Karlodinium elegans*	8.0–8.3/ 33.7–33.8	surface	1.6×10^3–1.46×10^4	Coastal/ Oceanic	LM*/ SEM	Yes	No	A
51	*Karlodinium veneficum*	N. S	N. S	N. S	Coastal	LM*	Yes	No	A
	Kirithra								
52	*Kirithra asteri*	7.2/ 33.72	0-5	N. S	Coastal	LM/ SEM/ TEM/ LSU rDNA	Yes	No	A
	Lebouridinium								
53	*Lebouridinium glaucum*	16.6	100-200	N. S	Coastal	LM*	Yes	No	H
	Levanderina								
54	*Levanderina fissa*	21.9–23/ 35.7–34.5	surface	0–9.52×10^2	Coastal	LM*	No	No	A
	Nematodinium								
55	*Nematodinium torpedo*	10–25	0–50	N. S	Coastal	LM*	Yes	No	H
	Polykrikos								
56	*Polykrikos schwartzii*	N. S	N. S	N. S	Coastal	LM*	No	No	H
	Protodinium								
57	*Protodinium simplicius*	16.6	0–25	N. S	Coastal/ Oceanic	LM*	Yes	No	H
58	*Protodinium simplex*	10–25	0–150	N. S	Coastal/ Oceanic	LM*	Yes	No	A
	Pseliodinium								
59	*Pseliodinium fusus*	18	0–100	0–9.52×10^2	Coastal	LM*	Yes	No	U
	Sclerodinium								
60	*Sclerodinium calyptroglyphe*	16.7–17.1	200	N. S	Coastal	LM*	Yes	Yes	H
	Takayama								
61	*Takayama helix*	N. S	N. S	N. S	Coastal	LM/ SEM/ TEM/ LSU rDNA, HPLC	Yes	Yes	A
	Torodinium								
62	*Torodinium robustum*	17.1–25	surface	N. S	Coastal	LM*	Yes	No	A
63	*Torodinium teredo*	17.1	surface	N. S	Coastal	LM*	Yes	No	A
	Warnowia								
64	*Warnowia cf. polyphemus*	N. S	N. S	N. S	Coastal	LM*	No	No	H
65	*Warnowia pulchra*	15.5/ 33.6	N.S	2.0×10^1	Coastal	LM*	Yes	Yes	H
66	*Warnowia purpurata*	18.5	0–100	N. S	Coastal	LM*	Yes	No	H
67	*Warnowia purpurescens*	16.7	0-50	N. S	Coastal	LM*	Yes	No	H
68	*Warnowia rubescens*	21.9–22.5	0-30	2.0×10^1–1.6×10^2	Coastal	LM*	Yes	No	H
69	*Warnowia violescens*	20–25	20-100	moderate	Coastal/ Oceanic	LM*	Yes	No	H

coastal shelf break (Negri et al. 1992). In contrast to the bloom of the same species in the tropical eastern South Atlantic Ocean (Braarud 1957), low temperatures and salinity join together to provide optimal conditions for *K. veneficum* to multiply in the shelf break front. Due to increased stratification, *K. veneficum* can spread for ~60 km, reaching a total number of 1.3×10^6 cells L^{-1}. The non-monospecific nature of *K. veneficum* blooms also provides leverage to other athecate dinoflagellates cooccurring in the same area (Negri et al. 1992) and is attributed to a strong coast-to-shelf break gradient. Since blooms occur in the spring, when the surface layer is enriched, bloom events were thought to be natural, in contrast to events recorded on the eastern side of the South Atlantic, where *K. veneficum* blooms are associated with pollution, eutrophication of surface waters and sewage discharge (Van der Lingen et al. 2016).

Species of *Karenia* are basically confined to the Subtropical portion of the eastern South Atlantic (Table I and II). We found that the only species-level records were made by Botes et al. (2003) and discussed by Stephen & Hockey (2007) who reported the occurrence of *Karenia bicuneiformis*, *Karenia cristata* and *Karenia mikimotoi(=Gymnodinium mikimotoi)*. Wind-driven temperature anomalies are linked to the frequent occurrence of *K. cristata* blooms in at least four distinct locations: Gordon's Bay, Lambert's Bay, False Bay, and Betty's Bay (Stephen
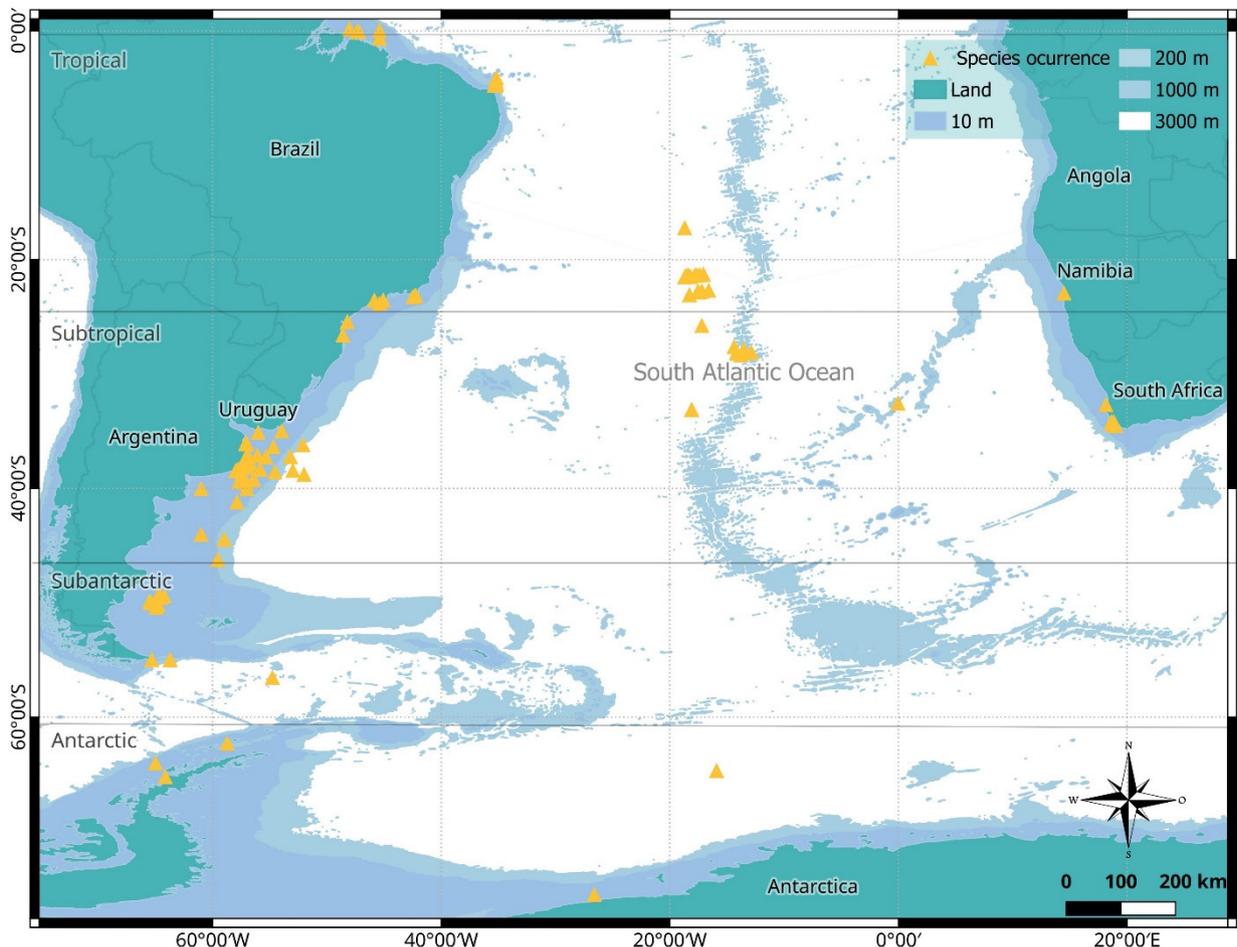
Figure 2. Occurrence of athecate dinoflagellates in the South Atlantic Ocean and Atlantic Sector of the Southern Ocean, according to the location provided in each checked reference.

& Hockey 2007). Northwesterly winds favor a shallower mixing layer, confining *K. cristata* cells on the surface, where they proliferate to bloom levels. Since cell density is highly dependent on water column structure (Smayda 2002 and previous studies), thermal stratification plays a central role in promoting *K. cristata* blooms. The other two species, *K. bicuneiformis*, and *K. mikimotoi*, were described in detail, but ecologic traits are not discussed, which leaves room only for assumptions that those organisms respond to the local environment at the intrageneric level.

The Subtropical region of Gordon's Bay and Walker's Bay are two hotspots for the occurrence of *Karenia cristata* and *Karenia bicuneiformis,* (Table I, II), but their occurrences do not overlap, indicating species-specific spatial differentiation, most likely related to the allelopathic behavior of *K. cristata* (Botes et al. 2003). While the occurrence of *K. bicuneiformis* is limited to the southern location represented by Walker's Bay, *K. cristata* is restricted to the northernmost location of Gordon's Bay. Only *K. cristata* is listed as a toxin-producing species based on field samples (Guiry & Guiry 2020), while *K. bicuneiformis* did not show any effects on marine fauna. Although there is no indication of toxin production in *K. bicuneiformis*, concentrations up to 0.5×10^6 cells L^{-1} were found to cause deleterious effects in bioassays primarily on fish and sea urchin larvae (Botes et al. 2003). Since the batch cultures of *K. cristata* were not subjected to any toxin quantification, such as enzyme-linked immunosorbent assay (ELISA) or High-Performance Liquid Chromatography (HPLC), it is still uncertain whether the cultured species found in Gordon's Bay were actually producing toxins at the time.

Subantarctic and Antarctic Zones

The southernmost region of the Atlantic Ocean displayed the lowest number of species recorded in the basin. Only 6 species are known to occupy solely Subantarctic (2) or Antarctic waters (4), even though nearly all of the species described in the first few years of dinoflagellate-related research activity belong to this area (see Table I. Balech & El-Sayed 1965, Balech 1971, 1976, 1979). The recorded occurrence is also low, accounting for 12 and 5 points of distribution, respectively (Figure 1b, 2). As a trend, heterotrophic species (34) in the South Atlantic Ocean are slightly more numerous than autotrophic species (31) while a few lack more detailed description, so their trophic mode remains uncertain (4) (Figure 1c). The same can be observed in both the Subantarctic and Antarctic zones, but especially in Antarctic coastal waters. In that case, one single researcher described the four species occurring in the Antarctic Zone: *Gymnodinium antarcticum* (=*Gymnodinium frigidum*), *Gymnodinium baccatum*, *Gyrodinium glaciale* and *Gyrodinium lachryma* (Balech & Sayed 1965, Balech 1971, 1976, 1979). At least *G. antarcticum* and *G. baccatum* seem to be endemic to the Atlantic sector of the Southern Ocean and are inherently linked to these cold waters. Even so, there are doubts about this conclusion due to 1) original descriptions based on a single/few specimens, 2) lack of micrographs, and 3) observation of the species only once and never again, which hampers our ability to make comparisons. In addition, these observations could be biased given that vertical net tows were used as the sampling strategy in the majority of the studies (Table II). Net tows select against larger and more robust specimens (Goméz 2005), which leads to a broad number of studies recording larger species such as heterotrophic *Gyrodinium*. This effect is enhanced by the use of harsh fixatives, usually formaldehyde, leading

to severe impairment of more delicate and smaller specimens (Goméz 2005).

It is only possible to infer methodological bias when dealing with first records, not to confirm it. For instance, net pore size selection against larger cells (>30 µm) and distortion caused by harsh fixatives such as formaldehyde (Table II, Balech & El-Sayed 1965) can select against the recording of larger and more robust specimens such as *Gyrodinium lachryma*, which gives the tendentious idea that a great part of dinoflagellates in the area are microplanktonic, which was recently shown to be a misleading conclusion (Ibarbalz et al. 2019).

The sampling effort and methodology used are decisive to the high rates of "oncers" (e.g., species only recorded once) observed by Thessen et al. (2012) and noted in our review as well. This scenario prevents advances in understanding species distribution, since the species recorded are either very rare, poorly described or wrongfully assigned (Thessen et al. 2012). This limitation remains in more modern research efforts, which still do not address athecate dinoflagellate distribution patterns or biogeographic dispersion in the South Atlantic Ocean. The lack of environmental data in the first, and most of the time only, species records (Table II) also prevent further discussions regarding this topic.

In the case of the Subantarctic Zone, the presence of heterotrophic species such *Gyrodinium fusiforme*, *Gyrodinium fusus* and *Gyrodinium spirale* (Table I) could indicate a transition between the Subantarctic and Antarctic zones. The highest contributions of dinoflagellates (15–42% relative abundance) are observed over the region under the influence of Subantarctic Shelf Water (SASW) (Gonçalves-Araujo et al. 2012).

The Subantarctic region is characterized by a strong thermohaline front with predominantly cold waters (8.1–18.8 °C) and low salinity (~33), especially in the inner shelf region. Most of the species reported in the region by Gonçalves-Araujo et al. (2012) were smaller than 20 µm, which raises questions about the role of body size as an ecological trait in Subantarctic waters. Additionally, the thermal variation provides an optimal condition for dinoflagellate occurrence over the Southern Patagonian Shelf, where a strong thermocline is the main oceanographic feature, and the Sigma-t indicates a more stratified state toward the northern part of the shelf at >52°S (Antacli et al. 2018). *Karenia cf. mikimotoi* can reach densities of 3.4×10^3 cells L^{-1} in the stratified zone of the Southern Patagonian Shelf while *Amphidinium* occurred once, primarily where warmer (11.4 °C), less salty (>33) and more stratified waters are predominant (Antacli et al. 2018). In this case, water temperature and inorganic nutrient concentrations seem to be the most important environmental features influencing the spatial distribution of dinoflagellates in the Subantarctic Zone. Additionally, the findings of Antacli et al. (2018) supplement the early observations made by Carreto (1995) and Hoffmeyer et al. (2018) that trophic behavior related to increasing stratification seems to be the most important factor for athecate dinoflagellates in the Subantarctic Zone.

In the Burdwood Bank protected area, stratification also plays a central role in athecate dinoflagellate distribution. The surface layer between the Beagle Channel and the Burdwood Bank contains Beagle-Magellan Water (BMW), SASW and Subantarctic Water (SAW), which contribute to the occurrence of *Torodinium robustum* (Table I, II) but in low abundance given the oligotrophic nature of most stratified waters in this region (Guinder et al. 2020).

The thermal and depth ranges of athecate dinoflagellate occurrence are narrow in the

Subantarctic and Antarctic zones (Balech & El-Sayed 1965, Balech 1973, 1976, 1979, Table II). However, the temperature range of Antarctic species remains between 6.29 °C and 7 °C, and the maximum depth of occurrence is within 150 m (Table II), which may favor heterotrophic *Gyrodinium*. Visualization of diatom cells in *Gyrodinium* food vacuoles has been mentioned at least three times before (see Balech 1958 and further references by this author) in Antarctic waters, indicating that this genus can act as a predator of diatom populations south of the Polar Front. However, the importance of predatory behavior of dinoflagellates in the Antarctic Zone is still an unexplored subject, especially considering their assumed importance in diatom bloom suppression. Considering recent predictions on climate-related increases in dinoflagellate heterotrophic activity in the Antarctic Zone, their grazing behavior is likely to increase along with water surface temperature (Deppeler & Davidson 2017). Even so, these affirmations are still generalizations based on studies of other flagellate groups, such as cryptophytes. Considering the highly specialized nature of dinoflagellates, it is important to address this matter with more thorough research efforts.

It is thought that specialized dinoflagellates present highly plastic behavior, which influences their distribution, leading to low rates of endemic species (Taylor et al. 2008). In the Subantarctic Zone, while some species, such as *Gymnodinium agiliforme*, were originally ascribed to warmer water flora (>20 °C) (Goméz 2005), the Antarctic specimens reported in Balech (1979) occurred in relatively cold waters: ~7 °C in the surface layer of the water column (Table II). The same is valid for other species mentioned by Balech, namely, *Gymnodinium flavum* and *Gymnodinium patagonicum*. These findings seem to corroborate the hypothesis

raised later by Taylor et al. (2008) that true endemism in dinoflagellates is rare. Instead, most species are cosmopolitan, and their occurrence and distribution are limited by their capacity to resist or thrive in local conditions, which is related to adaptive behavior rather than major biogeographic barriers/filters.

Previous reviews showed that biodiversity of many organisms is high in the Antarctic Zone, especially in the Antarctic Peninsula (Griffiths & Waller 2016) mostly due to higher number of published studies focused in the area. In our review, we found opposite results: the Antarctic Peninsula displays low diversity marked by seasonal patterns in temperature, salinity, stratification and chlorophyll *a* (Garcia et al. 2020), which are confirmed to favor only a few heterotrophic forms of athecate dinoflagellates such as *Gyrodinium*.

Feeding behavior seems to be an important factor driving species distribution in the Antarctic Zone as well. Balech (1973, 1976) theorized that the distribution of any species of the genus *Gyrodinium* can be a result of feeding behavior related to diatom blooms occurring in the area of the Gerlache Strait and Bellingshausen Sea. Since all species of *Gyrodinium* are phagotrophic, they engulf food as a preying strategy. In the case of the specimens reported in Balech & El-Sayed (1965), it was possible to identify food vacuoles filled with *Fragilariopsis*, another four unidentified diatoms, in addition to a small unidentified dinoflagellate. This observation is consistent with what Balech (1978) observed for *Gyrodinium lachryma*. Nevertheless, the discussion of the predatory role of larger species (>50 µm) of athecate heterotrophic dinoflagellates is still ongoing. Furthermore, the distribution of *Gyrodinium* in Antarctic ecosystems, mostly related to the mitigation of diatom blooms during the late summer, is unclear.

Climate change is known to drive major alterations in the Antarctic Zone, especially in the Western Antarctic Zone (Depeller & Davidson 2017). Differences in climatic conditions affect both the southern and northern sections of the Western Antarctic Peninsula (WAP), being more intense in the southern part of the permanent open ocean zone, mostly linked to increased stratification and shallowing of the mixed layer depth (MLD). Stratification induced by the freshening of surface waters triggered by glacier melting favors the dinoflagellate community, influencing the occurrence patterns of at least *Gyrodinium lachryma* (Table I) (Baylón et al. 2019). *G. lachryma* is associated with two water masses: Antarctic Bottom Water (AABW) and Antarctic Surface Water (AASW) (Baylón et al. 2019). This region presumably displays a strong interannual pattern according to data presented by Baylón et al. (2019) and Garcia et al. (2019), which, by extension, leads to the patchy distribution of other species.

Climate-induced glacier melting and freshwater runoff favors *Gyrodinium lachryma*, which plays a central role in the phytoplanktonic community (Baylón et al. 2019, Garcia et al. 2019, 2020). This species is responsible for approximately 37% of the phytoplankton composition variability during the summer in the WAP. Although it is not yet clear exactly how those environmental conditions benefit *G. lachryma*, its intimate relationship with glacier melting is certain. This result indicates that *G. lachryma* will play a central role in the WAP phytoplankton community in the future, even though research is still unclear on how.

Stratification and glacier melting are expected to increase in the future in the WAP region (Deppeler & Davidson 2017). Even so, glacier melting has already been documented, and it is related to the strengthening of the positive phase of the South Annular Mode

(SAM), which in turn enhances the athecate dinoflagellate contribution to the total phytoplankton community (Garcia et al. 2019, 2020). Small (<20 µm) athecate dinoflagellates are ubiquitous in the region, but it is only during sea ice cover retreats related to the positive SAM that they reach more than 20% of the community (Garcia et al. 2020). Sea ice cover and glacier melt seem to have greater influence over the dinoflagellate community on the WAP. This effect was previously observed to impact other flagellates, mainly cryptophytes (Mendes et al. 2018), leading to cryptophyte dominance over the southwestern Antarctic Peninsula region, but knowledge of the effects on dinoflagellates is still vague.

Common gaps in athecate dinoflagellate studies in the South Atlantic Ocean and future prospects for targeted research

In agreement with the findings of Thessen et al. (2012) for other athecate dinoflagellates, we recorded a low index of species records. Additionally, as Thessen et al. (2012) observed for the genus *Gymnodinium*, most of the species recorded in the South Atlantic were recorded only once or by a single researcher (see Table I and SI) or in a single study and never seen again after that. Specially regarding Antarctic species, this scenario jeopardizes advances in understanding species distribution and biogeography. For instance, searching for the original descriptions and then finding metadata such as geographical coordinates of plankton samples can be a challenging task. A large part of the species descriptions during the early research years did not include such metadata or additional environmental descriptors (see Tables II and SI). These issues tend to weaken the discussion about ecological traits, essentially because if no environmental data are added to the species records, there will be gaps that

will be difficult to fill since those species were recorded only once. These data indicate that either 1) those descriptions remain unknown to the general scientific community or 2) traditional taxonomic practices impair reidentification or include species as synonyms (Thessen et al. 2012).

Additionally, we found that a large part of what is understood as local biodiversity is actually an effect of research bias. Most of the species recorded in the South Atlantic Ocean occur in the west boundary in the Subtropical Zone (Figure 2). However, species records are clearly related to the number of publications and to local research effort rather than true biodiversity. For instance, a large part of the species records made between 1965 and 2002 are assigned to an Argentinian researcher (see Balech(& El-Sayed) 1965 to 2002). Additionally, more efforts have been made primarily within the continental shelves of Argentina and Uruguay. This scenario is related to the nature of extensive dinoflagellate blooms occurring in that area, which is of interest to researchers and results in more research material being available.

Another factor that leads us to believe that the local biodiversity has been underestimated in the South Atlantic Ocean is the rather small number of species recorded compared to other ocean basins, even smaller ones. In species lists from the Black Sea, around 74 athecate dinoflagellate species were found among the total of 267 species (Gómez & Boicenco 2004). Similar findings were made in the Mediterranean Sea, where around 179 species of athecate dinoflagellates are known to occur (Gómez 2003). Since we were able to identify only 69 species in a much larger basin, it is safe to conclude that most of the species living in the South Atlantic Ocean have not yet been described or recorded.

Even potentially toxic coastal athecate dinoflagellate species, which have been more often described in other oceanic regions (Gómez 2007), are less studied in the eastern and western boundaries of the South Atlantic Ocean. Therefore, we suggest that only research efforts focused on athecate dinoflagellates will fill those gaps for the South Atlantic Ocean.

The use of light microscopy as the main methodology in most of the studies and the little effort made to identify or describe athecate dinoflagellates with more accuracy can also be associated with the low biodiversity recorded for the South Atlantic Ocean. Virtually all species listed here (60 out of 69) were identified through light microscopy alone, and some type of fixative was used to examine non-living specimens under the microscope (Table II). As stated by Gómez (2007), athecate dinoflagellates are usually more prone to cell alterations due to the effects of fixatives, which jeopardizes species identification and enumeration under light microscopy. These issues may have contributed to the scenario reported in this review, as incomplete descriptions and records are often seen in the current database, including for the athecate dinoflagellates along the South Atlantic Ocean. To increase the athecate dinoflagellate species record in the South Atlantic Ocean and to enhance the quality and certainty of identifications, other methods, such as cultures and DNA sequencing, should be added to traditional light microscopy screening.

We noted that most records were concentrated in the western boundary of the South Atlantic Ocean, predominantly on the southern coast of Argentina and in the Subtropical Zone (Table I, Figure 2). Few species occurred within both boundaries of the South Atlantic Ocean. Differences in spatial distribution could be related to the plastic nature and ecological traits of dinoflagellates, but these differences

are more likely due to the disparity documented herein in terms of published articles between the eastern and western boundaries, as well as between the different climatic zones.

CONCLUSIONS

Athecate dinoflagellates have been unevenly studied within the South Atlantic Ocean. Distinct spatial distribution patterns of athecate dinoflagellates in general were due to differences in publication flow and dinoflagellate-focused research at each climatic zone rather than true diversity. Thus, the majority of scientific efforts toward understanding the spatial and temporal distribution of dinoflagellates have been focused on the Subtropical Zone.

On the eastern boundary, most studies have focused on the Southern Benguela Current System, mostly due to the higher incidence of bloom events or potential toxicity. The same can be said about the species recorded in the western boundary, where most of the records are tied to a region most prone to bloom events and deleterious effects to the local biota.

Despite our efforts, the available data did not allow for a robust definition of the distribution of athecate dinoflagellates in the South Atlantic Ocean, but we could enlist the species-level records in both the western and eastern boundaries of the South Atlantic Ocean. Among these species, heterotrophic *Gyrodinium* would play an important role as grazers of diatom blooms, at least along the Atlantic Sector of the Southern Ocean. Overall, the intrinsic morphology and size of many species of athecate dinoflagellates have impacted their diversity and biogeographic studies around the world, especially along the South Atlantic Ocean. Their first records were not descriptive enough or incomplete in terms of full taxonomic description, and were mostly based on a single or few specimens. There is a considerably high frequency of single records and major limitations posed by the absence of studies focused on athecate dinoflagellates along the South Atlantic Ocean that need to be consider and addressed in future studies targeting dinoflagellates.

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