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Changes in Phytoplankton Communities Along the Northern Antarctic Peninsula: Causes, Impacts and Research Priorities

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The Northern Antarctic Peninsula (NAP), located in West Antarctica, is amongst the most impacted regions by recent warming events. Its vulnerability to climate change has already led to an accumulation of severe changes along its ecosystems. This work reviews the current findings on impacts observed in phytoplankton communities occurring in the NAP, with a focus on its causes, consequences, and the potential research priorities toward an integrated comprehension of the physical–biological coupling and climate perspective. Evident changes in phytoplankton biomass, community composition and size structure, as well as potential bottom-up impacts to the ecosystem are discussed. Surface wind, sea ice and meltwater dynamics, as key drivers of the upper layer structure, are identified as the leading factors shaping phytoplankton. Short- and long-term scenarios are suggested for phytoplankton communities in the NAP, both indicating a future increase of the importance of small flagellates at the expense of diatoms, with potential devastating impacts for the ecosystem. Five main research gaps in the current understanding of the phytoplankton response to climate change in the region are identified: (i) anthropogenic signal has yet to be disentangled from natural climate variability; (ii) the influence of small-scale ocean circulation processes on phytoplankton is poorly understood; (iii) the potential consequences to regional food webs must be clarified; (iv) the magnitude and risk of potential changes in phytoplankton composition is relatively unknown; and (v) a better understanding of phytoplankton physiological responses to changes in the environmental conditions is required. Future research directions, along with specific suggestions on how to follow them, are equally suggested. Overall, while the current knowledge has shed light on the response of phytoplankton to climate change, in order to truly comprehend and predict changes in phytoplankton communities, there must be a robust collaboration effort integrating both Antarctic research programs and the whole scientific community under a common research framework.

Keywords: West Antarctica, phytoplankton response, climate change, bottom–up impacts to the ecosystem, research gaps and directions

INTRODUCTION

The Southern Ocean is instrumental in the functioning of the global ocean. It is responsible for over a third of the global CO_2 ocean sequestration, playing a key role in driving global biogeochemistry (Gruber et al., 2009). While covering only 30% of the global ocean's surface, it is predicted to account up to 75% of the heat uptake (Frölicher et al., 2015), underlining its importance under the reported and predicted impacts of anthropogenic-driven climate change. Thus, a better understanding of Southern Ocean processes on a circumpolar and regional scales and their vulnerability is urgent, especially considering that climate-driven changes over its biogeochemistry likely to impact from primary producers to changes on the ecosystem functioning (Henley et al., 2020).

Current knowledge shows that impacts of climate change in the Southern Ocean vary spatially. The Antarctic Peninsula, located in West Antarctica, is amongst the most rapidly warming regions worldwide, particularly its western (WAP) and northern (NAP) sectors (Clarke et al., 2007; Ducklow et al., 2012; Kerr et al., 2018b; Moffat and Meredith, 2018; Henley et al., 2019). Spatially, the NAP (**Figure 1**) roughly stretches from the Anvers Island to the oceanic waters surrounding the northern tip of the Antarctic Peninsula, including the Bransfield Strait, the southernmost Drake Passage and the NW Weddell Sea (Kerr et al., 2018b). Therefore, it is a diverse region, encompassing a range of oceanic and coastal ecosystems with complex hydrographic and biogeochemistry dynamics.

The NAP is highly relevant for the Southern Ocean dynamics, acting as a transition zone between sub-Antarctic and Antarctic waters. On the NAP's eastern boundary, the NW Weddell Sea acts as a critical site of formation and exportation of deep waters to the global ocean (Franco et al., 2007; de Carvalho Ferreira and Kerr, 2017; Kerr et al., 2018a). One of the source of this deep water is the relatively salty shelf water with temperatures near the freezing point (Huhn et al., 2008; Kerr et al., 2009; van Caspel et al., 2015; Kerr et al., 2018a), which is spread westward across the NAP environments by the coastal currents (Von Gyldenfeldt et al., 2002; Collares et al., 2018). On its western boundary, the Antarctic Circumpolar Current (ACC) transports relatively warm, salty, deoxygenated and nutrient- and carbon rich intermediate waters from the Bellingshausen Sea into the NAP, mainly influencing the shelf ecosystems along the west of the Antarctic Peninsula (Niller et al., 1991; Barlett et al., 2018). In-between, the Bransfield Strait is influenced by both Weddell and Bellingshausen-sourced waters, promoting a unique and varying blend that lead to changes in physical and chemical seawater conditions along the NAP (Dotto et al., 2016; Huneke et al., 2016).

Atmospheric warming in the northernmost region of the Peninsula has already exceeded 1.5°C since 1950 (Turner et al., 2005). The vulnerability of the NAP to climate change has led to an accumulation of severe changes along its ecosystems. In the western sector of NAP, sea surface temperatures are significantly rising (Vaughan et al., 2003; Meredith and King, 2005; Smith and Polvani, 2017), seasonal sea ice extent and duration are decreasing (Parkinson and Cavalieri, 2012), and glaciers are becoming thinner (Cook et al., 2016). Region-wise, the intrusion of anthropogenic carbon below 100 m in the Gerlache Strait (Kerr et al., 2018c) and deep-water cooling, freshening, and lightening in the Bransfield Strait have been reported (Azaneu et al., 2013; Dotto et al., 2016). Furthermore, tourism-related vessel traffic is intensifying (Bender et al., 2016) and marine debris concentrations are rising along the Antarctic Peninsula western coast (Waller et al., 2017; Lacerda et al., 2019). Marine debris are associated with the release of chemicals, which may be toxic, as well as with promoting the invasion of non-indigenous species (Oberbeckmann et al., 2015). Moreover, the microbial community associated with plastics – the plastisphere (Zettler et al., 2013) – includes microalgae and may alter the sinking rates of the surrounding waters phytoplankton (Long et al., 2015).

In the eastern sector of the NAP, studies have observed the disintegration and thinning of ice shelves (Pritchard et al., 2012; Paolo et al., 2015), as well as the freshening of shelf waters (Hellmer et al., 2011; Schmidtko et al., 2014). However, an increase of sea ice extent in the Weddell Sea has also been identified (Parkinson and Cavalieri, 2012). This recent reversal in sea ice decline, together with a plateau in atmospheric warming rates since the late 1990s along the region (Turner et al., 2016), have been associated with a short-term internal variability, due to periods of more neutral to negative Southern Annular Mode (SAM) frequencies or positive SAM offset by El Niño, which have currently superimposed on longer-term positive SAM trends (Henley et al., 2019). As a result, there has been occurring a large spatial-temporal variability of physical and biogeochemical changes between southern and northern regions along the NAP (Oliva et al., 2016; Monteiro et al., 2020a), as well as in other WAP coastal regions (Brown et al., 2019), although overall atmospheric warming and sea ice losses are still persistent and statistically significant (Henley et al., 2019).

While it is still uncertain how these stressors will shape biological communities along the NAP, several responses have already been observed across multiple trophic levels. At lower levels, repercussions include changes in phytoplankton biomass, composition and size (Montes-Hugo et al., 2009; Mendes et al., 2013; Schofield et al., 2017), as well as declines in Antarctic krill (*Euphausia superba*) biomass in favor of gelatinous

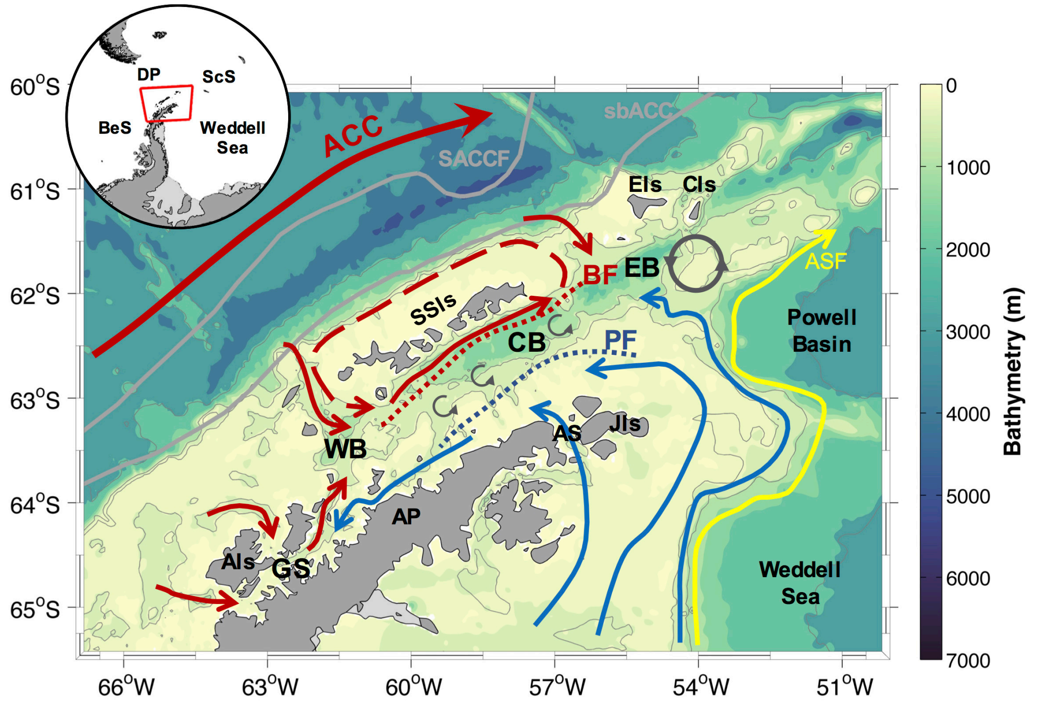

FIGURE 1 | Schematic of the ocean circulation patterns and mesoscale features in the Northern Antarctic Peninsula (NAP), following Smith et al. (1999); Garcia et al. (2002), Zhou et al. (2002); Savidge and Amft (2009), and Sangrà et al. (2017). The red arrows depict intrusion of warm waters, whereas the blue arrows depict the cold regime by Weddell Sea shelf waters advection into the NAP. The blue and red dotted lines show the surface Peninsula Front (PF) and the subsurface Bransfield Front (BF), respectively. The red dashed arrow depicts the recirculation around the South Shetland Islands (SSIs). The yellow arrow represents the location of the Antarctic Slope Front (ASF) and the flow associated to the Antarctic Slope Current, following Heywood et al. (2004). A stationary anticyclonic eddy south of Clarence Island (CIs), and the submesoscale eddies along the Bransfield Strait, are shown by dark gray arrows. The inset shows the location of the NAP, and the main areas surrounding the study region. Antarctic Circumpolar Current (ACC), Antarctic Peninsula (AP), Antarctic Sound (AS), Bellingshausen Sea (BeS), Drake Passage (DP), Scotia Sea (ScS), Anvers Island (AIs), Gerlache Strait (GS), Western basin (WB), Central basin (CB), Eastern basin (EB), Joinville Island (JIs), Elephant Island (EIs). The gray lines depict the Southern ACC Front (SACCF) and the southern boundary of the ACC (sbACC) following Orsi et al. (1995).

zooplankton taxa (Atkinson et al., 2004; Steinberg et al., 2015). Higher trophic levels have also been impacted: pack-ice seals habitats have reduced (Forcada et al., 2012) and ice-dependent penguin species are declining (Trivelpiece et al., 2011; Clucas et al., 2014). Tackling climate change in the NAP requires a deep understanding and constant monitoring of its biological communities.

Phytoplankton communities are expected to change across the Southern Ocean (Deppeler and Davidson, 2017) and monitoring their response is critical to predict the cascading effects of climate change within the NAP ecosystem. Despite top–down control having an important role in regulating the phytoplankton community composition and biomass during the austral summers (e.g., Mendes et al., 2012; Pillai et al., 2018), the bottom–up control effects have been more pronounced in both WAP (Venables et al., 2013; Saba et al., 2014) and NAP (Costa et al., 2020). This bottom–up control has been associated with sea ice cover season, which prevents wind mixing during winter and, along with glacial melting, provides meltwater to stabilize the upper ocean during summer, supporting phytoplankton growth (Venables et al., 2013). In addition, meltwater inputs further supply micronutrients to the upper ocean, such as iron, which may also be regulating biological production during summer along the Antarctic coastal waters (Boyd et al., 2007; Annett et al., 2015). Therefore, given the substantial physical changes over the past warming decades along the NAP, phytoplankton have long been regarded as a good indicator of change due to their sensitivity to effects of large scale climate oscillations, which drive sea ice season and glacial melting dynamics (Rozema et al., 2017; Brown et al., 2019).

For the past 20 years, the Brazilian High Latitude Oceanography Group (GOAL) has intensively studied the NAP (Kerr et al., 2018b; Mata et al., 2018). The work promoted by the GOAL has been instrumental to understand the evolving changes in phytoplankton communities in this region (Mendes et al., 2012, 2013, 2018a,b; Detoni et al., 2015; Gonçalves-Araújo et al., 2015; Costa et al., 2020), as studies have sought to disentangle the occurring high spatial variability within the region. While its southernmost sector, overlapping with the WAP, is relatively well studied for a Southern Ocean region (e.g., Ducklow et al., 2012), there are still many aspects of phytoplankton communities in the NAP that warrant future research. Moreover, the spatial variability inherent to the region must be considered as climate change impacts may also vary spatially. Finally, while several works have been performed over the past decades, this knowledge is scattered for most areas outside the WAP.

Over the next sections, this study reviews the regional ocean circulation and current findings on changes observed in phytoplankton communities occurring in the NAP. The main existing knowledge gaps are subsequently identified and addressed. For each gap, its main challenges are discussed, and suitable future research directions are proposed with the main goal of advancing our understanding in the NAP under the context of climate change.

OCEAN CIRCULATION IN THE NAP

The main pattern of the ocean circulation in the NAP (**Figure 1**) is formed by a complex current system governed by (i) the cyclonic gyre and the presence of a surface and a subsurface thermal fronts in the Bransfield Strait (i.e., the Bransfield and Peninsula fronts), (ii) the intrusions of relatively warm, salty and deoxygenated waters derived mainly from the Circumpolar Deep Water (CDW), which flow within the ACC, (iii) the advection of shelf waters by the Antarctic Coastal Current from the NW Weddell Sea continental shelf surrounding the Joinville Island and through the Antarctic Sound, (vi) the southward flow along the west coast of the Antarctic Peninsula toward the Gerlache Strait, and (v) the northward surface waters advection from the Gerlache Strait toward the Bransfield Strait (Smith et al., 1999; Garcia et al., 2002; Von Gyldenfeldt et al., 2002; Zhou et al., 2002, 2010; Heywood et al., 2004; Zhou et al., 2006; Savidge and Amft, 2009; Sangrà et al., 2011; Dotto et al., 2016; Huneke et al., 2016; Sangrà et al., 2017). In addition, a stationary eddy south of Clarence Island and other mesoscales features sourced by displacements of the ACC system and the Bransfield and Peninsula fronts, together with continental input of glacial meltwater, add complexity to the hydrography and ocean mixture along the NAP (Thompson et al., 2009; Azaneu et al., 2017; Moffat and Meredith, 2018).

In this context, the surface water masses characteristics are highly variable and likely essential in providing optimal conditions to the growth of specific phytoplankton blooms in the NAP (Mendes et al., 2012; Detoni et al., 2015; Costa et al., 2020). In general, the surface waters along the NAP zones can be split into cold and warm variety (Holm-Hansen et al., 1997). The former is derived mainly from the Weddell Sea shelf waters and it is located east of the Peninsula Front and southeast of the Elephant and Clarence islands (Holm-Hansen et al., 1997). This cold regime is sourced by waters with generally lower concentrations of macronutrients (a difference of at least ∼10 μM of nitrate and silicate than found in the Bransfield Strait; Kang et al., 2001), providing conditions less favorable for phytoplankton growth than that on the warm regime (Gonçalves-Araújo et al., 2015; Russo et al., 2018). The warm variety is mainly derived from the ACC surface waters (modified by CDW-sourced incursions from the southern region of the NAP), being distributed northwards along the NAP western shelves and the west of the Bransfield Front (Barlett et al., 2018). The warm conditions west of the Peninsula Front are enriched of macronutrients in subsurface waters as warm, nutrient- and carbon-rich CDW crosses the western Antarctic Peninsula shelves (Henley et al., 2017, 2018). This provides favorable conditions to a more productive environment (Smith et al., 1996; Prézelin et al., 2000; Mendes et al., 2012, 2013). Additionally, a northward surface water flow from the Gerlache Strait to the warmer side of the Bransfield Strait (Zhou et al., 2002) is responsible for advecting waters from a highly productive coastal zone to a more open region north of the NAP (Kerr et al., 2018b; Costa et al., 2020; Monteiro et al., 2020b).

The surface water properties of the sheltered zone of the Bransfield Strait (between the Bransfield and Peninsula fronts) are regulated by the strengthening of the mixing and volume of source waters (both cold and warm varieties). These waters intrude into the region, which is modulated by the dominant climate-driven mode of variability (Dotto et al., 2016; Barlett et al., 2018; van Caspel et al., 2018), modifying the location of the offshore ACC fronts (Loeb et al., 2010). During periods of El Niño conditions and negative SAM, the region receives higher amounts of cold waters derived from the Weddell Sea, while during La Niña conditions and positive SAM the region is flooded by the warm variety derived from the CDW (Dotto et al., 2016; Barlett et al., 2018). In addition, during positive SAM/La Niña conditions, warmer and stronger northerly winds blow across the NAP, resulting in a shortened sea ice season, while the opposite occurs during negative SAM/El Niño conditions (Stammerjohn et al., 2008; Henley et al., 2019). Nevertheless, the effects of positive SAM may also be offset by El Niño conditions, leading to colder winds and increased sea ice extent (Henley et al., 2019).

The main patterns and mechanisms controlling the ocean circulation in the NAP are well known (**Figure 1**). Nevertheless, some of the regional flows and physical processes that impact the water mass mixing, hydrography, and the advection of surface, intermediate and shelf waters in the region are still undetermined. For example, new information is needed for a better understanding of (i) intrusions of Warm Deep Water (a Weddell Sea local water mass sourced by CDW) at intermediate levels from the Powell Basin toward the Bransfield Strait (e.g., Azaneu et al., 2017); (ii) the periodicity and frequency of CDW intrusions along the western continental shelf of the NAP (e.g., Moffat et al., 2009; Couto et al., 2017; McKee et al., 2019); (iii) the rate of water masses mixing along the deep Bransfield basins (e.g., Brearley et al., 2017); and (iv) the rate of Weddell Sea shelf waters advection and renewal from the east (e.g., Renner et al., 2012; Dotto et al., 2016). All these unknown mechanisms directly impact the vertical stratification of the upper water column, consequently, impacting the development and distribution of the phytoplankton groups due the local and regional changes of the physical and chemical properties.

CHANGES IN THE PHYTOPLANKTON COMMUNITIES IN THE NAP

Current Knowledge

Most living organisms in the NAP are influenced by the advance and retreat timing of sea ice cover (Montes-Hugo et al., 2009; Trivelpiece et al., 2011). As sunlight increases and sea ice melts during spring, the mixed layer begins to shoal as a result of both thermal and freshwater stratification. Consequently, phytoplankton growth rates increase, particularly in the marginal sea ice zones (Arrigo et al., 2017; Schofield et al., 2018). Recent continuous high-resolution measurements (e.g., using autonomous floats) have also confirmed the importance of seasonal ice retreat for the timing and intensity of phytoplankton blooms (von Berg et al., 2020). Therefore, the beginning of sea ice melting in spring (September–November) linked to the increase of daylight length (Vernet et al., 2012), is the main factor that triggers phytoplankton blooms in the NAP (Varela et al., 2002; Garibotti et al., 2005b).

The variability of this overall bottom–up control (Saba et al., 2014; Petrou et al., 2016), associated with large-scale climate oscillations, is related to shifts in phytoplankton communities (Montes-Hugo et al., 2009; Schofield et al., 2010; Mendes et al., 2013, 2018a). Due to the north-south orientation of the Peninsula, changes in phytoplankton have exhibited different patterns according to latitude (Montes-Hugo et al., 2009). In the NAP, contrary to southernmost WAP, chlorophyll *a* has declined along with an increase (decrease) in the importance of nanophytoplankton (diatom) cells, particularly in areas of glacial ice melt (Montes-Hugo et al., 2009; Mendes et al., 2013, 2018b). These changes, verified using both *in situ* and satellite data, have been associated with an increase in cloudy days, shortened sea ice cover, glacier retreat, stronger winds and deeper summer mixed layer depths (MLDs) (Montes-Hugo et al., 2009).

The ongoing loss of winter sea-ice, associated to the recent rapid regional climate warming, has also been identified as an important factor modulating the dynamics of phytoplankton blooms in the region (Venables et al., 2013; Saba et al., 2014). Interannual differences in stratification have been shown to alter the intensity of phytoplankton blooms, with relatively low biomass concentrations generally following winters with low sea ice cover (Ducklow et al., 2013; Rozema et al., 2017). These results have been associated with light limitation, most severe following winters with low sea ice cover, due to weak stratification and anomalously deep mixed layers during spring/summer, resulting from higher exposure to winter winds (Venables et al., 2013; Arrigo et al., 2017). Therefore, due to the current downward trend in the NAP sea ice extent (Montes-Hugo et al., 2009; Venables et al., 2013; Saba et al., 2014; Schofield et al., 2018; Henley et al., 2019), mixed layers have been deeper and less stable, leading to overall lower phytoplankton biomass across the region (Montes-Hugo et al., 2009; Mendes et al., 2013, 2018b; Gonçalves-Araújo et al., 2015).

The NAP hosts high concentrations of Antarctic krill, mainly surrounding the South Shetland Islands (Atkinson et al., 2019), making it a highly productive marine ecosystem characterized as a key-feeding area for whales (Dalla Rosa et al., 2008; Secchi et al., 2011; Seyboth et al., 2018) and other krill-predators (e.g., Trivelpiece et al., 2011; Southwell et al., 2012). This reflects the NAP's high primary production potential, despite the substantial decline in phytoplankton biomass over the past warming decades (Holm-Hansen and Mitchell, 1991; Varela et al., 2002; Montes-Hugo et al., 2009; Russo et al., 2018; Costa et al., 2020).

Prior to the 1990s, the NAP austral summer, typically associated with high sea ice cover and negative SAM trend (Stammerjohn et al., 2008), exhibited high primary productivity linked to massive blooms and greater abundance of diatoms (Holm-Hansen and Mitchell, 1991 and references therein). From the 1990s to the early 2000s, studies also reported an abundant phytoplankton biomass (e.g., Castro et al., 2002; Rodriguez et al., 2002; Varela et al., 2002) and a community dominated by large diatoms, *Phaeocystis antarctica* and large flagellate *Pyramimonas* (a genus of unicellular green flagellates). However, this decade showed a greater positive SAM trend associated with higher sea ice retreat (Stammerjohn et al., 2008). In addition, cryptophytes were already observed in the southernmost regions of the NAP, particularly in the Gerlache Strait and adjacent waters (Castro et al., 2002; Rodriguez et al., 2002; Varela et al., 2002; Garibotti et al., 2005a). From the early 2000s onward, remote-sensing-derived phytoplankton biomass along the NAP during the austral summer has significantly decreased (Montes-Hugo et al., 2009). Corroborating this trend, *in situ* measurements have shown a sharp decline in diatom biomass coincident with an increase in nanophytoplankton abundance, such as cryptophytes (Mendes et al., 2013, 2018b). The dominance of cryptophytes over diatoms in the NAP is associated with low salinity and warm stratified waters (Moline and Prézelin, 1996; Moline et al., 2004; Mendes et al., 2018a). This marked shift from large to small phytoplankton cells has impacted high biomass development during the austral summers, overall decreasing primary productivity in the NAP (Montes-Hugo et al., 2009; Mendes et al., 2013, 2018a).

This shift in phytoplankton composition goes hand in hand with longer-term warming and deglaciation processes, which have been linked with anthropogenic CO_2 influence and coupled with the ongoing increase in positive SAM anomalies (Petrou et al., 2016). However, short-term natural variability must also be considered (Turner et al., 2016). Therefore, and contrary to the decreasing trend in phytoplankton biomass along the NAP, a recent study reported an intense diatom bloom (reaching > 45 mg m^{-3}) spanning a vast area of the NAP during a late summer oceanographic survey conducted in February 2016 (Costa et al., 2020). This bloom was mainly composed by a large centric diatom (*Odontella weissflogii*) and was linked to a significant local ocean carbon uptake (>60 mmol m^{-2} d^{-1}). This was likely associated with an atypical lag period in sea ice retreat caused by the first extreme El Niño of the 21st century (Santoso et al., 2017). Nevertheless, in the same austral summer, but during different sampling periods (December 2015 and April 2016), another work found an absence of diatom blooms in a NAP fjord (Andvord Bay, Gerlache Strait), despite abundant macronutrient and iron concentrations (Pan et al., 2020). On the contrary, a dominance of cryptophytes was reported in December, linked to glacial melting process and shallow mixed layers (Pan et al., 2020).

Although cryptophytes exhibit preference for growing in association with surface glacial melting waters, diatom blooms associated with the presence of freshwater plumes originating from glacier-melt outflow have also been registered (Mendes et al., 2012; Detoni et al., 2015; Höfer et al., 2019). This suggests that the shift from diatoms to cryptophytes in the NAP is not caused by physiological stress at low salinity and/or iron scarcity, as glacial ice melting is one of the main sources of both freshwater and iron input to surface waters around the Antarctic Peninsula (Dierssen et al., 2002; Annett et al., 2015). It should, however, be considered that early sea ice and glaciers retreat, together with the increase in sea surface temperature, may lead to the establishment of a shallow water column stratification, confining marine planktonic organisms near the surface and exposing them to high irradiance (Moreau et al., 2010). The recurrent growth of cryptophytes in the NAP could be attributed to their unique abilities to thrive under extremely high light levels normally found in confined stratified upper layers (Mendes et al., 2018a,b). Such conditions are becoming more frequent and intense in the NAP coastal waters and will probably have significant implications for the regional food web and biodiversity patterns (Henley et al., 2019). Recently, several studies have linked the decrease of Antarctic krill to the dominance of smaller phytoplankton cells in regional food webs, which favors salp-dominance (Atkinson et al., 2004, 2019; Moline et al., 2004; Montes-Hugo et al., 2009). Moreover, the dominant phytoplankton groups may have an influence on the local net sea-air CO_2 fluxes (Kerr et al., 2018c), given that diatoms achieve significantly higher biomass and oceanic CO_2 uptake than cryptophytes and other phytoplankton (Brown et al., 2019). For instance, observations in the WAP show an intensification of local CO_2 uptake during the austral summers driven by biological production (Brown et al., 2019; Monteiro et al., 2020b).

While ship-based surveys have shown that cryptophytes across the Antarctic Peninsula can occupy a range of distinct hydrographic niches (Henley et al., 2019), it is evident that these nanoflagellates are well-adapted to stable and shallow MLDs (preferentially < 20 m) under highly illuminated conditions (e.g., Mendes et al., 2018a,b). Nevertheless, despite the observed competition or niche segregation between diatoms and cryptophytes (Moline et al., 2004; Mendes et al., 2013, 2018a,b; Rozema et al., 2017; Schofield et al., 2017; Pan et al., 2020), the underlining critical factors and physiological evidences remain weakly understood.

Short- and Long-Term Changes Under A Climate Changing Scenario

The NAP coastal waters have been depicted as a significant source of dissolved iron (Annett et al., 2015, 2017; Sherrell et al., 2018), unlike most offshore waters in the Southern Ocean (Petrou et al., 2016). Consequently, light availability, as a function of water column structure, is usually the main driver of phytoplankton growth during the austral summer (Costa et al., 2020). As the MLD is controlled by wind, sea ice and meltwater dynamics, which in turn are driven by large scale climate oscillations (Stammerjohn et al., 2008; Venables et al., 2013; Saba et al., 2014; Brown et al., 2019), climatic changes at both short- and long-term scales shape phytoplankton communities and primary productivity through their influence on the physical compartments.

Anthropogenic greenhouse gas emission are predicted to continue to climb over the years (Santoso et al., 2017). Models also predict that the positive SAM frequency will increase for the next 50 years, contributing to persistent strong westerly winds and rising temperatures along the NAP. This will result in further glacial retreat and sea ice decline (Gillett and Fyfe, 2013; Turner et al., 2014). Due to increasing processes of deglaciation, in short-term, it is believed that the MLD will become shallower, leading to a strengthening of the already described increase in the integrated daily irradiance available to phytoplankton in surface waters (Marinov et al., 2010; Petrou et al., 2016). Thus, phytoplankton cells are expected to be more exposed to light stress in the upper shallower layers, which would present a fundamental niche favorable to the development of cryptophytes (Mendes et al., 2013, 2018a,b; **Figure 2**) and potentially lead to an increase in the overall abundance of these nanoflagellates.

In the long term (**Figure 2**), climate change effects in the NAP are expected to intensify (Montes-Hugo et al., 2009; Atkinson et al., 2019; Brown et al., 2019). Due to the projected stronger and persistent westerly winds and greater losses in the sea ice cover, the MLD will eventually deepen as the influence of sea ice in Antarctic coastal waters reduces. This could lead to a shift in the phytoplankton community to smaller cells adapted to low light conditions and deeper MLDs, such as *Phaeocystis antarctica* (Petrou et al., 2016). Although the glacial melting could offset the MLD deepening, this effect would likely be nearshore localized and still favor small cryptophytes (Mendes et al., 2013, 2018a; Schofield et al., 2017). Therefore, it is possible that phytoplankton communities, both in the short- and long-term, become nanoflagellates-dominated. Since high biomass is normally associated with a dominance of (large) diatoms, this would lead to a decrease in overall biomass and primary productivity, with myriad consequences in several compartments along the NAP ecosystem.

Ultimately, while the synergistic effects between natural internal variability and anthropogenic climate change on phytoplankton composition dynamics remain uncertain and/or poorly understood (Turner et al., 2016; Henley et al., 2019), impacts on phytoplankton communities in the NAP are ongoing and may follow one or more pathways in the future, likely following the short- and long-term scenarios suggested here.

MAIN KNOWLEDGE GAPS AND FUTURE RESEARCH DIRECTIONS

While the current knowledge gathered in the NAP has shed light on the response of phytoplankton to climate change, it should be noted that it is merely a glimpse of what may happen. A coordinated effort is needed to comprehensively understand and predict changes in the phytoplankton communities in the NAP.

The main knowledge gap in the NAP is the intrinsic elusive relationship between anthropogenic climate change and natural climate variability. The assessment of the impact of climate change requires disentangling natural internal variability from long-term alterations (Deser et al., 2012). This task becomes

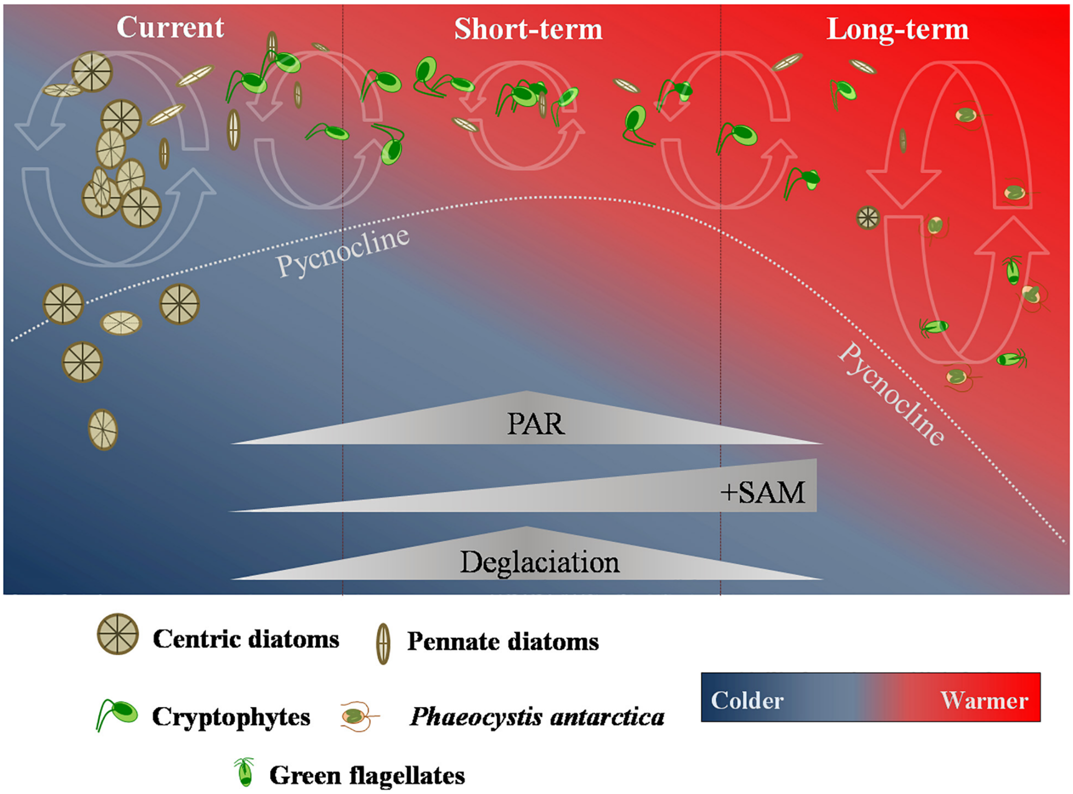

FIGURE 2 | Current and future short- and long-term scenarios of phytoplankton response to projected climate change impacts in the Northern Antarctic Peninsula suggested in this work. The coupled influence of the predicted changes in the mixed-layer available photosynthetic active radiation (PAR), the Southern Annular Mode (SAM) and deglaciation processes in the Northern Antarctic Peninsula are expected to significantly alter the phytoplankton community composition and size.

harder when facing shorter temporal or spatial scales, as the ratio of anthropogenic signal to noise is much lower (Stott and Tett, 1998). For instance, even at a global scale, a time series with a minimum length of 17 years or even longer is required for detecting human effects on mean air temperature (Santer et al., 2011; McKinley et al., 2016; Henson et al., 2018). In the Antarctic Peninsula, however, air temperature exhibits significant internal variability and it has been suggested that trends such as the rapid regional warming since the 1950s (Meredith and King, 2005) and the subsequent cooling since 1998 (Turner et al., 2016) could both be within the Peninsula's natural decadal variability (Turner et al., 2016; Smith and Polvani, 2017). A recent study for the Arctic, however, suggested that a similar cooling from 1998 onward may have been an artifact of missing data (Huang et al., 2017). Moreover, tracking biological changes has been proven to be particularly challenging (Hughes, 2000).

In the Antarctic Peninsula, continuous phytoplankton measurements only began in the second half of the 20th century and have been mostly focused in the WAP (Boyce et al., 2010). Despite spanning four decades, the sampling effort in the NAP is mainly limited to opportunistic summer oceanographic cruises. As a result, most studies capture a snapshot of the local phytoplankton communities (e.g., Rodriguez et al., 2002; Garibotti et al., 2003a,b; Mendes et al., 2012; Hernando et al., 2015; Costa et al., 2020) compared to the multidecadal-long studies in the WAP (e.g., Saba et al., 2014; Arrigo et al., 2017; Schofield et al., 2017, 2018). The yearly summer cruises led by GOAL have been important to begin understanding phytoplankton processes in the NAP, yet they only span 12 years (2008–2020) and are mainly limited to February. There is a need for continuous measurements that can help capture the biological and biogeochemical seasonality of this region (e.g., Monteiro et al., 2020a), particularly during late spring and the early summer period. Furthermore, decadal timeseries are insufficient to extract climate change-driven trends in phytoplankton (Henson et al., 2010), as studies suggest 30–60 years of data are required (Bopp et al., 2001; Boyd et al., 2008; Henson et al., 2010). Thus, the current uncertainty in the NAP must be considered when analyzing biological changes if the goal is to understand the impact of climate change in the Antarctic ecosystem.

To fill this gap, several research directions need to be followed (**Figure 3**). First and foremost, the current sampling effort in the NAP must be expanded. It is of paramount importance that current West Antarctic research programs collaborate, increasing the amount of data available and facilitating its dissemination among the scientific community (Schofield et al., 2010; Newman et al., 2019). Since many Antarctic research stations are in the NAP and research vessels are frequent during the summer, it would be possible to accurately cover the region's summer biological succession under a multi-national

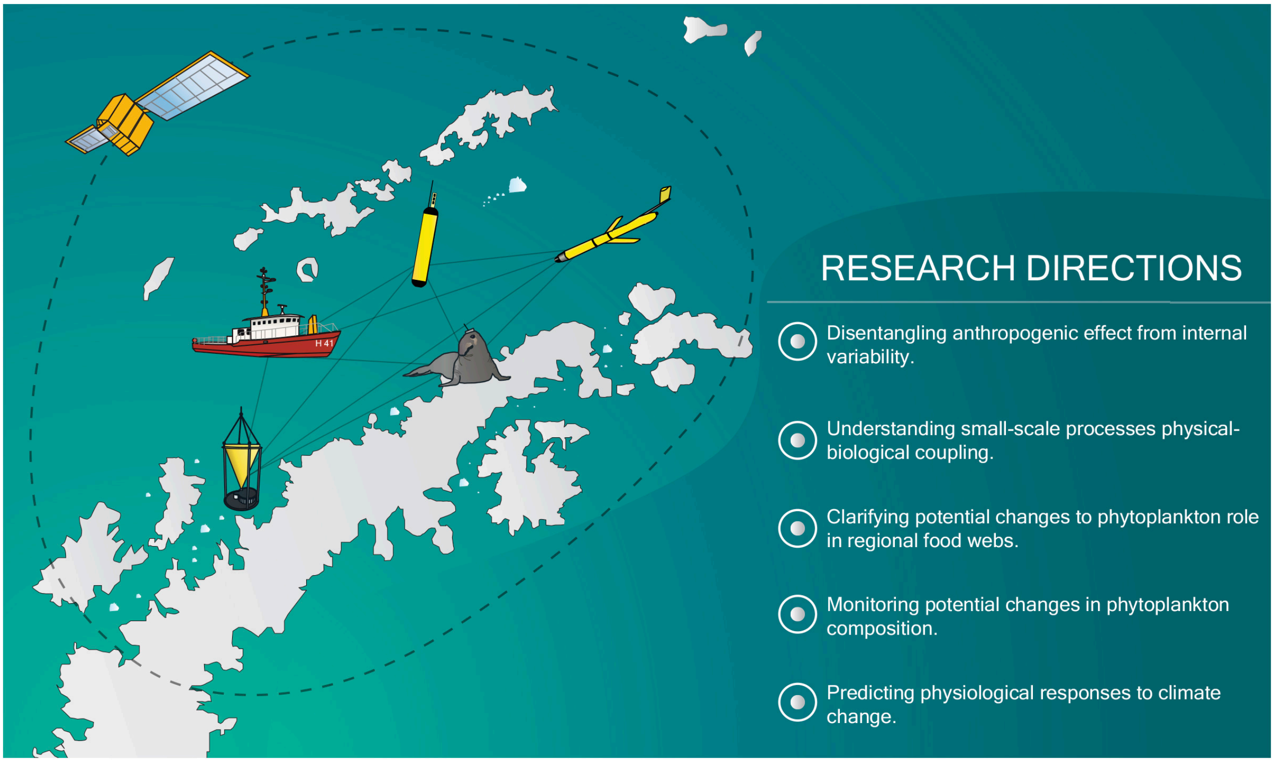

FIGURE 3 | Summary of the future main research directions required to accurately understand and predict the response of phytoplankton under climate change outlined in this work. Several *in situ* and remote-sensing tools, which will be essential toward this goal (e.g., animal-attached sensors, ocean color satellites, biogeochemical floats, underwater gliders), are represented.

cooperation framework. Kim et al. (2016, 2018) have shown how phytoplankton and nutrient data from stations spaced throughout the NAP can help unravel the importance of local-scale forcing on phytoplankton dynamics.

The projected increase in summer tourism along the NAP (Bender et al., 2016), despite its potential environmental impacts, may also be used as a platform to further monitor biological changes, whether through sensors attached to ships or through citizen science (Brosnan et al., 2015). Moreover, autonomous *in situ* data sources, such as underwater gliders, floats, drifters or animal-attached instruments, have already shown their potential to further increase the *in situ* data volume in the Southern Ocean (e.g., Meredith et al., 2013; Roquet et al., 2014; Haëntjens et al., 2017; Thomalla et al., 2017; Hindell et al., 2020). Autonomous data sources allow for the monitoring of the detailed seasonality of phytoplankton biomass and physical and chemical factors (Eriksen et al., 2018). While such sources do require extensive validation, they also offer very high spatial and temporal resolution. In some cases (e.g., floats, underwaters gliders, animal-attached instruments), they even allow for data along the water column. Autonomous *in situ* measurements will also allow for in-depth studies of the dynamics between phytoplankton and sea ice. While a few studies using floats already exist in marginal ice zones (e.g., Moreau et al., 2020; von Berg et al., 2020), further works would help reveal how phytoplankton changes with sea ice retreat at finer scales.

Ocean color remote sensing, i.e., satellite-based measurements of visible light reflected off the upper ocean, will be essential toward studying the NAP ecosystem. Benefiting from 20+ years of continuous, high-resolution data, ocean color remote sensing will complement *in situ* data, allowing for increased temporal and spatial coverage. Apart from its direct use to assess and monitor the impact and adaptation of anthropogenic climate change in phytoplankton communities, ocean color remote sensing has the potential to contribute to several study areas, including the validation and improvement of biogeochemical models, the global carbon cycle and ocean acidification (Groom et al., 2019).

Nevertheless, satellite data requires extensive validation with *in situ* data, particularly in polar regions, where cloud cover is ubiquitous and performance is typically poor (Dierssen and Smith, 2000; Cota et al., 2003). For instance, satellite chlorophyll *a* global algorithms have been seen to frequently underestimate *in situ* chlorophyll *a* in the Southern Ocean, which could be related to specific optical properties of the water in this region (e.g., Dierssen and Smith, 2000; Johnson et al., 2013). Despite efforts to create regional algorithms, these have either relied on relatively small *in situ* datasets (e.g., Garcia et al., 2005; Jena, 2017; Pereira and Garcia, 2018) or focused on large, heterogeneous regions (Johnson et al., 2013), limiting their applicability in Antarctic waters. An increase in *in situ* chlorophyll *a* measurements would be key in validating satellite data in the NAP, enabling the development of regionally tuned algorithms to produce accurate, multi-decadal phytoplankton data to monitor the region and quantify related uncertainties. For instance, in the Arctic, where *in situ* data is more abundant, Kahru et al. (2011) have estimated that phytoplankton blooms had advanced 50 days, within the period 1997–2009, attributing this shift to earlier ice melting. Moreover, this could pave the way to the use of satellite data to assess phytoplankton functional types, which would help assess changes through time in phytoplankton composition and structure.

Another important way to understand how phytoplankton communities in the NAP respond to climate change is through phytoplankton fossil records (Crampton et al., 2016). While limited to taxa with hard shells or coverings (e.g., diatoms, coccolithophores, dinoflagellate cysts), changes in their response to past warming conditions can provide an analog for present climate change (Wilson et al., 2018). Such studies could be essential to assess the natural variability of the NAP, as highlighted in recent studies (Houben et al., 2013; Crampton et al., 2016).

While solving the large-scale spatial and temporal variability should be the focus of future research in the NAP, there are other knowledge gaps which must be addressed. First, while studies have shown that ocean circulation within the NAP influence phytoplankton communities (e.g., Mendes et al., 2012, 2013, 2018a; Gonçalves-Araújo et al., 2015; Costa et al., 2020), a better understanding of the physical-biological coupling in the NAP is required. As mentioned in this work, several regional mesoscales processes (i.e., meanders, eddies, ocean fronts) still remain understudied, some of which have already been suggested to shape phytoplankton abundance and distributions, such as the advection processes from the Gerlache Strait into the Bransfield Basin, and the development of the Peninsula Front (Mendes et al., 2012, 2013; Russo et al., 2018; Costa et al., 2020). Therefore, a better understanding on how such processes change on both interannual and seasonal scales, and contribute to shape phytoplankton communities could be essential, particularly as climate change threatens to change regional circulation (Moffat and Meredith, 2018). Higher-resolution tools such as underwater gliders or animal-attached instruments may be extremely useful to this end.

Second, the role of phytoplankton in the food web and biological pump and carbon sequestration in the NAP must also be better understood. Climate change can threaten the future structure of regional food webs by leading to shifts in phytoplankton and zooplankton composition (e.g., Atkinson et al., 2004; Mendes et al., 2013; Steinberg et al., 2015). More fundamental studies on the structure and connectivity of the trophic web in the NAP are needed, building on past works (e.g., Cornejo-Donoso and Antezana, 2008; Seyboth et al., 2018). Only then it will be possible to accurately assess and predict how climate-derived changes in phytoplankton composition may shape the upper levels of the food web, as done for the WAP (Saba et al., 2014). Additionally, given that Antarctic krill biomass has been contracted in southward areas (Atkinson et al., 2019), it would also be possible to understand how this key species may be modulating the phytoplankton community composition and biomass in the NAP (top–down effects).

Furthermore, the predicted changes in phytoplankton composition toward smaller phytoplankton cells will likely affect the biological pump in the Antarctic Peninsula. It is of key importance to assess how a possible shift in phytoplankton composition may impact carbon uptake and further water column export, since smaller flagellates are more likely to be consumed, increasing remineralization, and ultimately decreasing carbon export due to their lower CO_2 uptake efficiency and sinking rates, contrasting large diatom cells (Brown et al., 2019; Trimborn et al., 2019). Thus, placing sediment traps throughout the NAP during the austral summer should also be a priority to allow for the estimate of regional organic carbon fluxes, along with monitoring diatom contribution over short-term scales (e.g., Ebersbach et al., 2011; Rembauville et al., 2015). This alternative approach would not only help to assess the local diatoms carbon export but also their variability in abundance and intraspecific contribution over time.

Third, one of the main impacts associated with climate change is the observed geographical shift of several marine taxa toward higher latitudes (Pinsky et al., 2013). Several studies have now documented southward expansion of coccolithophores and dinoflagellates in the Southern Ocean (McLeod et al., 2012; Winter et al., 2014). For instance, in recent years there has been a marked increase in the frequency and biomass of Gymnodinioid dinoflagellates along the NAP, apparently occupying sites/conditions less favorable to cryptophytes, i.e., with an adaptation/preference to deeper well-stratified mixed layers (e.g., Mendes et al., 2018b). The occurrence of dinoflagellates is of particular interest because they include toxic species adapted to disperse in coastal currents and frontal systems (Smayda, 2002). Although autotrophic dinoflagellates (mainly small Gymnodiniales $< 20\ \mu m$) have already been reported as important contributors to total biomass in some well-stratified Antarctic waters (Savidge et al., 1995; Kang et al., 2001; Mendes et al., 2012, 2013, 2018b), an ecological approach to explain the distribution patterns of this group in Antarctic environments has not yet been explicitly addressed. In the coccolithophores case, while rare south of the ACC, there is reason to believe that such poleward expansion may be facilitated by regional increases in temperature and stratification, promoting coccolithophore density in the sector of the NAP coinciding with the southern Drake Passage (Charalampopoulou et al., 2016). Furthermore, the introduction of non-native phytoplankton species into the NAP, whether from non-Antarctic ecosystems or from different parts of Antarctica, should also be considered (Frenot et al., 2005). While the current Antarctica-specific environmental protocols should reduce the risk of invasion, several studies have already highlighted potential introduction pathways as a result of increased anthropogenic presence in Antarctica (Lewis et al., 2003; Frenot et al., 2005). Since the current knowledge is not enough to estimate the risk of introduction or assess its potential impact, it remains unclear how the expansion or introduction of species could alter the phytoplankton community in the NAP. Nevertheless, *in situ* monitoring and specific actions focused on potential introduction pathways, such as ballast waters (Frenot et al., 2005) and marine plastic debris (Lacerda et al., 2019, 2020), should be introduced in the future.

Finally, understanding regional phytoplankton responses to climate change will be impossible without a better knowledge of phytoplankton physiology in the NAP. Experimental studies at a species level are key to predict how phytoplankton will modulate their internal processes under a changing climate (Petrou et al., 2016). While species-specific responses to warming and acidification have already been identified in the Southern Ocean (Petrou et al., 2016), similar works in the NAP are still scarce and typically test the response to individual stressors (e.g., Buck et al., 2010; Hernando et al., 2015; Trimborn et al., 2015). To truly understand and predict the physiological response of species to climate change, multi-stressors studies, focused on major phytoplankton species' response to factors such as Fe, CO_2, macronutrients, light, pH, salinity are required for the NAP (e.g., Boyd et al., 2016; Andrew et al., 2019; Boyd, 2019). Boyd et al. (2016) highlighted Fe and temperature as key factors modulating subantarctic phytoplankton growth, while CO_2, macronutrients and light were seen to be less important. Moreover, an emphasis should be placed on the potentially severe consequences of changes in phytoplankton composition to photosynthetic physiology due to its pivotal role in the ecosystem (Takao et al., 2014; Trimborn et al., 2015; Petrou et al., 2016; Brown et al., 2019).

CONCLUDING REMARKS

The NAP is one of the most vulnerable regions to anthropogenic climate change. As its effects on phytoplankton are becoming evident, the complex regional ocean circulation (**Figure 1**) may contribute to shape phytoplankton communities differently along the transition environments surrounding the NAP. While the response of regional phytoplankton communities is expected to differ at short- and long-term, an overall trend toward smaller flagellates is expected, with potential devastating impacts for the ecosystem (**Figure 2**). Five main research gaps in the current understanding on phytoplankton response to climate change in the NAP are identified. Future research directions (**Figure 3**), along with specific suggestions on how to tackle them, are suggested: (i) disentangling anthropogenic effect from internal variability; (ii) understanding the small-scale processes on the physical-biological coupling; (iii) clarifying potential changes to the role of phytoplankton in regional food webs; (iv) monitoring potential changes in phytoplankton composition; and (v) predicting physiological responses to climate change at species and community level. Achieving these goals will only be possible with the inter-collaboration of Antarctic research programs and scientific community under a common research framework.

AUTHOR CONTRIBUTIONS

AF, RC, and CM contributed to the conception and design of this work. AF, RC, TD, RK, and CM wrote the first draft of the manuscript. AF, RC, and TD designed the figures. VT, AB, VB, and ES contributed to the organization and writing of the final version of the manuscript. All the authors contributed to manuscript revision, read, and approved the submitted version.

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