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# Biological responses to change in Antarctic sea ice habitats

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Sea ice is a key habitat in the high latitude Southern Ocean and is predicted to change in its extent, thickness and duration in coming decades. The sea-ice cover is instrumental in mediating ocean–atmosphere exchanges and provides an important substrate for organisms from microbes and algae to predators. Antarctic krill, *Euphausia superba*, is reliant on sea ice during key phases of its life cycle, particularly during the larval stages, for food and refuge from their predators, while other small grazers, including copepods and amphipods, either live in the brine channel system or find food and shelter at the ice–water interface and in gaps between rafted ice blocks. Fish, such as the Antarctic silverfish *Pleuragramma antarcticum*, use platelet ice (loosely-formed frazil crystals) as an essential hatching and nursery ground. In this paper, we apply the framework of the Marine Ecosystem Assessment for the Southern Ocean (MEASO) to review current knowledge about relationships between sea ice and associated primary production and secondary consumers, their status and the drivers of sea-ice change in this ocean. We then use qualitative network

modelling to explore possible responses of lower trophic level sea-ice biota to different perturbations, including warming air and ocean temperatures, increased storminess and reduced annual sea-ice duration. This modelling shows that pelagic algae, copepods, krill and fish are likely to decrease in response to warming temperatures and reduced sea-ice duration, while salp populations will likely increase under conditions of reduced sea-ice duration and increased number of days of  $>0^{\circ}\text{C}$ . Differences in responses to these pressures between the five MEASO sectors were also explored. Greater impacts of environmental pressures on ice-related biota occurring presently were found for the West and East Pacific sectors (notably the Ross Sea and western Antarctic Peninsula), with likely flow-on effects to the wider ecosystem. All sectors are expected to be impacted over coming decades. Finally, we highlight priorities for future sea ice biological research to address knowledge gaps in this field.

#### KEYWORDS

Southern Ocean, storms, warming, copepods, fish, primary production, krill, MEASO

## 1. Introduction

Sea ice is a major structuring component in Antarctic marine ecosystems and a key driver of Southern Ocean biogeochemical cycles (Thomas, 2017; Henley et al., 2020). It forms a physical and chemically-active barrier on the surface of the ocean, and strongly affects fluxes of gas (e.g., climate-active gases such as carbon dioxide and various sulphur compounds, e.g., dimethyl sulphide) and energy across the atmosphere–ocean interface (Tison et al., 2017). Sea ice also forms a key habitat for ice algae (Arrigo, 2017); it is highly reflective (particularly when snow covered) and reduces light levels under the ice to 0.1%–1% of incoming surface radiation (Arndt et al., 2017), resulting in strong control on Southern Ocean phytoplankton production and phenology (Henley et al., 2020; Pinkerton et al., 2021). Sea-ice cover also decreases wind-driven mixing of the surface ocean, and its seasonal melt can induce stratification in the upper layers of the water column that is conducive for pelagic phytoplankton blooms during ice retreat in spring (Saba et al., 2014; Sabu et al., 2014; Kauko et al., 2021). Antarctic sea ice extent is sensitive to both atmospheric and oceanic forcing; however, regional-scale atmospheric circulation changes are thought to be the dominant driver of recent trends, i.e., a slight increasing overall trend in sea-ice extent since 1979 comprising different regional and seasonal contributions (Hobbs et al., 2016; Turner et al., 2022).

The life cycles of many Antarctic species are attuned to the seasonal cycle of sea-ice advance and retreat. For example, penguins and seals use sea ice as a resting and breeding platform; their sea-ice requirements are complex and include icescape variables such as landfast ice extent and duration, pack-ice concentration and seasonality and local snow cover thickness and surface roughness (e.g., Massom and Stammerjohn, 2010; Bestley et al., 2020). Sea ice also provides a substrate and habitat for ice-associated (sympagic) communities consisting of bacteria,

micro-algae, heterotrophic protists and small metazoans including copepods, flatworms, gastropods and ctenophores (Bluhm et al., 2017). Larger organisms living in the water column below can also use sea ice as a refuge from predators and/or as feeding grounds (Figure 1).

Ecosystem services provided by sea ice and their associated communities include biogeochemical cycling, food web maintenance, primary productivity and climate regulation, along with benefits for science, tourism and recreation, food security and fisheries (Grant et al., 2013, 2021; Cavanagh et al., 2021; Murphy et al., 2021; Steiner et al., 2021). At present, our understanding of how global environmental change will affect the biota associated with Antarctic sea ice is limited (IPCC, 2019, 2021). Here we apply the Marine Ecosystem Assessment of the Southern Ocean (MEASO) framework to synthesise the present state of knowledge of key lower trophic level biota that have strong connections with sea ice, either by occupying the sympagic habitat or by living in seasonally ice-covered waters. We then build a qualitative network model to show the interactions between these physical, chemical and biological components of the Southern Ocean ecosystem and explore how cascading feedback effects might affect the system under the influence of future global environmental change.

## 2. Sea ice

The annual cycle of Antarctic sea ice coverage represents the largest seasonal physical change on the surface of the Earth, varying between  $\sim 3.1$  million  $\text{km}^2$  in February and 18.5 million  $\text{km}^2$  in September (Eayrs et al., 2019; Parkinson, 2019). For ecosystems, a crucial distinction is between extensive mobile pack ice and stationary coastal landfast ice, because they provide different habitats for different species (e.g., Massom et al., 2009;

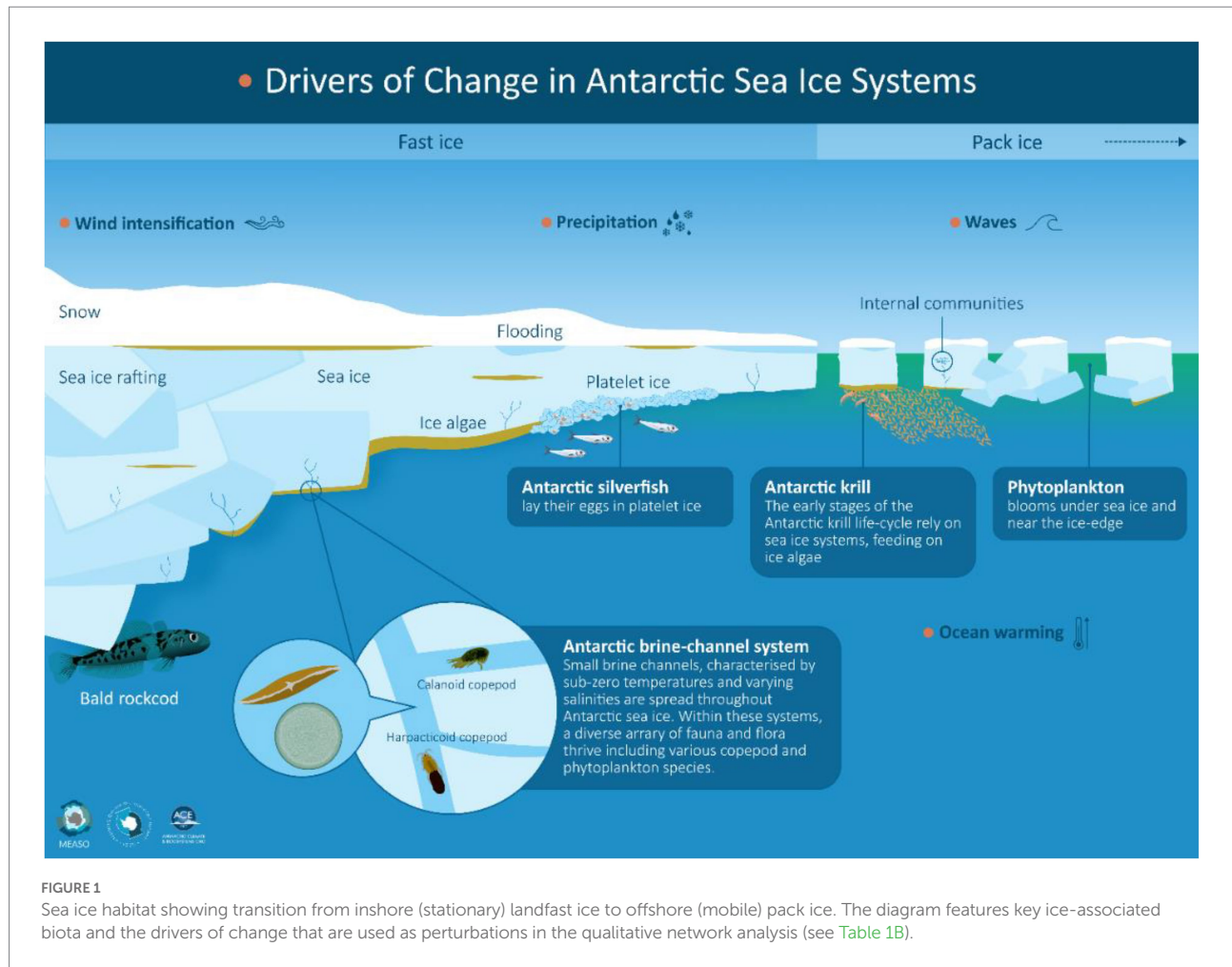


FIGURE 1

Sea ice habitat showing transition from inshore (stationary) landfast ice to offshore (mobile) pack ice. The diagram features key ice-associated biota and the drivers of change that are used as perturbations in the qualitative network analysis (see Table 1B).

Massom and Stammerjohn, 2010; Meiners et al., 2018; Labrousse et al., 2019). Around the Antarctic coast, landfast ice distribution is largely governed by coastal configuration and bathymetric depth (Fraser et al., 2012, 2020). Landfast ice can be either seasonally-recurring or perennial (persist through one or more summers), and the limit of its offshore coverage is generally determined by the location of icebergs grounded on seafloor shoals at a depth of ~400 m below sea level (Giles et al., 2008). The ice spanning from the coast to these pinning points can reach widths up to 300 km in certain areas, but is generally less extensive (Fraser et al., 2020). Although the spatial distribution and variability of Antarctic landfast ice are well-characterised (Fraser et al., 2021), detailed understanding of the drivers of its annual variation is currently lacking, though it is clear that it is affected by both oceanic and atmospheric forcing (Massom et al., 2009; Fraser, 2011; Aoki, 2017; Arndt et al., 2020). At some locations offshore from ice shelves, the shoaling of supercooled water originating from ice shelf basal melting, with its temperature below the freezing point, results in the formation of free-floating ice crystals that may form along the ice shelf gradient; these are known as platelet crystals, which accumulate and grow locally beneath fast ice (Foldvik and Kvinge, 1974; Langhorne et al.,

2015). As shown in Figure 1, platelet ice represents an important sub-habitat for some species. A comprehensive review of platelet ice and its role in the Antarctic ecosystem is provided by Hoppmann et al. (2020).

By comparison, pack-ice comprises a matrix of floes of varying size, age, concentration and thickness that are in constant motion in response to ocean currents and winds, which may cause complex rafting or dispersal of ice floes. In winter, the maximum width of Antarctica's pack-ice zone varies from a few hundred kilometres (e.g., off East Antarctica from 120°E to 135°E) to >2,000 km in the deep poleward embayment of the Weddell Sea. Antarctica's pack-ice zone is the dominant part of the sea-ice system that undergoes annual advance and retreat. Although Antarctic pack-ice thickness is a major unknown (IPCC, 2019), largely due to difficulties in making *in situ* measurements, it is thought to be typically 0.3–2.0 m thick (Worby et al., 2008), although larger thicknesses (of ~10 m) can occur through ice deformation where floes collide (Massom et al., 2006). Perennial ice is largely confined to the southwestern Weddell, Amundsen and eastern Ross seas (Parkinson, 2019).

The key attributes of Antarctic sea ice include areal coverage/extent, the thickness distributions of the ice and its snow cover,

rates and patterns of advance and retreat and resultant duration, and the associated variability (Massom and Stammerjohn, 2010). These attributes result from the complex interplay of both thermodynamic processes (freeze/formation and melt) and dynamic processes (movement and deformation of the ice by winds, ocean currents, swell and waves; Weeks, 2010). Although this combination of processes and the frequent passage of storms creates a highly heterogeneous mixture of different ice types, thickness, age and degree of deformation at small scales, overall the Antarctic sea-ice zone is characterised by distinctive large-scale zones (Massom and Stammerjohn, 2010). Moving from north to south, these are: (1) the marginal ice zone or MIZ (outer pack strongly influenced by the high-energy Southern Ocean and ocean waves); (2) the mid pack-ice zone, which is buffered by the MIZ and generally characterised by larger floes and thicker snow cover, but still influenced by storms; and (3) the coastal zone, where sea-ice conditions are strongly influenced by the Antarctic Coastal Current, coastal configuration and the distribution of icebergs; this is also the realm of landfast ice. Recurrent coastal polynyas (i.e., persistent areas of open water bounded by sea ice) are of particular importance as areas of both high sea-ice formation rates (during freezing months) and enhanced primary production in spring–summer (Barber and Massom, 2007). Around coastal Antarctica, polynyas generally form in the lee of blocking features such as coastal promontories and areas of landfast ice, where they are also maintained by strong katabatic winds blowing seawards from the ice-sheet interior (Nihashi and Ohshima, 2015).

At the microscale (millimetres), sea ice is made up of a matrix of ice crystals separated by small inclusions (pockets) of high-salinity brine (Petrich and Eicken, 2017), the characteristics of which are constantly modified by the interaction of physical, biological and chemical processes that vary in space and time. Regarding the ice crystals themselves, Antarctic sea ice comprises a mix of both granular (or “frazil” ice), which forms under turbulent conditions, and elongated columnar ice, which grows downwards under calmer conditions (Weeks and Ackley, 1986). Near peripheral ice shelves, platelet crystals form a porous layer beneath the sea ice called the sub-ice platelet layer which has a high liquid fraction (~75%, e.g., Wongpan et al., 2015). The columnar ice acts as an advancing interface, filling in the “interplateletary” space of the layer, and is where incorporated platelet ice is formed (e.g., Hoppmann et al., 2020).

Snow is a crucially-important part of the Antarctic sea-ice system, for both landfast and pack ice (Massom et al., 2001). It accumulates as an insulative and high-albedo blanket on the ice surface, to substantially modify the optical, thermodynamic and physico-chemical properties and evolution of the underlying ice (Sturm and Massom, 2017). Notably, and depending on its thickness and properties, which themselves change over space and time (Massom et al., 2001), snow exerts strong influence on the intensity and spectral properties of light available for algal growth both within and under the ice (Wongpan et al., 2018). It can also depress the ice surface below sea level (Massom et al., 2001),

leading to surface flooding and creation of an “infiltration community” (Fritsen et al., 1994; Kattner et al., 2004; Arrigo, 2017).

## 2.1. Variability in sea ice in Marine Ecosystem Assessment for the Southern Ocean sectors

Satellite passive microwave time series data obtained since 1978, when the records began, show a slight increasing trend in overall circumpolar Antarctic sea-ice extent (Parkinson, 2019). This overall extent masks contrasting sectoral contributions [i.e., loss in the Amundsen-Bellinghousen seas sector and gain elsewhere (Parkinson, 2019)], as well as widely-varying patterns of change and variability in sea-ice seasonality (i.e., the timings of annual advance and retreat and resultant duration of coverage Massom et al., 2013; Stammerjohn and Maksym, 2017). Moreover, the last decade has been characterised by extreme variability in overall Antarctic sea-ice extents, with record maxima in 2012–2014 (Reid and Massom, 2015) being followed by a strong negative anomaly beginning in 2015/2016 (e.g., Turner et al., 2017; Meehl et al., 2019), and, most recently, the lowest extent on record in 2021/2022 (Reid et al., 2022; Turner et al., 2022).

The MEASO framework divides Antarctica into five sectors, namely the Atlantic, Central Indian, East Indian, West Pacific and East Pacific sectors (Figure 2; Table 1). The Antarctic Peninsula, bordering the East Pacific and Atlantic sectors, is the best studied region biologically, with the western Antarctic Peninsula (wAP) currently the region of greatest environmental change, even when accounting for the cooling trend in the 1990s (Bozkurt et al.,

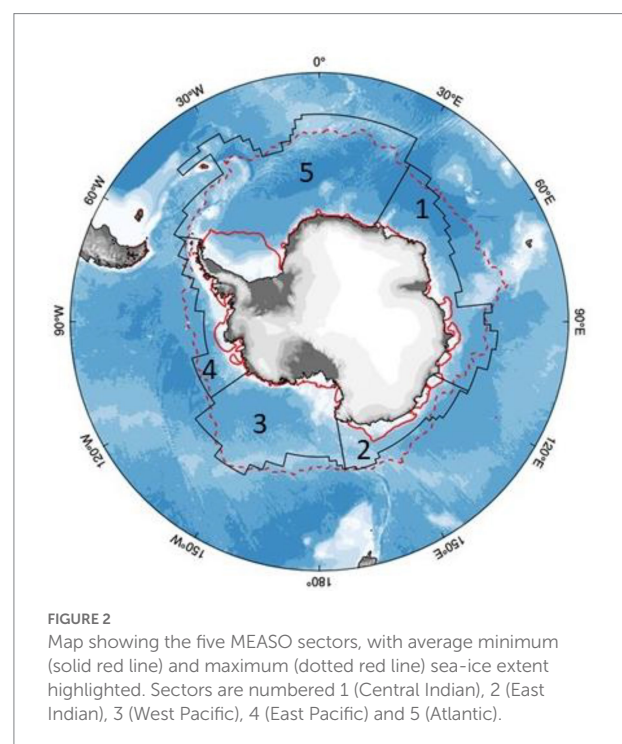


TABLE 1 Summary of the variation in physical factors of Antarctic sea ice between MEASO sectors (see Figure 2).

(a) Traits and trends of sea ice						
Features	Central Indian	East Indian	West Pacific	East Pacific	Atlantic	Ref
Minimum extent of sea ice reached (month/s)	February	February	February	February, March	February	<sup>1</sup>
Maximum extent reached (month/s)	October	September and October	Variable, July–November	August, September	Variable, August to October	<sup>1</sup>
Trend in sea ice extent over 40 years	Positive trends in all months	Positive trends for 10 months, negative trends for 2 months (September, November)	Positive trends for 10 months, negative trends for 2 months (February, March)	Summer and autumn trends are negative, winter are positive and autumn are mixed	Negative trends in winter and spring but positive trends in summer and autumn.	<sup>1</sup>
Trends in snow cover	Steady increase that reversed in late 20th century	Steady increase that reversed in late 20th century	Decreased accumulation over western WAIS*	Increased accumulation over Antarctic Peninsula and eastern WAIS	There was an overall increase in snow depth between 1986 and 2013	<sup>2,3</sup>
Platelet ice		Common offshore from Mirny, possible accretion adjacent to Mertz Glacier Tongue	In west McMurdo Sound occurs earlier in the season and makes up a high % of sea ice thickness; sometimes absent in east McMurdo Sound.	No platelets observed in Amundsen Seas or Bellingshausen, except for Pine Island	Platelets close to ice-shelf edge or coastal polynyas can be 4–10 m thick; 11–50% of total sea ice thickness	<sup>4</sup>
Fast ice, climatological minimum extent (km <sup>2</sup> ) <sup>†</sup>	66,534	68,960	25,092	20,982	33,504	<sup>5</sup>
Fast ice, climatological mean extent (km <sup>2</sup> ) <sup>†</sup>	157,452	145,996	35,561	49,726	63,663	<sup>5</sup>
Fast ice, climatological maximum extent (km <sup>2</sup> ) <sup>†</sup>	14,229	198,165	43,506	78,762	85,744	<sup>5</sup>
Pack ice, climatological minimum extent (10 <sup>6</sup> km <sup>2</sup> )	0.187	0.378	0.575	0.457	1.228	<sup>6</sup>
Pack ice, climatological mean extent (10 <sup>6</sup> km <sup>2</sup> )	1.896	1.232	2.846	1.413	4.244	<sup>6</sup>
Pack ice, climatological maximum extent (10 <sup>6</sup> km <sup>2</sup> )	3.778	2.000	4.142	2.258	6.643	<sup>6</sup>

(b) Summary of qualitative differences between drivers in MEASO sectors relative to the Atlantic Sector (based on Morley et al., 2020). Central and East Indian Sectors are combined

	West Pacific	East Pacific	Indian	Future
<i>Drivers</i>				
Temperature (T)	–	–	+	+
Storminess (S)	0	0	+	+
Time of freeze (F)	0	+	0	+
Time of melt (M)	+	0	+	–
Circumpolar Deep Water (C)	0	+	+	+
Latitude (L)	0	+	+	0

+ denotes change greater than the Atlantic, – change less than the Atlantic and 0 is no change.

<sup>1</sup>Parkinson (2019).

<sup>2</sup>Medley and Thomas (2019).

<sup>3</sup>Tison et al. (2017).

<sup>4</sup>Hoppmann et al. (2020).

<sup>5</sup>Fraser et al. (2020).

<sup>6</sup>Reid et al. (2022), values calculated based on satellite passive-microwave ice concentration data (Cavalieri et al., 1996).

\*West Antarctic Ice Sheet.

<sup>†</sup>Calculated for the years 2000–2018.

2021). Landfast ice represents between 4.0% (during winter) and 12.8% (during late summer) of total sea ice area, with the largest area found in the central and east Indian sectors, and only small areas in the remaining three sectors (Fraser et al., 2021). While circum-Antarctic sea-ice extent showed no significant changes based on satellite data from 1979 to 2018 (IPCC, 2019, 2021), the regional response is divergent, with the East Pacific sector (wAP, including Bellingshausen and Amundsen Seas) showing ice loss, while West Pacific (Ross Sea) and Atlantic (Weddell Sea) sectors gained sea ice and the Indian sectors show no clear trend. There is also significant seasonal variability in the trends (Table 1), such that some seasons are associated with decreases in the ice while others remain static; only the western Ross Sea shows a trend that is statistically significant during all seasons (Holland, 2014). The IPCC (2021) ranks meridional winds as an important driver of sea-ice extent with *high confidence*. Antarctic sea ice is changing at a rate that is much lower than observed for Arctic sea ice, which is likely due to Southern Ocean circulation driving surface heat from anthropogenic warming deeper into the water column. While the decrease in overall Antarctic sea-ice coverage is believed to be too modest to be separated from natural variability (*high confidence*; IPCC, 2021), it is probable that if anthropogenic greenhouse gas emissions continue at the current rate, the loss of seasonal sea ice within the next 50 years could be as high as 40% (Rintoul et al., 2018).

### 3. State of knowledge of the sea ice associated biota

Biogeographical patterns for Antarctic sea-ice biota are largely based on patchy sampling efforts in both time and space. However, there are considerable data available on the distribution, population structure and ecology of Antarctic krill (*Euphausia superba*), as a result of its importance as key species in the food web (Johnston et al., 2022), and in supporting an international fishery managed by the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The SCAR (Scientific Committee on Antarctic Research) Biogeographic Atlas of the Southern Ocean (De Broyer et al., 2014) summarised knowledge of distributions of many key species, including those that associate with sea ice (Duhamel et al., 2014; Swadling, 2014). Much of these data are geographically patchy and insufficient in duration for evaluating the current status of ice-associated species. In many cases chlorophyll *a* concentration is the only biological parameter recorded from ice cores and there are limited winter biological data available for most ice-covered regions (Meiners et al., 2012). Sampling of landfast ice habitats is biased in favour of locations close to Antarctic research stations (Meiners et al., 2018), while for the pack ice there is a strong seasonal emphasis on sampling during spring–summer marine research cruises, particularly around the Antarctic Peninsula and the Weddell Sea (Meiners et al., 2012). This paper focusses on the lower trophic

levels that are associated with sea ice, including algae, zooplankton and fish. Further analyses in relation to the MEASO can be found in Pinkerton et al. (2021) for phytoplankton and Johnston et al. (2022) for zooplankton. Pelagic marine predators are discussed in Bestley et al. (2020).

#### 3.1. Ice algae

The biomass of ice-associated communities is generally dominated by autotrophs, in particular pennate diatoms, but also flagellated algal species (e.g., van Leeuwe et al., 2018). Ice-algal communities form distinct communities in bottom, interior and surface layers of sea ice floes (Meiners et al., 2012, 2018). Spatial and temporal distributions of ice-algal communities, and their productivity, are strongly controlled by environmental processes, e.g., light availability and nutrients. Surface communities are promoted by snow loading resulting in surface flooding by seawater and brine, which creates surface-slush and gap layers that form habitat (Fritsen et al., 1994; Kattner et al., 2004; Ackley et al., 2008). In thicker pack ice, interior communities are likely to emerge following the rafting and ridging of ice floes, which are two processes that significantly contribute to the dynamical thickening of Antarctic sea ice (Worby et al., 2008). Furthermore, scavenging of phytoplankton during ice formation (and particularly frazil-ice formation Garrison et al., 1989; DeJong et al., 2018) and subsequent growth of incorporated algae may explain the occurrence of interior communities in undeformed sea ice (Arrigo et al., 2010). Bottom ice-algal communities thrive in the lowermost porous parts of sea ice floes characterised by favorable brine salinities and high nutrient availability. Surface and interior sea-ice algal communities are a characteristic feature of Antarctic pack ice (Meiners et al., 2012), while bottom algal communities generally dominate integrated ice algal biomass in Antarctic pack ice (Meiners et al., 2012). Extremely high ice algal biomass concentrations (with values >1,000 mg chlorophyll *a* m<sup>-3</sup> of melted ice) have been reported for Antarctic fast ice containing platelet ice (Arrigo et al., 1995; Günther and Dieckmann, 1999), which forms from super-cooled Ice Shelf Water at the base of sea ice adjacent to ice shelves (see Section 2; Langhorne et al., 2015; Hoppmann et al., 2020). This sub-ice platelet layer under landfast ice provides a large surface area that serves as an important algal micro-habitat and a critical hatching and nursery ground for Antarctic silverfish, *Pleuragramma antarcticum* (e.g., Vacchi et al., 2004, 2012; Ghigliotti et al., 2017).

Ice algae contribute substantially to the regional annual primary production of Southern Ocean ice-covered areas (Legendre et al., 1992; McMinn et al., 2010; Pinkerton et al., 2021). The ice algal communities are strongly affected by light availability and by the thermodynamic sea ice regime and its phase-equilibrium that regulates percolation and convection of sea ice brines, thereby controlling vertical material transport within the sea ice and across the ice-water interface (Saenz and Arrigo, 2014).

In general, there is an increase in the relative contribution of ice-algal production to overall production with increasing sea-ice cover duration. Model outputs suggest that ice algae contribute about 10%–20% to the overall sea-ice zone production of the Southern Ocean (Saenz and Arrigo, 2014). The ice algal production generally continues through the autumn and becomes re-invigorated in spring when light conditions for water column production is low, extending the productive season and reducing seasonal oscillations in food supply for pelagic and benthic food webs (Swadling et al., 2000, 2004; Kohlbach et al., 2018; Wing et al., 2018). Dominant taxa in pack ice include the diatoms *Fragilariopsis curta*, *Fragilariopsis cylindrus*, *Nitzschia stellata* and *Pseudonitzschia tugiduloides* while *F. curta*, *Entomeneis kjellmanii* and *N. stellata* (Scott et al., 1994; Takahashi et al., 2022) and *Berkeleya adeliensis* (Ryan et al., 2006) are more characteristic of fast ice. Surface communities tend to be dominated by flagellated taxa such as the dinoflagellate *Polarella glacialis* (Thompson et al., 2006).

### 3.2. Copepods (Arthropoda)

There are four common species of copepods that inhabit the brine channel system of sea ice, namely the calanoids *Stephos longipes* and *Paralabidocera antarctica* and the harpacticoids *Drescheriella glacialis* and *Harpacticus furcatus*. These copepods are small in size, measuring no more than 600 µm in width, and can number in the thousands of individuals per square metre of ice (Swadling et al., 1997, 2000; Kramer et al., 2011; Bluhm et al., 2017). All of these species have circum-Antarctic distributions, although *P. antarctica* is abundant along the East Antarctic coast (Tanimura et al., 1984; Swadling et al., 2000; Loots et al., 2009), while *S. longipes* is prevalent in the Weddell, Amundsen, Bellingshausen and Ross seas (Schnack Schiel et al., 1995, 1998; Guglielmo et al., 2007). Copepods are important in coastal sea-ice ecosystems as prey items for fish (e.g., *Trematomus borchgrevinki*, Hoshiai et al., 1989), which in turn are food for other marine predators (Johnston et al., 2022). Both *P. antarctica* and *S. longipes* have also been found in summer platelet ice (Günther et al., 1999) in the Drescher Inlet (72°50'S, 19°02'W) in the Weddell Sea. Kiko et al. (2008a) also found high abundances of *S. longipes* in the infiltration layer and Kiko (2010) argues that the acquisition of antifreeze properties via horizontal gene transfer might be an adaptation specifically to the occurrence of extremely low temperatures in this habitat. The four common ice-associated copepods use sea ice as a nursery ground, although the extent of their reliance on ice varies seasonally. *Paralabidocera antarctica* show synchronised development, with an unusually long overwintering phase as the naupliar stages that live within the brine channel system; when they reach late copepodid and adult stages in spring, they leave the sea ice to feed and reproduce at the under-ice surface (Tanimura et al., 1996; Swadling et al., 2004). *Stephos longipes* occupies the sea ice predominantly as nauplii

(Schnack Schiel et al., 1995; Costanzo et al., 2002) then relocates to the water column, with some individuals remaining in contact with the ice (Guglielmo et al., 2007) and others moving into deeper waters (Kurbjeweit et al., 1993). *Drescheriella glacialis* carry their eggs in paired sacs and show overlapping generations throughout the year. This species inhabits the interstices of the ice, feeding on ice algae and other particulate organic matter (Schmidt et al., 2003). These ice-associated species are also known to appear in the water column as sea ice is melting, highlighting the inter-relationships between sea ice and the pelagic systems (Makabe et al., 2022).

At the ice-water interface, a greater diversity of copepod species uses the ice as feeding grounds and/or for refuge. Frequently-recorded species include the calanoids *Ctenocalanus citer*, *Calanus propinquus* and *Microcalanus pygmaeus*, while cyclopoid copepods include *Oithona similis*, *Oncaea curvata* and *Pseudocyclopina belgicae*. *Calanus propinquus* is a biomass dominant species in the Southern Ocean; a proportion of the population remains in surface waters during winter where the individuals stay trophically active (Burghart et al., 1999), with stable isotope analysis suggesting this species could change its feeding mode to include sea-ice algae (Jia et al., 2016). *Calanus propinquus* also showed nocturnal feeding activity during winter and a modest vertical migration by descending into deeper layers during daytime (Hunt et al., 2014). *Pseudocyclopina belgicae* is the only cyclopoid copepod that might have a strong association with sea ice during its reproductive cycle, possibly overwintering in the ice as late-stage copepodites (Waghorn and Knox, 1988; Menshenina and Melnikov, 1995). Note that while copepods represent considerable diversity and biomass in ice-associated habitats, other groups including pteropods (Thibodeau et al., 2019) and amphipods (Rakusa Suszczewski, 1972; Richardson and Whitaker, 1979; Krapp et al., 2008) can be important in the under-ice environment. Moreover, ciliata, foraminifera, platyhelminthes, and rarer species such as the nudibranch *Tergipes antarcticus* and the anemone *Edwardsiella andrillae* (Daly et al., 2013) and even ctenophores are found inhabiting the brine channel system and/or the infiltration layer (e.g., Kiko et al., 2008a,b; Kramer et al., 2011 and references therein). These taxa are not addressed in this review.

### 3.3. Euphausiids (Arthropoda)

Antarctic krill, *Euphausia superba*, are a major link between primary producers and higher trophic levels, and use seasonal sea ice as habitat and as a potential source of their winter food supply (Quetin and Ross, 2009). Survival through the first winter is a critical time in the life cycle of krill (Kohlbach et al., 2018; Murphy et al., 2018; Johnston et al., 2022). Larval krill rely on habitat complexity (e.g., rafting, ridging) in sea ice for refuge from predators (Daly, 2004; Meyer, 2012; Meyer et al., 2017, 2020) and as a site of reduced competition for resources (David

et al., 2021). Recruitment is driven largely by winter survival of krill larval stages, which is the period of growth, when they are very susceptible to climate change (Flores et al., 2012; Meyer et al., 2020). Under poor feeding conditions, larval krill cannot grow and moult to their next stage of development (Ross and Quetin, 1991). Larval krill enter their first winter with no lipid reserve and, unlike adult krill, they need to feed continually to meet their energetic needs (Kohlbach et al., 2018; Thorpe et al., 2019). Without food they die within days (O'Brien et al., 2011). Furcilia larvae are capable of scraping ice algal films from the ice surface, especially from greenish sea ice (Hamner et al., 1989). However, as the larvae are not well-equipped to actively harvest sea ice-entrained algal cells in the winter when algal films on the ice surface are not well developed, they rely on the cells being released into the water column by physical processes including ice melting (Meyer et al., 2017). In the autumn, algae are entrained into sea ice as it grows, and these algae serve as potential food for larval krill (Kohlbach et al., 2018). Krill can exploit additional food sources in addition to sea ice algae, such as microzooplankton or detrital material within sea ice (Schmidt et al., 2014; Virtue et al., 2016). There is a strong correlation between sea ice extent and krill populations, which varies regionally (Massom et al., 2006; Atkinson et al., 2019), while the timings of annual sea-ice advance and retreat are another important factor (Quetin et al., 2007). In the Antarctic Peninsula region, krill recruitment is directly correlated with winter sea ice extent (Loeb and Siegel 1995; Johnston et al., 2022). Warming and ice loss has led krill populations in the Southwest Atlantic sector to contract southward. Numerical densities have declined sharply and the population has become more concentrated towards the Antarctic shelves (Atkinson et al., 2019). However, how representative these findings are for the entire Southern Ocean remains unknown and needs to be investigated.

Crystal krill, *Euphausia crystallorophias*, has a circumpolar distribution and is a smaller counterpart of Antarctic krill, replacing it in neritic environments (Harrington and Thomas, 1987; Thomas and Green, 1988; Ainley et al., 2004; Johnston et al., 2022). Highest crystal krill densities are generally associated with ice shelves and coastal polynyas (Boysen Ennen et al., 1991; Pakhomov and Perissinotto, 1996; La et al., 2015; Davis et al., 2017). The crystal krill synchronise their reproduction with coastal sea ice conditions including the appearance and persistence of polynyas. Spawning is initiated under fast ice but peaks during coastal polynya breakout (Pakhomov and Perissinotto, 1996). Eggs of crystal krill are neutrally buoyant, which allows them to concentrate in the upper layers, while hatched larvae are often associated with sea ice (Pakhomov and Perissinotto, 1996; Daly and Zimmerman, 2004; Wiebe et al., 2011). Crystal krill has a narrow thermal habitat restricted to coldest, coastal waters and thus can be vulnerable to climate change (Guglielmo et al., 2009; Papot et al., 2016). Changes in sea ice “dynamics”, potential pelagic

ecosystem modifications and shift of the Antarctic krill into the coastal environments under climate change may rebalance interactions and increase competition between two species, although with unknown outcomes at this point (Smith et al., 2014; Papot et al., 2016). Nevertheless, coastal seas with large continental shelves may provide crystal krill with refugia pockets, limiting its range.

### 3.4. Salps (Chordata)

Salps are gelatinous organisms that are found over a wide area of the Southern Ocean and are most numerous north and south of the Antarctic Polar Front (Foxton, 1966; Pakhomov et al., 2002; Johnston et al., 2022). Salps exhibit a complex life cycle and reproduction consisting of alternating generations of sexual (colonial forms or blastozoids) and asexual (single forms or oozoids) forms that differ morphologically (Foxton, 1966; Bone and Trueman, 1983). Salps can pump water through their internal cavity using their muscles, to create water currents that they use for propulsion, breathing, and feeding (Bone et al., 2000). Salps are indiscriminate filter feeders and ingest a wide range of particles, from 1  $\mu\text{m}$  (bacteria) to several mm (small crustaceans; Sutherland et al., 2010) in size and, based on lipids and molecular observations, flagellates are a large component of their diet (von Harbou et al., 2011; Metfies et al., 2014). It has been documented that at high chlorophyll *a* concentrations ( $>>1 \text{ mg m}^{-3}$ ) salps can suffer clogging of the feeding mesh and are rarely found in regions of dense phytoplankton blooms (Perissinotto and Pakhomov, 1998). Observations of the faecal pellets of salps suggest that some of these larger particles are passed through the digestive tract relatively intact and are therefore lost to epipelagic food webs as the heavy pellets sink rapidly out of the euphotic zone (Cabanes et al., 2017; Iversen et al., 2017; Pauli et al., 2021a). They appear to flourish in warmer waters in the Southern Ocean and in regions of low to moderate chlorophyll *a* concentration (Loeb et al., 1997; Pakhomov et al., 2002; Pillai et al., 2018). In the sea ice zones of the Southern Ocean, information about salps is limited but it is noted that in the Antarctic Peninsula region, where temperatures are warming much faster than the global average, they replace krill on a regular basis and this appears to be contingent on sea ice conditions (Pakhomov et al., 2002; Atkinson et al., 2004). Over the last century, salps expanded southward, which increased their spatial overlap with the Antarctic krill distribution range (Atkinson et al., 2004). However, salp populations in the high Antarctic are not permanently established (Pakhomov et al., 2011). Although salps have been observed under the seasonal sea ice (Perissinotto and Pakhomov, 1998; Pakhomov et al., 2018), krill are not yet replaced by salps because the species occupy different water masses and salps do not respond directly to sea ice conditions.



### 3.5. Fish (Chordata)

Sea ice in the Southern Ocean is an important habitat for a variety of notothenioid fish species, traditionally defined as “cryopelagic” species (Andriashev, 1987). *Trematomus borchgrevinki* is the best known ice-associated fish, with adaptations for cryopelagic life including camouflage against the background colour of the ice owing to silvery reflective layers beneath the skin and in the eyes, and protection from freezing provided by the high quantity of antifreeze glycoproteins in their body fluids (Eastman and DeVries, 1985). Other notothenioid species, which also contain antifreeze glycoproteins and associate with sea ice, include *Trematomus amphitreta*, *Trematomus* (=Pagothenia) *brachysoma* and *Trematomus* (=Cryothernia) *peninsulae* (Duhamel et al., 2014). Cryopelagic fishes often stay inactive, in an upside-down position, with their ventral side against the ice, and move erratically over short distances, possibly using the underside of the sea ice as a resting structure to reduce energetic requirements (Gon and Heemstra, 1990; Kock, 1992; Gutt, 2002). Large adult specimens of *T. borchgrevinki* swim slowly, in the normal position, in close vicinity to the sea ice, and hide between crevices (Eastman, 1993; Gutt, 2002), using the sea ice as a protective structure to avoid predation.

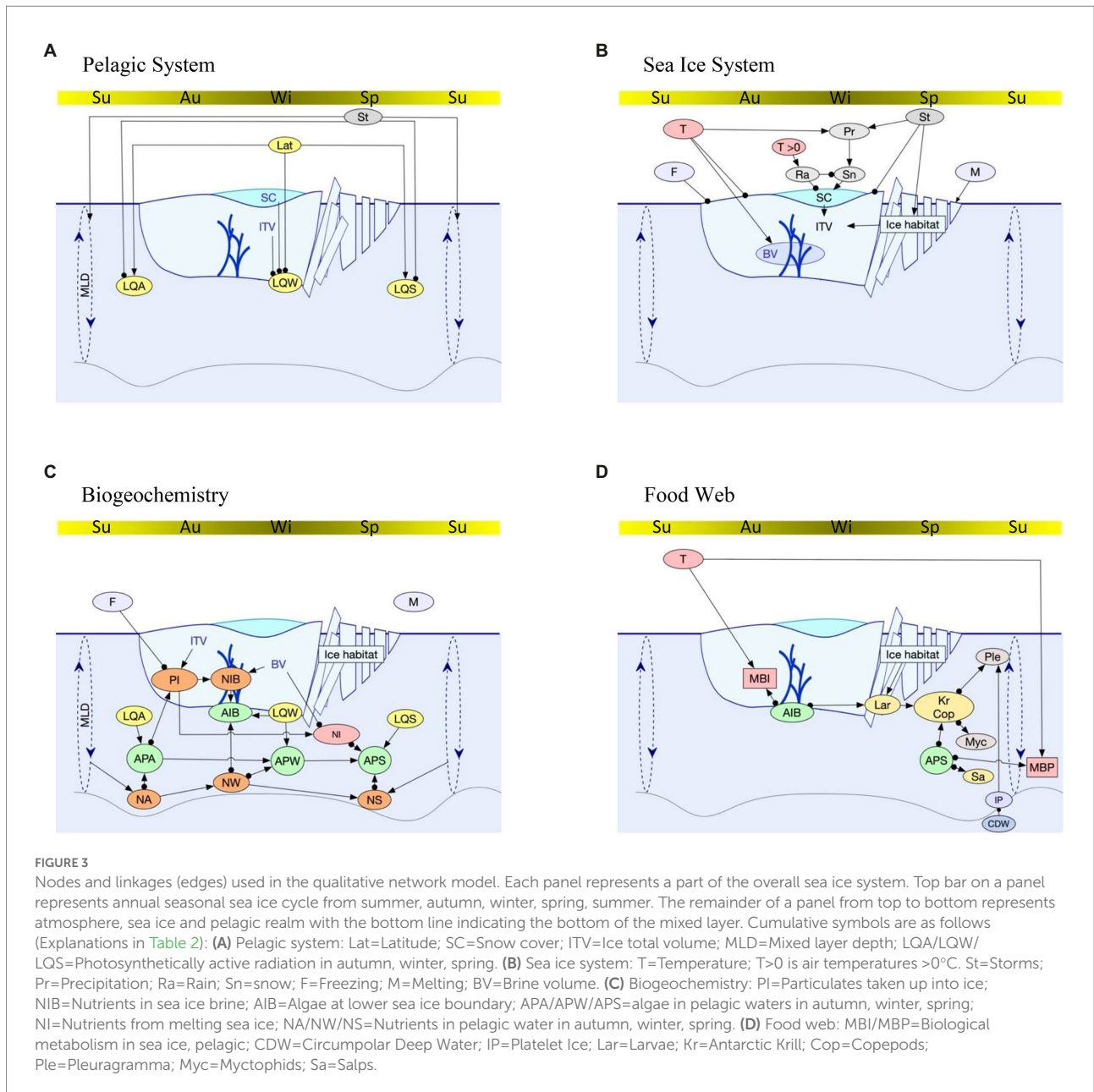
Although not included in the list of cryopelagic species, there are species whose distribution is influenced by the presence/absence of sea-ice cover; e.g. *Trematomus newnesi* occupy a cryopelagic niche as juveniles (Duhamel et al., 2014). Although living in swarms and being largely planktivorous, *T. newnesi* feeds on sea ice-associated fauna (Casaux et al., 1990; La Mesa et al., 2000). *Trematomus eulepidotus* occurs in the shallow coastal waters of Terra Nova Bay early in the summer, when the area is covered by sea ice, while moving into deep waters later in the season and after the sea-ice melting, thus suggesting an advantageous use of the sea-ice cover as shelter by this species (Vacchi, personal observation).

Some other fish species are linked to the sea ice during a crucial phase of their life, notably their embryonic development. Dragonfish *Gymnodraco acuticeps* eggs have been found in nests in shallow waters amongst anchor ice (submerged fast ice that is attached to the bottom), and ready-to-hatch eggs of *T. borchgrevinki* have been collected within a crevice on the side of an iceberg (Cziko et al., 2006). The most striking example is provided by the Antarctic silverfish *Pleuragramma antarcticum* (a commonly cited synonym is *P. antarctica*), whose developing eggs have been found dispersed in the platelet ice layer under the solid fast ice at Terra Nova Bay (Ross Sea), where they form the only known to-date silverfish hatching area (Ghigliotti et al., 2017). Survival of embryos and early larvae in that icy environment is possibly due to a suite of morphological adaptations (Cziko et al., 2006; Bottaro et al., 2009). Furthermore, the platelet-ice layer with its tridimensional crystal lattice structure provides protection from large predators (Guidetti et al., 2015).

## 4. Qualitative network modelling

In the following sections, we use qualitative network modelling (based on Melbourne-Thomas et al., 2012) to investigate potential synergistic, antagonistic and cascading effects on the ecosystem, given long-term change in the physical and chemical nature of the sea ice system. Details of the rationale behind qualitative network modelling are presented in Appendix. In short, we applied the network diagram approach of Melbourne-Thomas et al. (2012) to construct a qualitative network model where plausible interactions (edges) between the components (nodes) are either positive, neutral or negative, but with no quantitative magnitude of change. Such a network can be used to synthesise information on individual relationships between nodes to better capture the chains of interactions (cascades), compounding effects (synergisms, antagonisms) and positive and negative feedback loops. Many simulations (up to 10,000) can then determine probabilities of nodes increasing, decreasing or not changing when one or more of the physical attributes of the system are permanently changed (positively or negatively), in a process known as a press perturbation (Melbourne-Thomas et al., 2012). We undertook several press perturbations using the R package *QPress* (Melbourne-Thomas et al., 2012). In describing the outcomes, we focus on those impacted nodes where the directional change has a probability greater than or equal to 0.6, but report all probabilities.

The interactions between the different physical and biological components investigated are shown in Figure 3. The habitat variables that were considered in the model are precipitation (falling as rain or snow, depending on temperature), snow cover thickness, habitat in the sea ice (complexity, e.g., ridging and rafting, total ice volume, a function of area, duration, and thickness, and brine volume), platelet ice, nutrients in the ice and pelagic and light (in the autumn, winter and spring seasons; Table 2). Biotic variables that were included are ice algae and seasonal phytoplankton, copepods and Antarctic krill (with larvae of both groups as a separate node), salps, fish (myctophids, *Pleuragramma antarcticum*) and ecosystem metabolism in the ice and pelagic (Table 2). The nodes and edges are simplified from a more complex system structure. Nodes may represent many attributes that interact with other nodes in the same way. Most edges are self-explanatory and represent the links between nodes. Some edges represent the outcome of complex interactions rather than a full chain of events in order to avoid unwanted feedbacks in the qualitative model. For example, an increase in the proportion of ice that is brine will give rise to a decrease in nutrients released from the ice in spring. This is because the increase in brine increases the availability of particulate nutrients in the ice to algal production, which therefore reduces the particulate nutrients in the ice released in the spring melt. A different combination of edges would make this difficult to represent. Similarly, we have not represented the full complexity of the brine system food web, which in some regions contains many small meiofaunal species with numerous trophic interactions.



## 5. Response of sea ice and biota to spatial and temporal shifts in sea ice habitats

The primary drivers of sea ice habitats that are considered in this paper are ocean temperature, air temperatures changing the type of precipitation, storminess, change in the length of sea ice season, the potential effects of Circumpolar Deep Water, and the latitude in which the system is located. We use the qualitative network model to understand how changes in all of these drivers may impact the sea ice physical and biological systems. First, to assist our understanding of the roles of different drivers, we examined the effects of changes in individual drivers according to common hypotheses. Second, we applied known differences in the

drivers around Antarctica to investigate the likely differences in sea ice systems between MEASO sectors. Last, we examined the consequences of future change in the drivers for Antarctic sea ice systems.

### 5.1. Responses of sea ice systems to change in individual drivers

The following hypotheses were tested with the qualitative network model, with the results presented in Table 3:

1. Increasing temperature leads to an increase in the relative cost of sympagic and pelagic metabolism and a decrease in biomass;

TABLE 2 Description of the nodes used in the qualitative network model, as displayed in Figure 3.

Name	Code	Explanation
<i>Drivers</i>		
Latitude	L	Governs light available per day – higher latitude means more daylight hours in early autumn and late spring but less light in winter; 0–90°S
Time of freeze	F	Sea ice season – Timing of advance of sea ice formation in autumn likely to be later (Julian days)
Time of melt	M	Sea ice season – Timing of retreat of sea ice in spring likely to be earlier (Julian days)
Storms	S	Storms break up ice and give rise to rafting etc., thereby increasing habitat for krill. Storms also give rise to increased mixed layer depth, and increases in cloud cover, precipitation, wind strength and wave action
Temperature >0°C	Tg0	If temperature is >0°C, then precipitation falls as rain rather than snow; there is a likelihood of increased days at these temperatures
Temperature	T	Warming air temperature leads to increases in brine volume and brine channel connectivity (permeability) in ice, increases the metabolic rate for animals, and causes ice loss through melt (°C)
CDW with ice shelf cavity	C	Interaction of Circumpolar Deep Water with ice shelves causes formation of platelet ice
<i>Physical: Light</i>		
Light Autumn	LQA	Light available to pelagic algae in autumn, affected by latitude, cloud cover, sea ice cover, snow cover and mixed layer depth
Light Winter	LQW	Light available to pelagic algae in winter, affected by latitude, cloud cover, sea ice cover, snow cover and mixed layer depth
Light Spring	LQS	Light available to pelagic algae in spring, affected by latitude, cloud cover, sea ice cover, snow cover and mixed layer depth
<i>Physical: Precipitation</i>		
Precipitation	P	Total precipitation that could fall as snow or rain
Precipitation wet (rain)	PW	Precipitation will fall as rain if temperature is >0°C
Precipitation dry (snow)	PD	Precipitation will fall as snow if temperature is <0°C
Surface snow	IS	Snow cover that accumulates on the ice; thickness will vary in response to surface conditions (storms, temperature)
<i>Physical: Ice Processes</i>		
Ice total volume	ITV	Total volume of ice, proxy for available habitat, is a function of ice thickness, ice extent and age of ice. This node governs the relative importance of sea ice processes compared to pelagic processes, i.e., more sea ice results in more particulates taken up into the sea ice which means less remaining in the water column
Brine volume	IB	Proportion of the total ice volume that is brine, thereby influencing the proportion of particulates in the ice available as nutrients. The factors influencing this at present are temperature (modulated by snow cover), salinity, rate and mode of ice formation (frazil v columnar ice), and thickness
Habitat complexity	IH	Habitat complexity is a product of ice deformation (ridging, rafting) and reformation. It is influenced by storms as ice motion is a response to winds and currents
Platelet Ice	PI	Platelet ice is needed for reproduction of <i>Pleurogramma antarcticum</i> . Platelet ice results from the interaction of CDW and ice shelves
<i>Nutrient pools</i>		
Nutrients Winter	NW	Nutrients in the water in winter
Nutrients Autumn	NA	Nutrients in the water in autumn
Nutrients Spring/Summer	NS	Nutrients in the water in spring and summer
Ice Particulate Pool	IPP	Phytoplankton frozen into ice as a particulate pool during autumn freeze-up
Ice Available Nutrients	NI	Nutrients made available to the ice-dependent community through brine channels
Nutrient Pool Released from Ice	NIR	Nutrients released from ice upon melting in spring
<i>Biology: Algae</i>		
Algae Pelagic Autumn	APA	Phytoplankton in the water column in autumn

(Continued)

TABLE 2 (Continued)

Name	Code	Explanation
Algae Pelagic Winter	APW	Phytoplankton in the water column in winter
Algae Pelagic Spring	APS	Phytoplankton in the water column in spring, including that released from ice upon melting in spring
Ice Algae Bottom	AIB	Growing in the bottom of the ice and at the ice/water interface
Copepods and krill larvae	ZCKL	Copepods and krill larvae, in the sea ice and pelagos, grazing on algae
Copepods and krill	ZCK	Copepods and krill, in the sea ice and pelagos, grazing on algae
Salps	ZS	Salps feeding on pelagic algae
Myctophids	FM	Small pelagic fish – using the sea ice habitat as a feeding ground and/or refuge from predators
<i>Pleuragramma</i>	FP	Antarctic silverfish, <i>P. antarcticum</i> , require platelet ice as a nursery ground
Metabolism in sea ice food web	MI	Relative food web metabolism in sea ice, affected by temperature
Metabolism in pelagic food web	MP	Relative food web metabolism in pelagos, affected by temperature

- Increasing air temperatures (number of days when  $T > 0^{\circ}\text{C}$ ) will result in decreased habitat and increasing light, and therefore pelagic primary productivity will increase;
- Storminess will increase habitat complexity, which will lead to increases in sympagic biota;
- Later freezing will lead to less habitat space available for primary producers and ice algae biomass will decrease;
- Earlier melting of sea ice will lead to decreased abundance of ice-associated species;
- Increasing Circumpolar Deep Water (CDW) will result in less platelet ice and therefore the fish *Pleuragramma antarcticum* will decrease in abundance and biomass;
- Higher latitude ecosystems are subjected to less light from late autumn. Increased latitude means shorter days in winter and longer days in summer, shifting primary production away from winter to the advantage of the pelagic system.

### 5.1.1. Change in physical habitat

Increasing temperature would contribute to a decrease in total ice volume over a season, although the decrease would be most likely if atmospheric temperature was  $>0^{\circ}\text{C}$  due to an increase in precipitation as rain. The proportion of the ice as brine would also increase. Temperature of sea ice directly affects porosity and permeability, chemical composition of the pore microstructure and salinity. At  $-5^{\circ}\text{C}$ , the ice fraction of brine represents 35%, and the salinity of the brine is around 87 (Golden et al., 1998). At  $-30^{\circ}\text{C}$ , the brine fraction falls to below 8%, reducing the habitat available for microorganisms, while the salinity of brine increases (Ewert and Deming, 2013), consequently restricting the habitat space to only species that are tolerant to high salinities. Based on the relationships between temperature and brine volume, and given warming air temperatures ( $T_{g0}$  increasing), brine volume, and therefore available habitat, will increase on scales  $<10\text{mm}$ . However,

warming will also increase melting, leading to reduced duration and thickness of the ice cover on the larger scale.

Increased storminess can be described as increased wind speed, higher rates of precipitation (under blizzard conditions) and increased strength and duration of waves. These changes will have complex and possibly contradictory implications for the Southern Ocean sea ice system. Increased windiness will increase wave energy, possibly resulting in deeper ocean mixing while also bringing warmer waters to the surface; this could then increase the loss of ice through basal melt. Increased storminess could also enhance deformation of the ice, leading to greater habitat complexity (IH) and ice total volume (ITV, depending on coincident change in ice areal coverage – also affected by changes in wind direction). Notably, habitat complexity was directly related to storminess in our model. Yet the influences on sea ice-dependent species may be more complex than just the relationship with habitat complexity. Many of the responses relate to changes in extent and duration of sea ice, the timing of the sea ice season relative to the spring and autumn blooms, and the relative importance of pelagic algae and ice algae in the productivity of species.

### 5.1.2. Responses of the biological system

i. *Increasing temperature.* Warming produced positive responses in relative metabolism for both sympagic and pelagic communities, while negative or neutral responses in the algae, copepods, krill, salps and fish suggest that their overall numbers would either decrease (negative) or remain the same (neutral). An increase in temperature is likely to result in more resources going towards metabolism rather than growth of individuals and reproduction. Thus an increase in temperature means an increase in the cost of metabolism relative to the production of biomass, resulting in a reduction in biomass.

ii. *Increase in the number of days  $>0^{\circ}\text{C}$ .* Increases in the number of days that are above  $0^{\circ}\text{C}$  produced opposing responses in the two habitats, whereby sea ice metabolism

**TABLE 3** Assessment of the impacts of key physical drivers of change on the magnitude of food web components associated with sea ice, based on the Qualitative Network Modelling.

Node	Temperature (+)	Storms (+)	Temperature greater than zero (+)	Freezing (later)	Melt (earlier)	Circumpolar Deep Water (+)	Latitude (+)
Ice particulate pool frozen into ice (IPP)	0.50	0.72	-1.00	-1.00	-1.00	0.00	1.00
Nutrient pool released from ice (NIR)	-0.59	0.73	-0.96	-0.99	-0.98	0.99	0.64
Nutrients available in ice (NI)	0.81	0.72	-1.00	-1.00	-1.00	0.00	1.00
Nutrient supply autumn (NA)	0.50	0.97	-1.00	-1.00	-1.00	0.00	-1.00
Nutrient supply winter (NW)	0.61	0.81	-0.93	-0.82	-0.88	0.00	0.72
Nutrient supply spring (NS)	0.79	0.84	-0.59	0.51	-0.54	1.00	-0.79
Bottom ice algae (AIB)	-0.55	-0.63	-0.52	-0.76	-0.64	0.00	-0.57
Pelagic algae spring (APS)	-0.79	-0.57	0.59	-0.51	0.54	-1.00	0.79
Pelagic algae autumn (APA)	-0.50	-0.71	1.00	1.00	1.00	0.00	1.00
Pelagic algae winter (APW)	-0.60	-0.72	0.93	0.97	0.95	0.00	-0.69
Copepods & Antarctic krill (ZCK)	-0.68	0.61	0.54	-0.70	-0.59	1.00	0.64
Copepod nauplii and Antarctic krill (larvae) (ZCKL)	-0.55	0.71	-0.52	-0.76	-0.64	0.00	-0.57
Salps (ZS)	-0.79	-0.57	0.59	-0.51	0.54	-0.99	0.79
Metabolism in sea ice (MI)	0.77	-0.63	-0.52	-0.76	-0.64	0.00	-0.57
Metabolism in pelagic (MP)	0.66	-0.57	0.59	-0.51	0.54	-0.99	0.79
Myctophids (FM)	-0.68	0.61	0.54	-0.70	-0.59	1.00	0.64
<i>Pleuragramma antarctica</i> (FP)	-0.68	0.61	0.54	-0.70	-0.59	-1.00	0.64
Precipitation (P)	1.00	1.00	0.00	0.00	0.00	0.00	0.00
Precipitation – snow (PD)	1.00	1.00	-1.00	0.00	0.00	0.00	0.00
Precipitation – rain (PW)	0.00	0.00	1.00	0.00	0.00	0.00	0.00
Surface snow (IS)	1.00	1.00	-1.00	0.00	0.00	0.00	0.00
Habitat complexity (IH)	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Total ice volume (ITV)	0.50	0.77	-1.00	-1.00	-1.00	0.00	0.00
Brine volume (IB)	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Platelet ice (PI)	0.00	0.00	0.00	0.00	0.00	-1.00	0.00
Light autumn (LQA)	0.00	-1.00	0.00	0.00	0.00	0.00	1.00
Light winter (LQW)	-0.65	-0.84	1.00	1.00	1.00	0.00	-1.00
Light spring (LQS)	0.00	-1.00	0.00	0.00	0.00	0.00	1.00

Probability of a response from 10,000 simulations: the sign represents whether the probability is for a positive or negative response. Colours show responses with probability >0.6. Blue – negative response; Yellow – positive response; White – probability <0.6.

decreased and pelagic metabolism increased. As expected, pelagic algae increased due to the reduced ice cover and an increase in light. Ice algae decreased, most likely due to a reduction of the available habitat. There were increases in krill, copepods, salps and fish, though the larvae of krill and copepods decreased, indicating the contrasting influences of the pelagic and ice habitats, respectively. Larval and juvenile krill are highly ice-dependent, and consequently any perturbations in sea ice deformation, thickness and extent

(species-specific sea ice “quality”) will directly affect population dynamics (Melbourne-Thomas et al., 2016). Nevertheless, decreased survival of larvae may be offset by increased biomass accumulation by adults. The qualitative model is unable to differentiate between the relative importance of adult productivity and larval/juvenile survival to the overall dynamics of the populations. How increases in adult survival may balance out concurrent decreases in juvenile recruitment depends on the strength of the responses, and cannot

be determined from a qualitative network model. Thus the effects on the total population size are unknown.

iii. *Storminess*. Increased storminess led to decreased light, increased ice habitat and ice volume and concomitant decreases in ice algae and phytoplankton. Algae require a minimum day length to initiate growth so increased cloud cover, particularly in early spring, could decrease the growing season. In contrast, storminess could enhance deep mixing, bringing warmer, nutrient-rich, iron-rich water to the surface, resulting in favourable conditions for algal growth; overall, the model results suggests that light is the primary factor influencing algae in the sea ice and water column. Krill and copepods benefit from the increased habitat that can result from greater storminess, e.g., greater habitat area provides a refuge for krill (Meyer et al., 2017, 2020). The increases in prey could be beneficial for ice-associated fish that are feeding on crustaceans.

iv. *Later freezing and v. earlier melting*. The model simulations show negative responses from krill, copepods and fish and a decrease in larvae of krill and copepods, largely from the reduced volume of sea ice. Lower numbers of crustacean larvae could be a phenological response to reduced annual duration of the ice cover, preventing the ice-associated species from completing their life cycles; e.g. early retreat of sea ice leads to poor recruitment of krill in warm years (Loeb and Santora, 2015). Salps on the other hand responded positively to reduced sea ice coverage, which is to be expected based on observations that salps thrive under conditions of reduced ice cover (Quetin et al., 2007; Loeb and Santora, 2015). At the same time, lower duration of sea ice coverage could lead to increases in phytoplankton in spring as the amount of light reaching the surface layers is increased and sets off the open-ocean bloom earlier in the year.

vi. *Increasing Circumpolar Deep Water (CDW)*. Increased CDW resulted in a negative response in platelet ice and the fish *P. antarcticum*. Upwelled CDW near ice shelves leads to basal melting, and, consequently, platelet ice production is reduced (as per Hoppmann et al., 2020). As *P. antarcticum* requires platelet ice for early life stages (eggs and larvae; Guglielmo et al., 1998; Vacchi et al., 2004, 2012; Ghigliotti et al., 2017), reduction in this ice type leads to poor recruitment of the fish. Evidence from the Antarctic Peninsula (La Mesa et al., 2015; Corso et al., 2022) has shown that numbers of *P. antarcticum* have decreased substantially in line with reductions in sea ice. Consequent effects include increases in copepods and krill and their predators, myctophid fish, while salps decrease.

vii. *Increased Latitude (L)*. Increased latitude means shorter days in winter and longer days in summer, shifting primary production away from winter to the advantage of the pelagic system.

## 5.2. Expectations for differences between Marine Ecosystem Assessment for the Southern Ocean sectors

Using an assessment of drivers in each sector, following Morley et al. (2020), we examined how the response of biota

associated with the sea ice system might vary between the five MEASO sectors (Table 4). We compare how the different sectors might vary relative to the Atlantic Sector because of that sector having a mid-range sea-surface temperature regime in the Antarctic Zone compared to the other sectors.

Table 1 outlines differences in sectors based on available literature. If the global temperature warms by the expected 1.5°C by 2030, it is likely that the Antarctic Peninsula, particularly the northern region, will experience up to 130 days above 0°C (Siebert et al., 2019). Ocean-air interactions will lead to increased ocean turbulence resulting in shoaling of CDW. Increased heating in shallow waters is contributing to the basal melting of ice shelves and, consequently, a reduction in the formation of platelet ice (Hoppmann et al., 2020). Positive CDW incursions yield decreased platelet ice in the East Pacific and Indian sectors compared to the Atlantic, giving an expectation that *Pleuragramma antarcticum* would be less in number in those sectors than the Atlantic. In contrast, while CDW incursions are not expected to be different in the Atlantic sector and the West Pacific (Ross Sea), changes to *P. antarcticum* are expected to be larger in the Ross Sea due to other factors such as difference in productivity, through less metabolic demand in the Ross Sea and greater spring algal growth (Table 4). Silverfish comprise up to 90% of the mid-water fish biomass in the Ross Sea (Smith et al., 2007) and are prey for Weddell Seals, whales, Adélie penguins, emperor penguins and other seabirds (Smith et al., 2007). Sampling for *P. antarcticum* along the western Antarctic Peninsula (wAP) has shown that they are severely reduced in number around the central wAP, a region where they were historically abundant (La Mesa et al., 2015). This was linked by the authors to catastrophic loss of spawning habitat as a result of sea ice loss. The loss of silverfish as a prey item in the central wAP is likely leading to marine predators in the region exhibiting dietary switching, e.g., to myctophids (Moline et al., 2008), for which there is an expectation in our results that myctophids will be more abundant in the East Pacific.

The perturbation responses for the sea ice system in the Pacific sectors are consistent with observations. Sea ice extent and duration are currently increasing in the Ross Sea and decreasing in the Amundsen Sea (Comiso et al., 2011; Stammerjohn et al., 2012; Parkinson, 2019). In the Ross Sea, colder sea surface temperature (SST) and/or more southerly winds lead to a northward extensions of the productive marginal ice zone (MIZ), highlighted in Table 4 by an increase in pelagic algae in the East Pacific sector in spring, though no change occurred in the bottom ice algae. Algae contained in the ice are released by earlier melting, then mixed in the upper layers of the water column to be consumed by meso- and microzooplankton grazing (Hecq et al., 2000). Copepods and krill also increased, while their larvae decreased, perhaps indicating that earlier melting meant less habitat space available for the young stages, reinforcing the importance of adult productivity compared to recruitment driving this population. A reduction in light penetration through the ice may limit sea ice algal biomass, with consequences for krill and other zooplankton. Krill collected under less deformed, thinner ice with less snow cover had higher lipid levels as a result of a

**TABLE 4** Responses of attributes of the sea ice system from qualitative press perturbations of (i) differences in key drivers between MEASO sectors (see [Figure 2](#)) relative to the Atlantic Sector, and (ii) changes in the key drivers in all sectors into the future.

	(i) Differences of sectors compared to Atlantic	(ii) Change of all sectors in future		
	West Pacific	East Pacific	Indian	Future
<b>Drivers</b>				
Temperature (T)	–	–	+	+
Storminess (S)	0	0	+	+
Freezing (F)	0	+	0	+
Melting (M)	+	0	+	–
Circumpolar Deep Water (C)	0	+	+	+
Latitude (L)	0	+	+	0
<b>Responses</b>				
Ice particulate pool frozen into ice (IPP)	0.65	–0.72	0.84	–0.59
Nutrient pool released from ice (NIR)	0.69	–0.60	0.69	–0.58
Nutrients available in ice (NI)	–0.66	–0.85	0.92	0.59
Nutrient supply autumn (NA)	0.65	–0.92	0.84	0.68
Nutrient supply winter (NW)	0.50	–0.68	0.81	0.62
Nutrient supply spring (NS)	–0.74	–0.73	0.78	0.82
Bottom ice algae (AIB)	0.57	–0.58	–0.55	–0.66
Pelagic algae spring (APS)	0.74	0.73	–0.64	–0.70
Pelagic algae autumn (APA)	–0.65	0.92	–0.61	0.55
Pelagic algae winter (APW)	–0.53	0.75	–0.78	–0.52
Copepods & Antarctic krill (ZCK)	0.68	0.71	0.66	0.57
Copepod nauplii and Antarctic krill (larvae) (ZCKL)	0.57	–0.58	0.64	0.55
Salps (ZS)	0.74	0.73	–0.64	–0.70
Metabolism in sea ice (MI)	–0.71	–0.79	0.62	0.53
Metabolism in pelagic (MP)	–0.66	–0.57	0.58	0.53
Myctophids (FM)	0.68	0.71	0.66	0.57
<i>Pleurogramma antarctica</i> (FP)	0.68	–0.68	–0.64	–0.72
Precipitation (P)	–1.00	–1.00	1.00	1.00
Precipitation – snow (PD)	–1.00	–1.00	1.00	1.00
Precipitation – rain (PW)	0.00	0.00	0.00	0.00
Surface snow (IS)	–1.00	–1.00	1.00	1.00
Habitat complexity (IH)	0.00	0.00	1.00	1.00
Total ice volume (ITV)	0.65	–0.77	0.81	–0.52
Brine volume (IB)	–1.00	–1.00	1.00	1.00
Platelet ice (PI)	0.00	–1.00	–1.00	–1.00
Light autumn (LQA)	0.00	1.00	0.51	–1.00
Light winter (LQW)	0.50	0.65	–0.92	–0.61
Light spring (LQS)	0.00	1.00	0.50	–1.00

Key drivers are pressed according to the sign for set of perturbations. Responses show the largest proportion of outcomes of 10,000 simulations, with the sign and colour indicating whether the largest proportion was positive (increase, +, yellow) or negative (decrease, –, blue). Colours are only shown for responses that were >0.6 of outcomes.

higher biomass of sea ice biota ([Virtue et al., 2016](#)). Models also indicate that Antarctic marginal ice zones are important areas of carbon export driven by krill grazing and faecal pellet production

([Belcher et al., 2019](#)). Phytoplankton blooms form at retreating ice-edges due to a combination of melt-water stratification, and release of micronutrients (e.g., iron) and algae from the melting

sea ice (Lancelot et al., 1993; Lannuzel et al., 2016). Ice-edges serve as hotspots for pelagic food-web interactions by providing critical food for pelagic herbivores (Schmidt et al., 2018), which, in turn, are preyed on by higher trophic levels.

Antarctic krill, copepods and their larvae showed mixed responses to the environmental perturbations (Table 4). The Southwest Atlantic (20°W–80°W), which holds >50% of the circumpolar krill stock (Atkinson et al., 2019) has warmed rapidly over the last decades. Their distribution has contracted southward by ~440 km over the past 90 years and become centred more strongly over Antarctic continental shelves (Atkinson et al., 2019). Krill further showed an increase of ~75% in body mass, indicating the presence of more adults and less juveniles in the population and, consequently, a reduction in recruitment. No directional trends in krill population and sea ice have been established outside of the Atlantic sector (Flores et al., 2012).

Our perturbation experiments give an expectation that Antarctic krill would have better conditions in the other sectors in relation to the sea ice zone. These perturbations do not account for total productivity and the size of the area in which that occurs. Nevertheless Antarctic krill populations in other sectors may be relatively stable at present (Yang et al., 2020). With more stable sea ice coverage, no significant evidence for decline in krill stocks in the Indian sector was found (Nicol et al., 2000; Atkinson et al., 2017). The Ross Sea represents a mosaic of functionally different marine subsystems. The environmental changes in the Ross Sea could benefit diatoms and change krill distributions in future, although krill were not considered able to invade much of the continental shelf owing to the requirement for larval development at great depth (Smith et al., 2014). In Terra Nova Bay, large amounts of biopolymeric carbon accumulated in the bottom layer of the ice column concomitantly with the early spring increase in sympagic algal biomass. Such organic material, mostly accounted for by autotrophic biomass, was characterised by high food quality and was rapidly exported to the sea bottom during sea ice melting (Pusceddu et al., 2000). The Amundsen Sea was considered to be a potential new habitat supporting successful krill spawning in future due to delayed sea ice formation and smaller ice concentration which could benefit phytoplankton blooms and facilitate krill recruitment (Piñones and Fedorov, 2016). These models suggest that other regions besides the Atlantic sector could be potential krill biomass hotspots in future.

### 5.3. Expectations for future change

The fate of Antarctic sea ice under a range of greenhouse gas emissions scenarios to 2,100 has been investigated under the auspices of the IPCC's various assessment reports, underpinned by the Coupled Model Intercomparison Project (CMIPs). However, confidence in long-term projection of Antarctic sea ice extent is currently low due to the inability of many global climate models (GCMs) to accurately reproduce large-scale patterns observed by satellite, i.e., either the seasonal cycle or multi-decadal

trends (Turner et al., 2013). Moreover, model estimates of changes in Antarctic sea ice thickness (and hence volume) are of even lower confidence (IPCC, 2021). This is due to a lack (until recently) of reliable large-scale snow and ice freeboard estimates required for accurate computation of the thickness of both sea ice (Paul et al., 2018; Fons and Kurtz, 2019; Kacimi and Kwok, 2020) and its snow cover (Webster et al., 2018). Nevertheless, the former CMIP5 models project a range of decreases in Antarctic sea ice extent of between 8% and 67% for the 21st Century, depending on month of trend and emissions scenario (Collins et al., 2013). Most models predict nearly ice-free summertime (minimum extent) conditions by 2,100 under the highest emissions scenario, known as RCP 8.5 (Collins et al., 2013). There are currently no projections for coastal fast ice, since this ice type is currently not represented in any GCM.

Application of the environmental perturbations to future conditions produced only negative and neutral responses for krill and copepods, including their larvae (Table 4). Changes in the extent and area of the sea ice habitat have not been uniform or unidirectional, so the implications for sea ice-associated organisms are not clear. The magnitude and timing of the spring ice-associated algal bloom has changed over the last three decades and this change is directly related to sea-ice extent and duration of the previous winter (Stammerjohn et al., 2008, 2015). Changes in the timing of annual sea ice advance and retreat will impact the capacity for ice-associated microbes to initiate bloom events in spring. For example, ice algae are a food source for larval Antarctic krill during late winter and early spring. Other studies have highlighted the role of complex under- and intra-ice habitats in providing shelter for larval krill (Frazer et al., 2002; Massom et al., 2006; Meyer et al., 2017) and the importance of sea-ice drift patterns in transporting krill larvae to areas in which they can thrive in spring (Meyer et al., 2017). Strong relationships have also been established between sea-ice conditions (e.g., duration/persistence), their influence on ice algal carbon productivity and export, and subsequently, on coastal benthic community characteristics (e.g., Clark et al., 2017; Cummings et al., 2018). Few copepod species appear to be obligate ice dwellers. The harpacticoid copepod *Drescheriella glacialis* seems to be very ice-dependent due to its poor swimming capabilities, and *Stephos longipes* has acquired antifreeze protection (Kiko, 2010), which also indicates a high level of adaptation to the ice environment. It is possible that copepods can continue to thrive under scenarios of thinner or less frequent ice cover, as plasticity in their diets and life cycles might be the key to their continual success (e.g., Swadling et al., 2004). Understanding the relative importance of factors that drive organisms to colonise sea ice (e.g., response to predation versus reproductive needs) would enhance our ability to predict their responses to environmental change.

Salps responded positively to increased storminess and the number of days >0°C and negatively to a positive press perturbation of CDW (Table 4). There appears to be considerable spatial segregation between krill and salp populations (Nicol et al., 2000; Atkinson et al., 2004), although a comparative study of their



feeding behaviour showed similar diets, which might enhance the competition between both species (Pauli et al., 2021b). Currently it is assumed that temperature, sea ice and chlorophyll *a* drive large-scale population segregation between the two species, at least in the Indian sector (Nicol et al., 2000). Observations from the WAP also indicate that *E. superba* and *S. thompsoni* rarely, if ever, co-exist in high abundances in that region (Pakhomov et al., 2002; Steinberg et al., 2015) and instead oscillate between years of salp dominance and years of krill dominance (Ross et al., 2014). However, the rapid reproduction capacity of salps under favorable conditions could change current ecosystem structure and thus alter the behaviour and distribution of *E. superba*. The direct effect of increased *S. thompsoni* presence on *E. superba* populations, however, is unknown.

## 6. Discussion

The sea ice environment is pivotal for the Southern Ocean ecosystem and is likely to change (Meredith et al., 2019) over the 21st Century. There is *high confidence* that changes in meridional wind stress will have a strong effect on sea ice variability (IPCC, 2021), and Southern Ocean westerlies are expected to intensify. Understanding how sea ice will respond to environmental change is key to predicting the effects on the biota that rely on sea ice for all or part of their life cycles. Some species are already adapted to the ephemeral nature of sea ice, so it is the magnitude and rate of change to this habitat that might be key determinants of how well species fare in the future. For these species, developing a means of weighting CMIP models for their ability to represent the Southern Ocean sea ice system is an important step to making informative predictions about the future of sympagic and pelagic biota. Climate variations may influence the duration of sea ice by disrupting the timing of formation and retreat and thus primary productivity, with consequences for entire food webs (Seibel and Dierssen, 2003; McCormack et al., 2021; Murphy et al., 2021). One example is differences between phytoplankton assemblages, with blooms of *Phaeocystis antarctica* often dominating in the Ross Sea vs. diatoms occurring in the WAP (Ducklow et al., 2007; Smith et al., 2007; Mangoni et al., 2017; Schofield et al., 2017; Pinkerton et al., 2021).

Our qualitative network model showed realistic expectations for differences between sectors. For that reason, it is a useful tool for exploring different future scenarios for the ecosystems in different sectors, given that changes in the physical system are likely to vary in more nuanced ways than the future scenario we present here. A key lesson from our results is that different taxa did not respond in a consistent direction (positive or negative) across all environmental perturbations, highlighting the complexities of networks of interactions between the physical and biological variables. Increasing storminess produced positive responses in the pelagic nutrient pools, possibly due to deeper ocean mixing bringing nutrient-rich waters to the surface. At the same time, warming temperatures might lead to increased stratification trapping nutrients at depth. If

temperature is the more important driver, then we might expect to observe decreases in biomass of phytoplankton and grazers.

Species that require the presence of sea ice are more-or-less certain to fare badly under reduced ice scenarios, e.g., the dependency of the silverfish *P. antarcticum* on platelet ice during its early development. Kramer et al. (2011) also argued that the perennial sea ice of the Weddell Sea is colonised by highly adapted species that probably rely on year-round sea ice (e.g., *D. glacialis* and *T. antarcticus*), and therefore a change to a seasonal ice cover might be detrimental for these species. Also *S. longipes* might be adversely impacted by sea ice loss, as it seems to rely on sea ice as a nursery ground. In this case, the seasonal timing of sea ice formation and melting might also be important. Other species, such as *Paralabidocera antarctica*, appear to be facultative rather obligate inhabitants of sea ice (Arndt and Swadling, 2006) and might be able to adjust their life history strategies to meet their needs in a reduced sea-ice world.

Of course, it is most likely that species will have variable responses to changing sea-ice conditions and will depend upon how much their populations as a whole depend on a sea-ice phase in their overall dynamics, coupled with the potential for non-linear responses by various taxa (Constable et al., 2014). However, for benthic organisms it is already predicted that there will be “more losers than winners” (Griffiths et al., 2017). It is these complex adjustments in biology and ecology that will pose the biggest challenges to attempts to manage the Southern Ocean ecosystem (Atkinson et al., 2019).

Temperature affects sea ice structure, freeze/melt and extent and its carrying capacity for biota, expressed as biomass, at the same time as impacting metabolism in a system. The qualitative network model showed metabolism increased while primary producers and grazers decreased with increasing temperatures. However, as the model is purely qualitative, it is not possible to scale metabolism according to the biomass of each component and to obtain a measurable response from a change in temperature. Carrying capacity is determined by complex interactions between habitat complexity (e.g., deformation processes), the volume of brine available for colonisation and the total volume of the ice. Earlier we discussed how increased ice complexity can improve outcomes for larval krill (Frazer et al., 2002; Meyer et al., 2017) by providing them with refuge from predators and competitors. This underlines the importance of better defining the relationships between Antarctic sea ice physical properties and processes and biological and ecological processes, as they relate to optimal “habitat quality” for key species, including at different life stages (e.g., Quetin et al., 2007). As stated by Janssen et al. (2021), this is critical for robust projections of future states of the Southern Ocean ecosystem. A critical step will be to evolve the qualitative model into a quantitative model where the effects of quantitative change in the drivers can be better explored.

Understanding the ways that biota will respond between and within sectors is also a high priority. This research should be undertaken at a multi-national level, with sampling strategies designed to facilitate our understanding of poorly-studied regions along with those where we have better information (e.g., the Southern Ocean Observing System 2021–2025 Science and

Implementation Plan, Newman et al., 2022). There is patchy data coverage between sectors and the key taxonomic groups have been sampled on varying timescales. We know that sea ice is not changing uni-directionally, with some regions (primarily the southwestern Atlantic and eastern Pacific) showing rapid change while other regions (Ross, Indian) are showing some increases or not changing substantially – although there was an unexpected switch to high variability in 2012 (Parkinson, 2019). Additionally, as fast ice contains high biomass of true ice inhabitants (e.g., the algae and small grazers), being able to predict whether it will increase, decrease or stay the same is important and is an area needing attention.

Understanding and quantifying these changes will require rigorous scientific data collection drawn from species and ecosystems that are sensitive to multiple stressors of climate change, using novel field and laboratory technologies and methodologies to fill knowledge gaps in our understanding of the fundamental biology and ecology of many Southern Ocean species. This should ideally involve long-term cross-disciplinary monitoring of the coupled interactive sea ice-ocean-atmosphere-biology-biogeochemistry system in key regions, i.e., along the lines of the long-running Palmer Long-Term Ecological Research program (Ducklow et al., 2013) – noting that Antarctica's sea ice habitat is also affected by ice sheet and ice shelf melt and icebergs (Massom and Stammerjohn, 2010).

## 7. Key messages for policy makers

**Key message 1** Sea ice in the Southern Ocean is fundamentally important to the lower trophic levels of this ecosystem, including for primary productivity, krill and fish. This has major implications for marine predators, including marine mammals, penguins and other bird species, that collectively support different parts of the Antarctic marine food webs (very high confidence).

**Key message 2** The sea-ice-system, including fast ice and the marginal ice zone, is threatened by both atmospheric and ocean warming as well as strengthening oceanic winds as a result of climate change, but the timing and magnitude of these impacts is uncertain (high confidence).

**Key message 3** Reduction in global greenhouse gas emissions is the only mitigation approach as sea ice is too expansive to be manipulated by direct human intervention (statement of fact).

**Key message 4** While reduced sea-ice extent may impact the range of sea-ice dependent species examined here, such as Antarctic krill, the increased complexity of habitat may be a positive local benefit to these species (medium confidence).

**Key message 5** Whole-of-system research on the role of sea ice in Antarctic ecosystems needs to be extended beyond the Antarctic Peninsula and Weddell Sea to establish a circum-Antarctic understanding of the coupled physical-chemical-biological sea ice system.

**Key message 6** Predicting how perturbations in sea-ice extent and duration will impact Antarctic krill populations and

in turn the Southern Ocean ecosystem requires both regionally-focused and multidisciplinary experimental approaches, together with coupled physical and biological models of the sea-ice system embedded within Earth System models.

## Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

## Author contributions

KS and AC conceived the study. AF, RAM, MB, LGh, AG, LGu, NJ, SK, FK, RK, PK, RM, AMa, AMc, MM, EP, IP, JR, PR, KR, MV, PV, CW, PW, and SW wrote sections and/or provided comprehensive comments. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

AC is a Topic Editor of this MEASO Special Issue.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Appendix: Qualitative network modelling

There is often considerable uncertainty surrounding the strength, functional forms, and even occasionally the direction of interactions within an ecological community. If we are confident in the type of interaction (e.g., predator–prey), but not the strength, we face parametric uncertainty. If we lack confidence in the nature of an interaction (e.g., whether a relationship is parasitic or mutualistic), then we face structural uncertainty. Qualitative network models were first developed to provide insights into community dynamics in the presence of parametric uncertainty. Early efforts to take a qualitative approach to existing community network theory harnessed the tools of graph theory and matrix analysis (Levins, 1974; Puccia and Levins, 1985). By shifting the focus away from precisely specified interaction terms and towards capturing the general community structure qualitatively, qualitative models can provide insights into the cumulative effects of simultaneous direct and indirect community interactions.

Qualitative network models may be understood most intuitively through the construction of a directed graph representing a community assumed to be at equilibrium. Graph nodes represent community members (either species or functional groups) and edges represent interactions between community members. An arrow at the terminus of an edge represents a positive interaction effect for that node, while a dot is typically used to indicate a negative interaction effect. The directed graph has a corresponding signed community matrix,  $A$ , where entry  $a_{ij}$  is either +, −, or 0, denoting a positive, negative, or neutral effect of the density of node  $j$  on the density of node  $i$ . Insights are gained by analysing this signed community matrix (see Puccia and Levins, 1985; Dambacher et al., 2002, 2003 for a more thorough treatment of these topics). If all eigenvalues of  $A$  are negative, then the community structure is stable (May, 1973). The effects of sustained changes to a model parameter (a so-called press perturbation) can be seen in the signed entries of  $-A^{-1}$  (Bender et al., 1984), or, alternatively, by considering the signs of the adjoint matrix,  $\text{adj}(-A)$  (Dambacher et al., 2002). This analysis suggests whether the density of each node will increase, decrease, or experience no change in response to a press perturbation in each of the other nodes.

Qualitative network models have been used to address a wide range of topics, such as identifying indicators of the effects of fishing (Metcalf et al., 2011), interpreting marine ecosystem changes in response to climate warming (Melbourne-Thomas et al., 2013), and exploring alternative strategies for invasive species eradication (Raymond et al., 2011). Analyses based on qualitative network models have been extended to incorporate modified interactions, in which the strength of an interaction between two species is modified by the density of a third species (Dambacher and Ramos-Jiliberto, 2007), as well as structural uncertainty (Raymond et al., 2011; Melbourne-Thomas et al., 2012).