

**ADVANCED REVIEW**

Antarctic ecosystem responses following ice-shelf collapse and iceberg calving: Science review and future research

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Abstract

The calving of A-68, the 5,800-km², 1-trillion-ton iceberg shed from the Larsen C Ice Shelf in July 2017, is one of over 10 significant ice-shelf loss events in the past few decades resulting from rapid warming around the Antarctic Peninsula. The rapid thinning, retreat, and collapse of ice shelves along the Antarctic Peninsula are harbingers of warming effects around the entire continent. Ice shelves cover more than 1.5 million km² and fringe 75% of Antarctica's coastline, delineating the primary connections between the Antarctic continent, the continental ice, and the Southern Ocean. Changes in Antarctic ice shelves bring dramatic and large-scale modifications to Southern Ocean ecosystems and continental ice movements, with global-scale implications. The thinning and rate of future ice-shelf demise is notoriously unpredictable, but models suggest increased shelf-melt and calving will become more common. To date, little is known about sub-ice-shelf ecosystems, and our understanding of ecosystem change following collapse and calving is predominantly based on responsive science once collapses have occurred. In this review, we outline what is known about (a) ice-shelf melt, volume loss, retreat, and calving, (b) ice-shelf-associated ecosystems through sub-ice, sediment-core, and pre-collapse and post-collapse studies, and (c) ecological responses in pelagic, sympagic, and benthic ecosystems. We then discuss major knowledge gaps and how science might address these gaps.

This article is categorized under:

Climate, Ecology, and Conservation > Modeling Species and Community Interactions

KEYWORDS

Antarctic, climate change, ecosystems, ice shelf

1 | BACKGROUND

1.1 | Scientific momentum

The Earth is in the throes of the Anthropocene, and the Antarctic is no exception. The calving of A68, a 5,800 km² iceberg that shed in July 2017 from the Larsen C Ice Shelf, is one of over 10 significant ice-shelf-loss events in the past few decades driven by anthropogenically accelerated warming. The Antarctic Peninsula (AP) ice shelves are thinning rapidly (Pritchard et al., 2012; Shepherd, Wingham, Payne, & Skvarca, 2003; Shepherd, Wingham, & Rignot, 2004), retreating (Vaughan & Doake, 1996), losing volume, and suffering collapse (Doake & Vaughan, 1991; Rott, Skvarca, &

Nagler, 1996; Scambos et al., 2009). Despite the significant impacts such events have on glaciology, biogeochemistry, physical oceanography, and the structure and function of surrounding ecosystems, significant gaps still limit our understanding of ice-shelf systems, including poor knowledge of the process leading up to ice-shelf demise. During and after collapse, scientific studies typically are delayed by years owing to variable sea-ice conditions, logistical and infrastructural issues, and funding delays. Such studies are becoming increasingly multidisciplinary and more responsive, as demonstrated by rapid mobilization of researchers from the international community to the AP within months of the A68 calving. International consortia mounting rapid deployments included the British Antarctic Survey, the Korea Polar Research Institute with science support from the U.S. National Science Foundation, and the Alfred Wegener Institute (AWI, Germany), as well as the International Consortium of the Weddell Sea Expedition a year later. Scientists and the media followed the activities closely and supported the efforts, but there is still an urgent need for data and observations from collapsing ice-shelf systems so that the changing nature of these environments can be understood.

To address these concerns, an NSF-funded workshop “Antarctic Ecosystem Research Following Ice Shelf Collapse and Iceberg Calving Events” was organized in November 2017. Thirty-nine international researchers (all authors of this article) with a breadth of Antarctic scientific expertise gathered to share current knowledge of (a) sub-ice-shelf ecosystems, (b) how ice-shelf calving and collapse will affect these and adjacent ice-sheet, coastal, shelf/slope, and pelagic ecosystems, and (c) how the ecosystems will change over a range of time scales under climate-change scenarios. Since then, further ice-shelf retreats have added concern to the potential effects of ice-shelf collapse; these include the 1,600-km² Amery Ice Shelf calving event in September 2019, and the growing concern of progressive cracking around a similarly sized part of the Brunt Ice Shelf bordering the Weddell Sea.

The review presented here was conducted following initial discussions during the workshop and represents best-available knowledge. A brief synthesis of ecosystem changes following ice-shelf loss and the scientific response to ice-shelf collapse was provided in Ingels, Aronson, and Smith (2018). The present paper provides considerably more detail and focuses on what is known about ice-shelf-associated ecosystems prior to and following ice-shelf collapses, what our major knowledge gaps are, and how the international scientific community might address unanswered questions in future research.

1.2 | Ice shelves: Melt, volume loss, retreat, calving, and collapse

Ice shelves are thick, floating platforms of ice, 100 to over 1,500 m thick, which form where glaciers or ice sheets flow down onto the sea, creating Antarctica's primary connection between its ice sheet and the Southern Ocean. Ice shelves cover about three quarters of the Antarctic coastline and 11% of the total Antarctic area, playing an important role in the mass budget and dynamics of the Antarctic Ice Sheet (Rignot, Jacobs, Mouginot, & Scheuchl, 2013).

The AP is one of the most rapidly warming places on Earth, with average annual atmospheric temperature increases of 2–4°C, and midwinter temperature increases of 5–6°C since 1950 (Domack et al., 2013; Vaughan et al., 2003). Freshwater flows into the Southern Ocean from under-shelf melt, ice-sheet movement, and calving, affecting salinity, stratification, and global circulation patterns. Changing ocean circulation has contributed to the rapid regional warming and to increases in upper-layer salinity (Meredith & King, 2005).

Several observational studies over the past 60 years show that ice shelves are rapidly thinning, retreating, or collapsing (Pritchard et al., 2012; Scambos et al., 2009; Shepherd et al., 2003, 2004), with an estimated ice-area loss of >30,000 km² since the 1950s (Hogg & Gudmundsson, 2017; Peck, Barnes, Cook, Fleming, & Clarke, 2010), which is well over 18% of the total floating-ice area (Cook & Vaughan, 2010). Regional atmospheric and oceanic warming, in concert with wind forcing and upwelling, causes ongoing melting processes leading to gradual ice-shelf thinning. Thinning processes include both long-term basal melt and increased surface-melt, with melt-pond formation and potentially widespread risk of hydrofracture (Adusumilli et al., 2018; Bevan et al., 2017; Lai et al., 2020). Dickens et al. (2019) suggested that the ice shelves around the AP have been thinning for at least ~300 years, potentially predisposing them to collapse under continued anthropogenic warming. A warming ocean has the potential to erode these thick shelves at rates exceeding 10 m/year for each rise of 1°C (DeConto & Pollard, 2016; Shepherd et al., 2004), and a mean annual temperature of –9°C may demarcate a threshold of viability for ice shelves (Cook & Vaughan, 2010). Basal melt-rates beneath a thin and structurally important part of the Ross Ice Shelf are an order of magnitude higher than the shelf-wide average (Stewart, Christoffersen, Nicholls, Williams, & Dowdeswell, 2019; see Huettmann, Humphries, & Schmid, 2015 for available data). The 1970s seemed to mark the start of the steady decline in the total ice-shelf area along with the AP, a trend that continues today and is expected to increase in the next decades. The breakup of ice shelves has long been regarded as a harbinger of climate warming in Antarctica: for example, “One of the warning signs

that a dangerous warming trend is underway in Antarctica will be the breakup of ice shelves on both coasts of the Antarctic Peninsula, starting with the northernmost and extending gradually southward” (Mercer, 1978).

Ice-shelf loss occurs in a variety of ways: disintegration or collapse, rifting, and calving. Ice-shelf retreat and breakup are often associated with deeply embayed ice fronts, calving of numerous small icebergs in specific events, increasing flow speeds, and surface melt-ponds in the vicinity of the break-ups that cause crevasse propagation (Scambos, Hulbe, Fahnestock, & Bohlander, 2000). Of the 12 AP ice shelves, three have shown significant retreat (Larsen B, Muller, and Wilkins), and four have totally disintegrated (Kones, Wordie, Prince Gustav, and Larsen A) in the last half-century (Cook & Vaughan, 2010). In 2017, Larsen C also showed significant retreat, losing 9–12% of its area in the A68 break-off. Stewart et al. (2019) recently added the Ross Ice Shelf to the areas of concern, reporting rapid basal thinning; this shelf had lost an 11,000-km² iceberg by 2000. Currently, four ice shelves (George VI, Bach, Stange, and Larsen D) have more than 90% of their original area remaining and are not showing steady retreat (Cook & Vaughan, 2010), although George VI is thinning rapidly (Adusumilli et al., 2018). Cook and Vaughan (2010) give a relatively detailed account for each of the AP ice shelves.

Typically, more ice is lost each year through ice-sheet melting than calving (Rignot et al., 2013). Warm “foehn” winds contribute to surface melting and increase the risk of ice-shelf collapse in East Antarctica (Gagliardini, 2018; Lenaerts et al., 2017). These winds are thought to have precipitated the collapse of the Larsen B Ice Shelf (Cape et al., 2015). Ice-shelf retreat along the AP has also been occurring more southwardly, as the isotherm associated with their viability has been driven south by atmospheric warming (Vaughan & Doake, 1996). Crevasses formed through tidal flexure and plate bending can grow and lead to expanding rifts, eventually leading to calving once they surpass a critical threshold. Thinning from either surface or basal melt, as well as surface-melt ponding and filling of ice fractures, can cause loss of structural integrity of ice shelves (Scambos et al., 2000). In addition, the outer margins of ice shelves that are weakened through thinning and fractures are at increased risk of calving or collapse owing to the increased seasonal absence of protective sea-ice. Sea ice dampens the ocean swell, preventing wave-induced flexure (Massom & Stammerjohn, 2010; Miles, Stokes, & Jamieson, 2017). These processes can act cumulatively, accelerating ice-shelf disintegration. The collapse of the Larsen A Ice Shelf over a few days in 1995, for example, indicated that, after retreat beyond a critical limit, ice shelves may disintegrate very quickly indeed.

Ice-shelf retreat and collapse can have important upstream effects on Antarctic Ice Sheet dynamics. Ice shelves provide a buttressing or “doorstop” effect, preventing more rapid warming and melting of the grounded ice sheet and glaciers (Dupont & Alley, 2005; Fürst et al., 2016). The Ross and Weddell Sea ice shelves, and smaller shelves and ice tongues in the Amundsen and Bellinghausen Seas, provide such buttressing that prevents ocean-ward ice flow. Ice-shelf retreat and collapse allows glaciers to accelerate and thin (De Angelis & Skvarca, 2003; Rignot et al., 2004; Scambos, Bohlander, Shuman, & Skvarca, 2004), leading to ice-sheet flow up to eight times faster than normal (Rignot et al., 2004, 2008). Along with the AP, 87% of 244 marine glacier fronts retreated between 1940 and 2001, with retreats occurring progressively southward (Cook, Fox, Vaughan, & Ferrigno, 2005). Stark reminders of potential consequences are the recent calvings of the Pine Island Glacier in West Antarctica in 2017 and 2018 (with earlier calvings in 2007, 2013, and 2015) after long-term thinning, retreat, and dramatic increases of glacial flow rate (Rignot et al., 2004, 2008; Scambos et al., 2004, 2017). Such acceleration exacerbates glacial and ice-sheet discharge into the oceans, contributing to global sea-level rise, ocean freshening, and alteration of circulation patterns (Friedl, Seehaus, Wendt, Braun, & Höppner, 2018; Hogg & Gudmundsson, 2017). In the Bellinghausen Sea sector, ocean-driven thinning of ice shelves has been linked to grounded-ice-mass loss (Minchew, Gudmundsson, Gardner, Paolo, & Fricker, 2018). Several ice shelves, such as the Filchner-Ronne and Ross Ice Shelves, provide a strong buttressing effect along their grounding line. The grounded base is potentially also where the highest melting is observed, increasing the risk of reduced stability (Gagliardini, 2018; Lenaerts et al., 2017; Rignot et al., 2004). Moreover, highly localized ice-shelf thinning can cross the entire shelf and accelerate ice flow far away from the initial perturbation; this “tele-buttressing” can enhance outflow in response to thinning up to 1,000 km away (Reese, Gudmundsson, Levermann, & Winkelmann, 2018). The most critical regions in all major ice shelves are often located in areas easily accessible to the intrusion of warm ocean waters, which raises concern (Dutrieux et al., 2014; Hellmer, Kauker, Timmermann, Determann, & Rae, 2012; Reese et al., 2018; Rignot et al., 2013).

Ice-sheet–ocean interactions have important repercussions for the dynamics of glacial ice. Circumpolar Deep Water (CDW) forms a relatively salty and warm current (>3.5° above the freezing point of marine water; or >1.5°C) that flows onto the deep continental shelf in parts of the Antarctic, including the AP, contributing to grounding-line recessions and increased ice-shelf vulnerability to oceanic forcing (Adusumilli et al., 2018; Depoorter et al., 2013). The CDW has warmed and increased in volume, accelerating submarine melt of glaciers and ice shelves (Figure 1; Cook et al., 2016).

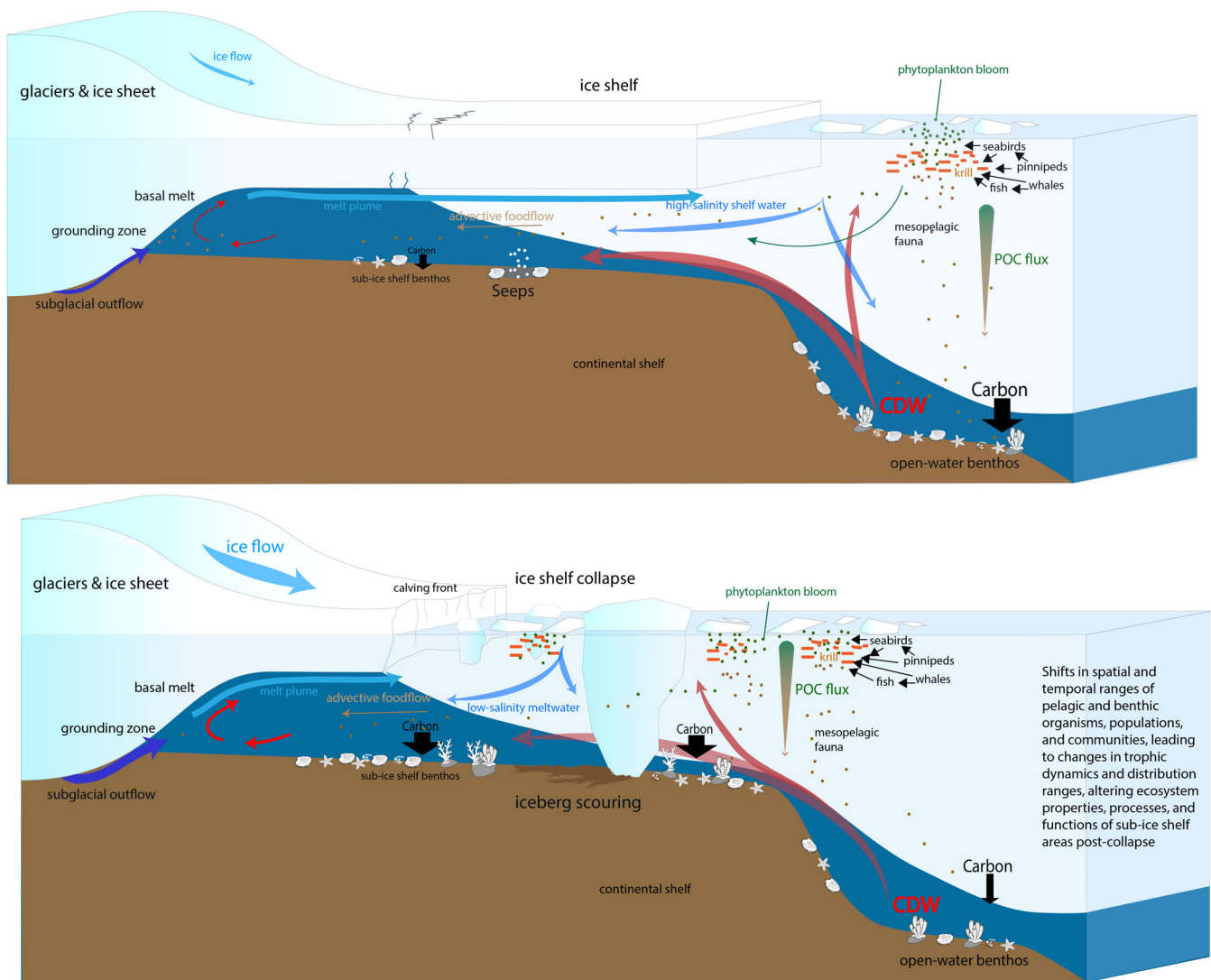


FIGURE 1 *Top*, pre-collapse. *Bottom*, post-collapse. Shifts in the spatial and temporal ranges of pelagic and benthic organisms, populations, and communities post-collapse lead to changes in trophic dynamics and species ranges, altering ecosystem properties, processes, and functions of sub-ice-shelf areas. Thin black arrows between pelagic and surface biota indicate trophic interactions. The color gradient of the particulate organic carbon flux indicates the change from fresh to more degraded/refractory material. Thicker arrows indicate higher fluxes. Reprinted with permission from Ingels et al. (2018)

In addition, Antarctic Surface Water (AASW) is a relatively fresh and buoyant water mass influenced by solar heating and sea-ice melting during summer (Orsi & Wiederwohl, 2009). The AASW can enter shelf cavities by wind and tidal forcing. Stewart et al. (2019) documented the important role of solar-heated surface water from Ross Sea polynyas in increasing summer basal melting by down-welling into the ice-shelf cavity. They concluded that solar heat absorbed in ice-front polynyas can make an important contribution to the mass balance of ice shelves, and ice-shelf melt driven by this process will increase in the future with predicted surface warming.

Conversely, export of freshwater as liquid or ice provides forcing on the ocean. Glacial freshwater can enter the sea surface as a result of surface runoff, or at depth at the margins of glaciers, ice shelves, and icebergs as a result of submarine melting. Whereas surface runoff can have far-ranging impacts on upper ocean stratification and heat exchange with the atmosphere (Silvano et al., 2018), freshwater input below the ocean surface (e.g., along glacial calving fronts) leads to the formation of rising buoyant plumes (Hewitt, 2020; Jenkins, 1999, 2011). This forcing drives vertical exchange of salt, heat, and nutrients sourced from both meltwater and deep ocean waters (Truffer & Motyka, 2016) that modify the physical and chemical properties of the water column, with feedbacks on downstream marine ecosystem processes (Section 4).

Computer models that couple ice sheet and climate dynamics with unabated emissions predict a potential global sea-level rise of >1 m by 2,100 and >15 m by 2,500 owing to Antarctic ice-sheet melt (DeConto & Pollard, 2016). When viewed in the long term, loss of Antarctic ice sheets exceeds all of the other predicted sources of sea-level rise, having a potential impact on sea-level rise of 58 m and adding significantly to the predicted 25–52 m of sea-level rise in the next 10,000 years (Clark et al., 2016). Although specific ice-shelf failures are difficult to predict, climate models suggest that shelf melt and calving will become more common (Gagliardini, 2018), and sea-level rise is among the greatest concerns for coastal ecosystems, and human populations and infrastructure globally as we progress through the Anthropocene.

2 | CURRENT KNOWLEDGE OF ICE-SHELF-ASSOCIATED ECOSYSTEMS

2.1 | Evidence from sub-ice and pre-collapse studies

Little is known about sub-ice-shelf ecosystems because of extremely difficult access through or beneath hundreds of meters of ice. In 1977–1978, The Ross Ice Shelf Project (RISP) drilled a hole through the 420-m-thick Ross Ice Shelf, 450 km from its seaward edge, allowing the first seafloor sampling under a permanent ice shelf (Clough & Hansen, 1979). A total of 250 amphipods (species of *Orchomene*) and one isopod (*Serolis trilobitoides*) were collected using baited traps on the seafloor 237 m below the bottom of the ice. Although no fish were caught, photographs showed *Trematomus* species, which are common at similar depths in McMurdo Sound and other parts of the Ross Sea. Biomass and abundance of microplankton and zooplankton assemblages were very low, similar to the oligotrophic deep sea (Bruchhausen et al., 1979; Clough & Hansen, 1979; Lipps, Ronan, & Delaca, 1979). Strangely, no signs of bioturbation or traces by benthic fauna were observed, and no live infauna were recovered from the RISP sediment samples, but there were skeletons from various meiofauna (32–1,000 μm , animals living in between sediment grains). More recently, a diverse foraminiferal assemblage was found under the Ross Ice Shelf 12 km from open water (Pawlowski et al., 2005), suggesting that the lack of recovered infauna in RISP was likely caused by sampling biases (Horrigan, 1981; Lipps et al., 1979; Stockton, 1982). Kim, Hammerstrom, and Dayton (2019) also reported a diverse sub-ice-shelf macrobenthos at 188 m depth, 80 km back from the edge of the McMurdo Ice Shelf. These communities inhabited fine-grained sediments with occasional drop-stones and were dominated by polychaetes and brittle stars on soft substrates, and by alcyonarian soft corals and sea anemones on hard substrates. This study also found abundant gelatinous animals above the seafloor, suggesting a pelagic food source for the benthic community (Kim, 2019). In summary, various sampling and videographic approaches confirm that life exists under the Ross Ice Shelf, contrary to the pre-RISP view that sub-ice-shelf habitats would be devoid of fauna because of a lack of food.

However, photosynthesis is not possible under ice shelves, so the benthic communities must depend on food advected from open-water areas or from sub-ice-shelf chemosynthesis (Azam et al., 1979; Domack et al., 2005; Horrigan, 1981). These findings imply that, aside from chemotrophic production, food sources are entrained in currents for >400 km while not descending more than 200 m, or that the local fauna is reliant on organisms that have died underneath the ice shelf (Stockton, 1982). In addition, some Antarctic organisms may be able to survive for long periods of time under extremely food-limited conditions (Kim, 2019). Such a scenario is reminiscent of the “food bank” hypothesis for benthos in the seasonal sea-ice zone in Antarctica (Smith et al., 2012), which suggests that phytodetrital material deposited from summer phytoplankton blooms provides a sustained source of food for benthic detritivores during winter months. For sub-ice-shelf ecosystems, advection of such food-bank material could accumulate in summer months, providing a sustaining source year-round. A potential evolutionary adaptation to such food limitation and benthic food storage is illustrated by the soft coral *Gersemia antarctica*, which has been observed bending its colony against the substrate and feeding to supplement pelagic food capture, in addition to relocation to undisturbed patches richer in available food (Slattery, McClintock, & Bowser, 1997). Along the Western Antarctic Peninsula (WAP), advected phytodetrital material may not only be derived from single-celled algae (ice-associated diatoms and planktonic phytoplankton), but also from rich, diverse, macro-algal coastal forests (Braeckman et al., 2019; Wiencke & Amsler, 2012). The “advective-food hypothesis” proposed for sub-ice-shelf systems was supported by Riddle, Craven, Goldsworthy, and Carsey (2007) and Post, Hemer, Brien, Roberts, and Craven (2007), who observed a diverse and complex benthic assemblage dominated by suspension feeders under the Amery Ice Shelf, 100 km from open water. This assemblage was similar to those characteristic of Antarctic coastal or deep-sea locations. Hemer and Harris (2003) documented marine diatoms in the surface sediments underneath the Amery Ice Shelf, further supporting advective transport under ice

shelves. Fresh water at the land-side of an ice shelf may play an important role in facilitating sub-ice-shelf advection of food by creating estuarine circulation, in which low-salinity waters flow outward in the upper water column and more saline open-ocean water carrying food flows in under the ice shelf in the lower water column.

Distinct functional communities were documented under ice shelves by Post et al. (2014), with sessile suspension feeders in sub-ice-shelf areas of strong marine inflow nearer the ice edge as well as grazers, deposit feeders, and only a few suspension feeders at sites more distant from the ice-shelf edge, where food supply was lower. Yet again, the role of advection in supplying sub-ice-shelf communities (and/or chemosynthetic sources) seems to be driving the composition and energetics of those communities.

There is very little information from the Antarctic concerning the role of glacial outflow and sympagic (within-ice) contributions to benthic sub-ice-shelf communities. However, sympagic production is of limited importance for benthos on the deep WAP shelf where annual sea-ice duration is moderate (Mincks, Smith, Jeffreys, & Sumida, 2008). In areas with extreme annual sea-ice duration such as the Ross Sea, sympagic production may be substantially more important for shallow-water benthos (Calizza, Careddu, Sporta Caputi, Rossi, & Costantini, 2018). In the Arctic, stable-isotope, biomarker, and feeding studies indicate that shelf-benthic communities utilize and may prefer organic matter from ice-algal production (e.g., McMahon et al., 2006; Morata & Renaud, 2008; Søreide et al., 2013). Gradinger (1999) suggested that sympagic production in the Arctic exceeds its consumption by ice-associated meiofaunal organisms, which suggests that excess production is released to sink to the seafloor.

The few studies available show that sub-ice-shelf communities do occur and appear to be supported by organic matter advected under the shelf (i.e., they appear to lack substantial in-situ production). Due to the remote and isolated nature of these habitats, sub-ice-shelf communities may also have distinct ecological and evolutionary trajectories that could be lost with ice-shelf retreat. There is an urgent need for a better understanding of these communities (e.g., by sampling immediately following ice-shelf collapse) and for advancing our knowledge of sedimentary and oceanographic processes within the sub-ice-shelf environment. Such knowledge will improve predictions of future changes and increase the availability of baseline data prior to ice-shelf disintegration.

2.2 | Evidence from post-collapse studies

A number of post-collapse studies have contributed to our understanding of what life under the ice shelf might have looked like prior to ice-shelf collapse. Faunal assemblages accustomed to the food-poor, sub-ice-shelf environment are altered by the new primary-production and export regimes (Figures 1 and 2; Gutt et al., 2011; Hauquier, Ballesteros-Redondo, Gutt, & Vanreusel, 2016; Hauquier, Ingels, Gutt, Raes, & Vanreusel, 2011; Niemann et al., 2009; Raes, Rose, & Vanreusel, 2010; Rose, Ingels, Raes, Vanreusel, & Arbizu, 2014). Data from the first benthic sampling 5 years after Larsen A and B collapse indicated low-density and low-diversity meiofauna communities (Raes et al., 2010). The meiofauna that was no longer under an ice shelf resembled more oligotrophic Weddell Sea deep-sea communities, compared with sites that had been receiving surface input for a longer period (Rose et al., 2014). However, tall hexactinellid sponges in newly opened shelf waters indicated that these suspension feeders were present before the ice-shelf broke up, as they are known to grow very slowly (Dayton et al., 2013, 2016; Gutt et al., 2011). At the same time, the presence of low densities of small and intermediate-sized sponges suggested limited or episodic post-collapse recruitment (Dayton et al., 2013). Recruitment limitations are likely set by the food-poor conditions for sensitive juvenile stages, while the few that survived the pre-collapse oligotrophy may have done so at the cost of a threshold in size. The presence of sponges prior to ice-shelf collapse in the Larsen B area has also been demonstrated by analyzing biogenic silica. Only the upper 2 cm of the sediments in that area contained silica originating from diatoms (i.e., primary production), whereas deeper in the sediment silica produced from sponge spicules was found, suggesting the pre-collapse presence of sponges (Sañé, Isla, Bárcena, & DeMaster, 2013).

Macrofaunal data from the expedition in 2000 to the Prince Gustav Channel (ice-free since 1992) and the Larsen A area (ice-free since 1995) showed distinctly different assemblages and dominance patterns between the two areas (e.g., Domack et al., 2001; J. A. Blake, personal communication). However, no comparison has been made with macrofauna data collected in these areas at later dates to investigate whether differences (if any occur) are in response to colonization and the opening up of the region following ice-shelf collapse or oceanographic conditions under the influence of the Weddell Sea. Gutt et al. (2011, 2013) observed low biomass and diversity of macrofauna and megafauna at their oligotrophic, sheltered, Larsen B study sites at a time when the ice-edge was relatively near (35–60 km), despite the presence of considerable amounts of deposited phytodetritus. A combined macrofauna–biogeochemical study

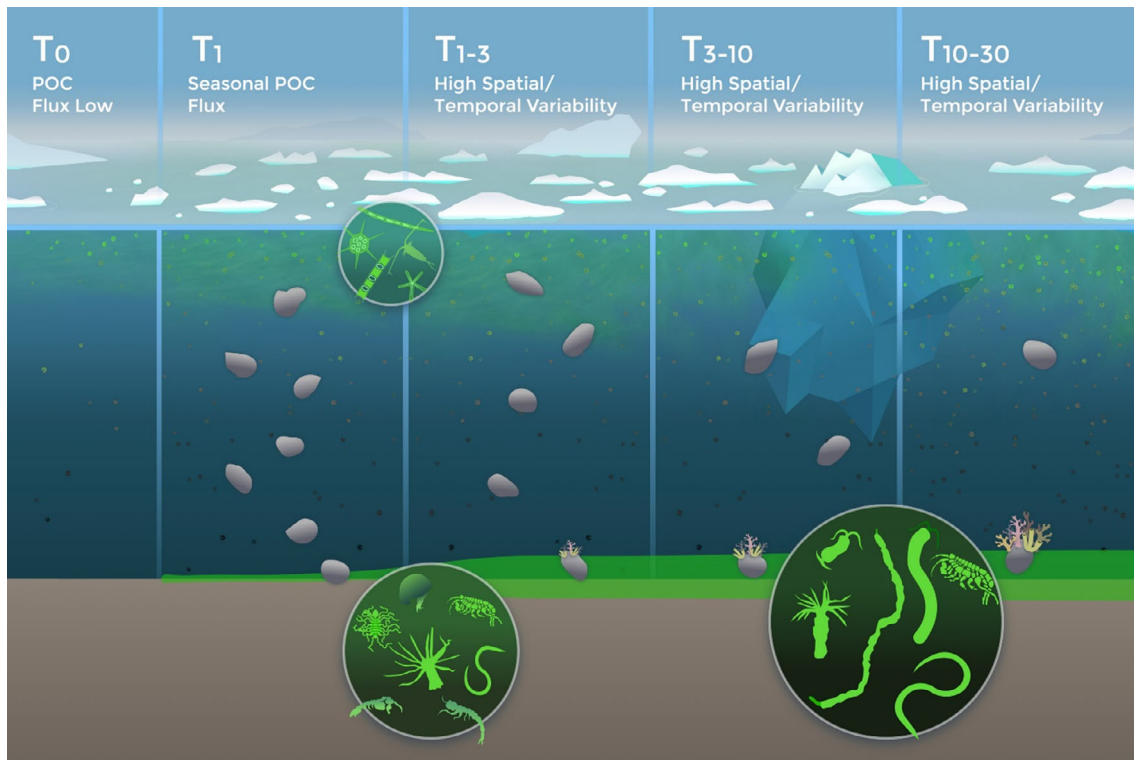


FIGURE 2 Expected changes in ice-shelf regions following ice-shelf retreat and collapse. Visualized are surface blooms and primary production, organic matter flux to the seafloor and provision of the food bank (the pool of labile and refractory matter), and drop-stone frequency. T0: During ice-shelf cover, there is very low input of organic and inorganic food sources; primarily through advection from open water and limited chemosynthetic sources. T1 year: In the year following ice-shelf collapse, an increase in drop-stones is expected from increasing supply of glacial-fed icebergs. Increased POC flux follows novel primary production and surface-water blooms in the newly-opened waters. T1–3 years: In the first years following ice-shelf collapse seasonality in primary production is introduced, with high spatiotemporal variability. Shifts in plankton composition are likely, yielding mismatches and changes trickling through the pelagic and benthic food webs. Drop-stone release continues, providing hard benthic substrates for new colonizers, but also disturbing the sediment. T3–10 years: Continued seasonal primary production feeds the benthic food bank resulting in increased biomass, potentially increasing diversity and shifting the composition of benthic assemblages. Increased glacial discharge may continue to deliver drop-stones, and iceberg calving can cause scouring disturbance. Deposition of terrigenous material possibly increases. High temporal and spatial variability in the deposition of food and disturbance remains. T10–30 years: High spatial and temporal variability of POC fluxes and organism distributions remain but could be more widespread following continued warming and potential reduction in seasonal sea-ice cover. Buildup of the food bank continues, with increased density and activity of organisms following enhanced food access. Increased bioturbation leads to increased oxygen penetration. However, oxygen penetration may shoal again if the flux of organic matter to the seafloor and subsequently organic matter deposition and biological activity increase. Image created by the Center for Environmental Visualization (CEV), University of Washington

indicated that the macrofauna at a recently exposed area on the East AP showed signs of only recent colonization. The macrofauna were feeding on lower-quality but more abundant organic matter compared with the macrofauna at a site that had been ice-free for thousands of years (Sañé, Isla, Gerdes, Montiel, & Gili, 2012). These observations suggest a near or complete absence of true sub-ice-shelf communities at Larsen A and B, and subsequent community development following ice-shelf retreat and collapse (Gutt et al., 2011, 2013). Biogeochemical studies have shown that phyto-detritus in the sediments of recently opened areas is produced locally rather than having been advected to that location pre-collapse (Sañé et al., 2011).

2.3 | Evidence from marine sediment core studies

Marine sedimentary records shed light on natural variability on decadal to millennial time scales, providing context for modern change and for the factors influencing the development of communities after ice-shelf collapse

(Brachfeld et al., 2003; Buffen, Leventer, Rubin, & Hutchins, 2007; Domack et al., 2003; Rebesco et al., 2014; Wellner et al., 2019). Sedimentologic, micropaleontologic, and biogeochemical data from marine sediment cores show that the Larsen A and Larsen B ice shelves have very different histories, with implications for sub-ice-shelf ecosystems. Both the Larsen A and B embayments suffered deglaciation and developed into ice shelves after the grounded ice retreated following the last glacial maximum. However, the Larsen A shelf was not consistently present through the Holocene (11,700 years ago to today), in contrast to the historical persistence of Larsen B. Holocene sediment cores from the Larsen A embayment record biosiliceous sediment deposition in a productive, open marine setting with seasonal sea-ice cover during the middle Holocene, whereas reduced abundance, but consistent presence, of diatom valves indicate the presence of an ice shelf in the early and late Holocene. During the latter, diatom input to the sediments was limited to advection from open water (Brachfeld et al., 2003; Domack et al., 2001; Wellner et al., 2019). Based on the presence of non-local, ice-rafted debris in marine sediment cores (further supporting a mid-Holocene absence of the Larsen A Ice Shelf), late Holocene regrowth of the ice shelf may have occurred during the Little Ice Age (Pudsey, Murray, Appleby, & Evans, 2006). Similar observations characterize the Prince Gustav Channel, just north of the Larsen A region (Pudsey & Evans, 2001). Cosmogenic-nuclide exposure ages from coastal sites also support a Larsen A ice-shelf collapse during the mid-Holocene (Balco et al., 2013). In contrast, the consistent presence of an overlying ice shelf in the Larsen B region through the entire Holocene has been documented (Domack et al., 2005; Rebesco et al., 2014). Following the Larsen B breakout, absolute diatom abundances increased rapidly from extremely low pre-breakout levels, suggesting that even if waters were advected from the Weddell Sea to the sub-ice cavity of the Larsen Ice Shelf, these advected waters were characterized by very limited productivity. Heavy sea-ice cover in the Weddell Sea likely causes this low productivity (Wellner et al., 2019). The contrast in ice-shelf history between Larsen A and Larsen B is further indicated by stable isotopic data from benthic and planktonic Foraminifera. Sediment cores from the Larsen B and C ice-shelf margins indicate productive sub-ice-shelf populations of benthic and planktonic Foraminifera in the absence of high overlying primary productivity (Domack, Ishman, et al., 2005).

Following ice-shelf collapse, the nature of the organic matter in the seabed becomes much more reactive and nutritive, as fresh organic matter from primary productivity in the recently open waters reaches the seabed and is bioturbated into the sediment column. The supply of fresh planktonic material (labile organic matter) transforms the seabed from a biological desert into an oasis of benthic biological activity (Section 3). This fresh planktonic material has been tracked into sediments beneath the collapsed Larsen ice shelves using chlorophyll and diatom abundances (Domack, Duran, et al., 2005; Sañé et al., 2011, 2013). More recently, the abundance and distribution of fresh planktonic material in the sediment column beneath the collapsed Larsen A and B ice shelves was assessed based on the difference in C-14 activity between recently deposited plankton and the much older organic material accumulated during times of ice-shelf existence (Isla & DeMaster, 2018; Taylor, 2018). Tracking of this labile organic matter is important because the colonizing benthic fauna almost exclusively assimilates this recently deposited, planktonic organic matter into their tissues (Isla & DeMaster, 2018). In addition, bioturbation intensities and mixing depths can be evaluated using naturally occurring Pb-210 distributions (a particle-reactive tracer reaching the seabed attached to recently deposited plankton), enabling diagenetic modeling of labile organic carbon (LOC) distributions.

This new approach for tracking freshly deposited phytodetritus in sediments beneath collapsed ice shelves has proven useful in contrasting the different ice-shelf histories of the Larsen A and B. At four Larsen A/B coring stations, Isla and DeMaster (2018) used radiochemical tracer distributions to obtain snapshots of the development of a labile-organic-carbon “food bank” (Mincks, Smith, & DeMaster, 2005) in the seabed at 5 years (2007) and 9 years after ice-shelf collapse. At these four seabed stations during 2007 and 2011, LOC inventories ranged from 1.5 to 22 mg LOC/cm² and LOC mean residence times ranged from 3.2 to 58 years. In Larsen A, the LOC inventory increased from 2.1 to 4.9 mg/cm² between 2007 and 2011, while the LOC mean residence time increased from 3.9 to 38 years over the same time period. Isla and DeMaster (2018) interpreted the increase in LOC inventory at this station as a consequence of four additional years of fresh plankton flux to the seabed (increasing the time since ice-shelf collapse by more than 30%). The increase in LOC mean residence time between 2007 and 2011 was attributed to benthic communities processing surface sediments for four additional years, degrading the fresh organic matter, and making the bulk organic matter more refractory.

In a complementary study, Taylor (2018) examined Larsen A LOC inventories, distributions, and mean residence times. Because the Larsen A Ice Shelf retreated westward over a period of nearly 200 years, the five selected Larsen A stations represented regimes of progressively longer times since ice-shelf collapse on a transect going from the western Larsen A (15 years since ice-shelf collapse) to the eastern Larsen A (170 years since ice-shelf collapse). With a longer time period to contrast sediment and LOC characteristics in the Larsen A deposits, the development of a labile “food bank” was more apparent, revealing increased inventories of LOC over time (10–75 mg/cm²), greater depths of LOC

penetration into the seabed (8–22 cm) with time, and longer LOC mean residence times (6–58 years) with increased age and duration of the food bank. These data are of vital importance as scientists try to unravel the complex ecological transitions occurring in post-collapse sediments.

3 | ICE-SHELF LOSS AND ECOLOGICAL RESPONSES

3.1 | Pelagic responses

3.1.1 | Pelagic changes following ice-shelf collapse

The thinning, calving, and collapse of ice shelves, and subsequently increased retreat of glaciers, will continue to expose increasingly large coastal areas to sunlight during periods of seasonally ice-free conditions, stimulating primary production. Pelagic ecosystems can be expected to respond rapidly as a result of the relatively short lifespans of most planktonic organisms, their rapid growth rates, and the fluid nature of their environment leading to high lateral exchange (Cape, Vernet, Kahru, & Spreen, 2014; Clarke et al., 2007). The dominant grazers in the epipelagic ecosystems of the AP (protists, copepods, krill, and salps) have life spans ranging from days (protists) to 6 years (Antarctic krill), suggesting similarly rapid adjustment to the altered physical environment (Atkinson et al., 2017; Bernard, Steinberg, & Schofield, 2012; Garzio, Steinberg, Erickson, & Ducklow, 2013; Gleiber, Steinberg, & Schofield, 2016). This is exemplified by the case of the Larsen A where high phytoplankton production and biomass, with a net CO₂ flux from the atmosphere to the ocean, were observed in newly open areas in less than 1 year following collapse (Bertolin & Schloss, 2009). Although the actual colonization of newly available pelagic habitat following ice-shelf collapse is difficult to study due to its rapidity and the logistics of scheduling ships in the region, we can gain understanding of these processes through analogy with other, similar ice-adjacent communities.

Study of the evolution of the coastal Northwest Weddell Sea following ice-shelf collapse has yielded insight into potential long-term trajectories. Following the Larsen A collapse in January 1995, Bertolin and Schloss (2009) observed high phytoplankton biomass and production in the freshly open area, suggesting that ice-shelf retreat and collapse leads to increased pelagic production, causing shifting food-web dynamics and potentially increased biological-pump activity (Bertolin & Schloss, 2009). They found that phytoplankton was dominated by siliceous diatoms species, but they also observed high *Phaeocystis* sp. abundances, implying newly open areas can contribute substantially to CO₂ drawdown into the Southern Ocean. As indicated by Cape et al. (2014), embayments uncovered by the Larsen A and B collapses have become seasonally productive polynyas, with the seasonal magnitude and spatial patterns of production controlled by the advance and retreat of sea ice in the Northwest Weddell Sea, much like along the WAP. Polynyas deserve special attention, not only as sites of incredibly high productivity within the ice pack (Arrigo & van Dijken, 2003), but also because they can contribute to ice-shelf basal melt as a result of solar-absorption and infiltration of warm water under the ice shelf. This process is lacking in the Larsen region, but has been observed in the Ross Sea Ice Shelf area (Stewart et al., 2019). Following ice-shelf collapse, polynya dynamics have become the primary driver of phytoplankton production in the Larsen A and B embayments (Cape et al., 2014). These polynyas are often dominated by *Phaeocystis* rather than diatom assemblages, leading to altered food-web pathways (Lee, Park, Jung, Yang, & Lee, 2016; Schofield et al., 2015). However, the significance of these changes for biogeochemical cycling is poorly understood.

3.1.2 | Antarctic ice sheet and glacial changes—The iron story

The export of glacial freshwater plays a fundamental role in structuring the physical and chemical properties of the Antarctic marine environment (Dinniman et al., 2016). Future changes in the Antarctic Ice Sheet, accelerated by ice-shelf collapse, may therefore have important consequences for pelagic marine ecosystems on scales ranging from centimeters to thousands of kilometers from the glacial margins. However, predictions of future ecosystem trajectories are complicated by the heterogeneous nature of ice-sheet–ocean exchanges. This fact may be best illustrated by considering the micronutrient iron. Research over the last decade has highlighted that glacial ice and meltwater contain high concentrations of iron (Raiswell et al., 2018). This suggests that the Antarctic Ice Sheet as a whole may be an important source of iron in pelagic biogeochemical cycling in the otherwise iron-limited Southern Ocean (Death et al., 2014; Hodson et al., 2017; Person et al., 2019; Wadham et al., 2013). The impact of this iron-rich freshwater input on the

marine environment is nevertheless mediated by the way it enters the ocean. Freshwater input is spatially and temporally variable and remains poorly constrained.

In the Amundsen Sea, vertical flux of iron at the glacier margin driven by meltwater input at depth serves as a primary source of micronutrients to phytoplankton in the productive Amundsen Sea Polynya (Gerringa et al., 2012). Iron-rich meltwater served as a similarly important physical and chemical forcing on the marine ecosystem of the WAP (Annett et al., 2017; Dierssen, Smith, & Vernet, 2002). In contrast, in the Ross Sea, glacial contributions of iron to regional primary production were found to be minor compared to other sources (McGillicuddy Jr et al., 2015). These contrasting examples highlight the variable importance of glacial iron sources to the marine environment. However, connections between iron-rich freshwater input and marine ecosystem processes may not always be as clear. Although observations in these cases showed that glacially-modified ocean waters ultimately reached the surface, these may also reach neutral buoyancy in the subsurface as a result of weak freshwater input and mixing with coastal ocean waters (Hewitt, 2020). This implies that a sub-surface export of iron may have little impact on ocean productivity if the water remains below the photic zone. Furthermore, solid-ice export (icebergs) constitutes a major freshwater export pathway from the Antarctic Ice Sheet, suggesting that iron input may be distributed over large oceanic regions (Lin & Twining, 2012; Raiswell et al., 2018). This is illustrated by the journey of the iceberg A-68A (the largest of three parts that formed A-68), which moved over 1,000 km north within 3 years after its separation from Larsen C.

Iceberg-export pathways (e.g., the Weddell Sea and Iceberg Alley) ultimately dictate the spatial footprint of glacially derived iron and freshwater-buoyancy on primary production (Smith et al., 2007; Vernet et al., 2012). Ice-shelf retreat and collapse, as well as subsequent acceleration of coastal glaciers, will ultimately lead to an increase in iceberg export from the Antarctic Ice Sheet (Liu et al., 2015; Scambos et al., 2004). Significant uncertainties remain as to the magnitude of the glacial iron source (e.g., Hopwood et al., 2019), the fate of that iron (Schroth, Crusius, Hoyer, & Campbell, 2014; Tagliabue et al., 2016), and pathways of glacial freshwater in the marine environment (Dinniman et al., 2016). These processes are poorly constrained and quantified, as are the rates of future ice-shelf collapse and glacial retreat. This results in a lack of good predictive modeling of impacts of future retreat on pelagic biogeochemical cycling, particularly when considering responses across the Southern Ocean as a whole.

3.1.3 | Sea-ice changes following ice-shelf collapse

As ice shelves retreat and collapse, newly open coastal regions become part of the Antarctic Sea Ice Zone. The sea-ice boundary will shift dramatically with ice-shelf loss, retreating south in some areas and displacing the suitable habitat for many sea-ice-dependent species like Antarctic krill, seabirds such as penguins, and marine mammals, but creating habitat for animals like Antarctic Minke whales and seals that feed on newly established krill and fish populations (Ducklow et al., 2013; Henley et al., 2019). In addition, sea ice may expand in other areas if surface water becomes fresher, allowing sea ice to form more easily. Direct modifications include changes within habitats and in environmental/habitat heterogeneity, while indirect changes include altered hydrography which can facilitate species invasions, decreased sea ice, CDW intrusion, warming, and volume increase. Warmer waters may introduce and favor different trophic assemblages (Atkinson, Siegel, Pakhomov, & Rothery, 2004) with long-term effects on bird and mammal breeding. On the other hand, as ice shelves and sea ice become thinner, more light will penetrate the ice, yielding more algal growth on the underside of the ice, affecting associated sympagic organisms (cf. Section 3.3.) and their contributions to pelagic food webs and nutrient cycles. Similarly, expansion of sea ice into previously ice-shelf-covered waters increases the surface area available for sea-ice algae production, an important contributor to the Southern Ocean food web. In the long term, there will be regions where ice-algal production will decline with the disappearance of the ice all together leading to new pelagic conditions, while in other areas sea ice will expand over previously ice-shelf covered waters.

Along the WAP, variability in sea-ice extent and duration appears to drive interannual patterns in primary productivity (Saba et al., 2014; Schofield et al., 2018; Vernet et al., 2008). Increased ice years lead to higher stratification (likely through increased meltwater supply during spring/summer) and greater light availability for phytoplankton (Ducklow et al., 2013; Saba et al., 2014). Sea-ice retreat in the southern WAP has opened available habitat and increased overall regional productivity, while inconsistent trends in sea ice in the northern WAP, potentially linked to natural variability in climate drivers, has obfuscated productivity and biomass patterns in this region (Kim et al., 2019; Schofield et al., 2018). Concomitant changes in the composition of the phytoplankton have also been noted, with shifts toward smaller phytoplankton cells in the now more seasonally ice-free and warmer reaches of the northern WAP, and blooms

composed of larger cells to the south (Montes-Hugo et al., 2009, and discussed in Rogers et al., 2020). Because the size structure of phytoplankton communities has important implications for the rate of carbon export (e.g., as a result of ballasting and sinking rates) and food–web interactions, these changes are thought to be important to the future of the WAP system.

3.1.4 | Spatial and temporal mismatches

Any change in primary production is likely to influence the rates of biogeochemical cycling, ocean–atmosphere gas exchange, and the viability and success of higher trophic levels (Moline et al., 2008; Moline, Claustre, Frazer, Schofield, & Vernet, 2004) through community and food–web dynamics (e.g., the shift from diatoms to cryptophytes). Thus, temporal and spatial trophic mismatches may occur. Phytoplankton production has evolved within particular temporal and spatial constraints, alongside the organisms that rely on it. Trophic interactions between prey and predators have evolved to synchronize (penguins and krill following 5-year patterns because of 4- to 5-year cycle of ideal phytoplankton ice conditions, the basis of the krill food stock; Ducklow et al., 2013; Kim et al., 2019; Saba et al., 2014). The concept of synchronicity in food requirement and food availability, and the subsequent impacts on energetics, survival, and reproduction, is cast in the match–mismatch hypothesis (Moline et al., 2008). Both phenological (temporal) and spatial overlap are important in trophic interactions that structure the food web. Ice-dependent organisms in pelagic habitats, such as krill (whose larvae depend on pack ice as shelter against predation and for food in the form of ice algae, Meyer et al., 2017), silverfish (dependent on ice as nursery, spawning, foraging/prey grounds), and penguins (with trophic links to ice-associated krill and phytoplankton), are heavily affected by ice-shelf changes. For instance, the 2017 Adélie penguin colony collapse in Petrels Island (18,000 breeding pairs) was linked to an unusually large extent of sea ice, causing penguins to travel longer distances to forage, yielding a spatial mismatch. Increasing sea ice in this particular area is likely caused by decreasing salinity driven by the Mertz Glacier collapse and melt discharge.

Reported replacement of phytoplankton by cryptophytes (Moline et al., 2004) may promote salp dominance rather than favoring krill populations (Atkinson et al., 2004, 2019; Constable et al., 2014). Cryptophytic dominance occurs during the summer when generally feeding activities are highest and shifting ice-free periods could further alter the duration that cryptophytes are present, highlighting the importance of the spatial–temporal match–mismatch (Moline et al., 2008). Increased salp numbers may have major implications for higher trophic levels, food–web structure, micro-nutrient and macronutrient cycling, and vertical export (Cavan et al., 2019). Salps are often thought of as trophic dead ends in pelagic food webs, although recent analyses suggest that this assumption may be related to the difficulty of recognizing salp remains within fish guts (Henschke, Everett, Richardson, & Suthers, 2016). Poleward range expansions in the warming AP region are predicted for a number of key pelagic species which prey both on krill and salps (Mackey et al., 2012), including the amphipod *Themisto gaudichaudii*, further influencing the gelatinous shift from krill to salps (Havermans et al., 2019).

A complex framework of temporal and spatial overlaps establishes the upper limits of matching and consumer–food interactions. Although specific predator–prey interactions are governed by this temporal and spatial dependency, overall productivity at the ecosystem level will be determined by matches and mismatches among all trophic levels (Franeker, Creuwels, Veer, Cleland, & Robertson, 2001; McMinn & Hodgson, 1993). Food abundance, food quality, condition of the food source, and thermal tolerances can offset synchronicity in a warming environment. Plasticity and phenology/life cycle characteristics are also involved in this process, and genetic variability and age structure, migration, and larval dispersal can be affected as well. Ice-shelf retreat and the environmental changes that follow are expected to weaken synchronization between food availability and food requirements, affecting predator–prey dependencies and, ultimately, ecosystem structure and function.

3.1.5 | Modification of benthopelagic coupling

Increased pelagic productivity following ice-sheet collapse will undoubtedly lead to strengthened benthopelagic coupling (Smith, Mincks, & DeMaster, 2006) and an increased supply of organic matter to the benthos (see Section 3.2, Figure 3). Moline et al. (2004) estimated that a shift from a diatom-dominated community to a cryptophyte-dominated community could lead to a 40–65% decrease in carbon transfer to higher trophic levels, and an increase of food to the benthos. Nevertheless, substantial uncertainty remains about how the biological carbon pump functions along the AP

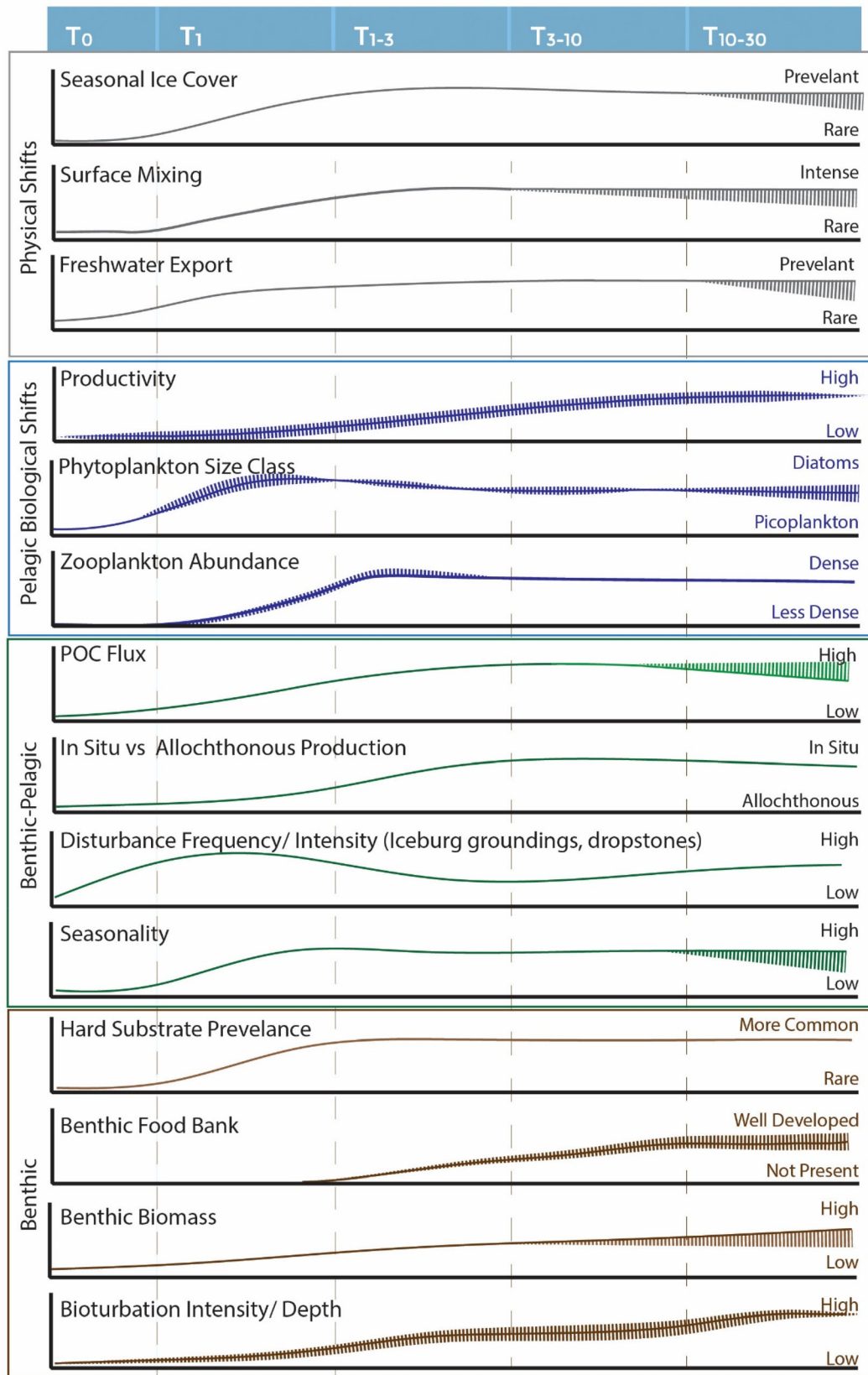


FIGURE 3 Expected changes in physical, pelagic biological, benthic-pelagic, and benthic parameters following ice-shelf collapse. Temporal scale corresponds with Figure 2; T₀: ice-shelf intact; T₁: first year following collapse; T₁₋₃: first 3 years following collapse; T₃₋₁₀: 3–10 years following collapse; T₁₀₋₃₀: 2–3 decades following collapse. Scale legend for each parameter appears on the right-hand side. Shading indicates uncertainty and variability, which generally increases over time. Owing to the diverse conditions that exist across the Antarctic in different ice-shelf regions and poor understanding of the ecological mechanisms and interactions between ecosystem components and processes, substantial uncertainty remains in predicting the different types and magnitudes of changes (cf. Section 4)

and in the open Southern Ocean beyond the shelf. Krill fecal pellets are often the dominant component of sinking material analyzed in sediment traps (Gleiber, Steinberg, & Ducklow, 2012). Transfer of these pellets to deeper depths can be extremely efficient, with minimum attenuation with depth, and their lateral transport enhances productivity through micronutrient and macronutrient recycling. These processes give the pellets a disproportionately important role in vertical carbon export (reviewed in Cavan et al., 2019). Depending on krill feeding, pellets present a “nutrient rain” that can be C- and N-rich and slower- or faster-sinking, affecting the nutrition that arrives at the seafloor following phytoplankton blooms and zooplankton grazing (Atkinson, Schmidt, Fielding, Kawaguchi, & Geissler, 2012). In addition, the notion that krill may feed on benthic resources in areas opened by ice-shelf collapse may influence estimates of uptake of fresh organic material by benthos as well as remove some of the organic material reaching the sea floor (Clarke & Tyler, 2008; Schmidt, Atkinson, Pond, & Ireland, 2014).

Salps are efficient grazers of small phytoplankton (consuming particles down to 4 μm), whereas krill only feed on particles $>20 \mu\text{m}$; thus, the input to the benthos should also shift following a change from diatoms to cryptophytes. Numerous lines of evidence suggest that salps have the potential to play a disproportionate role in transporting euphotic-zone production to the benthos through their rapidly-sinking fecal pellets and carcasses (Gili et al., 2006; Pakhomov, Froneman, & Perissinotto, 2002; Pfannkuche & Lochte, 1993; Phillips, Kremer, & Madin, 2009; Smith Jr. et al., 2014). Krill and salps are dominant grazers in the Southern Ocean, and their response to future climate change has implications for biogeochemical cycling and understanding the Southern Ocean carbon cycle (Pakhomov et al., 2002). For a thorough discussion of observed and future changes of krill and salps and its implications see Rogers et al. (2020).

Given that large phytoplankton and zooplankton dominate Antarctic systems and lead to high rates of new production and net community production (Huang, Ducklow, Vernet, Cassar, & Bender, 2012; Tortell et al., 2013; Weston et al., 2013), it is surprising that carbon-export efficiencies appear to be strikingly low (Ducklow et al., 2018; Lee et al., 2016; Stukel et al., 2015). This apparent imbalance may suggest that other processes, including subduction and vertical mixing of organic matter, are important components of vertical carbon flux (Llort et al., 2018; Stukel & Ducklow, 2017). However, it may also reflect an underlying uncertainty in the system that needs investigation in order to predict mechanistically the linkages between pelagic and benthic communities. In the East Antarctic, for example, the abundant and rich biota over Maud Rise is related to both oceanographic and sea-ice processes, fed by the richness of ice-edge blooms while transport of organic matter produced in the pelagic realm is more constant than elsewhere due to low lateral drift over the seamount (Brandt et al., 2011).

3.2 | Benthic responses

3.2.1 | Changes in organic matter flux to the benthos—Shifting food regimes

The sudden exposure of large areas of seafloor to phytodetrital input after ice-shelf collapse leads to a shift from an oligotrophic to a more eutrophic benthic system, initiating colonization processes and changing communities (Gutt et al., 2011; Hardy, David, Rigaud, De Ridder, & Saucède, 2011). These changes affect soft-sediment communities across species, size classes, and life stages (Ingels et al., 2012). Assessments of impacts on benthos must consider changes in the food sources they rely on. This comprises primarily the vertical and horizontal flux of particulate organic matter (including phytodetritus, zooplankton feces and carcasses, and associated microbes).

Organic flux to the seafloor in ecosystems surrounding ice shelves will be impacted by ice-shelf collapse in several ways (Figure 3).

- *Horizontal flux:* (a) The rates and direction of horizontal fluxes will vary on regional and local scales, depending on the nature and rates of primary production, as well as sediment resuspension and deposition. (b) Seafloor roughness and topography (driven by biology, iceberg scour, and geology) may modify horizontal flux. Horizontal flux or advection will also be affected by the flow dynamics of the benthic boundary layer and deposition patterns following ice-shelf loss, oceanographic, and hydrodynamic changes, as well as sources of currents, for example, buoyancy-driven flow from beneath the glacial versus flow into the sub-ice-shelf cavity (oceanography-driven flow).
- *Vertical flux:* (a) Input quality and quantity will change. (b) Temporal and spatial synchronicity and dependencies will change. (c) Variability in availability and quality of arriving food sources will change.
- Overall productivity from local to Antarctic spatial scales will change.
- Ice-shelf changes may enhance the chance of anthropogenic inputs arriving at previously isolated sites.

Changes in food quality and quantity arriving on the seafloor will likely cause substantial trophic effects on the seafloor. However, the very slow metabolic and physiological rates of benthic animals (e.g., Peck, Heiser, & Clark, 2016; Peck, Morley, Richard, & Clark, 2014) imply that individuals may be able to survive very long times without food; for example, the predatory snail *Trophon longstaffi* may survive up to 3 years with unaltered behavior on a single meal (Harper & Peck, 2003). This and other studies suggest a number of Antarctic benthic animals are likely well-adapted to extended periods of limited food availability (Harper & Peck, 2003). Mobile animals such as brittle stars could forage over larger areas and still only need infrequent meals to support their metabolism. However, in a shifting food regime, animals that are not adapted to greater food availability may move in and outcompete organisms adapted to food poverty (i.e., episodic and/or low food availability), creating the potential for biodiversity loss due to competition by fauna that expand their ranges from more eutrophic areas.

3.2.2 | Changes in benthic communities

Benthic community changes following ice-shelf collapse and subsequently changing food conditions have been observed in several studies. Increased primary production and subsequent benthic food influx result in higher-density meiofauna assemblages and, in the case of Foraminifera, to communities with more “live” calcareous species, as observed in the Larsen A area post-collapse (Murray & Pudsey, 2004). Pre-collapse, sub-ice nematode assemblages were impoverished and characterized by low densities and diversity, and high dominance by a few taxa. Such assemblages can still be present years after ice-shelf collapse, indicating that colonization there can be a slow process. The inner Larsen A nematode assemblage 12 years after ice-shelf collapse showed elevated diversity but low densities and a dominance of monhysterids, an opportunistic taxon taking advantage of the increased food supply. Five years after the ice-shelf collapse, nematode assemblages with low abundance, diversity, and dominance by opportunistic monhysterids were observed in the inner stations of Larsen B, between 50 and 100 km from the original shelf edge (Raes et al., 2010). The nematode assemblages near the former ice-shelf edge (outer Larsen B areas), on the other hand, appeared to be in a later stage of succession, with higher densities and diversities, but still with major differences from offshore shelf communities. Four years later (9 years after ice-shelf collapse) at the inner Larsen B stations, nematode densities had increased 10-fold but were still relatively low in diversity and dominated by opportunistic monhysterids (Hauquier et al., 2016). This indicates slow colonization (requiring more than 9 years) by nematode families other than monhysterids following ice-shelf collapse. The increase or dominance of bacterivorous taxa such as monhysterids following the collapse could be caused by the initiation of the microbial conveyor belt once particle fluxes increase.

Changes in benthic microbial communities have been indicated following ice-shelf collapse (Shimizu, 2016). In the Larsen A embayment, microbial analyses of sediments indicated that phytoplankton and bacterial lipid concentrations in the sediments were correlated with a gradient of increasing primary productivity from onshore to offshore. Furthermore, relative abundances of labile and phytoplankton-originated organic matter were positively correlated with relative abundances of chemoheterotrophic bacteria, while areas with lean or recalcitrant organic content were correlated with relative abundances of different species of recalcitrant organic matter degraders or chemoautotrophic archaea and bacteria. The findings of Shimizu (2016) imply that benthic microbial communities will respond to changes in overlying primary production, altering food webs and biogeochemical processes at the seafloor.

There is evidence that chemosynthetic communities, characterized by microbial mats and bivalves, may have occurred under the Larsen B ice shelf prior to breakout (Domack, Ishman, et al., 2005). Five years after ice-shelf collapse, microbial assemblages associated with this remnant seep were dominated by anaerobic methanotrophic archaea (ANME-3 and AAA) and sulfate-reducing bacteria, suggesting continued chemoautotrophic production (Niemann et al., 2009). This was the second report of a polar cold seep dominated by ANME-3, leading to speculation that this group specializes in cold environments, an observation supported by subsequent studies (Bhattarai, Cassarini, & Lens, 2019). However, 5 years after collapse, no live clams were found, and there was no evidence of utilization of chemoautotrophic production by the nematode assemblage (Hauquier et al., 2011).

Ice-shelf-induced changes in the benthic communities will affect trophic and other ecological processes, such as competition and predation. Many Southern Ocean benthic isopods and amphipods have a broad-spectrum diet, and predators are generally not selective, suggesting they may not be severely impacted by changes in food quality and quantity (Ingels et al., 2012). Furthermore, trophic flexibility and detritivory in sea urchins may reduce the impact of large fluctuations in the availability of primary production, seasonal or otherwise. However, some isopod and amphipod species are highly specialized, for example, by feeding on particular Foraminifera or sponge species (Nyssen, Brey,

Dauby, & Graeve, 2005; Würzberg, Peters, & Brandt, 2011). These taxa are much more likely to be impacted by the food and trophic changes that follow ice-shelf collapse. In general, reciprocal effects between different feeding and ontogenic stages makes it difficult to predict the response of most taxa to food changes because of potential but poorly-known tradeoffs between energy allocation, growth and reproduction, and differences between different species and their life-stages (Ingels et al., 2012 and references therein).

Our limited knowledge of in situ sub-ice-shelf biodiversity (Section 2.1) and post-collapse responses (Section 2.2), indicates that the benthic community type and, therefore, the biodiversity of these communities is largely dependent on their physical, chemical, and biological environmental setting. This means that not all benthic sub-ice-shelf communities will respond to the loss of ice in the same way. The diverse and complex benthic assemblages, dominated by suspension feeders, in areas of strong marine inflow such as those found underneath the Amery Ice Shelf (Post et al., 2007, 2014; Riddle et al., 2007) may not change dramatically in function or biodiversity. However, oligotrophic communities further from the ice-shelf edge, in an outflow area, or somewhere with little inflow from open water (e.g., Post et al., 2014), are likely to experience rapid and dramatic changes in community structure, abundance, and biodiversity. Research from the Amundsen Sea (Kaiser, Barnes, Sands, & Brandt, 2009; Linse et al., 2013) shows that the rich shelf-fauna may be the consequence of sub-ice, stable conditions in the area and the influence of the productive Pine Island Polynya (Arrigo, Lowry, & van Dijken, 2012), and potentially enhanced recruitment through dispersal facilitated by the CDW or migration from nearby areas that served as refuges during glacial maxima (Barnes & Hillenbrand, 2010).

3.2.3 | Ice impacts on benthic communities

Recent ice-shelf collapses have released thousands of small icebergs into open waters. Iceberg grounding and scouring can cause substantial damage to benthic communities and biodiversity loss up to 500 m water depth (Gutt et al., 2013; Gutt, Starman, & Dieckmann, 1996), causing communities of long-lived, slow-growing species with episodic reproduction to fluctuate between destruction and recovery (Barnes, 2017; Barnes & Conlan, 2007; Gutt et al., 1996). Although the impact of these processes on soft-sediment fauna is obvious, the interspersed hard substrates (rocks, boulders, and reefs) that provide habitat for numerous sessile species will also be affected (Gutt et al., 2011). With increasing iceberg calving, these disturbances are expected to increase both in number and frequency, until the supply of icebergs diminishes as ice shelves and glaciers disappear. However, an increase in fast ice over short-to-medium time scales could reduce iceberg movement by freezing in icebergs or by glacial buttressing (Massom & Stammerjohn, 2010).

Increased iceberg scouring disturbance can have devastating effects, but in shallow waters, increased disturbance can be followed by relatively rapid recolonization and succession through animal locomotion, advection, and larval recolonization over various time scales (Gutt et al., 1996; Gutt & Starman, 2001; Peck, Brockington, Vanhove, & Beghyn, 1999). For example, scouring can remove over 95% of the nematode assemblage and cause a drop in diversity (Lee, Gerdes, et al. 2001; Lee, Vanhove, et al., 2001). Recovery of the nematode assemblage from scouring can occur within weeks and without signs of community succession, suggesting the nematode fauna is relatively well adapted to frequent disturbance. However, in recently ice-free areas, there are signs that colonization leads to community succession, with dense communities of opportunistic species occupying scoured sediment areas, which were previously populated with low abundance, low-diversity nematode assemblages that are characteristic of sub-ice-shelf conditions (Hauquier et al., 2011, 2016; Raes et al., 2010). Foraminifera may also respond to drop-stone presence and frequency of occurrence, with a negative effect on infaunal Foraminifera, but the drop-stones may provide additional habitat for sessile Foraminifera (Ingels et al., 2012). In contrast, sessile organisms can be impacted by iceberg scour for years, decades, or potentially longer as it takes episodic recruitment followed by slow growth of certain taxa to repopulate these communities (Dayton et al., 2013).

Increased iceberg calving and melt, and ice-shelf and glacier retreat, will increase the amount and frequency of drop-stone deposition on the seafloor (up to 3,000 km from the source; Bond et al., 1992). This promotes heterogeneity, small-scale habitat diversity (Schulz, Bergmann, von Juterzenka, & Soltwedel, 2010), and increasing colonization potential for sessile species requiring hard substrate, in shallow as well as deep waters (Dayton, 1990; Ziegler, Smith, Edwards, & Vernet, 2017). Hard substrates present a considerable source of diversity in the Antarctic. On the Sabrina Shelf in East Antarctica, as well as in fjords and on the open shelf of the WAP, significant increases in taxonomic diversity, abundance, and biological cover were observed on hard substrates such as drop-stones and areas of exposed bedrock, compared with soft substrates (Post, Lavoie, Domack, Leventer, & Fernandez, 2020; Ziegler et al., 2017). Some

taxa, including the hexactinellid sponge *Anoxycalyx joubini*, branching hydrocorals, several gorgonians and bryozoans, and colonial ascidians, were found only on or around hard substrates. The distribution of drop-stones is partially random, creating fine-scale habitat heterogeneity that is important not only for the distribution of the seafloor biota but also for their reproduction, dispersal, and colonization (Post et al., 2020, Ziegler et al., 2017). At the same time, drop-stones can disturb the resident seafloor communities considerably (Barnes, 1999).

Ice-shelf collapse and melting will increase the availability of hard, drop-stone substrates, allowing the settlement of pelagic larvae, including those with very long pelagic durations arriving from distant sites. However, many species in Antarctica do not have long-distance pelagic larvae, but rather have short larval durations or brood their offspring (Poulin, Palma, & Féral, 2002; Smith et al., 2006). Communities living hundreds of kilometers under ice shelves are likely to include species that are mobile in the adult stages (e.g., Clough & Hansen, 1979; Stockton, 1982) and species with long-distance larvae transported from the ice edge. Currently, no analyses have tested whether sub-ice-shelf community compositions are increasingly skewed toward mobile species and/or those species with long pelagic duration with distance from the ice-shelf edge.

3.3 | Sympagic responses

Sea ice provides a habitat for many groups of organisms including bacteria, algae, fungi, heterotrophic protists, and invertebrates (e.g., Krapp, Berge, Flores, Gulliksen, & Werner, 2008). The brine-channel system in sea ice provides a complex network of living space (Thomas & Dieckmann, 2002), with varying temperature and salinity conditions to which the sympagic organisms are adapted, forming distinct communities (Arrigo et al., 2010; Meiners et al., 2011; Meiners, Papadimitriou, Thomas, Norman, & Dieckmann, 2009). Ice-algal biomass can be extremely high and exceed sub-ice phytoplankton biomass (Arrigo et al., 2010). Sea-ice algae have been estimated to contribute up to 25% of the overall primary production of the Antarctic sea ice zone (Arrigo & Thomas, 2004). Since they are adapted to low light levels, early growth in the bloom season means they provide an extended source of food for pelagic as well as benthic organisms. Areas previously covered with an ice shelf will likely transition to a state under the influence of sea ice and its sympagic production dynamics, enriching pelagic as well as benthic habitats, particularly in light of observations that sympagic production may exceed consumption within the sea ice at the ice boundary (Gradinger, 1999).

3.4 | Spatial and temporal scales of ice-shelf collapse consequences

Although a number of studies have reported the ecological consequences of catastrophic collapse or large iceberg calving of Antarctic ice shelves, there are few interdisciplinary efforts focusing on the consequences across the spatial and temporal scales over which impacts will occur. The majority of studies examining biological responses to ice-shelf retreat have focused on local scales (e.g., under the former ice sheet) or regional scales (e.g., in the northwest Weddell Sea). However, the export of freshwater from basal melt or export of icebergs can have significant impacts on primary production and the biological pump >1,000 km from the site of glacial retreat in some cases (Raiswell et al., 2018). Moreover, iceberg disturbance of the seafloor has been observed far away from the areas of ice-shelf disintegration (Gutt et al., 2011). To understand the consequences of ice-shelf collapse from ecosystem to global levels, interactions between physical, chemical, and biological processes must be considered across a wide range of scales within an interdisciplinary framework.

In general, although the adjacent pelagic systems have responded rapidly to ice-shelf collapse, benthic communities have shown a gradual succession from impoverished oligotrophic communities to diverse shelf assemblages. However, some fauna, such as hexactinellid sponges, are able to exploit newly favorable conditions and increase in abundance and biomass relatively rapidly (see Dayton et al., 2016), even over a decade after ice-shelf collapse (Fillinger, Janussen, Lundälv, & Richter, 2013). Following the Larsen A and Larsen B ice-shelf collapses, extensive changes in benthic marine ecosystems were documented in the year following collapse, but different ecosystem components responded over different time scales, from months to years, depending on mobility and colonization potential.

In addition, some studies indicate that there are significant and sometimes unexpected changes, with ramifications across levels of organization and disciplines. The combined effects of ice-shelf calving, ice-shelf collapse, fast- and sea-ice dynamics, and their downstream physical, biogeochemical, and ecological consequences are not “predictable”. Even when large icebergs calve, influences on the dynamics of the surrounding ecosystems are not well understood spatially,

temporally, or ecologically (Massom & Stammerjohn, 2010). Shifts in species ranges and altered phenological timings may lead to trophic mismatches, highlighting the importance of spatial and temporal scales of change following ice-shelf collapse.

The complexity of such spatial–temporal changes is further highlighted by studies of the effects on carbon fluxes within the ecosystem. Increased primary production following ice-shelf disintegration may have a cascading effect on carbon export (Peck et al., 2010). New organic-matter fluxes to the benthos can contribute to the development of sea-floor communities and the sequestration of carbon to the deep ocean via the biological pump (Peck et al., 2010). These shifts in benthic and pelagic communities, habitat availability, and food–web dynamics could ultimately contribute to the Southern Ocean's capacity as a carbon sink (Barnes, 2017; Peck et al., 2010). However, significant uncertainty on the temporal and spatial scales of such mechanisms exists owing to the complex nature of the carbon cycle of the Southern Ocean (Takahashi et al., 2012), the variable nature of marine-ecosystem processes (e.g., owing to variability in physical forcing), and the paucity of observational datasets spanning seasons to years that are needed to constrain these processes.

The findings summarized here present a complex set of responses of ecosystem components and interacting ecological niches. The interplay of changing processes (physical/oceanographic, chemical, and biological) in the wake of ice-shelf retreat and collapse in conjunction with regional warming trends will increase the spatial and temporal environmental heterogeneity to which the biotas will respond with similar spatial and temporal complexity (e.g., global niche decay due to anthropogenic global warming, Huettmann, 2017). Increases in environmental, habitat, and substrate heterogeneity will evoke ecosystem responses with dramatic population shifts, including most predator–prey relations and food webs, which are structured by sea-ice dynamics, oceanographic processes, geographical sequence of ice-shelf disintegration and ice-sheet dynamics, as well as biogeochemistry and biology (Gutt et al., 2011). In addition, ice-shelf collapse and retreat opens new pathways for potential redistribution of organisms and will cause mixing of previously isolated and genetically distinct populations (Halanych & Mahon, 2018). For instance, in the West Antarctic, evidence suggests that the land is more likely to be a series of archipelagoes than a single cohesive land mass, and different shelf areas have functioned as isolated refugia during glacial times, causing genetic structuring or cryptic speciation in several taxa (Harder, Halanych, & Mahon, 2016; Krabbe, Leese, Mayer, Tollrian, & Held, 2010; Wilson et al., 2007).

4 | OVERCOMING MAJOR KNOWLEDGE GAPS

Following the Larsen A and Larsen B ice-shelf collapses, several years passed before scientists could conduct comprehensive studies to document the consequent ecosystem changes. Relatively rapid responses to such events can be achieved, however, as demonstrated by the mobilization of researchers within months and 2 years after the A68 break-off (although access was still dependent on sea-ice conditions). Such efforts require concerted action from the international scientific community, a community that historically has relied on collaborative efforts to share existing samples and maximize interdisciplinary efforts on cruises of opportunity.

Despite efforts to investigate ice-shelf systems prior to and after their collapse, there are many scientific questions that remain—important questions relating to our ability to predict how the Southern Ocean and its ecosystems will respond to ice-shelf changes and their effects on Antarctica's ice-sheet dynamics. A major challenge is to document ecosystem responses at all levels of biological organization (genome to pan-Antarctic), and combine genomics/DNA approaches with multi-taxon studies that integrate taxonomic, biogeochemical, genomic, and community data followed by matching biological data with fluxes/transport measured by physical oceanographers, geochemists, and geologists (e.g., Halanych & Mahon, 2018). We also need a better understanding of the mechanistic linkages between climate, sea ice and ice shelves, ice sheets and icebergs, biogeochemical processes, food webs and organism interactions, and population and community dynamics (e.g., Lundesgaard et al., 2020; Ziegler, Cape, et al., 2020; Ziegler, Hahn-Woernle, et al., 2020). Linkages with glaciology, physical oceanography, biology, and ecological interactions are critical as both drivers and impacts of ice-shelf loss (Ducklow, 2008; Ducklow et al., 2007; Massom & Stammerjohn, 2010).

A better understanding of these complex relationships and links, and the ability to detect, monitor, and predict ecosystem responses to ice-shelf change, demands multidisciplinary research efforts. Additionally, in order to distinguish long-term anthropogenic trends from natural variability/fluctuations, and to predict future impacts more accurately, an integrated, long-term, circumpolar monitoring program of physical, biological, and biogeochemical factors is required. This critical need has been recognized with the establishment of the Integrating Climate and Ecosystem

Dynamics (ICED) in the Southern Ocean (Murphy, Cavanagh, Johnston, Reid, & Hofmann, 2008) and Southern Ocean Sentinel programs (Massom & Stammerjohn, 2010).

We envisage that advances in the development of marine scientific technology will be critical in achieving these aims. Study of sub-ice-shelf ecosystems before dramatic change occurs, and direct observations of the consequences of collapse and calving in its early stages, require a scientific infrastructure covering large spatial scales with scalable temporal resolution. Ocean and through-the-ice moorings with shallow-to-deep ocean samplers/sensors, automatic weather stations, automated underwater-vehicle surveys, and shipborne expeditions are but a few types of infrastructure needed to achieve a comprehensive approach. The Southern Ocean Observing System (SOOS), an international initiative that facilitates long-term observations of the dynamics and change of Southern Ocean systems, has supported ice-shelf studies as a priority, as well as data sharing, and data availability, as required under the Antarctic Treaty System and other regulatory structures.

Establishing an understanding of the physical and ecological consequences of ice-shelf collapse to Southern Ocean and global systems over a broad range of spatial and temporal scales is imperative. Therefore, improved international strategic planning and scientific investment in ice-shelf research are needed. The International Marine Ecosystem Assessment for the Southern Ocean (MEASO) aims to assess long-term status and trends in Southern Ocean biota and food webs, highlighting the need for increased scientific infrastructure and research to collect long-term observations. This certainly applies to research focused on the consequences of ice-shelf collapses.

Furthermore, initiation of networks of investigators to achieve enhanced collaboration in future ice-shelf research, international pooling of resources, and establishment of a multi-decadal plan are actions that would advance the field substantially. In recent years, and especially with the recent A-68 calving, there are signs that scientists are making increased efforts to share knowledge, identify important research priorities and knowledge gaps, and outline strategic plans to advance understanding of the changes that Antarctic ice shelves and surrounding ecosystems will experience in response to warming (Ingels et al., 2018). Moreover, ice-shelf collapse has important policy implications that have not been addressed sufficiently, requiring a future effort and review from the international community (e.g., Ingels et al., 2018).

Clearly, the international research community needs to put increased effort into establishing a better understanding of the complex responses to ice-shelf collapse; the relationships and links between changing ecosystem components; and detecting, monitoring, and predicting ecosystem responses to ice-shelf change. Evaluation of pre-collapse and immediately post-collapse conditions, and distinguishing between responses to ice-shelf disintegration and natural variability, are needed to accurately predict future warming impacts. This can only be achieved through integrated, highly coordinated, multidisciplinary international research, including long-term measurement and the combined analysis of physical, biological/ecological, and biogeochemical parameters.

Summary of some important knowledge gaps:

- Understanding of the response-times of pelagic and benthic organisms (on soft and hard substrates) to ice-shelf disintegration and collapse, including how these responses may vary seasonally and across size, taxonomic, and functional/trophic groups.
- Accurate and comprehensive knowledge of species, populations, and communities that inhabit sub-ice-shelf habitats, and improved knowledge of the distributions of those species, populations, and communities across ice shelves, fast-ice, and sea-ice zones.
- Knowledge of the quantity and quality of food sources that feed the pelagic fauna and are exported to the benthos, their remineralization during transit through the water column, and how the quantity and quality will change under ongoing ice-shelf changes.
- Understanding of advective and other processes feeding sub-ice-shelf communities, and how they will be affected by changes in ice-shelf coverage locally, regionally, and Antarctic-wide.
- Characterization of the distributions and fluxes of meltwater and associated nutrients to the upper water column and their effect on pelagic ecosystems far from the ice-shelf collapse.
- Knowledge of the timescales and spatial reach of iceberg advection, melting, and scouring, drop-stone and scouring frequencies and magnitude, and the effects of mass calving events on higher trophic levels, the biological pump, nutrient and sediment exports, and stratification of pelagic ecosystems far from the ice-shelf collapse.
- In-depth understanding of how the structure, function, and biodiversity of sedimentary ecosystems change in time and space following ice-shelf collapse, and how these link to marine ecosystem responses to abrupt large-scale environmental forcing (e.g., release from extreme food limitation, biogeochemical cycling, rates of carbon sequestration, and species invasions).

- Better predictions of ice-shelf retreat, disintegration, and collapse to be able to assess the magnitude of the changes that will occur in pelagic and seafloor habitats.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

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