Universidad de Concepción
Dirección de Postgrado
Facultad de Ciencias Naturales y Oceanográficas
Programa de Doctorado en Oceanografía

PERTURBACIÓN ANTRÓPICA EN LAS TRAMAS TRÓFICAS ANTÁRTICAS Y ECORREGIONALIZACIÓN DEL OCÉANO AUSTRAL (50-80°S)

Tesis presentada a la Facultad de Ciencias Naturales y Oceanográficas de la Universidad de Concepción para optar al grado académico de Doctor en Oceanografía

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diciembre 2021
Concepción, Chile

Universidad de Concepción
Dirección de Postgrado

La Tesis de "*Doctorado en Oceanografía*" titulada *"Perturbación antrópica en las tramas tróficas antárticas y ecorregionalización del Océano Austral (50-80°S)"*, del Sr*. "Giovanni Testa"* y realizada bajo la Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, ha sido aprobada por la siguiente Comisión de Evaluación:

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AGRADECIMIENTOS

Un sentido agradecimiento a Andrea y Leonardo por su apoyo, confianza y paciencia durante esta importante etapa de mi vida.

A Ricardo y Sergio, por sus consejos, atención y dedicación para mi crecimiento profesional. Sin ellos, el desarrollo de la presente Tesis no habría sido posible.

A Mauricio, por la disponibilidad y las prontas respuestas.

A Lorena, por entenderme, apoyarme y hacerme sonreír en todo momento.

A Ella, por las miradas llenas de inteligencia.

A Chiara, Roberto, Anna, Laura, Franco, Piera, Diego, Laura y Marco. Una parte de mi corazón que siempre me acompaña no obstante la distancia.

A la Agencia Nacional de Investigación y Desarrollo, Universidad de Concepción, Universidad Austral de Chile, Centro de Investigación Dinámica de Ecosistemas Marinos de Altas Latitudes y Centro de Investigación COPAS Sur Austral por el apoyo financiero recibido durante el desarrollo de la Tesis.

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RESUMEN

Perturbación antrópica en las tramas tróficas antárticas y ecorregionalización del Océano Austral (50-80°S)

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El Océano Austral (OA) juega un papel importante en el clima de la Tierra, proporciona productos pesqueros y ayuda al mantenimiento de la biodiversidad. El ecosistema de la Península Antártica (PA) es extremadamente sensible a la variabilidad climática y a la perturbación antrópica atribuida a la extracción de biomasa por las pesquerías. Este estudio tiene como objetivos evaluar el efecto del impacto antrópico sobre las tramas tróficas de la PA e identificar las principales ecorregiones físicas y biogeoquímicas en el OA y PA.

El grado de correspondencia entre la variabilidad espacial física, biogeoquímica y sus respectivas regionalizaciones se investigó mediante el cálculo de los principales factores físicos que explicaron estadísticamente la variabilidad biogeoquímica en el OA y la zona 48.1 de la Comisión para la Conservación de los Recursos Vivos Marinos Antárticos (CCAMLR). El valor promedio de las variables físicas y biogeoquímicas se estimó durante el verano austral dentro de una cuadrícula de 1° × 1° al sur de 50°S. La regionalización se desarrolló utilizando tanto el método de agrupamiento jerárquico y como el no jerárquico, mientras que se utilizó el paquete BIO-ENV y un análisis de redundancia basado en la distancia (db-RDA) para calcular qué factores físicos explicaron principalmente la variabilidad espacial biogeoquímica. Por otro lado, se forzó un modelo de la trama trófica de la PA usando el programa *Ecopath with Ecosim* calibrado para el período 1996-2012 y proyectando hasta 2100 con tres escenarios climáticos diferentes para variables ambientales (hielo marino, área de aguas abiertas y clorofila-a) y tres proyecciones de pesquería de kril (ausencia, capturas constantes y aumento decadal hasta duplicar las capturas actuales). El impacto de los diferentes factores sobre la trama trófica antártica se evaluó con un análisis de sensibilidad y con el estudio de la variabilidad temporal de varios grupos funcionales e indicadores ecosistémicos.

Se identificó un total de 12 regiones con características físicas significativas en el OA, mientras que las regiones biogeoquímicas fueron 18. La combinación de la batimetría y la cobertura de hielo marino fue el factor que explicó principalmente la variabilidad biogeoquímica (coeficiente de correlación de rango de Spearman: 0,68; p: 0,05) y el análisis db-RDA indicó que las variables físicas explicaron el 60,1% de la varianza en las variables biogeoquímica. Se identificaron 14 regiones físicas y 16 biogeoquímicas significativas para la zona 48.1 de la CCAMLR, donde la batimetría fue el factor principal que explicó la variabilidad biogeoquímica (coeficiente de Spearman: 0,81; p: 0,05) y el análisis db-RDA explicó el 77,1% de la varianza en las variables biogeoquímica. La correspondencia entre las regiones físicas y biogeoquímicas fue mayor para la zona CCAMLR 48.1 con respecto al OA. Por otra parte, la variabilidad ambiental ejercería un mayor impacto en la trama trófica antártica durante las proyecciones para 2100 en comparación con la pesquería de kril. La clorofila-a influyó fuertemente en la variabilidad temporal de los grupos funcionales, sugiriendo un control *bottom-up* sobre la trama trófica antártica. En los escenarios de las proyecciones al año 2100 se observó una modificación de la estructura de la trama trófica con una marcada disminución en la biomasa de kril (entre el 50% y la casi extinción según el escenario climático) y un aumento de salpas y otros grupos zooplanctónicos. También se detectó una reducción en los depredadores dependientes del hielo y del kril, como los pingüinos Adelia, Barbijo y la foca cangrejera. La ausencia de parametrización en la variabilidad espacial y estacional de la pesquería de kril podría causar una subestimación del impacto de esta componente sobre las tramas tróficas.

Los resultados de esta investigación proporcionan información novedosa y útil para la gestión de los ecosistemas del OA y de la zona CCAMLR 48.1, además de entregar una sólida base para la parametrización de futuros modelos ecosistémicos. La presente Tesis también presenta resultados innovadores con respecto a las posibles dinámicas de la trama trófica antártica bajo diferentes escenarios ambientales y de pesquerías de kril, destacando varios puntos críticos que deben abordarse para mejorar la comprensión y la parametrización de la futura variabilidad de grupos tróficos claves.

ABSTRACT

Anthropic disturbance in the Antarctic food web and Southern Ocean (50-80°S) ecoregionalization

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2021
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The Southern Ocean (SO) plays a major role in the Earth's climate, provides fishery products and help the maintenance of biodiversity. The Antarctic Peninsula (AP) ecosystems is extremely sensitive to climate variability and anthropogenic perturbance ascribed to biomass extraction from fisheries. This study aims to evaluate the anthropic impact on the AP food web and to identify the main physical and biogeochemical zones.

The degree of correspondence between physical and biogeochemical spatial variability and regionalization were investigated by calculating the main physical factors that statistically explained the biogeochemical variability within the SO and the 48.1 zone of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The mean value of physical and biogeochemical variables was estimated during austral summer within a grid of 1° x 1° south of 50°S. The regionalization was developed using both non-hierarchical and hierarchical clustering method, whereas BIO-ENV package and distance-based redundancy analysis (db-RDA) were applied in order to calculate which physical factors primarily explained the biogeochemical spatial variability. An Ecopath with Ecosim model calibrated for 1996-2012 period was forced to simulate different climatic scenarios for 2100 using environmental variables (sea ice, open water area and chlorophyll-a) and three krill fishery projections (no-take, constant and decadal increase until doubling the current catches). The relative impact of the different drivers on Antarctic food web was evaluated with a sensitivity analysis and the study of the temporal variability of several functional group and ecosystems indicators.

A total of 12 physical and 18 biogeochemical significant clusters were identified for the SO. The combination of bathymetry and sea ice coverage majorly explained biogeochemical variability (Spearman rank correlation coefficient: 0.68; p-value: 0.05) and db-RDA indicated that physical variables expressed the 60.1% of biogeochemical variance. On the other hand, 14 physical and 16 biogeochemical significant clusters were identified for 48.1 CCAMLR zone. Bathymetry was the main factor explaining biogeochemical variability (Spearman coefficient: 0.81; p-value: 0.05) and db-RDA analysis resulted in 77.1% of biogeochemical variance. The correspondence between physical and biogeochemical regions was higher for CCAMLR 48.1 zone with respect to the whole SO. The environmental variability exerted a greater impact on Antarctic food web in 2100 projections compared with krill fishery. Primary production strongly influenced the functional groups temporal variability, suggesting a bottom-up control on the food web. An alternative food web structure was observed in 2100, with a marked decline in krill population biomass (from -50% to nearly extinction depending on the environmental scenario) and an increase in salps and other zooplanktonic groups. A reduction in the biomass of ice and krill-dependent predators, such as Adélie and Chinstrap penguins and Crabeater seal, was also detected. The lack of parametrization in krill fishery spatial and seasonal variability might cause an underestimation of its impact.

The results of this dissertation provide novel and useful information for both SO and CCAMLR 48.1 zone ecosystem management and modeling parametrization. This work also provides useful insight into possible dynamics of the Antarctic food web during different environmental scenarios and highlights several critical points that need to be addressed to improve the understanding and parametrization of key trophic groups in the future.

1. INTRODUCCIÓN

1.1. Tramas tróficas antárticas

La huella del humano sobre el planeta es clara en cuanto a su influencia sobre los ecosistemas y clima global (IPCC 2014). Por lo tanto, de cara a nuestro presente y futuro, no es correcto estudiar el planeta y sus tramas tróficas sin considerar la presencia del *Homo sapiens* (O'Neill 2001). Una cadena trófica se puede definir como la transferencia secuencial de materia y energía de un organismo a otro. Las cadenas tróficas se entrelazan entre sí para formar una trama trófica debido a la interconexión que existe entre los hábitos alimentarios de diversas especies en una comunidad ecológica (Hui 2012). Como organismo heterótrofo, el hombre requiere carbono en forma orgánica para su asimilación. La explosión demográfica, acompañada por un desarrollo tecnológico sin precedentes, permitió a la humanidad tener un impacto desproporcionado en los ecosistemas terrestres y marinos, aumentando su poder depredador y, en algunos casos, incrementando su nivel trófico en la comunidad ecológica (Bonhommeau et al. 2013).

Debido a su ubicación y patrones oceanográficos, los ecosistemas del Océano Austral (OA) se pueden considerar como excelentes indicadores climáticos y del estado de la comunidad marina (Murphy et al. 2016). Los ecosistemas ártico y antártico comparten algunas propiedades (bajas temperaturas, marcada estacionalidad en el régimen de luz y dinámica de hielo marino) y difieren en otras, principalmente debido a la topografía y los patrones de circulación (McBride 2014; Murphy et al. 2016). Los flujos tróficos en los sistemas polares han sido considerados más simples por la baja cantidad de interacciones tróficas y a la menor diversidad de organismos comparados con sistemas de latitudes medias y bajas (Hill et al. 2006; Plagányi 2007). Suelen caracterizarse por una baja diversidad de metazooarios y la aparente dominancia de pocas especies en el flujo de energía (Murphy et al. 2012; **Figura 1.1**), generando una escasa redundancia funcional en el ecosistema (*i.e.*, pocas especies se encargan de las funciones ecológicas claves; Murphy et al. 2016). La baja redundancia funcional puede ser una ventaja a la hora de modelar los flujos del ecosistema ya que, conociendo las especies claves del ecosistema, se puede llegar a una simplificación en la parametrización de los flujos de energía y materia. Sin embargo, la baja diversdad de especies y redudancia funcional hace que los sistemas se puedan desestabilizar rápidamente cuando se altera algún componente de la trama trófica.

Productores primarios. Las diatomeas (microfitoplancton, >20 μm) son el componente de la comunidad fitoplanctónica que mayormente aporta a la productividad en el OA, aunque existen diferencias regionales en la estructura de la comunidad autótrofa y en la sucesión estacional de especies (McBride et al.

2014). Por otro lado, las criptófitas (nanofitoplancton, 2-20 μm) suelen aparecer después de la proliferación de diatomeas y suelen estar relacionadas con plumas de agua dulce asociadas con el derretimiento del hielo marino (Moline et al. 2004). La marcada estacionalidad del hielo marino afecta directamente la variabilidad espacio-temporal de la productividad primaria en las regiones polares, actuando como barrera física a la mezcla inducida por el viento, inhibiendo la penetración de la radiación lumínica y afectando la concentración

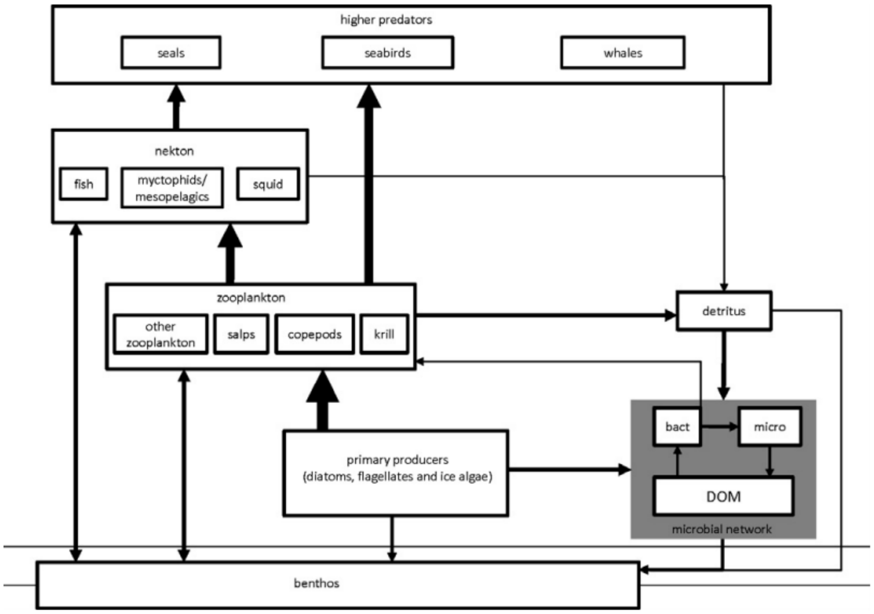

Figura 1.1. Esquema de las principales componentes y flujos de la trama trófica Antártica. Bact: bacterias; micro: microbios; DOM: Materia Orgánica Disuelta. Extraído de Murphy et al. (2012).

de micronutrientes (Vernet et al. 2008, Arrigo et al. 2012; Ducklow et al. 2013; Arrigo 2014; Constable et al. 2014; Murphy et al. 2016; Wu y Hou 2017). Debido a que el avance/retroceso de hielo marino depende en buena parte de la circulación atmosférica (Stammerjohn et al. 2003; Ducklow et al. 2007), se piensa que la productividad primaria (a escala interanual e interdecadal) podría en buena parte estar relacionada con anomalías atmosféricas, como con el Modo Anular del Sur y El Niño Oscilación del Sur (Arrigo et al. 2008; Saba et al. 2014).

Consumidores primarios. Por otro lado, *Euphausia superba* es la especie de eufáusido más abundante y dominante en el OA (McBride et al. 2014). *E. superba* está conectada directamente a niveles tróficos superiores (peces, ballenas, focas, pingüinos, albatros, etc.), creando una cadena trófica con pocos pasos intermedios y caracterizada por una elevada eficiencia en la transferencia de materia y energía (Hill et al. 2006). El ciclo de vida (entre 5 y 7 años; Hill et al. 2006) es complejo y depende del ciclo estacional del hielo marino y de las propiedades físico-químicas del ambiente (Piñones y Federov 2016). La mayor abundancia de kril se produce en el Mar de Escocia, probablemente asociada a movimientos advectivos desde la Península Antártica (PA) hacia esta zona (Hill et al. 2006). En zonas con baja densidad de kril, la comunidad zooplanctónica puede ser dominada por copépodos (*Rhincalanus gigas* y *Calanoides acutus;* McBride et al. 2014; Murphy et al. 2016), modificando la trama trófica a escala regional (Murphy et al. 2012). Las salpas (*Salpa thompsoni*) constituyen otro componente importante del zooplancton. El kril suele ser más abundante en aguas caracterizadas por una alta productividad primaria y la presencia de diatomeas, mientras que las salpas proliferan en aguas menos productivas y con abundancia de criptófitas (Atkinson et al. 2004; Moline et al. 2004). Las salpas podrían jugar un papel relevante en los ciclos biogeoquímicos, aunque no se consideran un enlace importante hacia los niveles tróficos superiores (Moline et al. 2004; Murphy et al. 2016).

Niveles tróficos superiores. Por lo general, las especies de peces antárticos suelen poseer características claras en sus ciclos vitales, entre ellas: bajas tasas de crecimiento, bajas tasas de mortalidad, gran tamaño corporal y ciclos de vida relativamente largos donde alcanzan la madurez sexual en una etapa tardía de su vida (Murphy et al. 2016). Las especies de peces antárticos pertenecen principalmente a una única familia (nototénidos) y en su mayoría tienen hábitos demersales o semi-demersales (con la excepción de *Pleuragramma antarticum*, una especie epipelágica cuyo ciclo de vida está fuertemente asociado al hielo marino; McBride et al. 2014).

Depredadores como aves (pingüinos y albatros) y mamíferos marinos (ballenas y focas) pueden sostener su dieta rica de lípidos y ácidos grasos a partir del consumo de zooplancton (Murphy et al. 2016). Este tipo de reservas energéticas se ven necesarias para realizar migraciones, sobrevivir al invierno y reproducirse en primavera. Dependiendo del organismo, los patrones migratorios pueden presentarse en diferentes escalas espacio-temporales: algunas especies (*e.g.*, *Megaptera novaeabgliae*) permanecen en el continente antártico sólo en ciertos periodos del año (Kraska et al. 2015), mientras que otras (*e.g.*, *Pygoscelis adeliae*) siguen las dinámicas del hielo marino (Takahashi et al. 2018).

Acoplamiento pelágico-bentónico. Al sur de los 50ºS la exportación de carbono orgánico particulado (COP) es 1000 Tg C año^{-1} (el 10% de la exportación global de COP), con una contribución significativa de carbono orgánico disuelto al flujo de carbono por debajo de 500 m (Schlitzer 2002). La mayoría de los estudios se han focalizado en el transporte activo de partículas orgánicas hacia las profundidades, aunque Stukel y Ducklow (2017) demostraron que el transporte pasivo por mezcla vertical y advección de COP también podría jugar un papel importante (un 54% de las exportaciones) en la bomba biológica de la PA y del OA (Henson et al. 2015). La plataforma continental estrecha y profunda en el OA disminuye la importancia del acople pelágico-bentónico con respecto a la zona polar del hemisferio boreal (Mc Bride et al. 2014). La mayor riqueza de especies bentónicas se encuentra en las proximidades de las islas Shetland del Sur, PA y en la zona oriental del Mar de Weddell (Kaiser et al. 2013). Por otro lado, Brandt et al. (2007) recopiló la distribución batimétrica de las especies claves de la comunidad bentónica en términos de meiofauna (sobre todo foraminíferos, nemátodos y copépodos), macrofauna (principalmente crustáceos e isópodos) y megafauna (donde los equinodermos dominan en términos de abundancia, biomasa y riqueza de especies) en el OA, sin encontrar una clara relación entre los patrones de biodiversidad y la profundidad, latitud, composición del sedimento y/o granulometría.

1.2. Impacto antrópico y modelación de trama trófica

La pesquería afecta las tramas tróficas marinas a través de la remoción directa de especies objetivo y no-objetivo (*e.g.*, *by-catch* y captura incidental), mediante la alteración de complejas interacciones biológicas, como la depredación y la competencia, y la alteración mecánica del hábitat que producen los artes de pesca (Trivelpiece et al. 2011). La explotación pesquera antártica empezó con la casi exterminación del lobo fino antártico (*Arctocephalus gazella*) en el siglo XVIII y XIX, seguida por la explotación masiva de las grandes ballenas (*Balenoptera* spp. y *Megaptera* spp.) en el siglo XX (Boyd 2009; Ainley y Pauly 2014). Entre 1960 y 1965 surgieron las pesquerías de peces demersales antárticos *Notothenia rossii, Lepidonotothen squamifrons* y *Gobionotothen gibberifrons* (Ainley y Pauly 2014). Cuando se agotaron estos recursos, la atención de las pesquerías se focalizó sobre *E. superba* y los peces *Dissostichus mawsoni*, *Dissostichus eleginoides* y *Champsocephalus gunnari* (Ainley y Pauly 2014). Desde finales de la década de los ‘70 las capturas de kril antártico superaron en gran medida las de otras especies en el OA (Hill et al. 2006; **Figura 1.2**).

A través de las pesquerías, la humanidad tiene un impacto directo (e indirecto) sobre las comunidades marinas, mientras que su contribución al cambio climático (a través de las emisiones de gases de efecto invernadero) repercute de una manera indirecta las tramas tróficas antárticas, induciendo un cambio en las dinámicas de hielo marino, patrones atmosféricos, corrientes oceánicas y generando cambios en la temperatura del mar. Los principales cambios oceanográficos comprenden: 1. calentamiento del mar; 2. desplazamiento meridional de los frentes oceánicos; 3. incremento de la actividad

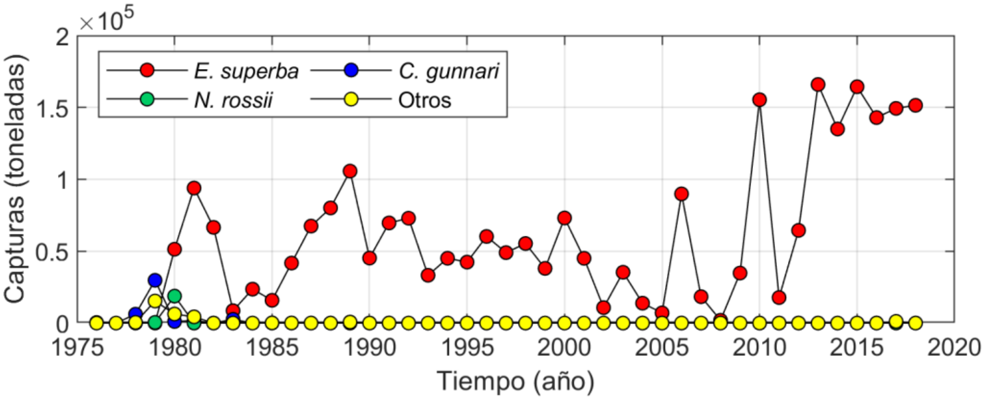

Figura 1.2. Evolución temporal de las capturas de las principales pesquerías en la región CCAMLR 48.1 durante el periodo 1975-2020.

de mesoescala; 4. aumento de la estratificación de la columna de agua (Constable et al. 2014; Schmidtko et al. 2014). Las variaciones interanuales en patrones físicos tienen repercusiones directas sobre los productores primarios (Arrigo et al. 2008; Wu y Hou 2017; Schofield et al. 2017) y la comunidad zooplanctónica (Atkinson et al. 2004; Hill et al. 2012; Piñones y Fedorov 2016; Murphy et al. 2017). Además, debido a la interconexión entre grupos tróficos, la variabilidad interanual en los eslabones inferiores puede llegar a tener repercusiones sobre los patrones espacio-temporales de abundancia y distribución de niveles tróficos superiores (*e.g.*, pingüinos, aves marinas y focas; Weimerskirch et al. 2003; Trivelpiece et al. 2011). No obstante, los cambios y tendencias interanuales se caracterizan por una elevada variabilidad y heterogeneidad espacial.

Con el fin de estudiar el impacto antrópico sobre las tramas tróficas antárticas, es imprescindible tener en cuenta dos factores. En primer lugar, la variabilidad espacio-temporal de los componentes del impacto antrópico (*e.g.*, en las tres zonas antárticas de la *Food and Agriculture Organization* (FAO) 48, 58 y 88; Ainley y Pauly 2014). En segundo lugar, es importante considerar la marcada heterogeneidad espacial que caracteriza los ecosistemas polares. Por lo general, se reconoce la división en tres zonas biogeográficas distintas: la zona oceánica permanentemente libre de hielo, la región afectada por el ciclo estacional del hielo marino y el área caracterizada por la presencia permanente de plataformas de hielo (Hill et al. 2006; Murphy et al. 2016). La mayor diferencia en las tramas tróficas antárticas se genera en la medida de la dominancia del kril con respecto a otros grupos zooplanctónicos (como copépodos, kril de hielo (*Euphausia crystallorophias*) y salpas (*Salpa thomsonii*); Murphy et al. 2012). Por otro lado, los trabajos de Murphy et al. (2013, 2016) estudiaron las principales similitudes y diferencias entre las tramas tróficas de PA (a través del modelo de Ballerini et al. (2014)) y la región de la plataforma continental de la Isla Georgia del Sur (utilizando el modelo de Hill et al. (2012)), revelando cómo el gradiente físico y la distancia entre ambos ecosistemas repercuten en la distribución espacial de especies clave de fitoplancton, pingüinos y focas, entre otras.

El conocimiento de la variabilidad temporal (a nivel estacional e interanual) de las tramas tróficas está fuertemente sesgada debido a la escasez de datos *in situ*; por lo tanto, una aproximación basada en un modelo *End-to-End* (E-E) podría ser útil desde este punto de vista. Travers et al. (2007) explicaron como la terminología E-E se refiere a una aproximación específica para el modelamiento de ecosistemas que: 1. pretende representar la trama trófica completa (incluyendo el componente humano) y al ambiente abiótico asociado; 2. requiere la integración de procesos físicos, químicos y biológicos de diferentes escalas; 3. utiliza una interacción de dos vías entre componentes del ecosistema; 4. tiene en cuenta el efecto, en forma de forzamiento dinámico, del clima y del impacto humano sobre múltiples niveles tróficos. El concepto de ecosistema se fundamenta sobre algunas suposiciones implícitas, como la definición de limites espaciales cerrados, la homogeneidad espacial dentro del mismo ecosistema, la ausencia de selección natural y suele considerar el *H. sapiens* como un componente externo (O'Neill 2001).

Para el desarrollo del modelo se eligió el área CCAMLR 48.1 debido a que la mayoría de los datos para la zona antártica se concentran en dicha zona y que es una zona sujeta a fuerte presión pesquera y variabilidad ambiental a escala interanual. Es importante mencionar que el modelo exclusivamente reproduce el estado del ecosistema durante la temporada de verano, debido a que la extensión del hielo marino durante el invierno austral reduce la cobertura de los productos satelitales y dificulta la recopilación de datos *in situ* a incorporar en el modelo trófico.

1.3. Zonas biogeográficas antárticas

Una zona biogeográfica se define como un área con una composición relativamente homogénea de especies, diferente con respecto a sistemas adyacentes. La determinación de la composición de especies suele ser determinada por la predominancia de un reducido número de ecosistemas y/o un conjunto de patrones oceanográficos o topográficos (*i.e.*, temperatura, cobertura de hielo, etc.; Spalding et al. (2007)). A nivel biogeográfico existe una marcada heterogeneidad espacial en los ecosistemas polares. Por lo general, se reconoce la división en tres zonas biogeográficas distintas: la zona oceánica permanentemente libre de hielo, la región afectada por el ciclo estacional del hielo marino y el área caracterizada por la presencia permanente de plataformas de hielo (Hill et al. 2006; Murphy et al. 2016). Con un enfoque más detallado, Grant et al. (2006) utilizaron un análisis de agrupación para dividir el OA en 14 regiones distintas, mientras que el trabajo de Constable et al. (2014) dividió el OA en 20 regiones biogeográficas distintas. Además, los trabajos de Spalding et al. (2007; 2012) identificaron diferentes ecorregiones y provincias pelágicas en los ecosistemas marinos del OA (**Figura 1.3**).

La presente Tesis se plantea como objetivo principal evaluar la perturbación antrópica en los flujos tróficos y dinámicas de los ecosistemas de la zona CCAMLR 48.1 a través de un enfoque de modelación de trama trófica. Además, se estudió la variabilidad espacial de parámetros físicos y biogeoquímicos en la zona de estudio, y en el OA en general, con el fin de evaluar el grado de homogeneidad de estas variables e individualizar regiones físicas y biogeoquímicas. Primero, se estudió la variabilidad espacial de variables físicas y biogeoquímicas de los ecosistemas del OA, recopilando diferentes bases de

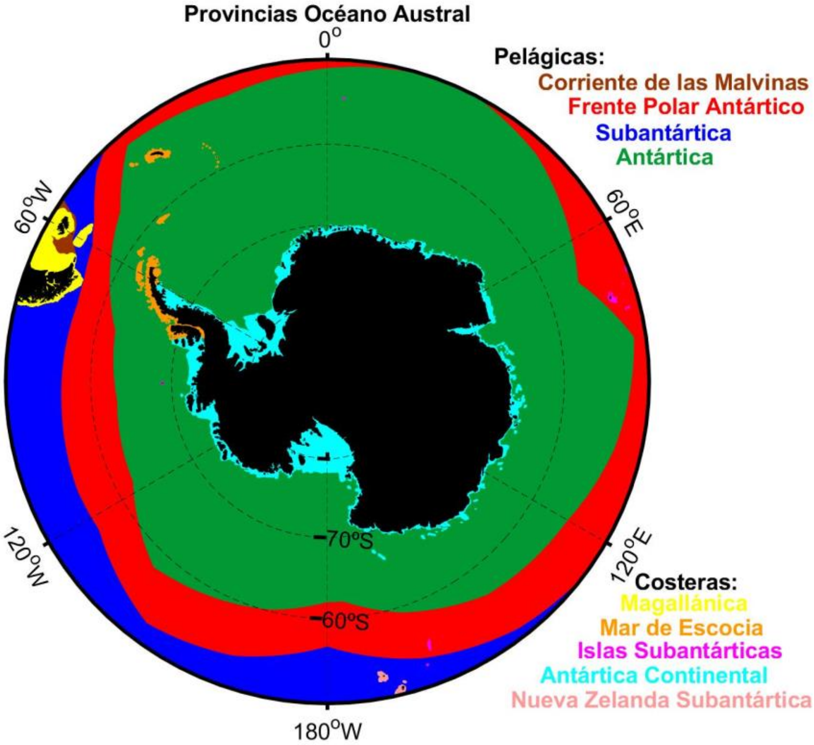

Figura 1.3. Principales provincias pelágicas y costeras en el Océano Austral. Elaboración propia a partir de los datos de Spalding et al. (2007; 2012).

datos a partir de productos satelitales y salidas de modelos. *A posteriori*, se realizará un análisis de agrupación para identificar macroecorregiones en el OA. Se evaluará el impacto antrópico a escala interanual causado por variables ambientales y el efecto de las pesquerías de kril sobre la trama trófica de la zona CCAMLR 48.1, simulando las respuestas dinámicas del ecosistema frente a perturbaciones antrópicas variables en su magnitud y características.

2. HIPÓTESIS DE TRABAJO Y OBJETIVOS ESPECÍFICOS

2.1. Hipótesis

Hipótesis 1: Procesos físicos determinan la zonificación de zonas biogeográficas del Océano Austral y en la zona CCAMLR 48.1.

Hipótesis 2: La pesquería de kril es la componente de la perturbación antrópica que más afectará el estado del ecosistema de la zona CCAMLR 48.1 en las proyecciones para el 2100.

2.2. Objetivos

2.2.1. Objetivo principal: Evaluar el efecto del impacto antrópico (*e.g.*, cambios en hielo marino y pesquerías) sobre las tramas tróficas en la zona CCAMLR 48.1.

2.2.2. Objetivos específicos:

1. Identificar zonas biogeográficas en la zona CCAMLR 48.1 y en el Océano Austral basándose en el análisis de la variabilidad espacial de variables físicas y biogeoquímicas y su grado de homogeneidad.
2. Describir los cambios en el ecosistema de la zona CCAMLR 48.1 en dos periodos diferentes (décadas de los ’90 y 2100) a través de modelos tróficos.

3. Evaluar el potencial impacto de la perturbación antrópica causada por diferentes forzantes (*i.e.*, hielo marino y pesquerías) sobre las tramas tróficas de la zona CCAMLR 48.1 mediante simulaciones dinámicas en base a proyecciones de clorofila-a y hielo marino de CMIP6 (*Coupled Model Intercomparison Project*) y proyecciones hipotéticas de capturas para el periodo 2020-2100.

3. MATERIAL Y MÉTODOS

3.1. Identificación de zonas biogeográficas del Océano Austral y de la zona CCAMLR 48.1

A la hora de dividir el Océano Austral (OA) en macroregiones físicas y biogeoquímicas se determinó enfocarse en las condiciones promedio de las diferentes variables durante la "época productiva" (diciembre-marzo). Se utilizó este intervalo temporal, y no el promedio anual (enero-diciembre) debido a los escasos datos *in situ* recopilados durante la temporada invernal, la mayor extensión del hielo marino durante el invierno que reduce la cobertura de los productos satelitales, la fenología (meses de inicio y fin) de las proliferaciones de diatomeas (Soppa et al. 2016) y la eclosión de las larvas de kril durante este periodo (Piñones y Federov 2016). Debido a que la mayoría de los productos satelitales utilizados provienen del sensor *Moderate Resolution Imaging Spectroradiometer* (MODIS, con datos de 2003 en adelante), se definió acortar la cobertura temporal de algunas variables (*e.g.*, la cobertura de hielo) para un intervalo de tiempo comparable. Por otro lado, los datos presentaron diferente resolución espacial (desde 500 m hasta 1º), por lo que se uniformó la escala espacial calculando el valor promedio en una grilla de 1º por 1º. Para cada variable se buscó un compromiso entre la mayor resolución y cobertura espacio-temporal. Se utilizaron estadísticos básicos (desviación estándar, intervalos de confianza) para medir el grado de heterogeneidad para variables físicas y biogeoquímicas en el OA y en la zona CCAMLR 48.1. Además, se analizó el número de zonas biogeográficas para la zona CCAMLR 48.1 con el fin de discutir la suposición implícita de la homogeneidad espacial de variables físicas (*e.g.*, temperatura y capa de mezcla), químicas (*e.g.*, concentración de hierro) y biológicas (*e.g.*, productividad primaria) dentro del mismo ecosistema.

El estudio de Grant et al. (2006) utilizó un análisis de agrupación basado en datos de batimetría, temperatura superficial del mar y concentración de nutrientes para dividir el OA en 14 regiones distintas. De similar manera, el trabajo de Constable et al. (2014) dividió el OA en 20 regiones biogeográficas distintas a partir de datos batimétricos, de temperatura superficial del mar y de superficie cubierta por hielo marino. Por otro lado, utilizando la misma metodología que los estudios anteriores, los trabajos de Spalding et al. (2007; 2012) identificaron 7 diferentes zonas biogeográficas en el OA. Se planea utilizar la misma metodología propuesta por Grant et al. (2006) con el fin de identificar regiones biogeoquímicas y físicas en el OA y en la zona CCAMLR 48.1. En resumen, la metodología se puede resumir como: I) Reemplazar los pixeles en tierra con NaN; II) Eliminar las filas sin datos (en cualquier variable); III) Cambiar datos de batimetría (Z) en $\log_{10}(Z)$; IV) Normalizar todos los datos entre 0 y 1; V) Realizar el análisis de agrupación no jerárquica CLARA (*Clustering Large Applications*) para encontrar 250 grupos; VI) Calcular el valor promedio para cada grupo CLARA (utilizando los datos originales); VII) Normalizar datos entre 0 y 1; IX) Realizar el análisis de agrupación jerárquica UPGMA (*Unweighted Pair Group Method using Arithmetic averages*); X) Establecer el número de grupos significativos según Clarke et al. (2008). Las variables seleccionadas para la regionalización física y biogeoquímica se resumen en la **Tabla 3.1**. Se utilizó el paquete BIO-ENV y el análisis de redundancia basado en la distancia (db-RDA) para averiguar qué factores físicos explicaron principalmente la varianza espacial de variables biogeoquímica.

3.2 Modelamiento de tramas tróficas antárticas y de la perturbación antrópica

Ecopath with Ecosim (EwE) es una herramienta de modelamiento utilizada desde la década de los ‘80 para crear modelos con balance de masa en sistemas marinos (Polovina 1984; Christensen y Pauly 1992; Walters et al. 1997) y que hasta la actualidad cuenta con más de 400 modelos desarrollados en distintos ecosistemas acuáticos alrededor del planeta (Heymans et al. 2016). Plagányi (2007) identifica la amplia difusión de EwE y el enfoque estructurado dedicado a la parametrización como las ventajas de EwE, mientras que las mayores limitaciones se asocian a la calidad y cantidad de los datos disponibles y la estructura espacial no explicita presente en *Ecosim*.

Tabla 3.1. Variables incluidas en los análisis de agrupación. CHM: Cobertura de Hielo Marino; TSM: Temperatura Superficial del Mar; PAR: Radiación Fotosintéticamente Activa; COP exp.: Exportación de Carbono Orgánico Particulado; Nanofit.: Concentración de nanofitoplancton; PPN: Producción Primaria Neta. NOAA: https://coastwatch.pfeg.noaa.gov/.

Regionalización física		**Regionalización biogeoquímica**	
Variable	**Referencia**	**Variable**	**Referencia**
Batimetría	Olson et al. 2016	Hierro disuelto	Verdy y Mazloff 2017
CHM	Titchner y Rayner 2014	Diatomeas	Soppa et al. 2016
TSM	NOAA	Nanofit.	Kostadinov et al. 2016
Capa de mezcla	Mazloff et al. 2010	PPN	Behrenfeld y Falkowski 1997
PAR	NOAA	COP exp.	Guillaumot et al. 2017

El balance de masa para cada grupo *i* se modela a través de la ecuación (1) (Christensen y Walters 2004):

$$P_i = Y_i + M2_i \cdot B_i + E_i + BA_i + M0_i \cdot B_i \qquad (1)$$

Los parámetros de la ecuación (1) se detallan en la **Tabla 3.2**. Al incluir una componente de acumulación de biomasa (*BA*, que puede ser positiva, negativa o cero) la ecuación admite situaciones alejadas del estado-estable. Por otro lado, Christensen y Pauly (1992) calculan el balance de energía para cada grupo funcional de consumidores acorde a la ecuación (2):

$$Q = P + R + U \qquad (2)$$

Una breve explicación de cada término se encuentra en la **Tabla 3.2**. Para cada grupo funcional del modelo trófico se necesitan los siguientes parámetros de entrada: 1) Biomasa (*B*); 2) la razón producción biomasa *P/B*; 3) la razón consumo biomasa *Q/B*; 4) la composición de la dieta (*Dc*); 5) las capturas (*Y*). Para niveles tróficos inferiores (*i.e.*, fitoplancton) los parámetros *B* y *P/B* pueden obtenerse a partir de datos satelitales de clorofila-a y de productividad primaria (*e.g.*, Beherenfeld y Falkowski 1997). Mientras que para conocer la biomasa de la comunidad zooplanctónica hay que conocer la estructura de la comunidad según sus diferentes estadios y un peso promedio para cada uno de ellos. Las variables de entrada para los grupos funcionales de interés pesquero pertenecientes a los peces se suelen obtener desde cruceros de evaluación de stock (estimando la abundancia de los diferentes estadios, junto al peso promedio de cada individuo). Por otro lado, la información para niveles tróficos superiores suele venir de censos. El *H. sapiens* será considerado como un factor externo que remueve recursos del ecosistema, debido a que la gran mayoría de las capturas no son consumidas *in situ*, ninguna fracción vuelve al ecosistema en forma de detritus y no interactúa tróficamente como otros depredadores.

Después de balancear el modelo (*i.e.*, ajustar los parámetros de entrada del modelo de manera que se equilibre la producción con la remoción para cada grupo en el periodo considerado) siguiendo las reglas ecológicas y termodinámicas resumidas por Heymans et al. (2016), la herramienta *Ecosim* permite expresar la dinámica temporal de la biomasa de los diferentes grupos

Tabla 3.2. Parámetros de las ecuaciones de *Ecopath with Ecosim*.

Variable	**Explicación**
Ecuación (1)	
P	Tasa total de producción. P_i se calcula como el producto de B_i con la razón P/B_i; la tasa (P/B) en muchas ocasiones corresponde a la tasa de mortandad total ($Z_i = Y_i + M2_i + M0_i$).
Y	Capturas totales por pesquería
$M2$	Tasa total de depredación
B	Biomasa
E	Tasa neta de migraciones (emigración - inmigración). E_i suele considerarse igual a cero, ya que de normal el sistema comprende el hábitat completo de los principales grupos funcionales de interés.
BA	Tasa de acumulación de biomasa
$M0$	Tasa de otra mortalidad (independientes de predación y pesca)
Ecuación (2)	
Q	Consumo
P	Producción
U	Alimento no asimilado (i.e., egestión y excreción)
Ecuación (3)	
$\partial Bi/\partial t$	Tasa de cambio en la biomasa del grupo i durante el intervalo de tiempo ∂t
g_i	Eficiencia bruta de conversión de alimento (expresada como el cociente P/Q del grupo i)
$M0_i$	Tasa de otras mortalidades (independientes de predación y pesca) del grupo i
F_i	Tasa de mortalidad por pesca
e_i	Tasa de emigración
I_i	Tasa de inmigración
Q_{ji}	Tasa de consumo del depredador j sobre la presa i basada en el concepto de “arena de forrajeo” (Walters et al. 1997).

funcionales del ecosistema a través de una serie de ecuaciones diferenciales acopladas entre sí. La ecuación (3) se deriva de la ecuación (1) y se expresa, según Christensen y Walters (2004), como:

$$\frac{\partial B_i}{\partial t} = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (M0_i + F_i + e_i) \times B_i \qquad (3)$$

Los términos de la ecuación se explican en la **Tabla 3.2**.

Los límites espaciales de la zona CCAMLR 48.1 se definieron acorde a criterios pesqueros y no ecológicos; de esta manera se encontraron en su interior zonas oceanográficas heterogéneas, como regiones costeras y oceánica, zonas con hielo permanente y estacional. Debido a que la mayoría del kril de la zona CCAMLR 48.1 se reproduce alrededor de las Shetland del Sur y después es advectada hacia la isla de Georgia del Sur (Murphy et al. 2013), la captura de kril cerca de la PA podría tener un mayor impacto sobre la población total de kril con respecto al kril capturado cerca de las Shetland del Sur.

El modelo de Dahood et al. (2019) para la zona CCAMLR 48.1 fue calibrado utilizando series de tiempo biológicas, la dinámica de hielo marino y la clorofila-a para el periodo 1996-2012, aunque no se incluyeron las pesquerías. Debido a eso, el primer paso fue crear un nuevo modelo a partir del trabajo de Dahood et al. (2019) con los valores de pesquerías de kril para el periodo indicado. *A posteriori*, se proyectó el modelo calibrado para el periodo 1996-2012 hasta el año 2100 simulando diferentes escenarios donde se varió la magnitud de las diferentes componentes antrópicas (*i.e.*, pesca y calentamiento global). En específico, se simuló el impacto de tres escenarios climáticos diferentes (*Shared Socioeconomic Pathways* (ssp) 126, 370 y 585; https://es-doc.org/cmip6/; O'Neill et al. 2017) sobre las variables ambientales (hielo marino, superficie libre de hielo y clorofila-a) y la influencia de tres proyecciones teóricas de presión pesquera (*i.e.,* ausencia de capturas, pesquerías constantes y aumento gradual y decadal de las pesquerías hasta alcanzar el doble de las capturas actuales en 2100). Se utilizaron las proyecciones CMIP6 (*Coupled Model Intercomparison Project*; Eyring et al. 2016) para los escenarios de hielo marino y clorofila-a esperados para el año 2100. La variabilidad ambiental afectó la relación depredador-presa para varios grupos funcionales y la productividad primaria, mientras que el hielo marino afectó directamente la dinámica poblacional del kril y de *G. gibberifrons*. Por lo tanto, las variables forzantes del modelo impactaron para diferentes grupos funcionales los parámetros de consumo total, la eficiencia bruta de conversión de alimento y la mortalidad por pesca en la Ecuación 3. Para evaluar el impacto de las diferentes componentes antrópicas sobre la trama trófica antártica se analizó la variabilidad temporal de varios grupos funcionales y de indicadores ecológicos basados en biomasa y nivel trófico (Shin et al. 2010; Coll y Steenbeek 2017), enfocándonos en aquellos que tengan significancia ecológica, sensibilidad a la actividad pesquera, además de ser utilizables para medir el estado y tendencia del ecosistema. La magnitud del impacto de las diferentes forzantes sobre la trama trófica antártica fue evaluada a través de un análisis de sensibilidad.

4. RESULTADOS

4.1. Capítulo 1. Regionalización física y biogeoquímica del Océano Austral y de la zona CCAMLR 48.1

Artículo publicado en la revista *Frontiers in Marine Science*: 8(592378) doi:10.3389/fmars.2021.592378. Testa, G., Piñones, A., Castro, L.R. (2021).

Resumen

El Océano Austral juega un papel importante en el clima de la Tierra, proporciona productos pesqueros y ayuda al mantenimiento de la biodiversidad. El grado de correspondencia entre la variabilidad espacial física, biogeoquímica y las respectivas regionalizaciones se investigó mediante el cálculo de los principales factores físicos que explicaron estadísticamente la variabilidad biogeoquímica dentro del Océano Austral y la zona 48.1 de la Comisión para la Conservación de los Recursos Vivos Marinos Antárticos (CCAMLR). El valor promedio de las variables físicas y biogeoquímicas se estimó durante el verano austral dentro de una cuadrícula de 1° × 1° al sur de 50°S. La regionalización se desarrolló utilizando el método de agrupamiento tanto jerárquico como no jerárquico, mientras que el paquete BIO-ENV y el análisis de redundancia basado en la distancia (db-RDA) se aplicaron para identificar qué factores físicos explicaron principalmente la variabilidad espacial biogeoquímica. Se identificaron

un total de 12 regiones físicas y 18 biogeoquímicas significativas para el Océano Austral (alfa: 0,05). La combinación de la batimetría y la cobertura de hielo marino explicó principalmente la variabilidad biogeoquímica (coeficiente de correlación de rango de Spearman: 0,68) y el análisis db-RDA indicó que las variables físicas expresaron el 60,1% de la varianza biogeoquímica. Por otro lado, se identificaron 14 regiones físicas y 16 biogeoquímicas significativas para la zona 48.1 de la CCAMLR. La batimetría fue el factor principal que explicó la variabilidad biogeoquímica (coeficiente de Spearman: 0,81) y el análisis db-RDA explicó el 77,1% de la varianza biogeoquímica. La correspondencia entre las regiones físicas y biogeoquímicas fue mayor para la zona CCAMLR 48.1 con respecto a todo el Océano Austral. Nuestros resultados proporcionan información útil para la gestión de ecosistemas del Océano Austral, de la zona CCAMLR 48.1 y para la parametrización de modelos.

frontiers in Marine Science

ORIGINAL RESEARCH
published: 18 March 2021
doi: 10.3389/fmars.2021.592378

Physical and Biogeochemical Regionalization of the Southern Ocean and the CCAMLR Zone 48.1

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The Southern Ocean plays a major role in the Earth's climate, provides fisheries products and help the maintenance of biodiversity. The degree of correspondence between physical and biogeochemical spatial variability and regionalization were investigated by calculating the main physical factors that statistically explained the biogeochemical variability within the Southern Ocean and the 48.1 zone of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The mean value of physical and biogeochemical variables was estimated during austral summer within a grid of 1° × 1° south of 50°S. The regionalization was developed using both non-hierarchical and hierarchical clustering method, whereas BIO-ENV package and distance-based redundancy analysis (db-RDA) were applied in order to calculate which physical factors primarily explained the biogeochemical spatial variability. A total of 12 physical and 18 biogeochemical significant clusters were identified for the Southern Ocean (alpha: 0.05). The combination of bathymetry and sea ice coverage majorly explained biogeochemical variability (Spearman rank correlation coefficient: 0.68) and db-RDA indicated that physical variables expressed the 60.1% of biogeochemical variance. On the other hand, 14 physical and 16 biogeochemical significant clusters were identified for 48.1 CCAMLR zone. Bathymetry was the main factor explaining biogeochemical variability (Spearman coefficient: 0.81) and db-RDA analysis resulted in 77.1% of biogeochemical variance. The correspondence between physical and biogeochemical regions was higher for CCAMLR 48.1 zone with respect to the whole Southern Ocean. Our results provide useful information for both Southern Ocean and CCAMLR 48.1 zone ecosystem management and modeling parametrization.

Keywords: Southern Ocean, CCAMLR 48.1, regionalization, spatial variability, biogeochemistry

OPEN ACCESS

Edited by:
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Reviewed by:
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Specialty section:
This article was submitted to Marine Biogeochemistry, a section of the journal Frontiers in Marine Science

Received: *07 August 2020*
Accepted: *26 February 2021*
Published: *18 March 2021*

Citation:
Testa G, Piñones A and Castro LR (2021) Physical and Biogeochemical Regionalization of the Southern Ocean and the CCAMLR Zone 48.1. Front. Mar. Sci. 8:592378. doi: 10.3389/fmars.2021.592378

INTRODUCTION

The Southern Ocean plays a major role in the Earth's climate since the opening of the Drake Passage approximately 41 Ma ago (Scher and Martin, 2006). The Antarctic Circumpolar Current is the major current of the planet (with a transport of 137 Sv; Rintoul and da Silva, 2019) and it connects the Pacific, Indian and Atlantic Ocean basins isolating the Antarctic continent from lower latitudes.

The Antarctic Circumpolar Current and the Southern Ocean influence heat and salt balances and biogeochemical cycles (e.g., C, N, P; Sallée, 2018). The combination of the thermohaline gradient, sea-ice cycle and atmospheric patterns creates a meridional overturning circulation in the Southern Ocean (Tomczak and Godfrey, 2003; Morrison et al., 2015) which is a sensitive mechanism able to influence the greenhouse gases budget between the atmosphere and the ocean (Reid et al., 2009; Gruber et al., 2019). The export of Particulate Organic Carbon (POC) south of 50°S is 1000 Tg C yr^{-1} corresponding to 10% of the global POC export, with a significant contribution of dissolved organic carbon in the top 500 m of the water column (Schlitzer, 2002). The Southern Ocean has also been identified as a region providing important ecosystem services, particularly fisheries (CCAMLR, 2018; FAO, 2018) and maintenance of biodiversity (Grant et al., 2013; David and Saucède, 2015).

The Southern Ocean is recognized as a High Nutrient Low Chlorophyll region, approximately 48% of the Southern Ocean mean surface Chlorophyll-a (Chl-a) concentration is lower than 0.25 mg m^{-3} despite high macronutrients concentration (Pollard et al., 2006). Different hypotheses have been proposed, from light limitation due to deep mixing (Venables and Moore, 2010) to zooplankton grazing pressure (Le Quéré et al., 2016) and bioavailable dissolved iron depletion (Martin et al., 1990; Wadley et al., 2014). The iron limitation hypothesis leaded to several expeditions between 1993 and 2011 to artificially fertilize the photic layer of the Southern Ocean, these experiments increased surface Chl-a up to 15-fold (Boyd et al., 2007; Yoon et al., 2018). Pitchford and Brindley (1999) suggested that different explanations should be regarded as complementary, rather than alternative. The oceanic islands of the Southern Ocean (e.g., South Georgia Islands) stand out from High Nutrient Low Chlorophyll productivity patterns, mainly due to local input of dissolved iron and shallower bathymetry (Venables and Moore, 2010).

The 48.1 zone of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is a key region for monitoring the Antarctic ecosystem. This area is experimenting strong interannual variability and trends in sea ice coverage and water column temperature (Schmidtko et al., 2014; Jones et al., 2016) that turn this zone in one of the most climate sensitive region of the planet and most variable (Hendry et al., 2018). Recent studies (Murphy et al., 2016; Comiso et al., 2017) suggested that the interannual oceanographic variability is partly linked with atmospheric patterns, such as El Niño-Southern Oscillation and the Southern Annular Mode. This region is subject to strong anthropic influence via krill fisheries (Boyd, 2009; Ainley and Pauly, 2014; McBride et al., 2014) and local contamination by increasing tourist's presence (Bargagli, 2008; Waller et al., 2017). Intense Antarctic krill (*Euphausia superba*) fisheries within the 48.1 zone (Brooks et al., 2018) might have important repercussion on the trophic structure and the trophic pathways due to the reduced functional redundancy of polar ecosystems (i.e., few species perform most of the ecological functions; Murphy et al., 2016), the key role of krill within the Antarctic food web (Trivelpiece et al., 2011; Murphy et al., 2012; McBride et al., 2014) and the importance of this region for krill spawning and nursery (Piñones and Fedorov, 2016; Henley et al., 2019; Perry et al., 2019). A specific focus was given to CCAMLR 48.1 zone because of the ecological importance of this climate sensitive area and since no other biogeochemical regionalization study has been previously developed for this region according to our knowledge.

Regionalization is an important tool for conservation and management of the marine environment and marine resources, since it can provide useful information for identification of protected areas and fisheries zones (Berline et al., 2014). Marine protected areas are multi-purpose regions that provide protection for the natural resources they contain and can help marine ecosystems be resilient to natural and anthropic-driven climate changes (Roberts et al., 2017). Currently, the Ross Sea and the South Orkney Islands are the only established marine protected areas within the Southern Ocean, while three more proposal have been submitted for East Antarctica, the Antarctic Peninsula and the Weddell Sea (Sylvester and Brooks, 2020). The terrestrial ice-free area of Antarctica was divided in 16 biogeographic regions by Terauds and Lee (2016), whereas various studies of bioregionalization have been previously performed for the Southern Ocean pelagic (i.e., Grant et al., 2006; Spalding et al., 2007, 2012; Cabré et al., 2016) and benthic communities (Griffiths et al., 2009; Pierrat et al., 2013; Douglass et al., 2014; Hogg et al., 2016; Teschke et al., 2016; Fabri-Ruiz et al., 2020). A new physical and biogeochemical regionalization is needed to fill the existing gap in the understanding of the physical forcing on biogeochemical cycles spatial heterogeneity (Hendry et al., 2018) and to generate useful information for marine protected areas proposals and marine ecosystem modeling.

This study will generate new physical and biogeochemical regionalization utilizing the Southern Ocean data available from satellite-derived and model output databases. The degree of similarity between physical and biogeochemical characteristics obtained with this new regionalization will be compared with previously existing regionalization. In addition, the physical variable that primarily control biogeochemical variability in the Southern Ocean and CCAMLR 48.1 zone will be identified. The work will deliver useful information to the scientific community in order to identify highly productive areas and to understand and predict future changes in the context of the current climate crisis.

MATERIALS AND METHODS

Study Zone

The International Hydrographic Organization (IHO, 2002) defined the northerner limits of the Southern Ocean at 60°S. For the purpose of this study, the northern limit of the Southern Ocean was set at 50°S due to the spatial distribution of the Polar and Subantarctic Fronts (Orsi et al., 1995; Sallée et al., 2008; Koshlyakov and Tarakanov, 2011), especially in the Atlantic and western Indian Ocean (**Figure 1**). The proposed limit allowed the inclusion of the entire Drake Passage and the Southern Patagonia, permitting the analysis of differences and similarities

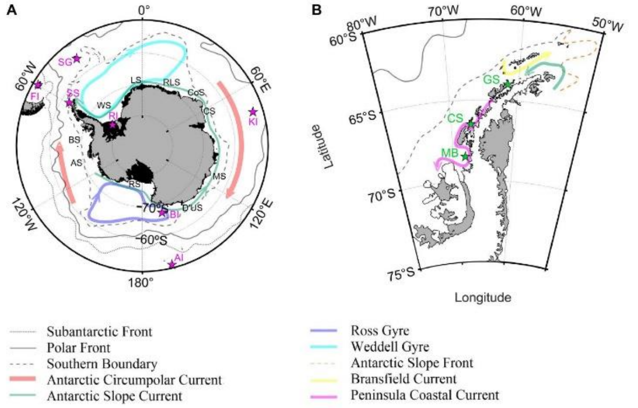

FIGURE 1 | Geographic location of the main islands, places, fronts, seas and circulation patterns for the Southern Ocean **(A)** and CCAMLR 48.1 zone **(B)**. Magenta and green stars indicated the location of Falkland Islands (FI); SG,South Georgia Island; SS, South Shetland Islands; RI, Ronne ice shelf; BI, Balleny Islands; AI, Auckland Islands; KI, Kerguelen Islands; MB, Marguerite Bay; CS, Crystal Sound; GS, Gerlache Strait. Black letters indicated the location of the main Antarctic seas: Bellingshausen Sea (BS); AS, Amundsen Sea; RS, Ross Sea; D'US, D'Urville Sea; MS, Mawson Sea; CS, Cooperation Sea; CoS, Cosmonaut Sea; RLS, Riiser-Larsen Sea; LS, Lazarev Sea; WS, Weddell Sea. Fronts location was obtained from Orsi et al. (1995), whereas the circulation patterns were reproduced combining the information from Heywood et al. (2004); Thompson et al. (2009), Armitage et al. (2018); Moffat and Meredith (2018), Thompson et al. (2018), and Vernet et al. (2019).

between Antarctic and Subantarctic habitats from a physical and a biogeochemical oceanographic point of view.

The limits of the CCAMLR 48.1 zone (50–70°W, 60–70°S with the exclusion of the of the southern part of the Weddell Sea) are in fact very similar to those that define the Western Antarctic Peninsula and Scotia Arc zone identified by the Southern Ocean Observing System[1]. The 48.1 zone include the shelves and pelagic areas off the Western Antarctic Peninsula from Margarite Bay to the tip of the Peninsula (**Figure 1**), coastal islands such as the South Shetland Islands and the northern part of the Eastern Antarctic Peninsula. This study dedicated a special focus on the CCAMLR 48.1 zone because it is one of the most important spawning regions for Antarctic krill (Perry et al., 2019) that is directly affected by fisheries (Ainley and Pauly, 2014; Brooks et al., 2018) and has experienced one of the fastest temperature increase of the planet (Turner et al., 2005, 2016). Krill was the main fishery target within the 48.1 zone and represented the 99.9% of the catches in the area since 2000 (CCAMLR, 2018). Krill landings from the 48.1 zone accounted for 45% of total Southern Ocean krill catches and the eastern and western part of the Bransfield Strait were the regions where most of the 48.1 krill catches occurred (62%), followed by the western pelagic area of the Drake Passage (15%). Most of these catches were made with midwater otter trawls (CCAMLR, 2018).

Physical and Biogeochemical Variables

The variables selected for the physical and biogeochemical regionalization, along with their characteristics, are presented in **Table 1**. The mean value of the physical and biogeochemical parameters during the "productivity season" (December–March; **Supplementary Figures 1, 2**) was calculated in a 1° × 1° latitude/longitude grid south of 50°S. The study focused on this period based on the phenology of phytoplankton proliferations (Soppa et al., 2016), the higher krill abundances (Atkinson et al., 2017) and the higher proportion of valid satellite data with respect to austral winter. The majority of the analyzed variables covered a time span of 15 years (2003–2018), with the significant exception of iron concentration and mixed layer depth (MLD) estimations that only were available for a period of 5 years (**Table 1**). These model-output databases were chosen despite of their limited time frame because they guaranteed a higher spatial coverage with respect to others *in situ* databases (i.e., Tagliabue et al., 2012; Li et al., 2017; Holte et al., 2017), especially in the coastal areas of the Antarctic continent.

Olson et al. (2016) bathymetry data was obtained from the data.gov portal[2], whereas Titchner and Rayner (2014) sea ice estimations were downloaded from the Met Office Hadley Center page[3]. Monthly composite of satellite-derived variables (sea surface temperature, photosynthetically active radiation and chlorophyll-a; SST, PAR and Chl-a, respectively) were extracted from the CoastWatch project of the National Oceanic and Atmosphere Administration[4]. Model output variables, such as MLD and iron concentration in the surface water, were

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[1] http://www.soos.aq/activities/rwg/wapsa

[2] https://catalog.data.gov/dataset

[3] https://www.metoffice.gov.uk/hadobs

[4] https://coastwatch.pfeg.noaa.gov/

TABLE 1 | Spatio-temporal characteristics of the physical and biogeochemical variables used in this study.

Variable	Database	Spatial resolution	Temporal resolution	Temporal span	References
Physical					
Bathymetry	SRTM 15 + v1	500 m			Olson et al., 2016
Ice coverage	HadISST.2.2.0.0	1°	Monthly	2003–2018	Titchner and Rayner, 2014
Sea surface temperature	MODIS Aqua	9 km	Monthly	2003–2018	NOAA Coastwatch
Mixed layer depth	SOSE	0.17°	Monthly	2005–2010	Mazloff et al., 2010
Photosynthetically active radiation	MODIS Aqua	9 km	Monthly	2003–2018	NOAA Coastwatch
Biogeochemical					
Iron concentration×	B-SOSE	0.33° lon × 0.17° lat	Monthly	2008–2013	Verdy and Mazloff, 2017
Net primary production	VGPM	9 km	Monthly	2003–2018	Behrenfeld and Falkowski, 1997
Diatoms contribution to Chl-a$^{\beta}$	MODIS Aqua	9 km	Monthly	2003–2018	Soppa et al., 2016
Nanophytoplankton biomass	SeaWiFS	9 km	Monthly	2003–2010	Kostadinov et al., 2016
Particulate organic carbon export*	AADC	0.1°	Monthly	2003–2015	Guillaumot et al., 2017

SRTM, Shuttle Radar Topography Mission; HadISST, Hadley Centre Global Sea Ice and Sea Surface Temperature; MODIS, Moderate-Resolution Imaging Spectroradiometer; SOSE, Southern Ocean State Estimates; B-SOSE, Biogeochemical Southern Ocean State Estimate; SeaWiFS, Sea-Viewing Wide Field-of-View Sensor; VGPM, Vertically Generalized Production Model; AADC, Australian Antarctic Data Centre; NOAA, National Oceanic and Atmospheric Administration. NOAA Coastwatch link: https://coastwatch.pfeg.noaa.gov/erddap/index.html.

×Iron surface concentration (0–50 m).

$^{\beta}$Diatoms was derived from Chl-a MODIS.

**Summer season was defined by Lutz et al. (2007).*

obtained from the Southern Ocean State Estimation page[5]. Net Primary Production (NPP) estimations calculated with the "standard" Vertically Generalized Production Model (Behrenfeld and Falkowski, 1997) were acquired from the Ocean Productivity page[6]. Finally, Kostadinov et al. (2016) nanophytoplankton concentration was achieved from the PANGEA data center[7] and Particulate Organic Carbon (POC) exports were extracted from the Australian Antarctic Data Center[8].

It is important to consider that satellite-derived Chl-a was directly used as input parameter for NPP, diatoms and POC export estimations, which may cause redundancy in the spatial variability of these variables and the biogeochemical regionalization. In spite of this, the treatment of Chl-a data was different for each product, since only diatoms concentration exclusively relies on Chl-a concentration and NPP and POC estimations used multiple input variables along with Chl-a data. Soppa et al. (2016) equation was used for diatoms concentration: $\log_{10}(\text{Diatom}) = 1.1559 \cdot \log_{10}(\text{Chl-a}) - 0.2901$. Behrenfeld and Falkowski (1997) equation for NPP estimations might be summarized as: $\text{NPP} = f(\text{Chl-a}) \cdot f(\text{SST}) \cdot D_L \cdot f(\text{PAR})$; where $f(\text{Chl-a})$ represents a function of surface Chlorophyll-a estimation, $f(\text{SST})$ indicates a function of Sea Surface Temperature, D_L is the day length and f(PAR) represents a function of Photosynthetically Active Radiation. On the other hand, POC export flux was calculated by Guillaumot et al. (2017) using: $\text{POC export} = \text{NPP}_c \cdot f(Z_{eu}) \cdot f(Z_0)$; where NPP_c is the Net Primary Production in the surface water calculated with the Carbon-based Production Model (Westberry et al., 2008), Z_{eu} indicates the depth of the euphotic zone and Z_0 the depth of the sea floor. The simplified equation for NPP_c might be summarize as: $\text{NPP}_c = f(\text{Chl-a}) \cdot f(\text{bbp}) \cdot f(\text{PAR}) \cdot f(Z_{NO3}) \cdot D_L \cdot f(\text{MLD}) \cdot f(k_{490})$; where $f(\text{bbp})$ indicates a function of the particulate backscattering coefficient at 443 nm, $f(Z_{NO3})$ is a function of nitracline depth, $f(\text{MLD})$ represents a function of Mixed Layer Depth and $f(k_{490})$ is a function of the diffuse attenuation coefficient at 490 nm.

Estimates of Regionalization

Regionalization is a useful methodological tool that allows to identify similarities and dissimilarities between adjacent and remote areas according to different *criteria* and to group regions with analogous properties. Indeed, a regionalization developed using physical variables might provide the degree of similarity (expressed as distance in a dendrogram) between regions from a physical standpoint. On the other hand, the use of biogeochemical variables will result in a regionalization according to a biogeochemical point of view. The number of regions provided by this analysis is an indicator of heterogeneity; whereas the mean value for each group (i.e., cluster) might help the identification of areas with similar temperature and sea ice patterns as well as high and low productivity zones. The comparison between physical and biogeochemical regionalization can provide useful information about physical and biogeochemical patterns within a defined area.

The Southern Ocean regionalization was developed following the methodology of Grant et al. (2006) and Raymond (2014). The main steps for this analysis were: (I) The mean bathymetry for each pixel was transformed in $\log_{10}$(bathymetry); (II) the pixels with at least a missing value among all variables were eliminated (i.e., no interpolation was used); (III) all the variables were normalized between 0 and 1; (IV) non-hierarchical Clustering Large Application (CLARA; Kaufman and Rousseeuw, 1990) was applied to group all the pixels within 250 clusters using Manhattan distance for both datasets as indicated by

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[5] http://sose.ucsd.edu

[6] http://sites.science.oregonstate.edu/ocean.productivity/

[7] https://www.pangaea.de/

[8] https://data.aad.gov.au/

Grant et al. (2006) and Raymond (2014); (V) the mean value for each of the 250 groups was calculated; (VI) an agglomerative hierarchical clustering method (Unweighted Pair Group Method with Arithmetic mean, UPGMA; Sokal and Michener, 1958) was applied to the results of the previous step; (VII) the number of significant clusters within the data was identified using the Clarke et al. (2008) statistical method (1000 permutations and an alpha value of 0.05 with the assumption of no *a priori* groups). This section slightly modified the original methodology proposed by Grant et al. (2006), which incorporated a cutoff method for dendrograms. Indeed, the cutoff technique strongly depends on authors criteria, whereas other "traditional" methods to determine numbers of clusters within a dendrogram (i.e., elbow, silhouette, gap statistic and Charrad et al. (2014) methods) were unsuccessful when applied to the data (**Supplementary Table 1**). On the contrary, the regionalization of CCAMLR 48.1 zone was performed exclusively with UPGMA agglomerative cluster due to reduced sample size. The analyses were carried out using R[9] and Matlab[10].

The regionalization methodology applied in this study is accompanied by different sources of uncertainties in the pixels grouping and boundaries location between areas. Among different factors, uncertainty might be ascribed to imprecision in the data and epistemic uncertainty related to the knowledge of regionalization process (Grant et al., 2006). Data imprecisions comprise satellite or model estimations errors and bias due to incomplete observations, whereas knowledge errors include the data selection and the processing steps, such as the clustering method.

Relationship Between Physical and Biogeochemical Variables and Regions

The Pearson linear correlation coefficient (p-value: 0.05) between physical and biogeochemical variables, along with the geographical coordinates, was estimated. The BIO-ENV package from Clarke and Ainsworth (1993) was used in order to find the best subset of physical variables that have maximum correlation with biogeochemical dissimilarities throughout Spearman rank correlation coefficient. In addition, Distance-Based Redundancy Analysis (db-RDA; Legendre and Andersson, 1999), which is the direct extension of multiple regression to the multivariate scale and it allows non-Euclidean dissimilarity indices (i.e., Manhattan distance), was performed with 1,000 permutations and a p-value of 0.001. Throughout db-RDA analysis the ordination process was constrained by the biogeochemical variables and the ordination sought the axes that were best explained by a linear combination of explanatory physical variables (Kindt and Coe, 2005; Borcard et al., 2018). An analysis of variance (ANOVA) was performed to assess the significance of constraints. Both BIO-ENV and db-RDA analysis were realized using the R package Vegan from Oksanen et al. (2019).

For every biogeochemical region the number of physical clusters in which it was divided (and *vice versa*) were calculated in order to evaluate the degree of agreement between physical and biogeochemical regionalization. The clusters that represented less than 20% of total pixels of the corresponding region were filtered to identify the zones that majorly contributes to its surface. Finally, a non-parametric Mann–Kendall test for significance (with a p-value < 0.05) was used to assess the statistical significance of sea ice trend.

RESULTS

Southern Ocean

Physical Regionalization

The Southern Ocean presented very heterogenous physical conditions during the biological productive season (December to March). Sea ice coverage, indeed, ranged from 0 to 99%, whereas MLD varied between 12 and 103 m and SST (with a mean value of 2°C) oscillated between −1 and 12°C (**Table 2**). Physical variables were grouped in an agglomerative hierarchical cluster tree with a cophenetic correlation coefficient of 0.73 (**Figure 2A**) and 12 significant clusters were identified within the dendrogram (**Figure 2B**). Two oceanic ice-free zones north of 60°S (clusters n° 11 and 12) characterized by deep bathymetry and MLD (**Supplementary Table 2**) covered approximately the 53% of the study zone (38 and 15%, respectively). On the other hand, regions south of the Polar Front (clusters from n° 1 to 9) were characterized by low SST (mean values ranged from −0.96 to 0.47°C), shallow MLD (varying between 23.13 to 34.42 m) and reduced PAR values (from 14.34 to 27.87 E m^{-2} d^{-1}). The areas of Falkland Islands and South America were merged within one cluster (n° 10) that presented few pixels with shallow bathymetry, no ice coverage and highest PAR and SST values. Clear circum-Antarctic patterns were detected in several oceanic regions north (n° 8, 11, and 12) and south (n° 2 and 3) of 60°S, whereas this circumpolar structure was absent for coastal clusters (**Figure 2B**).

Biogeochemical Regionalization

The dendrogram of biogeochemical variables (**Figure 2C**; cophenetic correlation coefficient: 0.78) was divided into 18 significant clusters. Four oceanic groups of the Atlantic, Indian and Pacific sectors (n° 5, 6, 7, and 11; **Figure 2D**) were characterized by low POC export (ranging from 4.15 to 5.07 mg C m^{-2} d^{-1}), diminished diatoms concentrations (varying between 0.26 and 0.44 mg Chl-a m^{-3}) and covered approximately 52% of the Southern Ocean surface (**Supplementary Table 3**). In contrary, coastal Antarctic and Southern Patagonian areas (clusters n° 16, 17, and 18) presented elevated NPP values (ranging from 0.44 to 1.98 g C m^{-2} d^{-1}), diatoms concentrations between 0.55 and 1.06 mg Chl-a m^{-3}, nanophytoplankton concentrations from 37.85 to 45.45 mg C m^{-3} and POC export between 39.90 and 53.06 mg C m^{-2} d^{-1}. Group n° 1 enclosed remote areas from the Weddell Sea (close to the Ronne ice shelf) and the area around the Balleny Islands (near the Ross Sea; **Figures 1**, **2D**), probably because these regions shared the highest dissolved iron concentration in the surface of the Southern Ocean (0.2 nM) and intermediate productivity. The pixels belonging to the Weddell Sea (cluster n° 17) also presented elevated iron concentration, but the productivity and POC export were higher compared with Balleny Islands and

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[9] https://cran.r-project.org/

[10] https://mathworks.com/

TABLE 2 | Basic statistics of physical and biogeochemical variables within Southern Ocean and CCAMLR 48.1 zone.

	Southern Ocean				CCAMLR 48.1			
Variable	**n**	**Min**	**Max**	**Mean ± CI**	**n**	**Min**	**Max**	**Mean ± CI**
Physical								
Bathymetry (m)	7772	0.30	6595.60	3633.71 ± 30.50	123	48.11	4104.10	1899.20 ± 267.73
Ice coverage (%)	8081	0.00	99.16	15.37 ± 0.56	120	0.00	81.57	15.61 ± 4.44
SST (°C)	8016	−1.35	11.62	2.01 ± 0.07	121	−0.71	3.42	0.69 ± 0.17
MLD (m)	7889	11.94	103.02	39.54 ± 0.27	114	15.40	40.51	30.37 ± 1.00
PAR (E m^{-2} d^{-1})	7860	2.73	45.50	26.91 ± 0.13	121	15.48	30.90	26.64 ± 0.60
Biogeochemical								
Iron (nM)	7965	0.10	0.28	0.13 ± 0.00	119	0.11	0.20	0.14 ± 0.00
Diatoms (mg Chl m^{-3})	7879	0.17	1.21	0.38 ± 0.00	120	0.25	0.92	0.42 ± 0.03
NPP (g C m^{-2} d^{-1})	7764	0.04	2.22	0.27 ± 0.00	119	0.14	0.81	0.25 ± 0.02
Nanophytoplankton (mg C m^{-3})	7898	1.11	67.21	10.17 ± 0.21	118	1.50	51.47	14.00 ± 2.01
POC export (mg C m^{-2} d^{-1})	7801	3.36	103.63	8.53 ± 0.26	119	4.37	46.44	18.72 ± 2.4

Min, minimum; Max, maximum; n, number of valid pixels; CI: 95% Confidence Interval; SST, sea surface temperature; MLD, mixed layer depth; PAR, photosynthetically active radiation; NPP, net primary production; POC, particulate organic carbon.

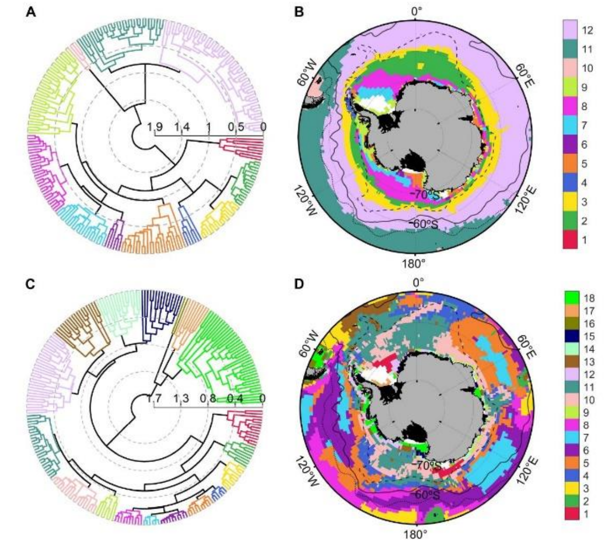

FIGURE 2 | Polar dendrogram and spatial distribution of the clusters obtained from physical **(A,B)** and biogeochemical **(C,D)** variables for the Southern Ocean. Black solid, dotted and dashed lines within Southern Ocean map indicated the geographic position of the Polar, Subantarctic and Southern Boundary fronts, respectively.

Ronne ice shelf (cluster n° 1). The circum-Antarctic pattern identified for oceanic physical regions was less clear during the biogeochemical regionalization. Oceanic island such as South Georgia, Auckland and Kerguelen were grouped in a separate region (n° 2) with much higher POC exports (29.03 mg C m^{-2} d^{-1}) with respect to the oceanic areas of the Indian and Pacific Ocean (n° 6, 7, and 8). The physical properties of the South America coastal region were significantly unique for this zone, whereas the biogeochemical regionalization showed that Southern Patagonia shared biogeochemical properties with coastal Antarctic regions of Ross, Bellingshausen, Amundsen and Cooperation Sea (cluster n°18).

Physical Variables That Explain Biogeochemical Spatial Variability

The latitude showed the highest Pearson linear correlation coefficient (*p*-value: 0.05) with physical variables (0.77, −0.77, −0.80, and −0.83 for sea ice concentration, SST, MLD, and PAR, respectively; **Table 3**). On the other hand, the neritic-pelagic gradient seemed to majorly control NPP, diatoms concentration, nanophytoplankton and POC export (with correlation coefficient of 0.55, 0.42, 0.68, and 0.81, respectively), whereas dissolved iron concentration in the photic layer appeared to be mainly controlled by sea-ice dynamics (Pearson linear correlation coefficient: 0.71).

The BIO-ENV analysis identified the combination of bathymetry and sea-ice coverage as the subset of environmental variables with best correlation to biogeochemical spatial variability, with a Spearman rank correlation coefficient of 0.68. Db-RDA (**Supplementary Figure 3A**) indicated that physical variables expressed the 60.1% of total biogeochemical variance.

CCAMLR Zone 48.1

Physical Regionalization

Important heterogeneity was found in physical variables within the 48.1 CCAMLR zone, with sea ice coverage varying between 0 and 82%, and SST ranging from −0.7 and 3.4°C (**Table 2**). The agglomerative hierarchical cluster tree for physical variables showed a cophenetic correlation coefficient of 0.78 (**Figure 3A**), whereas 14 significant clusters were identified. A region with an average sea ice coverage of 3% (n° 5) occupied approximately 33% of the entire 48.1 zone with a southwest (SW)-northeast (NE) distribution that included Shetland Islands (**Figure 3B**). This cluster presented intermediate depth (mean value: 1,168 m), SST (0.55°C) and MLD (31.8 m) values as compared with other groups (**Supplementary Table 4**). The SW-NE spatial pattern also appeared for warmer free-ice oceanic clusters located toward the Drake Passage (n° 1, 2, and 4), with the regions n° 2 and 5 that seemed to be separated by the Southern Boundary (**Figure 1**). The zone of the 48.1 zone closer to the Weddell Sea (clusters n° 9 and 10) exhibited the highest sea ice concentrations (from 64.3 to 69.1%) and coolest waters (between −0.68 and −0.61°C). Marguerite Bay, Gerlache Strait and Crystal Sound (biological hotspots along the Western Antarctic Peninsula; Costa et al., 2007; **Figure 1**) were clustered into group n° 14, which was characterized by elevated sea ice coverage (mean value: 55%), the shallowest MLD (21 m) and lowest PAR value (20 E m^{-2} d^{-1}) within CCAMLR 48.1 zone. These zones shared physical conditions with the southern part of the Eastern Antarctic Peninsula shelf. Finally, one singleton cluster (n° 6) was observed in the northern tip of Antarctic Peninsula.

Biogeochemical Regionalization

We identified 16 significant clusters within the dendrogram of biogeochemical variables (**Figure 3C**; cophenetic correlation coefficient: 0.84). Gerlache Strait, the eastern part of Marguerite Bay and one oceanic pixel were identified as singleton biogeochemical clusters (n° 2, 9, and 13) in the CCAMLR zone 48.1 (**Figure 3D**). Marguerite Bay, the coastal zone of the Eastern Antarctic Peninsula and the area around Crystal Sound (clusters n° 1, 2, 3, and 16) were the most productive clusters in terms of NPP, diatoms, nanophytoplankton concentrations and POC exports (**Supplementary Table 5**). Conversely, the oceanic region off the Western Antarctic Peninsula (clusters from n° 4 to 10) were the most oligotrophic and presented the least POC export within the 48.1 zone. Pixels belonging to group n° 12 appeared to accurately follow the continental shelf slope and the southern Antarctic Circumpolar Current boundary along the Western Antarctic Peninsula (Moffat and Meredith, 2018). The division marked by the Southern Boundary in physical regionalization appeared less evident in the biogeochemical, whereas a separation between the eastern (n° 14) and western part (n° 15 and 16) of the Bransfield Strait was found (**Figure 3D**). The similarity between Marguerite Bay and the southern shelf of the Eastern Antarctic Peninsula physical conditions was also observed in the biogeochemical properties (n°1, 2, and 3).

Physical Variables That Explain Biogeochemical Spatial Variability

The longitudinal gradient in CCAMLR zone had a stronger influence in sea ice concentration and SST (**Table 4**) as compared with the results of the entire Southern Ocean (**Table 3**). On the other hand, the latitudinal gradient strongly influenced both physical (especially MLD and PAR, with −0.81 and −0.87, respectively) and biogeochemical properties in 48.1 zone (NPP and nanophytoplankton concentrations). Pearson linear correlation coefficient suggested that bathymetry was the main physical factor affecting biogeochemical properties as iron (0.65), POC export (0.96) and diatoms concentrations (0.77; **Table 4**).

Indeed, BIO-ENV analysis indicated bathymetry as the physical variable with higher correlation to biogeochemical spatial variability (Spearman rank correlation coefficient: 0.81). Additionally, db-RDA (**Supplementary Figure 3B**) showed that physical variables explained the 77.1% of biogeochemical variance.

Physical and Biogeochemical Regionalization Correspondence

The pixels of each Southern Ocean biogeochemical region belonged on average to 6 different physical zones (± a 95% confidence interval of ±1.5), whereas each physical region was divided in 9 ± 1.4 biogeochemical zones (**Figures 4A,B**). However, by filtering the results it was calculated that every biogeochemical (physical) region of Southern Ocean averagely corresponded to 1.8 ± 0.2 different physical (biogeochemical) zones. On the contrary, the correspondence degree between biogeochemical and physical regions was higher for CCAMLR 48.1 zone compared with the entire Southern Ocean, since the pixels of each biogeochemical (physical) region on average belonged to 2.3 ± 0.7 (2.7 ± 0.9) physical (biogeochemical) regions (**Figures 4C,D**). The results decreased to 1.5 ± 0.3 and 1.7 ± 0.4, respectively, when only the pixels that represented more than 20% of total pixels of the corresponding region were considered.

DISCUSSION

Comparison Between Physical and Biogeochemical Regionalization

This study allowed the identification of new physical and biogeochemical regions within the Southern Ocean, enabled

TABLE 3 | Pearson linear correlation coefficient between geographical coordinates, physical and biogeochemical variables within Southern Ocean.

	Lon	**Lat**	**Bat**	**Ice**	**SST**	**MLD**	**PAR**	**Fe**	**Dia**	**NPP**	**Nano**	**POC**
Lon	1	−0.18	0.08	−0.10	−0.03	0.14	0.20	*0.01*	−0.14	−0.13	−0.09	0.05
Lat		1	0.33	0.77	−0.77	−0.80	−0.83	0.63	0.44	−0.06	0.50	0.40
Bat			1	0.50	−0.19	−0.24	−0.19	0.39	0.55	0.42	0.68	0.81
Ice				1	−0.56	−0.66	−0.74	0.71	0.49	0.09	0.63	0.48
SST					1	0.66	0.78	−0.62	−0.31	0.34	−0.30	−0.17
MLD						1	0.73	−0.64	−0.41	0.04	−0.40	−0.22
PAR							1	−0.65	−0.28	0.29	−0.33	−0.14
Fe								1	0.41	−0.04	0.46	0.30
Dia									1	0.72	0.82	0.58
NPP										1	0.58	0.49
Nano											1	0.75
POC												1

Italics numbers indicated the results not statistically significant (p-value: 0.05). Lon, longitude; Lat, latitude; Bat, bathymetry; Ice, ice coverage; SST, sea surface temperature; MLD, mixed layer depth; PAR, photosynthetically active radiation; Iron, iron concentration in the surface layer (0–50 m); Dia, diatoms concentration; NPP, net primary production; Nano, nanophytoplankton biomass; POC, particulate organic carbon export.

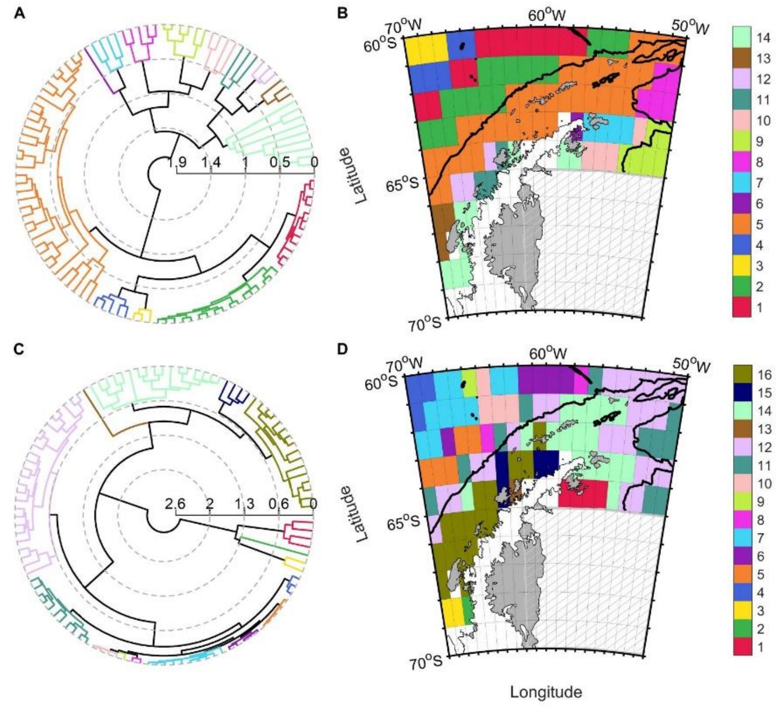

FIGURE 3 | Polar dendrogram and spatial distribution of the clusters obtained from physical **(A,B)** and biogeochemical **(C,D)** variables for the CCAMLR 48.1 zone. The black continuous line within 48.1 map indicated the 2,000 m isobath, whereas the gray hatched area represented the zone not included within the CCAMLR 48.1 zone.

TABLE 4 | Pearson linear correlation coefficient between geographical coordinates, physical and biogeochemical variables within CCAMLR 48.1 zone.

	Lon	Lat	Bat	Ice	SST	MLD	PAR	Fe	Dia	NPP	Nano	POC
Lon	1	−0.32	*0.13*	0.38	−0.68	*−0.07*	*0.08*	*−0.11*	*0.07*	*−0.19*	*0.01*	*0.01*
Lat		1	0.63	0.53	−0.40	−0.81	−0.87	0.58	0.69	0.70	0.70	0.66
Bat			1	0.38	−0.53	−0.53	−0.63	0.65	0.77	0.65	0.85	0.96
Ice				1	−0.67	−0.71	−0.63	*0.08*	0.58	0.43	0.51	0.39
SST					1	0.59	0.49	−0.21	−0.50	−0.24	−0.42	−0.42
MLD						1	0.83	−0.53	−0.62	−0.57	−0.63	−0.50
PAR							1	−0.61	−0.67	−0.65	−0.77	−0.65
Fe								1	0.49	0.53	0.65	0.63
Dia									1	0.94	0.88	0.79
NPP										1	0.84	0.73
Nano											1	0.90
POC												1

Italics numbers shown the results not statistically significant (p-value: 0.05). See ***Table 3*** *for acronyms definitions.*

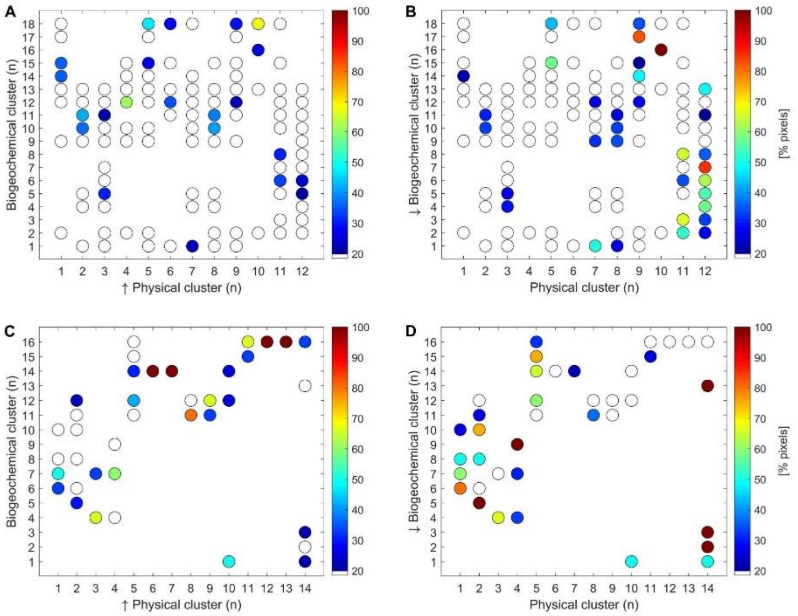

FIGURE 4 | Correspondence (expressed as% of pixels) between physical and biogeochemical clusters within Southern Ocean **(A,B)** and CCAMLR 48.1 zone **(C,D)**. The white (colored) dots represent the clusters that cover less (more) of 20%. Panels **(A,C)** show the pixels distribution for every physical cluster within the biogeochemical clusters, whereas panels **(B,D)** indicated the pixels distribution for every biogeochemical cluster within the physical clusters.

the comparison with previous regionalization and provided more explanatory information with respect to other studies. In addition, setting the northern limits at 50°S enabled the creation of new clusters and the study of similarities and differences between Antarctic and Southern Patagonian environments.

Cluster analysis revealed a higher number of significant biogeochemical regions with respect to physical zones. The number of Southern Ocean regions identified in the present work (12 and 18 for physical and biogeochemical variables, respectively) was comparable with other studies of bioregionalization. Indeed, the study of Grant et al. (2006) divided Southern Ocean in 14 different regions based on bathymetry, SST and nutrients concentration, whereas 20 regions were established by Raymond (2014) using bathymetry, SST and ice coverage. Instead, the study of regionalization for CCAMLR 48.1 zone is the first of our knowledge and identifies a surprisingly high number of significant zones (14 physical and 16 biogeochemical regions), probably due to absence of *a priori* non-hierarchical grouping. The observed circumpolar distribution of physical oceanic clusters marked by the oceanic fronts pattern was similar with the findings of previous regionalization studies (Grant et al., 2006; Spalding et al., 2012; Raymond, 2014). Additionally, Falkland Islands and the coastal zone of the Southern Patagonian were grouped into one physical cluster, which was in agreement with previous works. This work divided the Antarctic coastal area in seven different clusters, which coincided with Raymond (2014) and differed with the regionalization of Grant et al. (2006) that grouped the entire Antarctic coastal area into one region. Grant et al. (2006) additionally identified a separated cluster for the oceanic area of the Weddell gyre, in contrast with the division of this area into four different regions shown by this research and supported by the results of Raymond (2014). The inclusion of sea ice spatial variability into the regionalization variables (Raymond, 2014; this study) might originate higher physical heterogeneity with respect to a regionalization (Grant et al., 2006) that incorporated nitrate and silicate concentrations, since elevated and homogenous macronutrient concentrations are generally observed south of the Southern Boundary and along the Antarctic coastal area (Pollard et al., 2006; Sigman and Hain, 2012).

As expected, the Subantarctic and the Polar Fronts spatial variability influenced the Southern Ocean physical regionalization generating circum-Antarctic clustering (**Figure 2B**). On the contrary, the spatial variability of oceanic fronts was not reflected in biogeochemical regionalization (**Figure 2D**), since biogeochemical regions were identified crossing the oceanic fronts in the Indian and Pacific Ocean. In fact, the distinction was not reflected in NPP and phytoplanktonic groups distribution despite the clear difference in SST and MLD at both sides of the fronts (**Supplementary Figure 1**). Low NPP estimations might be explained by a combination of light limitation (Venables and Moore, 2010), zooplankton grazing (Le Quéré et al., 2016) and dissolved iron depletion (Tagliabue et al., 2014; Wadley et al., 2014).

The coastal zones around South America and Falkland Islands were merged into one physical cluster significantly different from all others in the Southern Ocean (**Figure 2B**). Contrarily, the coastal region around the southern part of Patagonia was divided in two regions according to biogeochemical variables (i.e., 16 and 18) and the cluster n° 18 also appeared near the coastal zone of Ross, Bellingshausen, Amundsen and Cooperation Sea (**Figures 1**, **2D**). This suggested that coastal zones of Patagonia and some Antarctic zones shared common biogeochemical features (high NPP estimations and diatoms concentrations; **Supplementary Table 3**), but not physical dynamics. The high productivity of coastal Antarctic zones might be fueled by marginal sea-ice melting during austral summer, injecting micronutrients (Lannuzel et al., 2016) and increasing the photic layer stability (Taylor et al., 2013), whereas the high NPP around the southern part of the Patagonia might be sustained by high tidal energy dissipation and mixing above the continental shelf (Romero et al., 2006), continental freshwater discharges (Cuevas et al., 2019) and the possible iron supply by shelf transport (Garcia et al., 2008) or atmospheric dust (Jickells et al., 2005). Future modeling studies might test the influence of physical and chemical factors on primary production and carbon export in Antarctic and Southern Patagonian related biogeochemical zones under different climate change scenarios.

Additionally, Southern Ocean waters surrounding oceanic islands as Auckland, Kerguelen and South Georgia (**Figure 1**) were grouped in separated biogeochemical clusters (n°2 and 13; **Figure 2D**), whereas this distinction was not revealed by physical regionalization. The elevated NPP rates (**Supplementary Table 3**) and the annual bloom around these oceanic islands can be explained by an "island mass effect" primary produced by downstream iron fertilization via advection (Boyd et al., 2004; Robinson et al., 2016). Sediment pore waters of oceanic islands are a key source of iron in the Southern Ocean (Graham et al., 2015), since iron is released into the photic layer via internal waves and mixing (Korb et al., 2008) and can fuel phytoplankton blooms. In spite of this, interannual variability in the magnitude and extension of the island mass effect might also be influenced by macronutrients and light limitation (Robinson et al., 2016).

The spatial distribution of the Southern Boundary and the Polar Front influenced the physical regionalization of the NW zone of the CCAMLR 48.1 region (clusters n° 2 and 5) but this division was not clearly detected in the biogeochemical regionalization (**Figures 1**, **3**). On the other hand, the physical regionalization of the CCAMLR 48.1 zone didn't identified a difference between the eastern and western parts of the Bransfield Strait which, on the contrary, was observed in the biogeochemical regionalization (**Figure 3**). Intense continental meltwater input and the influence of the Antarctic Slope Current (**Figure 1**) that brings waters from the Weddell Sea (Sangrà et al., 2011; Moffat and Meredith, 2018) might cause the biogeochemical division between the western and eastern part of the Bransfield Strait. Marguerite Bay and the southern shelf of the Eastern Antarctic Peninsula presented similar physical and biogeochemical conditions, with the shallowest MLD and highest NPP estimations and diatoms concentrations, probably due to the elevated presence of sea ice during the austral summer and its influence on biogeochemical cycles (Hyatt et al., 2011; Siegert et al., 2019).

No strong consistency was observed between the physical and biogeochemical regionalization of the Southern Ocean (**Figure 4**), whereas this correlation was higher for CCAMLR 48.1 zone. The higher consistency between physical and biogeochemical regionalization for 48.1 zone might be explained by either the reduced sample size and/or the response of both biogeochemical and physical regions to the spatial patterns of the shelf slope (**Figure 3**), as also pointed out by Heywood et al. (2014). The inconsistency detected for the Southern Ocean might be ascribed to the lower spatial variability of biogeochemical variables explained by physical factors as compared with the CCAMLR 48.1 area (60 and 77%, respectively). Indeed, Southern Ocean regions with different physical conditions might present the same biogeochemical features (and High Nutrient Low Chlorophyll patterns), as resulted from oceanic areas around the Subantarctic and the Polar Fronts (**Figures 2B–D**). This difference might induce a more comparable number of physical and biogeochemical clusters for CCAMLR 48.1 zone (14 and 16, respectively) with respect to the Southern Ocean (12 and 18).

Neither physical nor biogeochemical Southern Ocean regionalization identified a separated cluster for CCAMLR 48.1 zone. Indeed, the limits of the CCAMLR zone included heterogeneous zones with coastal and open water areas, islands, as well as areas belonging to either the Western or Eastern part of the Antarctic Peninsula. This heterogeneity was reflected in elevated number of biogeochemical and physical clusters within CCAMLR 48.1 zone, suggesting that the 48.1 limits were identified exclusively for statistical purposes[11] and should be revised following biogeochemical *criteria*.

Main Physical Factors Explaining Biogeochemical Spatial Variability

BIO-ENV analysis revealed that the combination of bathymetry and sea-ice concentration majorly controlled the biogeochemical spatial variability in the Southern Ocean. Both the neritic-pelagic gradient and sea ice variability affect nutrients and iron cycles and stoichiometry (Garcia et al., 2008; Torres et al., 2014; Annett et al., 2017; Cuevas et al., 2019; Henley et al., 2020), water column stability (Hellmer, 2004; Romero et al., 2006; Cuevas et al., 2019) and irradiance balance (Smith Jr. and Comiso, 2008). In addition, bathymetry directly affects the POC oxygen exposure time to remineralization (Dunne et al., 2007), whereas high pulses of krill fecal pellets that strongly contribute to POC exports (Henley et al., 2020) have been discovered near the marginal ice zone (Belcher et al., 2019). As a result, sea ice variability is a sensible mechanism able to influence NPP rates, POC exports and phytoplankton species composition (Deppeler and Davidson, 2017). Changes in dissolved iron supply, light availability, stratification and ice-free period are projected to affect the biogeochemical cycles and increase Southern Ocean NPP rates up to 50%, in contrast with global trend of declining NPP (Henley et al., 2020). Sea ice variability also influence the production of dimethyl sulfide, a climate-active gas with high concentration in the marginal ice zone (Meredith et al., 2017; Hendry et al., 2018; Henley et al., 2019), and plays an important role in controlling the amount of organic matter that reaches the benthic community (Hendry et al., 2018; Henley et al., 2019). The strong interdependency between sea ice and phytoplankton abundance and size spectrum implies that its variability is also able to alter higher trophic levels of the food web, changing the structure and functioning of the entire ecosystem (Kerr et al., 2018). Indeed, a reduction in sea ice coverage and a shift from a cold and dry climate toward maritime conditions might disadvantage some species (such as Adélie penguins, Weddell seals and minke whales) and favor others (e.g., gentoo penguins and humpback whales; Henley et al., 2019 and references therein).

Bathymetry was identified as the physical variable that majorly described the biogeochemical spatial variability in the CCAMLR 48.1 zone, contrarily to the Southern Ocean where the combination of bathymetry and sea ice was established as the main feature controlling biogeochemical variability. The exclusion of sea ice variability in the 48.1 area might be ascribed to the low spatial heterogeneity in sea ice concentration during the austral summer, since most of the Antarctic Peninsula exhibited low sea ice concentrations with exception of Marguerite Bay and the southern part of the Eastern Antarctic Peninsula (**Supplementary Figure 2**).

The number and extension of biogeochemical regions might be affected by future variability since both sea ice and bathymetry will experiment changes (on different time scale). Indeed, changes in continental shelf width and bathymetry might occur on decadal to century time scales because of the balance between glacial isostatic adjustment (+41 mm yr^{-1}; Barletta et al., 2018) and sea level rise (+1.2 mm yr^{-1}; King et al., 2012). The spatial variability of sea ice trends for the Southern Ocean during 40 years (from 1978 to 2018; **Figure 5**) showed significant heterogenous trends along the major Antarctic marginal sea ice zones and the CCAMLR 48.1 zone, mainly explained by surface atmospheric circulation patterns (Eayrs et al., 2019) and deep ocean warming (Meredith et al., 2017). Despite the negative sea ice trend detected in the Western Antarctic Peninsula since 1978, a hiatus in atmospheric temperature and sea ice trend has been recorded in this area during the last two decades as part of the natural interdecadal climate variability (Meredith et al., 2017; Henley et al., 2019). Parkinson (2019) shown that sea ice coverage trends were reversed during the 2014–2018 period with sea ice loss in the Weddell and Ross Sea and in the Indian and Western Pacific Ocean; whereas a sea ice gain was observed for the Bellingshausen and Amundsen Sea. These opposite sea ice trends were mainly explained by the combination of atmospheric events (El Niño-Southern Oscillation, the Southern Annular Mode fluctuations and regional circulation flows) and oceanic variability (subsurface heat anomalies and polynyas creation; Parkinson, 2019; Turner et al., 2020). Oceanic biogeochemical regions of the Southern Ocean might also be affected by climate variability, since a poleward expansion of subantarctic waters and a contraction in biogeochemical regions closer to the Antarctic continent were projected for 2100 (Reygondeau et al., 2020).

Future Challenges

This work provides useful information for future parametrization and calibration of biogeochemical models for both the Southern Ocean and the 48.1 zone. Further subjective clustering methods might allow the identification of macro physical and biogeochemical provinces (Spalding et al., 2012) in the Southern Ocean in order to facilitate modeling purposes. The results of the biogeochemical regionalization suggested the division of the 48.1 zone in two provinces (the region above the continental shelf and the deeper ocean) for future ecosystem

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[11] https://www.ccamlr.org/en/organisation/explanation-terms

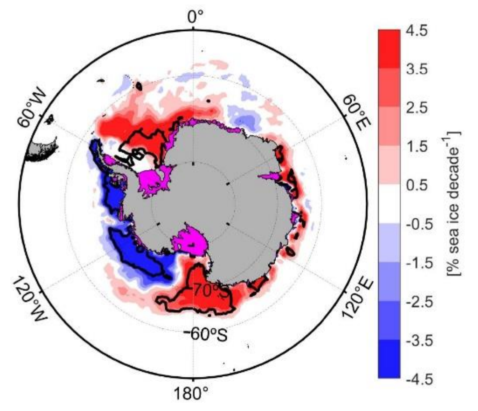

FIGURE 5 | Sea-ice coverage spatial trend during the last 40 years (1978–2018). Black contour line indicated zones with a significant trend (*p*-value: 0.05).

parametrizations. The study additionally suggests the exclusion of the northerner part of the Eastern Antarctic Peninsula and Marguerite Bay during the parametrization of the 48.1 zone because the physical and biogeochemical dynamics seemed to be strongly affected by either higher presence of sea ice for Marguerite Bay (Hyatt et al., 2011; Siegert et al., 2019; **Figure 1**) or inflow from Weddell Sea in the Eastern Antarctic Peninsula (Moffat and Meredith, 2018).

This study identified the most productive biogeochemical regions for both the Southern Ocean and CCMAR 48.1 zone. This valuable information will be useful in the development and support of marine protected area proposals, although additional information, such as the spatial variability of higher trophic levels (i.e., zooplankton, zoobenthos, fish, birds, and marine mammals), is needed to create a more solid proposition. The biogeochemical regionalization was initially designed with the inclusion of intermediate trophic levels (i.e., zooplankton abundances). Unfortunately, even the largest *Euphausia superba* and *Salpa thompsoni* abundance database for the Southern Ocean (i.e., KRILLBASE; Atkinson et al., 2017) presented extended regions with missing data (**Supplementary Figures 4A,B**). A continuous updating of krill and salp abundance databases within the Southern Ocean is a must, in order to develop detailed studies regarding food web spatial variability. Abundance data of copepods such as *Calanoides acutus* and *Rhincalanus gigas* were even sparser in the Southern Ocean (**Supplementary Figures 4C,D**), despite of merging the Coastal and Oceanic Plankton Ecology, Production, and Observation Database[12], the Southern Ocean Continuous Plankton Record database[13] and the database provided by Cornils et al. (2018). The summary and standardization of published copepods data within a new Southern Ocean database is considered an important challenge ahead for the scientific community. A regionalization for 48.1 zone including zooplankton abundances is also needed in the near future in order to develop and improve ecosystem management, such as regulation of fisheries, tourism, contamination and creation of marine and terrestrial protected areas and sanctuaries.

The dataset containing the gridded mean value for physical and biogeochemical variables from December to March within the entire Southern Ocean will be shared with colleagues, consistent with the principle of free-access data and analysis in order to face the actual social and climate crisis.

CONCLUSION

This regionalization study allowed the identification of new regions within the Southern Ocean and comparisons with previous regionalization developed using physical and biogeochemical variables. The number of the physical and biogeochemical Southern Ocean regions identified in this study (12 and 18, respectively) was comparable with previous studies of bioregionalization. However, southern Patagonian coastal areas were merged into a physical cluster significantly different from all others in the Southern Ocean, whereas biogeochemical patterns were shared with coastal Antarctic areas (i.e., Ross, Bellingshausen, Amundsen, and Cooperation Sea). The combination of bathymetry and sea ice coverage majorly explained biogeochemical variability within the Southern Ocean (Spearman rank correlation coefficient: 0.68). Since both sea ice and bathymetry will experiment changes, although on different time scale, our results suggest the number and extension of biogeochemical regions might be affected in the future.

Fourteen physical and 16 biogeochemical significant clusters were identified for 48.1 CCAMLR zone, where bathymetry was the main factor explaining biogeochemical spatial variability (0.81). The results suggested the division of the 48.1 zone in two main provinces separated by the shelf slope during future ecosystem parametrizations, with the exclusion of the northerner part of the Eastern Antarctic Peninsula and Marguerite Bay, because those regions were affected by either higher presence of sea ice (for Marguerite Bay) or inflow from Weddell Sea (in the Eastern Antarctic Peninsula).

The correspondence between physical and biogeochemical regions was higher for CCAMLR 48.1 zone with respect to the entire Southern Ocean, probably ascribed to the lower spatial variability of biogeochemical variables explained by physical factors in the Southern Ocean as compared with the CCAMLR 48.1 area (60 and 77%, respectively). Both physical and biogeochemical Southern Ocean regionalization failed to identify a separated cluster for CCAMLR 48.1 zone, suggesting that the 48.1 limits should be revised following biogeochemical *criteria*.

This study provides useful data for both Southern Ocean and CCAMLR 48.1 zone management and ecosystem parametrization purposes.

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[12] https://www.st.nmfs.noaa.gov/copepod/

[13] https://www.scar.org/science/cpr/

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

GT, AP, and LC analyzed the data and wrote the manuscript. All authors contributed to the article and approved the submitted version.

FUNDING

This study was supported by FONDECYT 11170913, FONDAP 15150003, National Agency for Research and Development (ANID)/PFCHA/Doctorado Nacional/2017-21170561, and COPAS Sur Austral ANID PIA Apoyo CCTE AFB 170006.

ACKNOWLEDGMENTS

We thank R. Giesecke, S. Neira, the associate editor, and reviewers for their valuable comments and suggestions.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.592378/full#supplementary-material

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Conflict of Interest: The 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.

4.2. Capítulo 2. Proyección del impacto ambiental y de la pesquería de kril sobre la trama trófica de la Península Antártica en 2100

Artículo enviado a la revista *Progress in Oceanography*

Testa, G., Neira, S., Giesecke, R., Piñones, A.

Resumen

El ecosistema de la Península Antártica es extremadamente sensible a la variabilidad climática y la perturbación antrópica asociada a la extracción de biomasa por las pesquerías. Se corrió un modelo Ecopath con Ecosim, calibrado para el período 1996-2012, hasta el año 2100 considerando tres escenarios climáticos de variables ambientales (hielo marino, área libre de hielo y clorofila-a) y tres proyecciones de pesquería de kril (ausencia de capturas, capturas constantes, aumento decadal gradual hasta duplicar las capturas actuales). El impacto relativo de las diferentes forzantes sobre la trama trófica antártica se evaluó con un análisis de sensibilidad y también se analizó la variabilidad temporal de varios grupos funcionales e indicadores ecosistémicos. La variabilidad ambiental pareció tener un mayor impacto sobre la trama trófica antártica en las proyecciones para 2100 en comparación con la pesquería de kril. La clorofila-a influyó fuertemente en la variabilidad temporal de los grupos funcionales, lo que sugiere un control principalmente *bottom-up* en la trama trófica. En el año 2100 se observó una estructura trófica alternativa, con una

marcada disminución en la biomasa de kril (entre -50% y la casi extinción según el escenario ambiental) y un aumento de salpas y otros grupos de zooplancton. Se detectó también una reducción en la biomasa de los depredadores dependientes del kril y del hielo, como los pingüinos Adelia y Barbijo y la foca cangrejera. La falta de parametrización en la variabilidad espacial y estacional de la pesquería de kril podría causar una subestimación de su impacto. Este trabajo proporciona información útil sobre posibles dinámicas de la trama trófica antártica ante diferentes escenarios ambientales y destaca varios puntos críticos que deben abordarse para mejorar la comprensión y la parametrización de modelos que exploren su variabilidad futura.

Progress in Oceanography

Projecting environmental and krill fishery impacts on the Antarctic Peninsula food web in 2100

--Manuscript Draft--

Manuscript Number:	
Article Type:	Full Length Article
Section/Category:	Interdisciplinary
Keywords:	Antarctic Peninsula; food web modeling; environmental variability; krill fishery; climate change
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Abstract:	The Antarctic Peninsula ecosystems is extremely sensitive to climate variability and anthropogenic perturbance ascribed to biomass extraction by the fisheries. An Ecopath with Ecosim model calibrated for the 1996-2012 period was projected in to the future (year 2100) under three different climatic scenarios for environmental variables (sea ice, open water area and chlorophyll-a) and three krill fishery projections (no-take, constant and decadal increase until doubling the current catches). The relative impact of different drivers controlling Antarctic food web dynamics was evaluated with a sensitivity analysis and the temporal variability of several functional group and ecosystems indicators. Under these scenarios the environmental variability resulted in a greater impact on Antarctic food web in 2100 projections compared to krill fishery. Chlorophyll-a biomass strongly influenced the temporal variability of functional groups, suggesting a predominantly bottom-up control on the food web. An alternative food web structure was observed in 2100, with a marked decline in krill population biomass (from less than 50% to nearly extinction depending on the environmental scenario) and an increase in salps and other zooplankton groups. A reduction in the biomass of sea-ice and krill-dependent predators, such as Adélie, Chinstrap penguins and Crabeater seals, was also observed. The lack of parametrization in the spatial and seasonal variability of krill fishery might cause an underestimation of its ecosystem impacts. This work provides useful insights on the dynamic responses of the Antarctic food web under likely environmental scenarios and highlights critical points that need to be addressed to improve the understanding and parametrization of the Antarctic food web to anticipate future variability.
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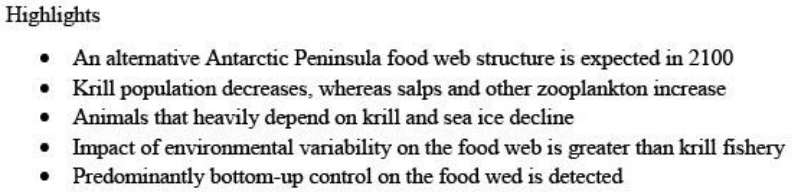
Highlights



Highlights

- An alternative Antarctic Peninsula food web structure is expected in 2100
- Krill population decreases, whereas salps and other zooplankton increase
- Animals that heavily depend on krill and sea ice decline
- Impact of environmental variability on the food web is greater than krill fishery
- Predominantly bottom-up control on the food wed is detected

Projecting environmental and krill fishery impacts on the Antarctic Peninsula food web in 2100

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ABSTRACT

The Antarctic Peninsula ecosystems is extremely sensitive to climate variability and anthropogenic perturbance ascribed to biomass extraction by the fisheries. An Ecopath with Ecosim model calibrated for the 1996-2012 period was projected in to the future (year 2100) under three different climatic scenarios for environmental variables (sea ice, open water area and chlorophyll-a) and three krill fishery projections (no-take, constant and decadal increase until doubling the current catches). The relative impact of different drivers controlling Antarctic food web dynamics was evaluated with a sensitivity analysis and the temporal variability of several functional group and ecosystems indicators. Under these scenarios the environmental variability resulted in a greater impact on Antarctic food web in 2100 projections compared to krill fishery. Chlorophyll-a biomass strongly influenced the temporal variability of functional groups, suggesting a predominantly bottom-up control on the food web. An alternative food web structure was observed in 2100, with a marked decline in krill population biomass (from less than 50% to nearly extinction depending on the environmental scenario) and an increase in salps and other zooplankton groups. A reduction in the biomass of sea-ice and krill-dependent predators, such as Adélie, Chinstrap penguins and Crabeater seals, was also observed. The lack of parametrization in the spatial and seasonal variability of krill fishery might cause an underestimation of its ecosystem impacts. This work provides useful insights on the dynamic responses of the Antarctic food web under likely environmental scenarios and highlights critical points that need to be addressed to improve the understanding and parametrization of the Antarctic food web to anticipate future variability.

Keywords: Antarctic Peninsula, food web modeling, environmental variability, krill fishery, climate change.

1. INTRODUCTION

Antarctic ecosystems are extremely sensitive to climate variability. Temperature and sea ice spatiotemporal dynamics affect food webs, from phytoplankton growth and krill life cycle to seal and penguin's food habits (Trivelpiece et al., 2011; Flores et al., 2012; Meade et al., 2015; Coello-Camba and Agustí, 2017; Watanabe et al., 2020). Although the human impact on the Antarctic food web is far to be fully understood, anthropogenic disturbance on Antarctic ecosystems is majorly ascribed to its contribution to climate change and the biomass removed by the fisheries.

Arctic and Antarctic ecosystems share common features (*i.e.*, low temperatures, marked seasonality in light and sea ice variability) and present several differences (*e.g.*, nutrient availability, primary production magnitude and endemism degree) mainly explained by topography and circulation patterns (McBride et al., 2014; Murphy et al., 2016). Trophic flows in polar systems are less complex compared with others marine ecosystems (Hill et al., 2006; Plagányi, 2007) and low metazoan diversity and the apparent dominance of few species in energy flows results in diminished functional redundancy in the Antarctic ecosystem (Murphy et al., 2016). Despite of this, high environmental heterogeneity and geographical isolation produce unexpected high levels of Antarctic marine biodiversity (Convey and Peck, 2019).

Diatoms (microphytoplankton >20 μm) are the major component of phytoplankton community that contribute to the Southern Ocean (SO) productivity (McBride et al., 2014), whereas cryptophytes (nanophytoplankton, <10 μm) usually dominate after diatoms proliferation and are related with the occurrence of low salinity waters associated with ice melting (Moline et al., 2004; Hernando et al., 2020). *Euphausia superba* is the most abundant and dominant krill species in the SO with an estimated biomass of 379 million tonnes (Atkinson et al., 2009; McBride et al., 2014) and it is connected to its consumers (fish, penguins, seals, albatrosses and whales) through few trophic links, increasing the transfer efficiency of energy and carbon along the food web (Hill et al. 2006). Murphy et al. (2016) estimated that krill covered on average the 43% of all metabolic requirements of Antarctic predators occupying higher trophic levels. However, this percentage was greater for sea birds and marine mammals and lower for fish and cephalopods. Despite the key role that Antarctic krill plays as prey for high trophic levels species, only a small fraction (3-5%) of the primary production is channeled through this group towards larger organisms (Murphy et al., 2016). Areas with low krill density might be dominated by copepods (*Rhincalanus gigas* and *Calanoides acutus*) with a modification of the food chain at regional scale (Murphy et al., 2012; McBride et al., 2014; Murphy et al., 2016). Krill usually dominates in high productivity waters characterized by the presence of diatoms, whereas salps (*Salpa thompsoni*) proliferate in less productive waters where cryptophytes dominate (Atkinson et al., 2004; Moline et al., 2004). Salps might play an important role in biogeochemical cycles, although they are usually not considered as a critical link to higher trophic levels (Moline et al., 2004; Murphy et al. 2016).

Marked spatial variability in Antarctic food webs, majorly expressed as krill dominance with respect to other zooplanktonic groups (*i.e.*, copepods, salps and ice krill), might be explained by physical (circulation and sea ice dynamics) and chemical (concentration of macro and micro nutrients) patterns that control biological dynamics (Murphy et al., 2012). The works of Murphy et al. (2013, 2016) identified the physical gradient and geographical distance as the main factors explaining the differences in penguins and seals species abundances between the Western Antarctic Peninsula (WAP) and the South Georgia ecosystems.

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) strongly regulate Antarctic fisheries since 1982, with a management that recognizes the interdependency of fisheries with the entire ecosystems (Constable et al., 2000; Hill et al., 2006; Kock et al., 2007; Constable, 2011). Indeed, fisheries might affect the food web via the direct removal of target and non-target (*i.e.*, by-catch) species and the alteration of complex biological interactions such as predation and competition (Trivelpiece et al., 2011). The Antarctic environment experimented a "fishing down the food web" process (Ainley and Pauly, 2014), since the exploitation of Antarctic living resources began with the near extinction of the Antarctic fur seal (*Arctocephalus gazella*) during the 18th and 19th centuries, followed by whales catches (*Balenoptera* y *Megaptera* spp.) in the 20th century (Ainley and Pauly, 2014; Lowther, 2018). Since 1960 demersal fish (*Notothenia rossii, Champsocephalus gunnari, Lepidonotothen squamifrons* y *Gobionotothen gibberifrons*) were the next main target for Antarctic fisheries (Ainley and Pauly, 2014), with a decrease of up to 80% of fish population (McBride et al., 2014). Since then, the human focused their attention upon krill (*E. superba*) and Antarctic and Patagonian toothfish (*Dissostichus mawsoni* and *Dissostichus eleginoides*). Krill catches within the CCAMLR 48.1 zone were approximately the 35% of the total krill catches in the SO since 1980, although this proportion was higher (53%) during the period 2010-2018 (**Supplementary Figure 1**).

Sea ice is a key component to complete the life cycle of several Antarctic organisms, since the timing of *E. superba* and several fish life cycles is strongly related with sea ice extent (Flores et al., 2012). Sea ice dynamics, statistically explained by wind-driven advective and thermodynamic effects (Holland and Kwok, 2014), also affect open ocean where photosynthesis can occur. Sea and continental ice are also recognized as the main stressors for the benthic community (Barnes and Conlan, 2007). During the second part of the 20th century WAP air temperature increased between 2 and 3°C (Stark, 1994). In addition, an increase in both surface and bottom ocean temperature was observed (Schmidtko et al., 2014; Comiso et al., 2017) which induced a decrease in sea ice. Despite the recent plateau in atmospheric warming of the Antarctic Peninsula, coastal sea ice is still retreating (Convey and Peck, 2019). Piñones and Fedorov (2016) predicted a change in krill habitat and a modification in its life cycle by 2100 due to ocean temperature rise and changes in sea ice dynamics. A decrease in sea ice extension (along with a rise in ocean temperature) might induce a movement toward higher latitudes and cause a transition to a copepods-dominated trophic web (Hill et al., 2012). A negative trend was observed for Adélie (*Pygoscelis adeliae*) and Chinstrap penguin (*Pygoscelis antartica*) populations within the South Shetland Islands from 1997 to 2007, mainly ascribed to a reduction in krill population due to a combination of sea ice cover retreat, krill fisheries and higher predation induced by a recovery in marine mammal populations (Trivelpiece et al., 2011).

The end to end food web modelling approach through the implementation of Ecopath with Ecosim (EwE), a modelling software used since 1984 to create mass balanced models for marine systems (Polovina, 1984; Christensen and Pauly, 1992; Walters et al., 1997), has been used to develop more than 400 models for aquatic systems around the planet (Heymans et al., 2016). Plagányi (2007) identified the flexibility of the parametrization framework as the main advantage of this approach, whereas the major limitation lies in the quantity and quality of available data and the absence of explicit spatial structure in Ecosim. For the study area, there are only two validated EwE models (Hoover et al., 2012; Dahood et al., 2019). These models are calibrated for a long period of time (1978-2007 and 1996-2012, respectively), other end to end modeling approaches for the Antarctic Peninsula (*i.e.*, Cornejo-Donoso and Antezana, 2008; Ballerini et al., 2014) are representative snapshots for a specific average year. On the other hand, the Coupled Model Intercomparison Project (CMIP) has coordinated climate model experiments since 1995 and its current phase 6 has led to a better understanding of climate changes arising from natural variability or in response to radiative forcing variability (CMIP6; Eyring et al., 2016).

The aim of this work is to evaluate the relative impact of environmental variability (sea ice extent and chlorophyll-a concentration) and krill fisheries on the marine food web of CCAMLR 48.1 zone under different scenarios projected toward the end of the century. To achieve this goal, a previously published and calibrated food web model for the study zone was used (Dahood et al., 2019) and forced with environmental and fisheries forcing factors developing several scenarios. Sea ice and chlorophyll-a projections were obtained from the CMIP6, whereas theoretical scenarios were developed for the temporal evolution of krill fisheries. The identification of the variables that majorly influenced the ecosystem response was evaluated through a sensitivity analysis for ecological indices and functional groups variability.

2. MATERIAL AND METHODS

2.1. Study area

The CCAMLR 48.1 zone extends over 658739 km^2 (**Figure 1**). The 55% of this region has a bathymetry deeper than 1000 m and only the 9% of the bathymetry is shallower than 200 m (**Supplementary Figure 2**). The region shows low sea-ice concentrations (*i.e.*, pixels with an annual mean in ice coverage below 10%) identified in 42% of the study zone, and higher sea ice concentrations (more than 50%) in 23% of the area. The SO is recognized as High Nutrient Low Chlorophyll zone (Martin, 1990; Pollard et al., 2006; Venables and Moore, 2010), although only the 28% of the marine surface in CCAMLR 48.1 zone showed concentrations higher than 0.5 mg m^{-3} and the 36% presented mean annual surface chlorophyll-a concentrations lower than 0.25 mg m^{-3}. Several permanent top-predator hotspots were identified within this area based on species richness and abundance of seabirds and marine mammals from historical observations obtained by the Antarctic Marine Living Resources program between 2003 and 2011 (Santora and Veit, 2013). Krill is the main fishery within 48.1 zone since 1980, followed by the fisheries targeting Mackerel icefish (*C. gunnari*) and Marbled rockcod (*N. rossii*; **Supplementary Figure 1**). The highest krill catches for CCAMLR 48.1 zone were reported during the period 2010-2018, with an average value of $12.7 \cdot 10^4$ tonnes.

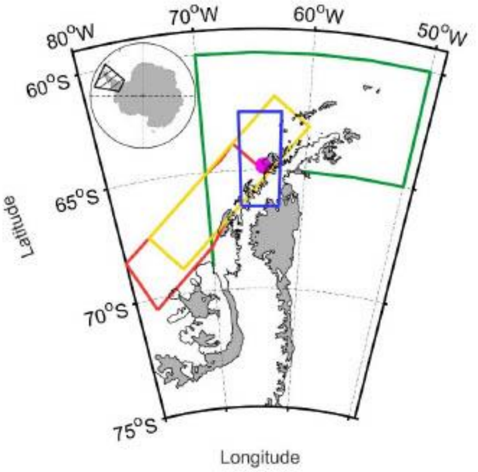


Figure 1. Study area and data source location. Green line indicates the CCAMLR 48.1 zone limits; Yellow: LTER stations area; magenta point: Palmer Station; Blue polygon: chlorophyll-a; Red polygon: sea ice

2.2. Model specifications

The Dahood et al. (2019) EwE model for CCAMLR 48.1 zone was used in this study since the Hoover et al. (2012) model only used sea ice to force juvenile krill rather than adult krill and failed to reproduce penguins trends. The model was calibrated for the 1996-2012 period with eight biological time series (abundances of Antarctic fur seal, Adélie, Chinstrap, Gentoo penguins, Mackerel icefish, Humped rockcod, Marbled rockcod and krill) and included 34 functional groups (plus one detritus group; **Figure 2**), representing the main components of the Antarctic food web. Krill was represented as a multi-stanza age groups by splitting this group into small (<24 months) and large (>24 months) organisms based on ontogenetic predator-prey interaction shift. The multi-stanza approach supposes a von Bertalanffy curve for body growth of krill and that the population has met a stable age-size distribution, which seems valid for Antarctic krill (Astheimer et al., 1985; Hofmann and Lascara, 2000; Candy and Kawaguchi, 2006). The data used to develop and validate the model were obtained from the Long-Term Ecological Research (LTER) at Palmer Station (**Figure 1**), indicating that the model was especially representative for the food web dynamics in the coastal WAP. Annual biomass accumulation rates of 2.9 and 3.9% were originally considered for fin whales and humpback whales, respectively. Since a full recovery of humpback whale population is expected by 2030 (Zerbini et al., 2019), the biomass increase rate was maintained up to this year. On the other hand, fin whale annual biomass accumulation rate was kept constant until the end of the century because no full recovery of pre-exploitation levels was expected before 2100 (Tulloch et al., 2019).

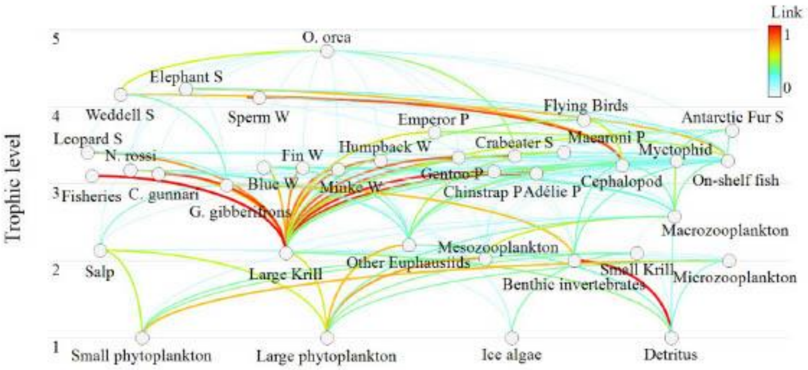


Figure 2. Energy flow diagram for the Ecopath food web model used in this study. Functional groups and fleets are represented by nodes, whereas lines represent the flow of energy. Colors indicate the relative magnitude of energy flows between functional groups.

Temporal biomass simulations for the different functional groups (Christensen y Walters, 2004) were expressed following the equation (1):

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ji} + I_i - (M0_i + F_i + e_i)B_i \qquad (1)$$

where dBi/dt indicates the i group biomass change over the time interval t, g_i represents the net growth efficiency, $\sum_j Q_{ji}$ is the total consumption on group i and I_i and e_i are the immigration and emigration rates, respectively. F_i represents the fishing mortality rate, $M0_i$ indicates the other mortality term and B_i is the initial biomass.

Four time series were originally used to force the model (**Supplementary Figure 3**): I) Monthly sea-ice area (expressed as sea-ice index) over an area of approx. 194320 km^2 (Palmer Station Antarctica LTER and Stammerjohn, 2020; **Figure 1**). The annual index was calculated as the ratio between annual sea-ice area minimum and the 1996-2012 average minimum sea-ice area. II) Open water area inside the ice edge was computed as the difference between sea-ice extent (*i.e.*, total area with sea-ice between 15 and 100%) and the area covered by sea-ice. III) Monthly chlorophyll-a concentration from continuous inflow near the Palmer station (Palmer Station Antarctica LTER and Schofield, 2020; **Figure 1**). IV) Observed leopard seal predation mortality rate on Antarctic fur seal pups from South Shetland islands (Goebel and Reiss, 2014). The leopard seal predation mortality rate on Antarctic fur seal pups was kept constant during our simulations (the mean value for the period 2002-2012 was used) since the magnitude increase in predation rate detected by Goebel and Reiss (2014) was not considered statistically significant due to the diminished sample size.

2.3. CMIP6 scenarios and projections

Three concentration-driven Shared Socioeconomic Pathways (ssp) were explored (ssp126, ssp370 and ssp585) from the CMIP6 (Eyring et al., 2016). The ssp126 scenario

predicts a radiative forcing reaching 2.6 W m^{-2} in 2100 (https://es-doc.org/cmip6/) with ssp1 socioeconomic conditions (O'Neill et al., 2017) and represents the "best case" of the range of possible future pathways. On the other hand, the ssp370 scenario considers a medium to high radiative forcing (7 W m^{-2}) by the end of century. Finally, the ssp585 scenario is characterized by ssp5 socioeconomic conditions (O'Neill et al., 2017) and represents the "worst case" scenario with emissions able to produce a radiative forcing of 8.5 W m^{-2} in 2100.

Sea ice and chlorophyll-a projections were obtained from the Earth System Grid Federation page (https://esgf-node.llnl.gov/search/cmip6/). The different runs for both variables included the same ensemble member (r1i1p1f1), which certify the same initial conditions and procedures, physic version and variants of forcing applied (Taylor et al., 2018). We extracted the monthly sea ice area fraction (with a spatial resolution of 50 km) developed by the Geophysical Fluid Dynamic Laboratory (GFDL) Earth System 4 (Krasting et al., 2018) of the National Oceanic and Atmospheric Administration (NOAA). Despite the underestimation in the austral summer sea ice minimum and the inability to reproduce the spatial trend of sea ice concentration between 1979 and 2014 (Roach et al., 2020; Shu et al., 2020), a moderately higher confidence in Antarctic sea ice CMIP6 projections with respect to previous generations was found (Roach et al., 2020). The sea-ice area value for a surface of approximately $187 \cdot 10^3$ km^2 (**Figure 1**) was calculated from 2015 to 2100 (**Supplementary Figure 4**). **On the other hand, we analyzed the monthly mass concentration of phytoplankton expressed as chlorophyll-a in sea water (with a spatial resolution of 1°) produced by the** GFDL Earth System 4 (Krasting et al., 2018). **The chlorophyll-a time series used to force the model represents the mean value for an area around the Palmer Station (Figure 1** and **Supplementary Figure 4**). In order to obtain representative chlorophyll-a projections, we compared *in situ* data from Palmer Station Antarctica LTER and Schofield (2020) and model outputs for the overlapping period (2015-2019) using basic statistics parameters for different pixel boxes (**Supplementary Table 1** and **Supplementary Figure 5**; Świrgoń and Stramska, 2015). Comparison revealed higher correlation between *in situ* and model output chlorophyll-a, and lower errors, within a box with dimensions of 5° longitude and 5° latitude (**Figure 1** and **Supplementary Table 1**). Linear regressions were carried out using model II reduced major axis regression following Legendre and Legendre (1998). The mean value for each box was calculated, except in the case of the pixel nearest to Palmer Station which used a single estimation. The original GFDL chlorophyll-a estimations were significantly lower than *in situ* measurements for the period 2015-2019 (mean value: 2.6, 0.5, 0.6, 0.6 mg m^{-3} for *in situ*, ssp126, ssp370 and ssp585 scenarios, respectively). When running the model with the original chlorophyll-a projection, a strong and doubtful collapse of the entire ecosystem was detected. Thus, the projected scenarios were recalibrated using the linear equations calculated in **Supplementary Table 1** with 2015-2019 *in situ* measurements: $\log_{10}(\mathrm{Chl}_{126m}) = [\log_{10}(\mathrm{Chl}_{126orig.}) + 0.4695] / 0.5615$; $\log_{10}(\mathrm{Chl}_{370m}) = [\log_{10}(\mathrm{Chl}_{370orig.}) + 0.4606] / 0.6091$ and $\log_{10}(\mathrm{Chl}_{585m}) = [\log_{10}(\mathrm{Chl}_{585orig.}) + 0.4635] / 0.59810$; where Chl_{126m}, Chl_{370m}, Chl_{585m} represented the modified chlorophyll-a estimations for three climatic scenarios, whereas $\mathrm{Chl}_{126\ orig.}$, $\mathrm{Chl}_{370orig.}$, $\mathrm{Chl}_{585orig.}$ were the original GFDL values. The Pearson linear correlation coefficient did not detect significant correlation between environmental forcing factors along the time series (**Supplementary Table 2**).

A constant leopard seal predation rate on Antarctic fur seal pups (*i.e.*, the mean value of 2002-2012 period) was maintained constant up to 2100, since Antarctic fur seal populations seemed to majorly respond to bottom-up control (availability of Antarctic krill to be predated) rather than top-down dynamic (leopard seal predation; Goebel and Reiss, 2014).

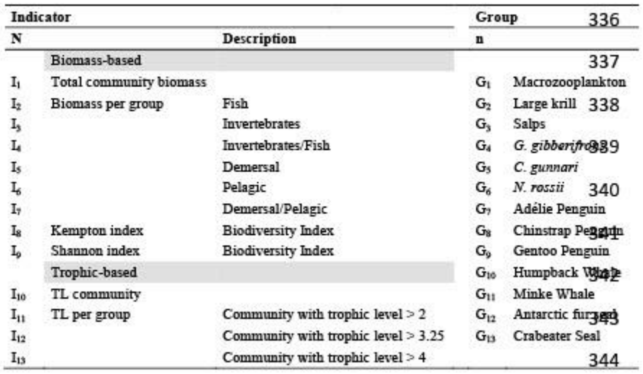
The average krill catches from 1996 to 2012 (~51900 tonnes yr^{-1}) were included during the model balancing. No other fisheries (*i.e.*, *C. gunnari* and *N. rossii*) were included in the model since krill fisheries accounted for 99.9% of total catches of CCAMLR 48.1 zone during the last 20 years (CCAMLR, 2019; **Supplementary Figure 1**). No bycatch was additionally considered during krill fisheries in CCAMLR 48.1 zone since incidental catches were negligible (0.07%) with respect to krill landings during the 2012-2016 period (Arana and Rolleri, 2020) and the species biomass caught during krill fishery were minimal compared with the modelled initial biomass (**Supplementary Table 3**). Three future krill fisheries scenarios were explored: absence of krill catches, constant krill catches (*i.e.*, the mean value of the last two decades was keep constant until 2100) and krill fisheries with a gradual and decadal increase until doubling the catches by 2100 (**Supplementary Figure 4**). A decadal variation in krill landings is a plausible scenario due to the historic changes in krill quotas (*i.e.*, 1993, 2000, 2009, 2021; CCAMLR, 2020). The actual krill quota for CCAMLR 48.1 zone is set to 155,000 tonnes (CCAMLR, 2020) in the presence of a krill biomass estimated in 17.3 million tonnes for the study zone (Nicol et al., 2000). Since the krill quota has been completed within the study zone during the last five years (**Figure S1**), an increase in krill catches is reasonable towards the end of the century (Hill et al., 2016).

Sea-ice, open water area and chlorophyll-a time series were used as forcing functions impacting different specific predator-prey interactions (*i.e.*, search rate, vulnerability, foraging arena area or a combination of those). Chlorophyll-a variability was also applied as a multiplier on production rate, whereas krill and Humped rockcod biomass were directly driven by sea-ice temporal variability (with a sigmoidal and normal functional response, respectively). Thus, the environmental variability influenced the total consumption on each group and the net growth efficiency (the production/consumption ratio), whereas krill fishery impacted the fishing mortality rate in the Ecosim Equation 1.

2.4 Estimations of anthropogenic influence

Environmental and fishery perturbances on CCAMLR 48.1 ecosystem were estimated through the temporal variability of functional groups biomass and ecological indicators for exploited marine systems (**Table 1**). Biomass and trophic-based indicators were selected from Coll and Steenbeek (2017) ECOIND package (**Table 1**), with the input data required to calculate the ecological indicators shown in **Supplementary Table 4**. No catch-based indicators were considered since only krill fisheries were included in the trophic model. Indeed, the mean krill fisheries for the study period (0.08 t km^{-2} yr^{-1}) accounted for the 0.1% of the input large krill biomass used in the model, whereas *C. gunnari* and *N. rossii* fisheries only accounted for the $9 \cdot 10^{-4}$ and $2 \cdot 10^{-3}$% of the initial biomass, respectively. Biodiversity indices, such as the Shannon (Shannon, 1948) and Kempton Index (Kempton and Taylor, 1976; Ainsworth and Pitcher, 2006), were considered in the study to analyze the temporal variability of ecosystem biodiversity.

Table 1. Ecological indicators and functional groups used in this study to evaluate the environmental and anthropogenic influence on the CCAMLR 48.1 food web.



Indicator			**Group**	
N		**Description**	**n**	
	Biomass-based			
I_1	Total community biomass		G_1	Macrozooplankton
I_2	Biomass per group	Fish	G_2	Large krill
I_3		Invertebrates	G_3	Salps
I_4		Invertebrates/Fish	G_4	*G. gibberifrons*
I_5		Demersal	G_5	*C. gunnari*
I_6		Pelagic	G_6	*N. rossii*
I_7		Demersal/Pelagic	G_7	Adélie Penguin
I_8	Kempton index	Biodiversity Index	G_8	Chinstrap Penguin
I_9	Shannon index	Biodiversity Index	G_9	Gentoo Penguin
	Trophic-based		G_{10}	Humpback Whale
I_{10}	TL community		G_{11}	Minke Whale
I_{11}	TL per group	Community with trophic level > 2	G_{12}	Antarctic fur seal
I_{12}		Community with trophic level > 3.25	G_{13}	Crabeater Seal
I_{13}		Community with trophic level > 4		

The sensitivity analysis is a useful methodological tool to assess how the uncertainty in the model output can be apportioned to different sources of uncertainty in its inputs (Saltelli, 2002). Several experiments were performed to identify the relative influence of the different forcing elements on the Antarctic ecosystem (**Table 2**). The n°11 scenario (constant sea ice index, open water, chlorophyll-a and fishery) was used as reference and the results of other simulations were expressed as percentage with respect to this projection. The mean value of the final five years of the simulations (2095-2100) was used during the sensitivity analysis. The mean annual sea ice index value during the period 1996-2012 was computed for the reference scenario, whereas the mean annual cycle during the same timeframe was calculated for open water area and chlorophyll-a estimations.

The comparison between the initial (1996) and 2100 ecosystem was done using the mean value for 1996-2001 and 2095-2100 ecosystems in order to reduce the seasonal variability. The effect of uncertainty in EwE input parameters was assessed running Monte Carlo simulations (100 iterations) with a coefficient of variation of 0.1 around the input Ecopath values (Heymans et al., 2016). The mean value and the 95% confidence interval were calculated during the sensitivity analysis and the study of temporal variability for every functional group and ecological indicator.

Table 2. Experimental design. SI index: Sea Ice Index; Chl-a: Chlorophyll-a; const: Constant value; ssp126, ssp370, ssp585: values corresponding to Shared Socioeconomic Pathways 126, 370 and 585 scenarios, respectively.

Scenario	Variable			
(n)	SI index	Open Water	Chl-a	Fishery
	Sensitivity analysis			
1	ssp126	const	const	const
2	ssp370	const	const	const
3	ssp585	const	const	const
4	const	ssp126	const	const
5	const	ssp370	const	const
6	const	ssp585	const	const
7	const	const	ssp126	const
8	const	const	ssp370	const
9	const	const	ssp585	const
10	const	const	const	0
11	const	const	const	const
12	const	const	const	double
	Impact of fisheries			
13	ssp126	ssp126	ssp126	0
14	ssp126	ssp126	ssp126	const
15	ssp126	ssp126	ssp126	double
16	ssp370	ssp370	ssp370	0
17	ssp370	ssp370	ssp370	const
18	ssp370	ssp370	ssp370	double
19	ssp585	ssp585	ssp585	0
20	ssp585	ssp585	ssp585	const
21	ssp585	ssp585	ssp585	double

3. RESULTS

3.1. The importance of different forcing factors for the 2100 Antarctic ecosystem

3.1.1. Ecosystem indicators

Sensitivity analysis for ecosystem indicators variability revealed that total biomass of the 48.1 zone (I_1) greatly responded to chlorophyll-a scenarios in 2100, whereas fish biomass (I_2) widely varied with both open water area and chlorophyll-a variability (30.1 and 132.0% difference was found between the ssp126, ssp370 and ssp585 scenarios with respect to the reference simulation, respectively; **Figure 3**). Invertebrate biomass (I_3) heavily oscillated according to chlorophyll-a scenarios (104.1% difference, respectively) and no clear sensitivity ascribed to a single forcing factor was observed for the invertebrates/fish biomass ratio (I_4). Chlorophyll-a scenarios also caused the greatest variability in both demersal (I_5; 118.9%) and pelagic biomass (I_6; 97.9%), whereas the demersal/pelagic ratio biomass (I_7) varied mainly with open water area (10.2%) and chlorophyll-a (15.2%) between scenarios. The Kempton index (I_8) majorly varied because of chlorophyll-a scenarios (8.5%), whereas the sensitivity analysis of other ecosystem indicators (I_9 to I_{13}) did not reveal important variability that could be attributed to a particular forcing factor.

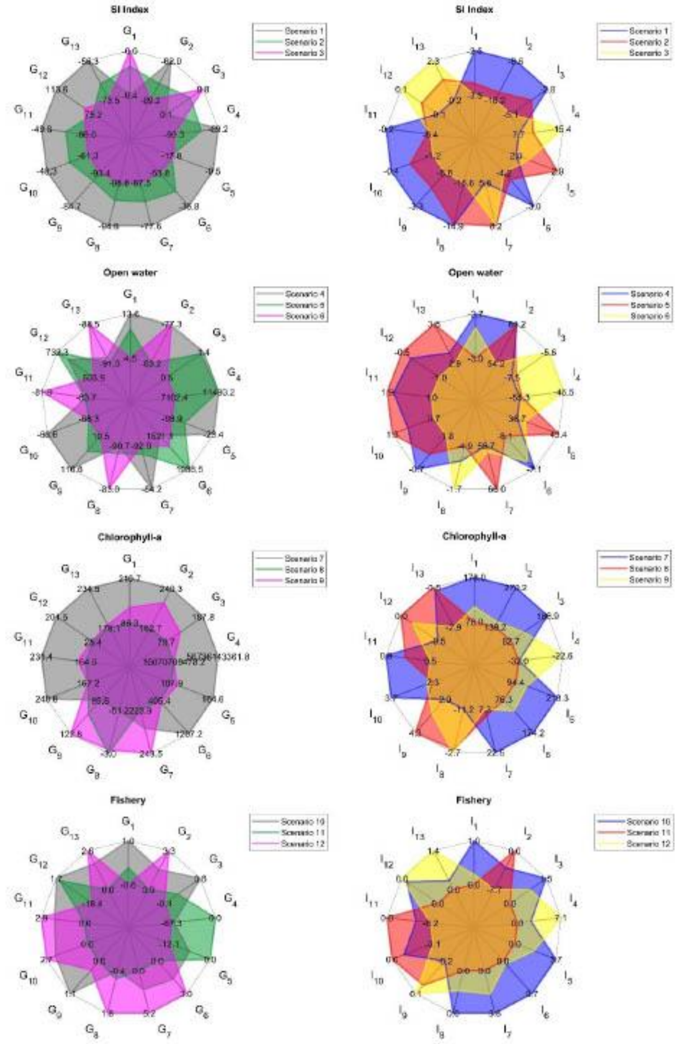


Figure 3. Sensitivity analysis for 13 selected functional groups (left panels) and ecological indicators (right panels). The numbers correspond to each group and indicator in Table 1, whereas the characteristics of each scenario are shown in Table 2.

3.1.2. Functional groups

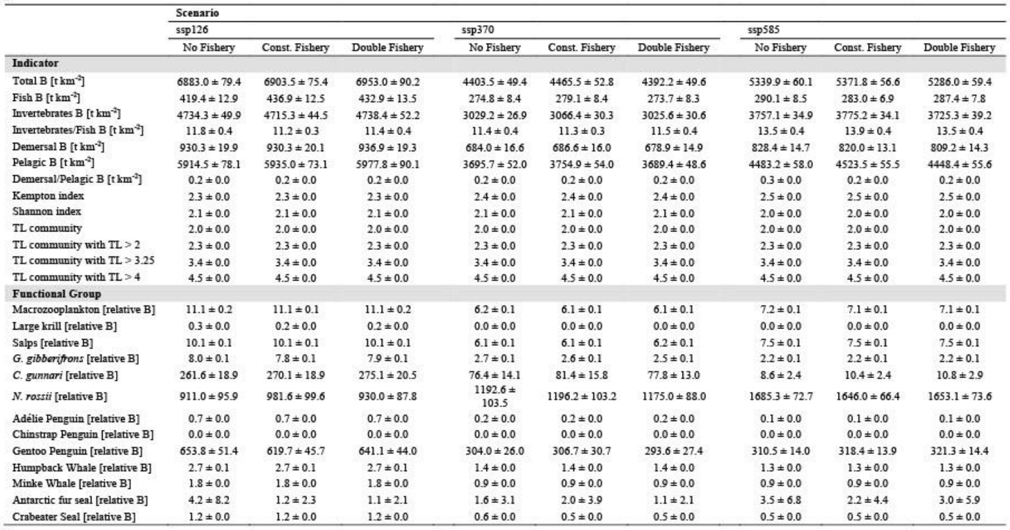
Macrozooplankton biomass (G_1) showed higher variability between environmental scenarios induced by open water area (9.1%) and chlorophyll-a scenarios (124.4%) with respect to sea ice index (0.4%) and krill fishery (1.6%; **Figure 3**). Large krill (G_2) majorly varied because of sea ice index and chlorophyll-a (27.2 and 77.5% difference between scenario, respectively), whereas salps (G_3) showed strong variability according to chlorophyll-a oscillations (111.1%). Humped rockcod (G_4), Mackerel icefish (G_5) and Marbled rockcod (G_6) biomass variability highly fluctuated with both chlorophyll-a and open water area forcing, whereas chlorophyll-a induced the greatest variability in Adélie (G_7) and Chinstrap (G_8) penguin biomass (19.6 and 48.1%, respectively). Contrarily, open water area was the principal forcing factor that impacted the Gentoo penguin (G_9) biomass (100.1% difference between scenarios). Humpback (G_{10}) and Minke (G_{11}) whales majorly responded to both sea ice index (13 and 16.2%, respectively) and chlorophyll-a (73.7 and 67.4%, respectively), whereas open water area and chlorophyll-a scenarios influenced the Antarctic fur seal (G_{12}) biomass (128.3 and 173%, respectively). Finally, Crabeater seal (G_{13}) biomass impact was higher for chlorophyll-a forcing (56.4%) with respect to sea ice index (17.2%), open water area (2.5%) and krill fishery (2.6%; **Figure 3**). The sensitivity analysis for all functional groups is available in **Supplementary Table 5** for interested readers.

3.2. Impact of environmental variability on 2100 Antarctic ecosystem compared with krill fishery pressure.

3.2.1. Ecosystem indicators

The total biomass of the ecosystem, along with fish biomass, decreased with rising radiative forcing (**Table 3**), since the highest estimations for both indicators were recorded under ssp126 scenario independently of krill fishery projections. Contrarily, the invertebrates/fish biomass ratio was the highest (from 13.5 to 13.9) with the "worst case" scenario (ssp585). Both pelagic and demersal biomass were higher during ssp126 scenarios (between 930 and 937 t km^{-2} and from 5914 and 5978 t km^{-2}) compared with spp370 and ssp585 projections in 2100. No clear trend was observed in demersal/pelagic ratio during either environmental or krill fishery scenarios (**Table 3**). Shannon index decreased with higher radiative forcing scenarios (from 2.1 to 2.0), whereas the Kempton Q index increased between ssp126, ssp370 and ssp585 projections (2.3, 2.4 and 2.5, respectively). The trophic level indicators were not altered by environmental and fishery variability. Krill fisheries projections did not have noticeable influence in any of the analyzed Antarctic ecosystem indicators.

Table 3. Impact of climatic variability and fisheries by year 2100. Mean values ± 95% confidence interval. The climatic and fishery-related characteristics of each scenario are shown in Table 2. B: Biomass. The temporal evolution of the ecosystem indicators and groups is displayed in the **Supplementary Figures 6**-7.



	Scenario								
	ssp126			ssp370			ssp585		
	No Fishery	Const. Fishery	Double Fishery	No Fishery	Const. Fishery	Double Fishery	No Fishery	Const. Fishery	Double Fishery
Indicator									
Total B [t km^{-2}]	6883.0 ± 79.4	6903.5 ± 75.4	6953.0 ± 90.2	4403.5 ± 49.4	4465.5 ± 52.8	4392.2 ± 49.6	5339.9 ± 60.1	5371.8 ± 56.6	5286.0 ± 59.4
Fish B [t km^{-2}]	419.4 ± 12.9	436.9 ± 12.5	432.9 ± 13.5	274.8 ± 8.4	279.1 ± 8.4	273.7 ± 8.3	290.1 ± 8.5	283.0 ± 6.9	287.4 ± 7.8
Invertebrates B [t km^{-2}]	4734.3 ± 49.9	4715.3 ± 44.5	4738.4 ± 52.2	3029.2 ± 26.9	3066.4 ± 30.3	3025.6 ± 30.6	3757.1 ± 34.9	3775.2 ± 34.1	3725.3 ± 39.2
Invertebrates/Fish B [t km^{-2}]	11.8 ± 0.4	11.2 ± 0.3	11.4 ± 0.4	11.4 ± 0.4	11.3 ± 0.3	11.5 ± 0.4	13.5 ± 0.4	13.9 ± 0.4	13.5 ± 0.4
Demersal B [t km^{-2}]	930.3 ± 19.9	930.3 ± 20.1	936.9 ± 19.3	684.0 ± 16.6	686.6 ± 16.0	678.9 ± 14.9	828.4 ± 14.7	820.0 ± 13.1	809.2 ± 14.3
Pelagic B [t km^{-2}]	5914.5 ± 78.1	5935.0 ± 73.1	5977.8 ± 90.1	3695.7 ± 52.0	3754.9 ± 54.0	3689.4 ± 48.6	4483.2 ± 58.0	4523.5 ± 55.5	4448.4 ± 55.6
Demersal/Pelagic B [t km^{-2}]	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
Kempton index	2.3 ± 0.0	2.3 ± 0.0	2.3 ± 0.0	2.4 ± 0.0	2.4 ± 0.0	2.4 ± 0.0	2.5 ± 0.0	2.5 ± 0.0	2.5 ± 0.0
Shannon index	2.1 ± 0.0	2.1 ± 0.0	2.1 ± 0.0	2.1 ± 0.0	2.1 ± 0.0	2.1 ± 0.0	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0
TL community	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0	2.0 ± 0.0
TL community with TL > 2	2.3 ± 0.0	2.3 ± 0.0	2.3 ± 0.0	2.3 ± 0.0	2.3 ± 0.0	2.3 ± 0.0	2.3 ± 0.0	2.3 ± 0.0	2.3 ± 0.0
TL community with TL > 3.25	3.4 ± 0.0	3.4 ± 0.0	3.4 ± 0.0	3.4 ± 0.0	3.4 ± 0.0	3.4 ± 0.0	3.4 ± 0.0	3.4 ± 0.0	3.4 ± 0.0
TL community with TL > 4	4.5 ± 0.0	4.5 ± 0.0	4.5 ± 0.0	4.5 ± 0.0	4.5 ± 0.0	4.5 ± 0.0	4.5 ± 0.0	4.5 ± 0.0	4.5 ± 0.0
Functional Group									
Macrozooplankton [relative B]	11.1 ± 0.2	11.1 ± 0.1	11.1 ± 0.2	6.2 ± 0.1	6.1 ± 0.1	6.1 ± 0.1	7.2 ± 0.1	7.1 ± 0.1	7.1 ± 0.1
Large krill [relative B]	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Salps [relative B]	10.1 ± 0.1	10.1 ± 0.1	10.1 ± 0.1	6.1 ± 0.1	6.1 ± 0.1	6.2 ± 0.1	7.5 ± 0.1	7.5 ± 0.1	7.5 ± 0.1
G. gibberifrons [relative B]	8.0 ± 0.1	7.8 ± 0.1	7.9 ± 0.1	2.7 ± 0.1	2.6 ± 0.1	2.5 ± 0.1	2.2 ± 0.1	2.2 ± 0.1	2.2 ± 0.1
C. gunnari [relative B]	261.6 ± 18.9	270.1 ± 18.9	275.1 ± 20.5	76.4 ± 14.1	81.4 ± 15.8	77.8 ± 13.0	8.6 ± 2.4	10.4 ± 2.4	10.8 ± 2.9
N. rossii [relative B]	911.0 ± 95.9	981.6 ± 99.6	930.0 ± 87.8	1192.6 ± 103.5	1196.2 ± 103.2	1175.0 ± 88.0	1685.3 ± 72.7	1646.0 ± 66.4	1653.1 ± 73.6
Adélie Penguin [relative B]	0.7 ± 0.0	0.7 ± 0.0	0.7 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
Chinstrap Penguin [relative B]	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Gentoo Penguin [relative B]	653.8 ± 51.4	619.7 ± 45.7	641.1 ± 44.0	304.0 ± 26.0	306.7 ± 30.7	293.6 ± 27.4	310.5 ± 14.0	318.4 ± 13.9	321.3 ± 14.4
Humpback Whale [relative B]	2.7 ± 0.1	2.7 ± 0.1	2.7 ± 0.1	1.4 ± 0.0	1.4 ± 0.0	1.4 ± 0.0	1.3 ± 0.0	1.3 ± 0.0	1.3 ± 0.0
Minke Whale [relative B]	1.8 ± 0.0	1.8 ± 0.0	1.8 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0
Antarctic fur seal [relative B]	4.2 ± 8.2	1.2 ± 2.3	1.1 ± 2.1	1.6 ± 3.1	2.0 ± 3.9	1.1 ± 2.1	3.5 ± 6.8	2.2 ± 4.4	3.0 ± 5.9
Crabeater Seal [relative B]	1.2 ± 0.0	1.2 ± 0.0	1.2 ± 0.0	0.6 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0

3.2.2. Functional groups

Large krill biomass decreased with high radiative forcing, with a near depletion under ssp370 and ssp585 projections (**Table 3**). Biomass decline with warmer conditions (ssp370 and ssp585) was also observed for Humped rockcod and Mackerel icefish. Contrarily, Marbled rockcod seemed to be beneficiated by increasing radiative forcing. Adélie and Chinstrap shown almost extinction patterns in 2100 under ssp585 scenario, being ssp126 the more favorable projection for Adélie penguin. The biomass reduction with increasing temperature also characterized Gentoo penguin, Humpback and Minke whales and Crabeater seal biomass variability. No significant variability ascribed to fishery projections was observed in the relative biomass of macrozooplankton and salps in 2100, whereas lower biomass was detected during ssp370 and ssp585 compared with the "best case" scenario (ssp126). The results suggested that krill fishery slightly influenced large krill, Humped rockcod and Antarctic fur seal biomass, with the highest biomass estimations recorded with no catch scenarios (**Table 3**). The remaining functional groups seemed not to be strongly affected by the projected krill fishery levels in 2100. The impact of both environmental and fishery variability on all functional groups is available in **Supplementary Table 6**.

3.3. Temporal variability of ecosystem indicators and functional groups from 1996 to 2100

3.3.1. Ecosystem indicators

An overall increase in ecosystem total biomass was observed under all three climatic scenarios in 2100 compared with the initial (1996-2001) values (**Table 4**). Fish biomass strongly raised during all scenarios (from 10 t km^{-2} to 275-429 t km^{-2}), along with the moderate increase in invertebrate biomass caused a relevant decline in invertebrates/fish ratio in 2100 (from -85 to -82% with respect to 1996-2001 estimations). Contrarily, the demersal/pelagic ratio grew approximately 53% with respect to initial condition due to important (less marked) rise in demersal (pelagic) biomass (+857 and +337%, respectively). Both ecosystem diversity indicators decreased with ssp585 scenario during the period 1996-2100, although the loss in Kempton index (-3%) was greater compared with Shannon index (-1%). The community trophic level increased (approx. +10%), despite the reduction in the trophic level of the highest functional groups (from -5.4 to -6.1% and -1.6% for the community with trophic level higher than 3.25 and 4, respectively; **Table 4**). Krill fisheries seemed not to heavily influence the temporal variability of ecosystem indicators (**Supplementary Figure 6**).

3.3.2. Functional groups

Strong increase in macrozooplankton and salp biomass (a mean of +885 and +842%, respectively) was detected in 2100 compared with 1996, although high variability was recorded between environmental scenarios (**Table 4**). Contrarily, large krill biomass only maintained a 49% of its initial values under ssp126 conditions and was nearly depleted with ssp370 and ssp585 scenarios. Fish biomass (Mackerel icefish, Marbled and Humped rockcod) shown a noticeable rise in 2095-2100 compared with the 1996-2001 estimations, although environmental variability seemed to have a strong impact in the increase magnitude. Temporal dynamics in penguins biomass were very different: with an almost extinction of Chinstrap penguin, a decrease in Adélie penguin biomass according to environmental scenarios (-24, -74 and -83% with respect to initial values for ssp126, ssp370 and ssp585, respectively) and the increase in Gentoo Penguin (mean value: +40598%). Simulations predicted a doubling biomass for Minke whale under ssp126 conditions, whereas a slight decrease was observed with ssp370 and ssp585 projections (-1 and -4%, respectively). A similar temporal pattern was detected for Crabeater seal, whereas Humpback whale and Antarctic fur seal shown a variable increase in biomass by 2100. Overall, krill fisheries seemed not to strongly influence the temporal variability of the studied functional groups (**Supplementary Figure** 7).

Table 4. Mean value for ecosystems indicators and relative biomass groups during the period 2095-2100 compared with the reference period 1996-2001. Values are expressed as percentage.

	Scenario		
	ssp126 (%)	ssp370 (%)	ssp585 (%)
Indicator			
Total B	490.3	276.4	354.7
Fish B	4352.8	2755.5	2861.4
Invertebrates B	569.9	329.4	428.4
Invertebrates/Fish B	-85.2	-85.3	-82.4
Demersal B	998.4	704.8	868.1
Pelagic B	451.3	243.4	315.3
Demersal/Pelagic B	46.8	55.7	58.5
Kempton index	-11.9	-6.4	-2.7
Shannon index	1.3	1.8	-0.8
TL community	10.6	9.2	9.5
TL community with TL > 2	4.4	4.2	4.0
TL community with TL > 3.25	-5.4	-6.1	-5.4
TL community with TL > 4	-1.6	-1.6	-1.7
Group			
Macrozooplankton	1251.5	644.1	762.1
Large krill	-51.4	-94.6	-100.0
Salps	1103.2	631.5	793.3
G. gibberifrons	2419.1	731.8	604.4
C. gunnari	13548.3	4022.0	410.2
N. rossii	61084.2	77488.3	108213.2
Adélie Penguin	-24.5	-73.9	-83.4
Chinstrap Penguin	-100.0	-99.1	-99.5
Gentoo Penguin	61902.6	29228.0	30663.4
Humpback Whale	149.5	29.6	18.9
Minke Whale	95.2	-1.2	-4.2
Antarctic fur seal	91.2	38.5	160.2
Crabeater Seal	28.6	-40.7	-47.8

4. DISCUSSION

4.1. Main factors impacting the Antarctic food web

The sensitivity analysis showed how several functional groups were influenced by sea ice and open water area dynamics, although the most deciding factor was chlorophyll-a variability, suggesting a bottom-up control on the food web. The study of Suprenand and Ainsworth (2017) highlighted the importance of both sea ice algae and phytoplankton production on the mean trophic level, biomass and diversity of the WAP ecosystem from now to 2050. A strong bottom-up interaction in the WAP food web was also identified by the EwE model of Hoover et al. (2012). Indeed, the Antarctic ecosystem was heavily affected by both primary production control and Particulate Organic Carbon (POC) export that influence benthic community (Henley et al., 2019). The lack of a specific parametrization for thermal and sea ice optimum range of each functional group (*e.g.*, Serpetti et al., 2017) might induce similar responses for species with different temperature and sea ice tolerance.

On the other hand, krill fishery seemed not to be a crucial factor in the temporal dynamics of functional groups and ecological indicators. The current exploitation rate is set at a precautionary level to maintain the krill stock and support the krill predators at regional scale (Nicol et al., 2012; Hill et al., 2016; Watters et al., 2020). The increase in krill fishery projected in this study was below the biomass level that generates the maximum sustainable yield, which was estimated at 25-50% of unexploited biomass (Hill et al., 2016). Additionally, the present work did not consider the spatial and seasonal variability in krill catches. Indeed, the Bransfield Strait was the main location of 48.1 krill fishery (62%), followed by the western pelagic area of the Drake Passage (15%; CCAMLR, 2019). Krill fisheries have shifted from summer to autumn and winter periods due to a reduction in sea ice coverage (Smetacek and Nicol, 2005; Nicol et al., 2012; Brooks et al., 2018), causing a possible overlap between fishery, successful spawning stock (Meyer et al., 2020) and krill-dependent predators on small spatiotemporal scales (Hinke et al., 2017; Atkinson et al., 2019). The lack of parametrization regarding spatial and seasonal variability in krill abundance, life cycle and fishery might induce an underestimation of the krill fishery influence in the model since Watters et al. (2020) identified the impact of krill fishery on their predators similar to that of climatic phenomena such as El Niño Southern Oscillation and the Southern Annular Mode.

4.2. Krill scenarios and trends

Krill variability is mainly associated with primary production and sea ice dynamics (Smetacek, 2008; Piñones and Fedorov, 2016). Indeed, the winter sea ice coverage is crucial for krill spawning success, larval survivals and recruitment following the summer (Smetacek and Nicol, 2005; Saba et al., 2014; Henley et al., 2019; Rogers et al., 2020), whereas zooplankton abundance, distribution and species assemblage depend on the availability and composition of phytoplankton community and the water column structure (Henley et al., 2019). The effect of large marine mammals on krill stock dynamics is still unclear due to the lack of information on the interplay between predation (top-down) and fertilization of phytoplankton (bottom-up) via iron cycling by whales (Smetacek, 2008; Surma et al., 2014; Maldonado et al., 2016; Cavan et al., 2019).

A strong decline in krill biomass (*E. superba*), with a nearly extinction under ssp370 and ssp585 scenarios and a 51% decrease in its biomass with ssp126 environmental conditions was observed in the simulations. The study of Meredith et al., (2019) identified a decline in krill biomass under both "best" and "worst case scenarios for greenhouse gases projections (*i.e.*, Representative Concentration Pathway 2.6 and 8.5). Despite of this, the natural climate variability, especially in a short time span (<20 years), seemed to be an important driver in regional Antarctic krill dynamics (Henley et al., 2019; Sylvester et al., 2021). A debate on the magnitude and apparent decline of krill have emerged in recent years (Hill et al., 2016; Cox et al., 2018; Meyer et al., 2020), although the work of Hill et al., (2019) seemed to reaffirm the decrease in Antarctic krill density in the Southwestern part of the Atlantic sector of the SO (Atkinson et al., 2019). Climatic variability in the last four decades have caused a poleward displacement of the spawning ground for krill, affecting population growth and a general contraction in SO krill habitat, especially over Antarctic continental shelves and the southern part of the CCAMLR 48.1 zone (Piñones and Fedorov, 2016; Atkinson et al., 2019; Perry et al., 2019; Sylvester et al., 2021). Additional changes in krill behavior, physiology and distribution are to be expected under increasing temperature scenarios (Piñones and Fedorov, 2016; Murphy et al., 2017; Siegert et al., 2019; Veytia et al., 2020), along with high spatial variability in climate change impact on krill and its predators within the CCAMR 48.1 zone (Klein et al., 2018).

4.3. The Antarctic food web in 2100

Model simulations did not predict changes in phytoplankton community structure since no specific phytoplankton size-related parametrization was included. A shift in phytoplankton community towards smaller phytoplankton have been predicted (Deppeler and Davidson, 2017; Antoni et al., 2020), although recent *in* situ evidence did not reveal significant trends (Schofield et al., 2017). Alteration of phytoplankton size spectrum might change the structure and functioning of the entire ecosystem (Saba et al., 2014; Deppeler and Davidson, 2017; Kerr et al., 2018) and favor proliferation of salps (Atkinson et al, 2004, 2019; Moline et al., 2004; Ferreira et al., 2020).

The environmental projections simulated in this study resulted in a modified zooplankton community, with a decrease in krill and an increase in salps and other zooplankton groups (**Figure 4**), similar to predictions by Suprenand and Ainsworth (2017) under different primary production scenarios in 2050. A shift in zooplankton community might affect POC export toward the deep ocean and the efficiency of the carbon pump since krill fecal pellets represents a large proportion of total POC exports in the SO, with large pulses near the marginal sea ice zone (Belcher et al., 2019; Cavan et al., 2019; Henley et al., 2020). Despite of this, the increase in copepods and salps fecal pellets, along with an increased phytodetrital flux caused by a decline in krill grazing, might partly counterbalance the krill loss although the different size and swarming behavior could alter the biogeochemical cycles (Cavan et al., 2019). Salps fecal pellets have shown to have the ability to boost primary production by releasing elevated concentrations of bioavailable dissolved iron (3.3 times as much dissolved iron as krill fecal pellets; Böckmann et al., 2021), which coupled with the projected increase in salp abundance (this study) could enhance the efficiency of the biological carbon pump by the year 2100 and could promote the sink of anthropogenic released CO_2.

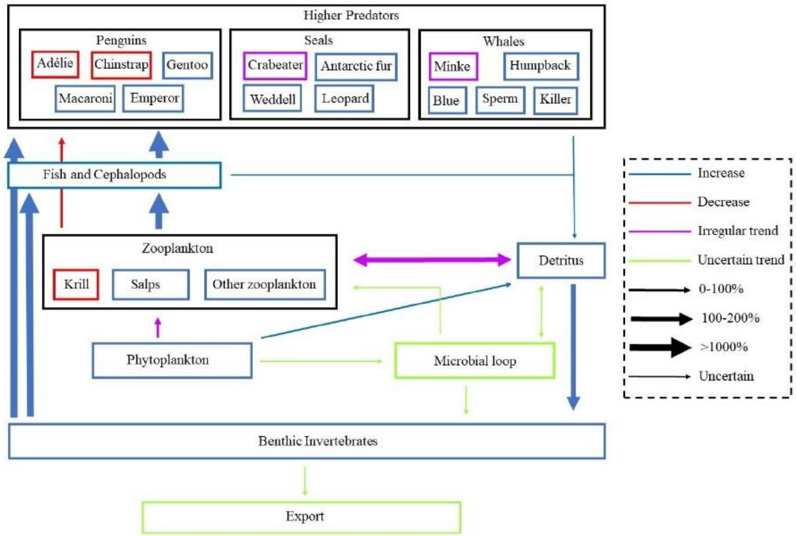


Figure 4. Schematic representation of the major functional groups (boxes) and pathways (arrows) variability in Antarctic marine food web by year 2100. Red boxes indicated a decrease in the component biomass compared with the initial values of the trophic model; blue: increase; magenta: irregular trend according to the climatic scenario; green: uncertain trend. This figure was inspired by the diagram of Murphy et al. (2012).

The model outputs showed a strong increase in fish biomass assuming fisheries absence from now to 2100. A recovery in fish populations is therefore predicted after the heavy extraction that decimated the Antarctic fish populations during the 1960-1980 period (Ainley and Pauly, 2014; McBride et al., 2014). The majority of fish stocks is currently below its pre-fishing level and has not been fully recovered (O'Brien and Crockett, 2013). Fishes and whales are predicted to be largely unaffected by warming effects on krill growth, whereas penguins seemed the most sensitive since a 30% decrease have been projected (Klein et al., 2018). Significant decline in ice and krill-dependent Adélie and Chinstrap penguins have been observed in the WAP (Ducklow et al., 2013; Saba et al., 2014) in good agreement with the simulations of this study, suggesting a drastic decline (almost depletion) of Adélie (Chinstrap) penguin biomass in 2100. The lack of recovery in Adélie and Chinstrap penguins' population, even in the absence of fishing pressure, has also been predicted by other model outcomes (Watters et al., 2013). Contrarily, the less ice-dependent Gentoo penguin population has increased in recent years making up over half the total penguin breeding community in the WAP (Ducklow et al., 2013; Henley et al., 2019), which agree with our findings. Other ice and krill dependent species, such as Crabeater seal and Minke whale, might experiment a habitat contraction because a shift toward a more maritime climate is expected for WAP (Henley et al., 2019; Hückstädt et al., 2020). An and Minke whale, might experiment a habitat contraction because a shift toward a more maritime climate is expected for WAP (Henley et al., 2019; Hückstädt et al., 2020). An increase in these species biomass is predicted under the "best case" scenario (ssp126), while a decrease was registered with ssp370 and 585 projections. Less ice and krill dependent species like Humpback whale and Antarctic fur seal showed an increase in their biomass under all the climatic and fishery scenarios presented in this study and it is in line with observations done by Ducklow et al., (2013) who predicted a lower impact on these species due to climate change. It is important to consider when analyzing the functional groups trends obtained in this study that crucial factors such as phenotypic plasticity, dietary shift and evolutionary genetic response, which are key for species survival over decades (Convey and Peck, 2019), were not considered in the model.

The reduction in sea ice coverage is expected to favor pelagic and benthic ecosystem productivity (Henley et al., 2019), which might increase the demersal biomass, the demersal/pelagic ratio and favor the benthopelagic coupling of the food web. A decline in Kempton biodiversity index under all environmental scenarios was observed, whereas the Shannon index revealed a decrease only under a ssp585 scenario. A similar decrease in Kempton Index for Antarctic ecosystem was also evidenced by Suprenand and Ainsworth (2017) by 2050. Climate variability is able to affect both pelagic and benthic biodiversity (Griffiths, 2010; Chown et al., 2015), although vulnerability is highest in shallow waters and coastal ecosystem (Rogers et al., 2020). Finally, an increase in the overall trophic level of the Antarctic community was detected, similarly to the study of Suprenand and Ainsworth (2017), whereas the observed decline in the trophic level of the highest trophic groups might suggest a trophodynamic shift of the Antarctic food web structure by 2100.

4.4. Model limitations

The geographical location of the data source used to develop the EwE model (**Figure 1**) suggest that the results obtained in this study might be representative only for coastal WAP ecosystem. Indeed, the CCAMLR 48.1 zone is characterized by strong spatial variability in physical (Stammerjohn et al., 2008; Comiso et al., 2017; Kumar et al., 2021; Santamaría-del-Ángel et al., 2021), biogeochemical (Ducklow et al., 2007; Marrani et al., 2008; Constable et al., 2014; Schofield et al., 2017; Hendry et al., 2018; Testa et al., 2021) and high trophic levels patterns (Weimerskirch et al., 2003; Thiele et al., 2004; Trivelpiece et al., 2011; Ducklow et al., 2013; Murphy et al., 2013). Indeed, the zooplanktonic dominant population can vary between krill, salps, copepods and ice krill according to the sea ice gradient (Murphy et al., 2016) and a variability in the abundance of several key species (such as fishes, penguins and seals) have also been detected (Murphy et al., 2013).

We believe that the increased magnitude in the biomass of several functional groups delivered by the model from 1996 to 2100 could be exaggerated and might be ascribed to an overestimation in chlorophyll-a projections. The original CMPI6 chlorophyll-a projections underestimated the phytoplankton biomass of the WAP, whereas our calibrations might have produced the opposite result. Additionally, chlorophyll-a forcing function was applied to primary producers as a constant multiplier of production rate, although the carbon-to-chlorophyll-a ratio can vary between phytoplankton functional groups and locations within the CCAMLR 48.1 zone (Aracena et al., 2018). Despite the concern regarding the magnitude of phytoplankton biomass, the chlorophyll-a trends remain valid for future projections and the observed tendencies for several functional groups agreed with previously published studies (Ducklow et al., 2013; Saba et al., 2014; Henley et al., 2019).

Mortality caused by contamination was not included in the model since its effects on Antarctic ecosystem are still not fully understood. Bioaccumulation and biomagnification of potentially toxic trace elements (*i.e.*, Cd y Hg) is a reality in all levels of marine food webs (Bargagli, 2008; Seco et al., 2021) and micro, mesoplastics and paint particle have been detected in Antarctic deep sea sediments and surface waters (Waller et al., 2017; Lacerda et al., 2019). Zooplanktonic filter feeders might be affected by microplastic ingestion (Li et al., 2016), although Dawson et al. (2018) demonstrated the krill capacity of turning microplastics into nanoplastics through digestive fragmentation, potentially affecting the Antarctic pelagic ecosystem and the global biogeochemical cycles due to an impact on krill moulting and krill fecal pellets sinking (Bergami et al., 2020). Additionally, the effect of acidification was not included in the present model. Despite the influence of acidification on the lower trophic levels (Hancock et al., 2020), its impact on Antarctic ecosystem is thought to be lower compared with the influence of temperature increase on marine organisms (Convey and Peck, 2019).

4.5. Future challenges

Fishery products have significant importance among the several SO ecosystem services (*i.e.*, benefits that humanity obtain from natural ecosystem; Nicol et al., 2012; Rogers et al., 2020; Cavanagh et al., 2021) and a three-way tradeoff between fishery performances, the krill stock status and predators' populations have been proposed (Grant et al., 2013). Despite of this, the uncertainty regarding krill dynamics in a changing climate scenario might suggest imposing a moratorium under a precatory principle as a protection measure (Cheung, 2018) until we better understand krill trend and impact in the WAP. A similar decision has been adopted in 2017 by the States bordering the Central Artic Ocean in the Artic agreement for the Northern hemisphere polar ecosystem (Brooks et al., 2018). We consider this political measure as necessary due to the destabilization of Antarctic food web for the last 200 years of sequential over-exploitation of whales, seals and fishes which makes difficult to differentiate the effect of overexploitation from the impact induced by climate change (Trivelpiece et al., 2011). A fishing moratorium could help to counterbalance the climate change-related risks for several WAP biological hotspots (Santora and Veit, 2013) and reduce the probability of population collapse for various functional groups (Klein et al., 2018; Dahood et al., 2020). The creation of marine protected areas in the SO might be a complementary protection measure useful to maintain the population of vulnerable species. The Ross Sea and the South Orkney Islands are currently the only established marine protected areas in the SO while East Antarctica, the Antarctic Peninsula and the Weddell Sea have been proposed recently (Sylvester and Brooks, 2020).

The bottom-up sensitivity of the Antarctic food web evidenced in this study urges the development of more accurate Antarctic chlorophyll-a projections, since the current CMIP6 projections might have low degree of reliability. Regional projections are specifically needed, with a recommended calibration with *in situ* data for the overlapping period. Additionally, the top-down control on Antarctic ecosystem dynamics needs to be further investigated during future modeling applications, along with a specifically designed trophic model for the pelagic ecosystem of the WAP. The study of similarities and differences between the pelagic and neritic ecosystems might provide useful information to predict the different response of the two environments under climate change scenarios. Further investigation is also needed to predict the dynamics of key component of the Antarctic food web such as the microbial loop, detritus fate and organic matter export **(Figure 4)**.

More *in situ* data from year-round stations (such as the US Palmer Antarctica LTER project, the Rothera Time Series of the British Antarctic Survey, and other programs resumed in Henley et al. (2019)) are necessary to better parametrize and understand the spatiotemporal variability of the main functional groups that constitute the Antarctic food web. An additional effort should be considered for the methodological standardization between different research and monitoring programs. The collection of all data in a single database is suggested to facilitate researchers and future investigations.

The trophic model used during this work will be shared with colleagues to allow its study, modification and improvement. Free-access data, along with the cooperation principle, might help mankind to face the current social and climate hard circumstances.

5. CONCLUSIONS

The outcomes of our model under different scenarios suggest that the environmental variability (mainly chlorophyll-a and sea ice extend) play a key role on the expected Antarctic food web structure and ecosystem functioning for 2100, while krill fishery under a gradual fishery increase scenario seems to have a lower impact on the food web. Despite of this, the lack of parametrization in spatial and seasonal variability of krill fishery might cause an underestimation of its impact. Among different environmental variables (*i.e.*, sea ice, open water area and chlorophyll-a), the chlorophyll-a variability appeared to have the strongest impact on functional groups biomass and ecosystems indicators, suggesting a primary bottom-up control on the food web. A trophodynamic shift of the food web structure is observed in 2100, with a marked decline in krill population and an increase in salps and other zooplanktonic groups. While ice and krill-dependent species, such as Crabeater seal, Adélie and Chinstrap penguins, show a significant decline towards to the end of this century. More accurate chlorophyll-a projections are needed for future Antarctic ecosystem parametrizations and further studies are required to better understand the role of top-down forcing on the food web dynamics.

6. FUNDING

This study was supported by FONDAP 15150003, National Agency for Research and Development (ANID)/PFCHA/Doctorado Nacional/2017-21170561 and ANID-FONDECYT 1210988.

7. ACKNOWLEDGMENTS

We thank L. Castro, T. Russell, G. Watters, the associate editor, and reviewers for their valuable help, comments and suggestions.

8. AUTHOR CONTRIBUTIONS

Giovanni Testa: Conceptualization, Methodology, Software, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Visualization, Project administration. **Sergio Neira**: Conceptualization, Methodology, Validation, Writing – Review and Editing, Visualization, Supervision. **Ricardo Giesecke**: Conceptualization, Methodology, Writing – Review and Editing, Visualization. **Andrea Piñones**:

Conceptualization, Writing – Review and Editing, Visualization, Funding Acquisition. All authors contributed to the article and approved the submitted version.

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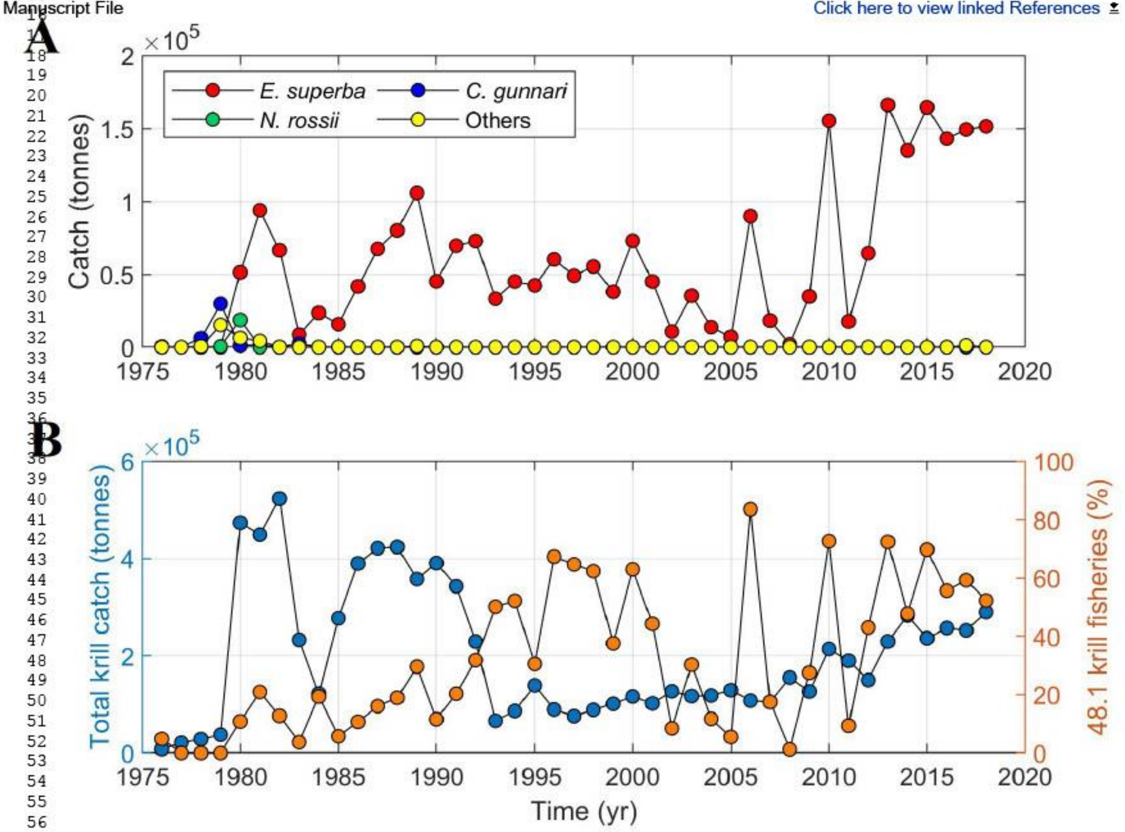
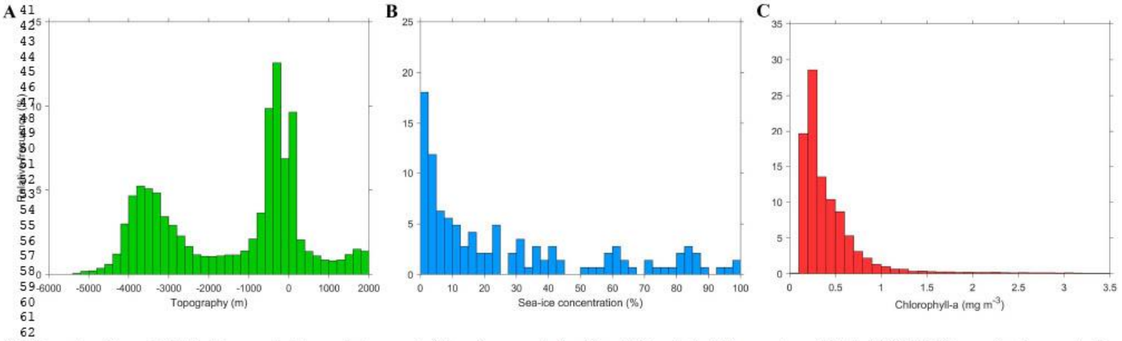
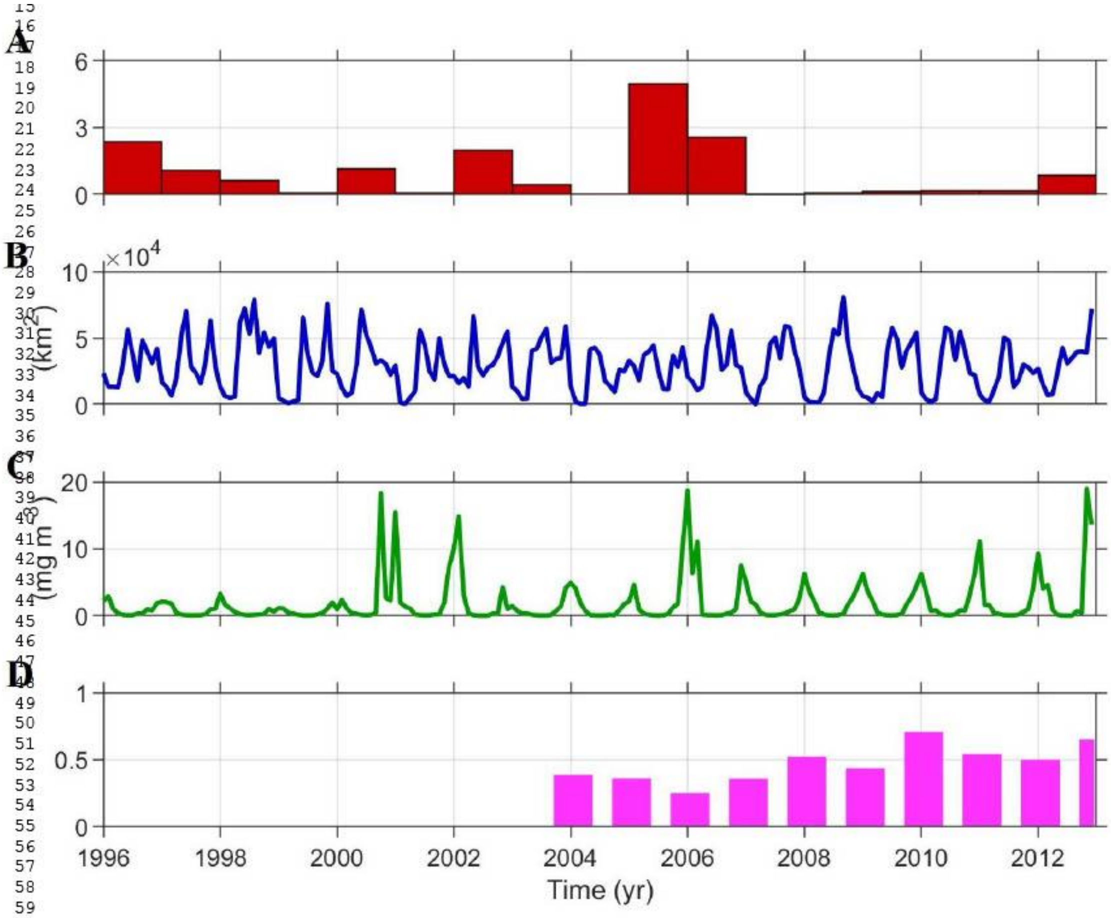


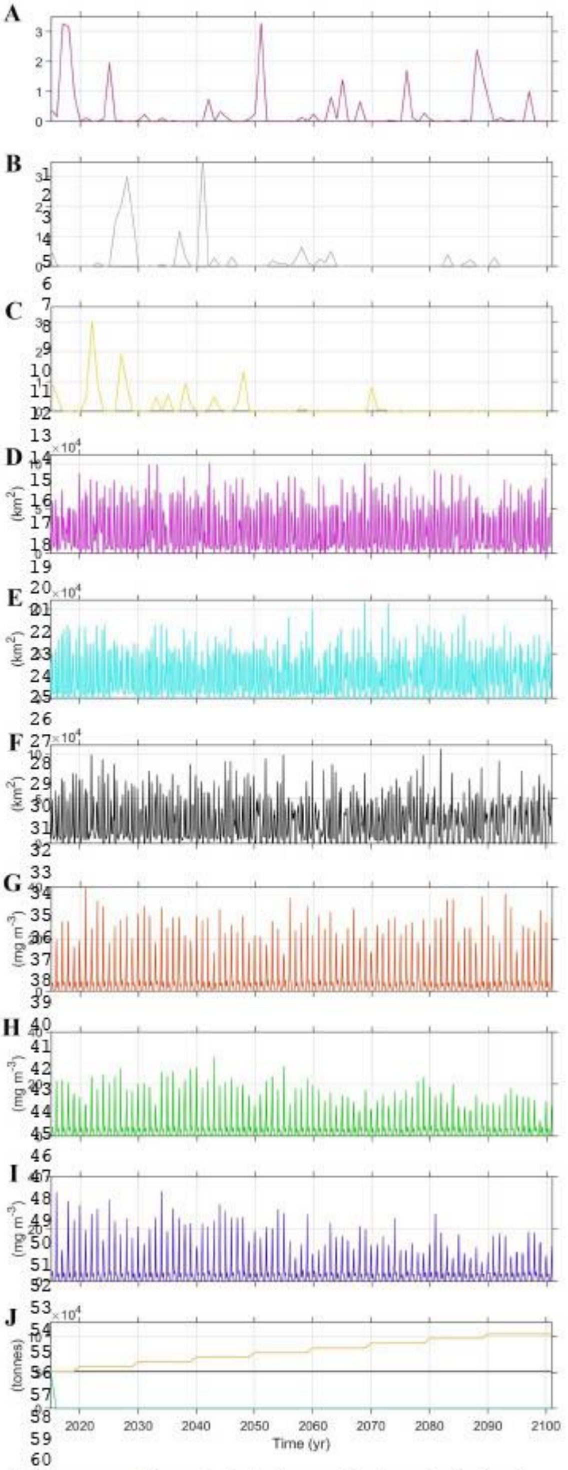
Supplementary Figure 1. Main fisheries time series within the CCAMLR 48.1 zone **(A)** and total krill catches time series within the Southern Ocean and the relative proportion of CCAMLR 48.1 zone catches with respect to the total catches **(B)**. Values were obtained from the Statistical Bulletin (Volume 31) of the CCAMLR.



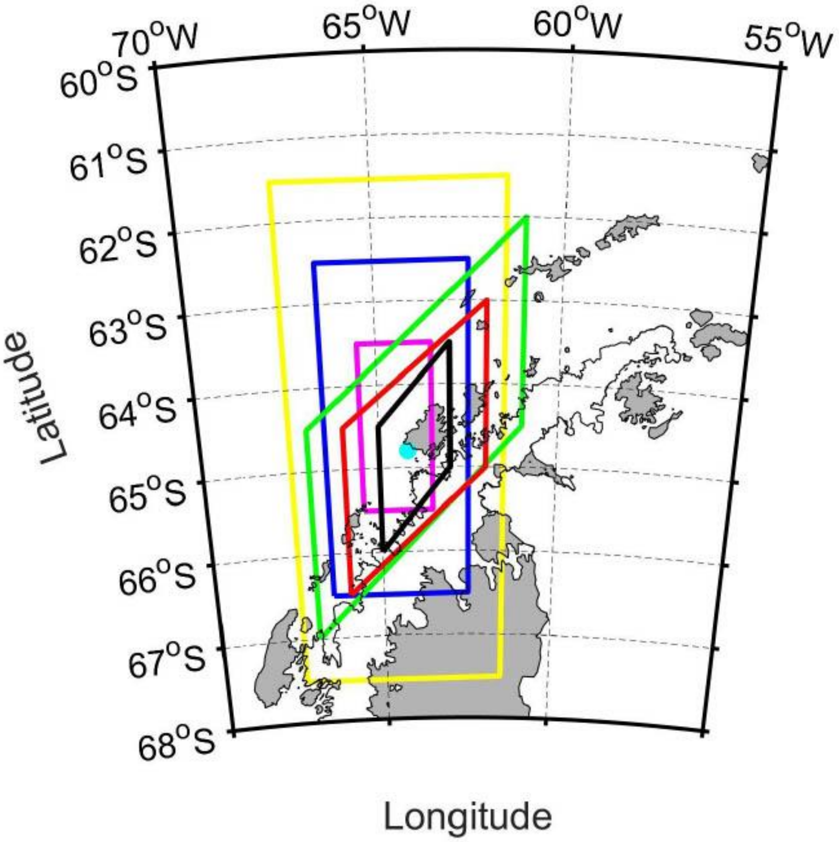
Supplementary Figure 2. Relative frequency dendrogram for topography **(A)**, sea-ice concentration **(B)** and Chlorophyll-a **(C)** mean values within the CCAMLR 48.1 zone. Sea ice concentration and chlorophyll-a mean values were extracted between 2003 and 2019. Values were obtained using the CoastWatch project of the National Oceanic and Atmospheric Administration (https://coastwatch.pfeg.noaa.gov/).



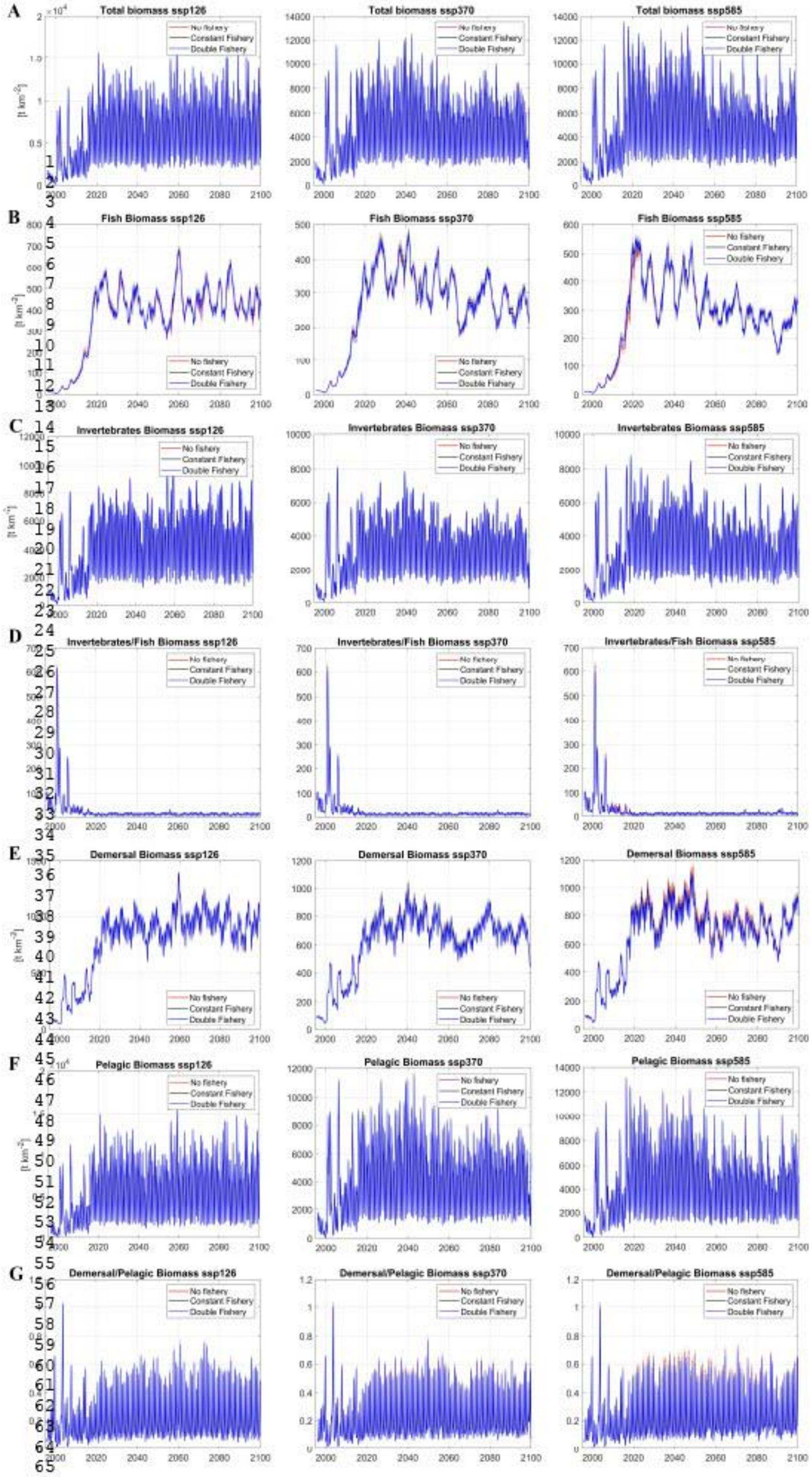
Supplementary Figure 3. Time series of forcing factors used in Dahood et al. (2019) model: sea-ice index **(A)**, open water area **(B)**, chlorophyll-a **(C)** and leopard seal predation mortality rate on Antarctic fur seal pups **(D)**.



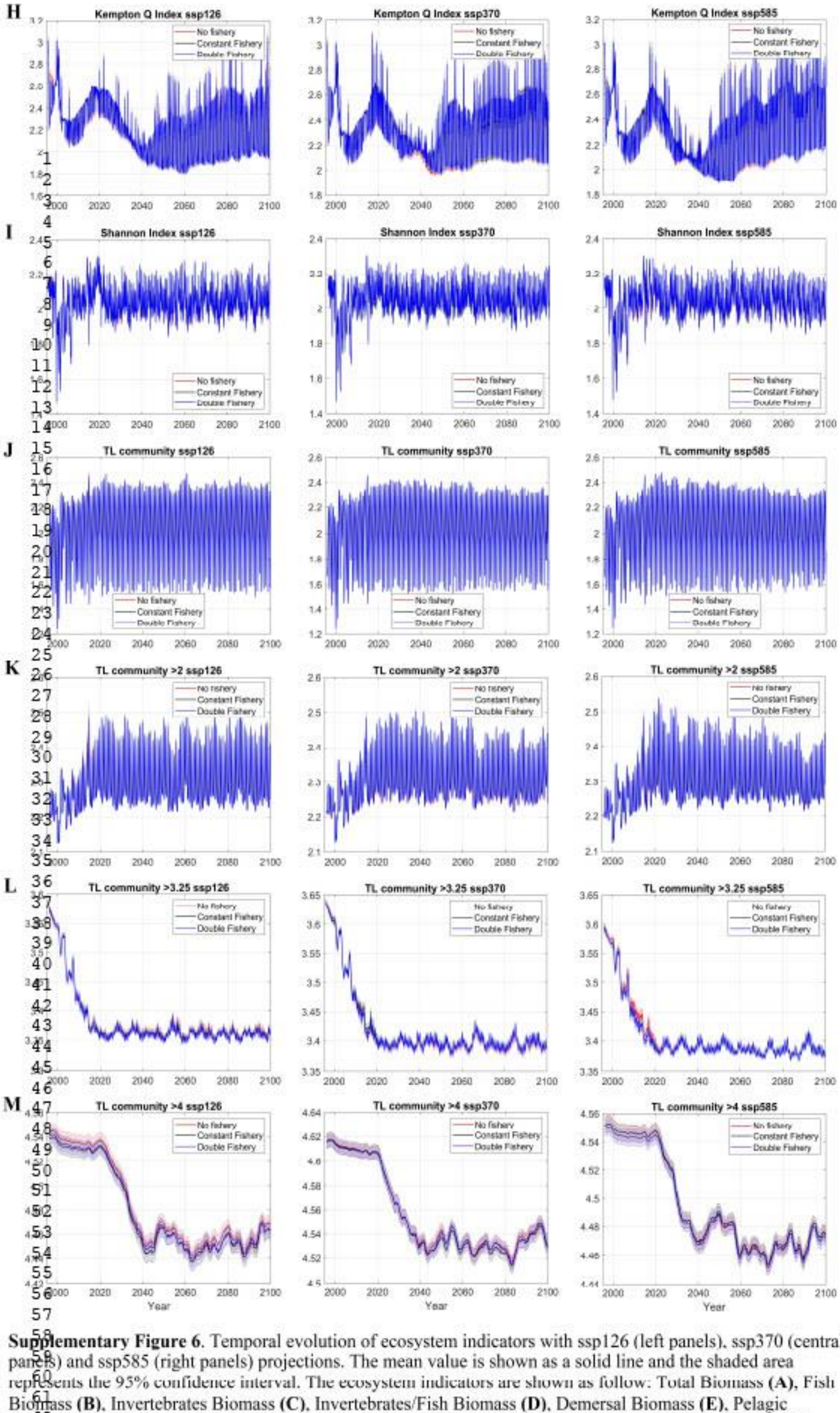
Supplementary Figure 4. Projections used to force the food web model for the period 2015-2100. Sea-ice index time series for ssp126 **(A)**, ssp370 **(B)** and ssp585 **(C)** scenarios; open water area time series for ssp126 **(D)**, ssp370 **(E)** and ssp585 **(F)** scenarios; chlorophyll-a time series for ssp126 **(G)**, ssp370 **(H)** and ssp585 **(I)** scenarios; krill fisheries **(J)** scenarios.



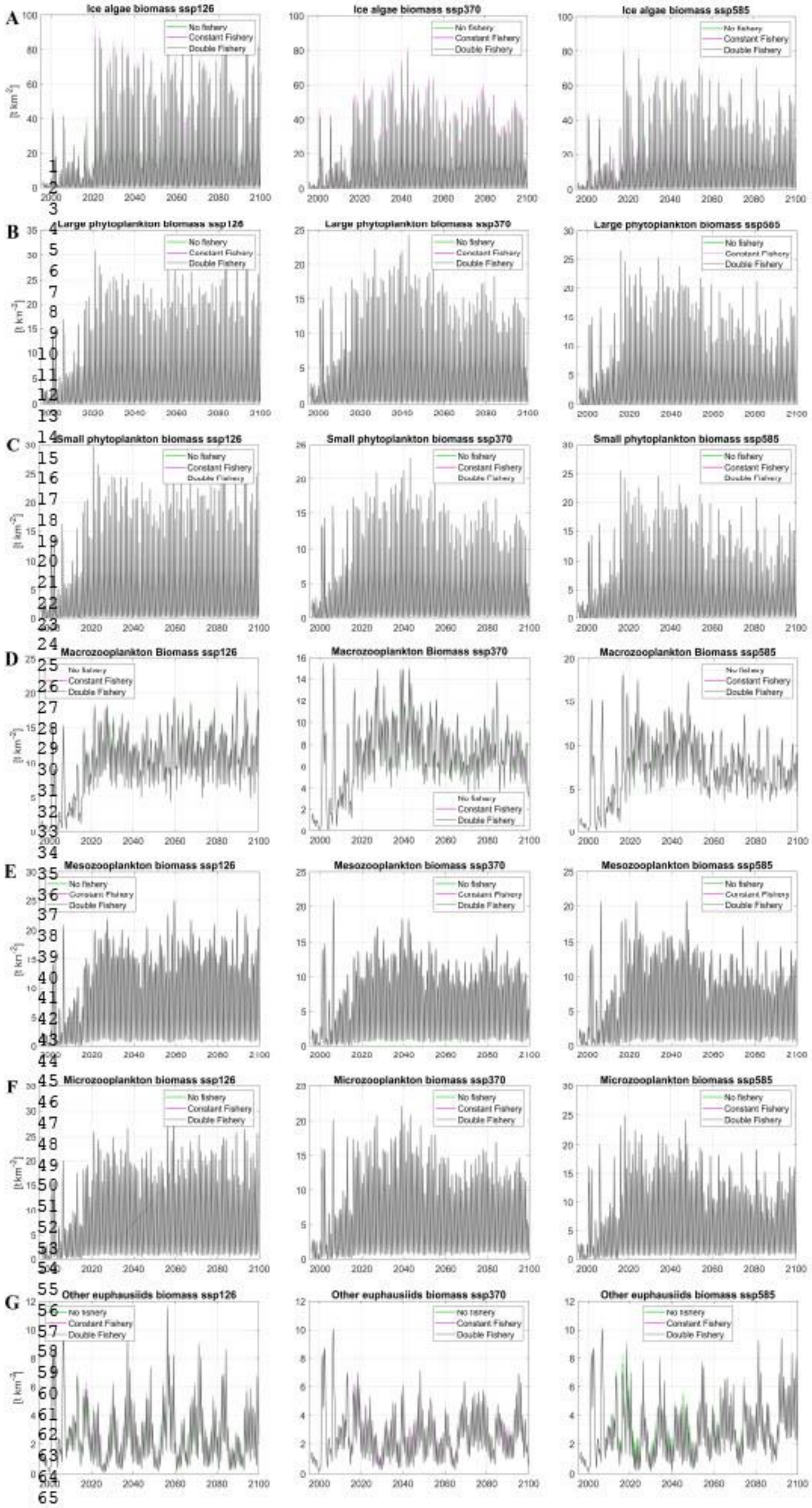
Supplementary Figure 5. Geographic location of the grids used during the comparison of *in situ* and model output chlorophyll-a in Supplementary Table 1.


A
Total biomass ssp126
Total biomass ssp370
Total biomass ssp585
B
Fish Biomass ssp126
Fish Biomass ssp370
Fish Biomass ssp585
C
Invertebrates Biomass ssp126
Invertebrates Biomass ssp370
Invertebrates Biomass ssp585
D
Invertebrates/Fish Biomass ssp126
Invertebrates/Fish Biomass ssp370
Invertebrates/Fish Biomass ssp585
E
Demersal Biomass ssp126
Demersal Biomass ssp370
Demersal Biomass ssp585
F
Pelagic Biomass ssp126
Pelagic Biomass ssp370
Pelagic Biomass ssp585
G
Demersal/Pelagic Biomass ssp126
Demersal/Pelagic Biomass ssp370
Demersal/Pelagic Biomass ssp585
No fishery
Constant Fishery
Double Fishery
[t km⁻²]
2000
2020
2040
2060
2080
2100

continue



Supplementary Figure 6. Temporal evolution of ecosystem indicators with ssp126 (left panels), ssp370 (central panels) and ssp585 (right panels) projections. The mean value is shown as a solid line and the shaded area represents the 95% confidence interval. The ecosystem indicators are shown as follow: Total Biomass **(A)**, Fish Biomass **(B)**, Invertebrates Biomass **(C)**, Invertebrates/Fish Biomass **(D)**, Demersal Biomass **(E)**, Pelagic Biomass **(F)**, Demersal/Pelagic Biomass **(G)**, Kempton Q Index **(H)**, Shannon Index **(I)**, Trophic Level of the community **(J)**, Trophic Level of the community with trophic level higher than 2 **(K)**, Trophic Level of the community with trophic level higher than 3.25 **(L)** and Trophic Level of the community with trophic level higher than 4 **(M)**.


A
Ice algae biomass ssp126
Ice algae biomass ssp370
Ice algae biomass ssp585
B
Large phytoplankton biomass ssp126
Large phytoplankton biomass ssp370
Large phytoplankton biomass ssp585
C
Small phytoplankton biomass ssp126
Small phytoplankton biomass ssp370
Small phytoplankton biomass ssp585
D
Macrozooplankton Biomass ssp126
Macrozooplankton Biomass ssp370
Macrozooplankton Biomass ssp585
E
Mesozooplankton biomass ssp126
Mesozooplankton biomass ssp370
Mesozooplankton biomass ssp585
F
Microzooplankton biomass ssp126
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G
Other euphausiids biomass ssp126
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Other euphausiids biomass ssp585
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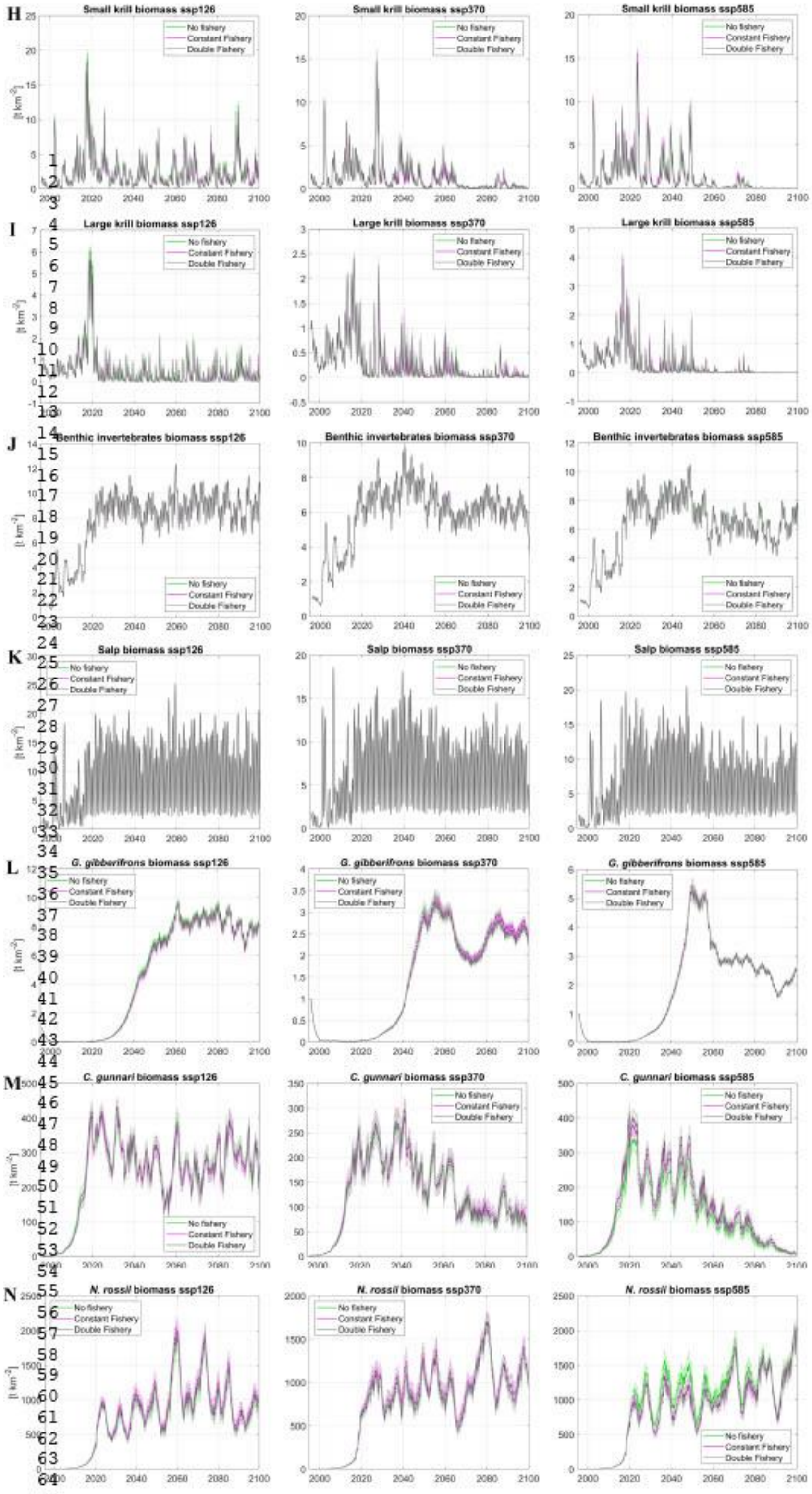
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Salp biomass ssp126
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G. gibberifrons biomass ssp126
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C. gunnari biomass ssp126
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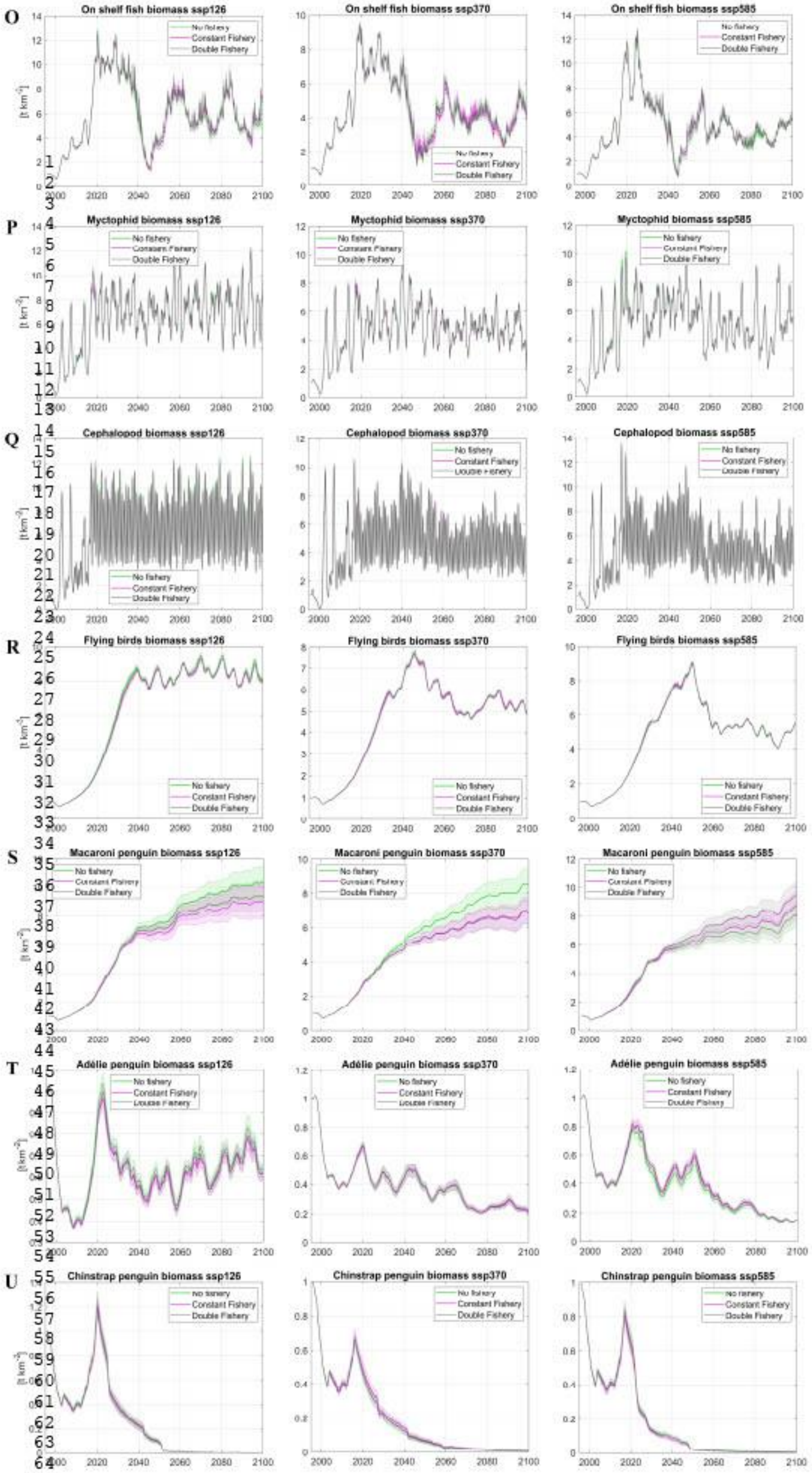
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Flying birds biomass ssp126
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Adélie penguin biomass ssp126
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Chinstrap penguin biomass ssp126
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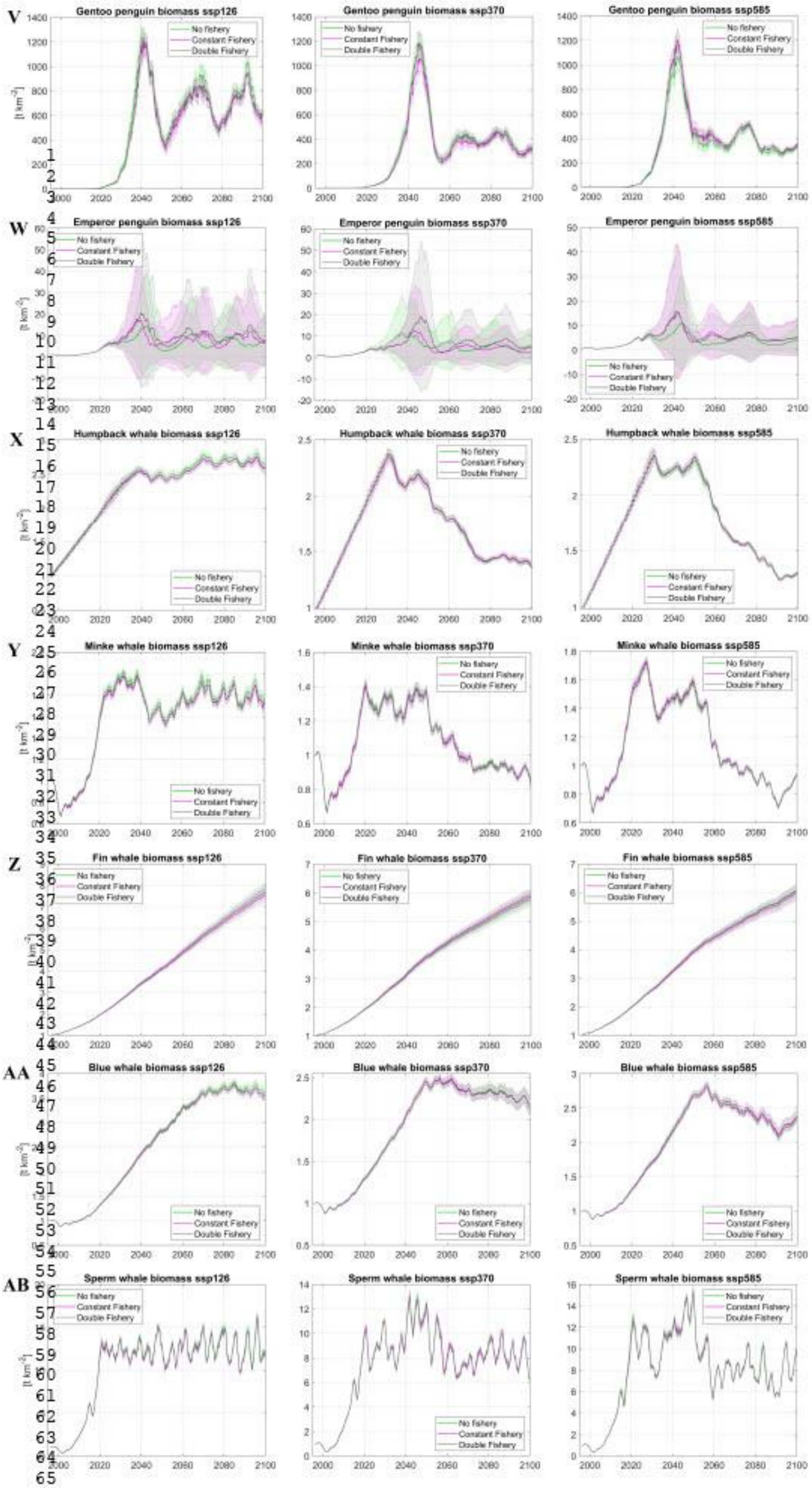
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Gentoo penguin biomass ssp126
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Gentoo penguin biomass ssp585
W
Emperor penguin biomass ssp126
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Emperor penguin biomass ssp585
X
Humpback whale biomass ssp126
Humpback whale biomass ssp370
Humpback whale biomass ssp585
Y
Minke whale biomass ssp126
Minke whale biomass ssp370
Minke whale biomass ssp585
Z
Fin whale biomass ssp126
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Fin whale biomass ssp585
AA
Blue whale biomass ssp126
Blue whale biomass ssp370
Blue whale biomass ssp585
AB
Sperm whale biomass ssp126
Sperm whale biomass ssp370
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[t km^{-2}]
No fishery
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Double Fishery
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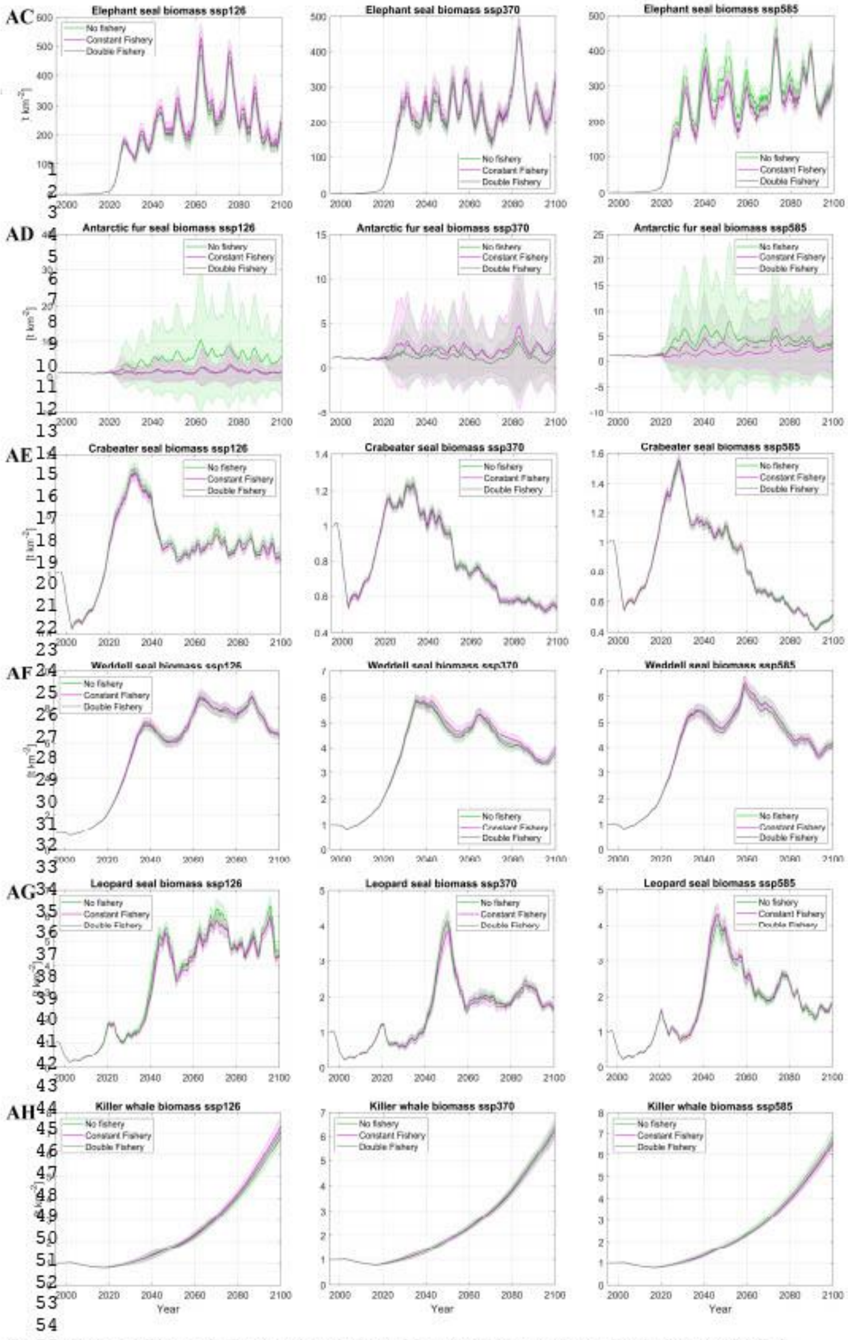
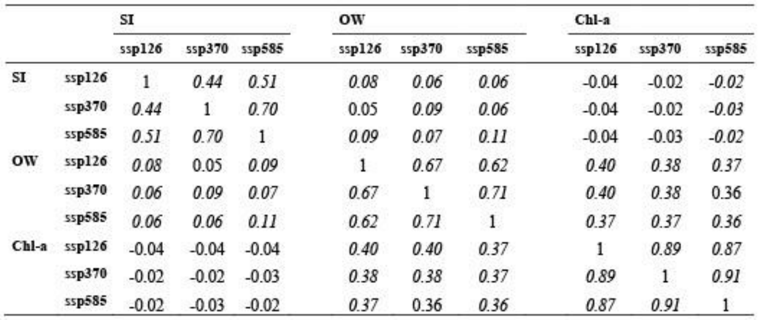


Supplementary Figure 7. Temporal evolution of functional groups dynamics during ssp126 (left panels), ssp370 (central panels) and ssp585 (right panels). The mean value is shown as a solid line and the shaded area represents the 95% confidence interval. Functional groups biomass is displayed as follow: Ice algae **(A)**, Large phytoplankton **(B)**, Small phytoplankton **(C)**, Macrozooplankton **(D)**, Mesozooplankton **(E)**, Microzooplankton **(F)**, Other euphausiids **(G)**, Small krill **(H)**, Large krill **(I)**, Benthic invertebrates **(J)**, Salps **(K)**, *Gobionotothen gibberifrons* **(L)**, *Champsocephalus gunnari* **(M)**, *Notothenia rossii* **(N)**, On shelf fish **(O)**, Myctophid **(P)**, Cephalopod **(Q)**, Flying birds **(R)**, Macaroni penguin **(S)**, Adélic penguin **(T)**, Chinstrap penguin **(U)**, Gentoo penguin **(V)**, Emperor penguin **(W)**, Humpback whale **(X)**, Minke whale **(Y)**, Fin whale **(Z)**, Blue whale **(AA)**, Sperm whale **(AB)**, Elephant seal **(AC)**, Antarctic fur seal **(AD)**, Crabeater seal **(AE)**, Weddell seal **(AF)**, Leopard seal **(AG)** and Killer whale **(AH)**.

Supplementary Table 1. Summary of error statistics, i.e., Absolute Average Error (AAE), Root Mean Square Error (RMSE), Bias Mean Normalized Bias (PBIAS), Mean Absolute Percentage Error (MPE) and r^2 coefficients for different Chlorophyll areas and scenarios.

Scenario	Box (lon x lat)	Details	AAE	RMSE	BIAS	Pbias	MPE	r^2
ssp126								
	1x1	Pixel nearest to Palmer Station	2.31	4.97	-2.27	-86.16	71.61	0.48
	3x3	Pixel nearest to Palmer Stationin the center of the grid	2.25	4.91	-2.19	-83.17	69.72	0.49
	5x5	Pixel nearest to Palmer Stationin the center of the grid	2.19	4.84	-2.09	-79.40	68.37	0.51
	7x7	Pixel nearest to Palmer Stationin the center of the grid	2.22	4.88	-2.12	-80.81	66.66	0.47
	2x2	63°-65°W; 64°30'-66°S and 63°30'-65°S	2.27	4.92	-2.21	-84.14	71.26	0.52
	4x3	62°-66°W; 64°30'-66°30'S and 63°-65°S	2.25	4.90	-2.18	-82.99	70.69	0.52
	6x4	61°-67°W; 64°30'-67°S and 62°-64°30'S	2.26	4.92	-2.19	-83.30	68.60	0.48
ssp370								
	1x1	Pixel nearest to Palmer Station	2.29	4.94	-2.25	-85.69	69.98	0.53
	3x3	Pixel nearest to Palmer Stationin the center of the grid	2.22	4.87	-2.17	-82.49	65.23	0.55
	5x5	Pixel nearest to Palmer Stationin the center of the grid	2.14	4.77	-2.05	-78.09	64.26	0.56
	7x7	Pixel nearest to Palmer Stationin the center of the grid	2.18	4.83	-2.10	-79.94	61.99	0.52
	2x2	63°-65°W; 64°30'-66°S and 63°30'-65°S	2.23	4.88	-2.19	-83.40	68.67	0.56
	4x3	62°-66°W; 64°30'-66°30'S and 63°-65°S	2.21	4.85	-2.16	-82.10	66.09	0.57
	6x4	61°-67°W; 64°30'-67°S and 62°-64°30'S	2.22	4.88	-2.17	-82.55	64.72	0.54
ssp585								
	1x1	Pixel nearest to Palmer Station	2.27	4.94	-2.23	-84.72	69.91	0.51
	3x3	Pixel nearest to Palmer Stationin the center of the grid	2.20	4.88	-2.14	-81.36	67.67	0.51
	5x5	Pixel nearest to Palmer Stationin the center of the grid	2.16	4.82	-2.04	-77.49	66.89	0.51
	7x7	Pixel nearest to Palmer Stationin the center of the grid	2.18	4.86	-2.08	-79.10	65.51	0.47
	2x2	63°-65°W; 64°30'-66°S and 63°30'-65°S	2.21	4.88	-2.16	-82.22	68.38	0.54
	4x3	62°-66°W; 64°30'-66°30'S and 63°-65°S	2.19	4.86	-2.13	-80.87	67.75	0.54
	6x4	61°-67°W; 64°30'-67°S and 62°-64°30'S	2.21	4.89	-2.14	-81.53	66.24	0.50

Supplementary Table 2. Pearson linear correlation coefficient between the forcing time series. SI: Sea Ice Index; OW: Open Water area; Chl-a: Chlorophyll-a. Values in italic were characterized by a p-value < 0.05.



		SI			**OW**			**Chl-a**		
		ssp126	**ssp370**	**ssp585**	**ssp126**	**ssp370**	**ssp585**	**ssp126**	**ssp370**	**ssp585**
SI	**ssp126**	1	*0.44*	*0.51*	*0.08*	*0.06*	*0.06*	-0.04	-0.02	*-0.02*
	ssp370	*0.44*	1	*0.70*	0.05	*0.09*	*0.06*	-0.04	-0.02	*-0.03*
	ssp585	*0.51*	*0.70*	1	*0.09*	*0.07*	*0.11*	-0.04	-0.03	*-0.02*
OW	**ssp126**	*0.08*	0.05	*0.09*	1	*0.67*	*0.62*	*0.40*	*0.38*	*0.37*
	ssp370	*0.06*	*0.09*	*0.07*	*0.67*	1	*0.71*	*0.40*	*0.38*	0.36
	ssp585	*0.06*	*0.06*	*0.11*	*0.62*	*0.71*	1	*0.37*	*0.37*	*0.36*
Chl-a	**ssp126**	-0.04	-0.04	-0.04	*0.40*	*0.40*	*0.37*	1	*0.89*	*0.87*
	ssp370	-0.02	-0.02	-0.03	*0.38*	*0.38*	*0.37*	*0.89*	1	*0.91*
	ssp585	-0.02	-0.03	-0.02	*0.37*	0.36	*0.36*	*0.87*	*0.91*	1

Supplementary Table 3. Summary of the main incidental catches during the period 2010-2018 for krill fisheries. The mean annual incidental catches per specie were compared with the initial biomass of the trophic model to calculate the percentage of the incidental catches to the biomass of the species.

Specie	**Catch ($t\ km^{-2}\ yr^{-1}$)**	**Model biomass ($t\ km^{-2}$)**	**Bycatch (%)**
Salpa thompsoni	$5.88 \cdot 10^{-4}$	160	$3.68 \cdot 10^{-4}$
Champsocephalus gunnari	$5.01 \cdot 10^{-6}$	0.9	$5.56 \cdot 10^{-4}$
Pleuragramma antarctica	$2.71 \cdot 10^{-6}$	5.25	$5.17 \cdot 10^{-5}$
Nototheniops nybelini	$1.15 \cdot 10^{-5}$	5.25	$2.20 \cdot 10^{-4}$
Pseudochaenichthys georgianus	$1.23 \cdot 10^{-6}$	5.25	$2.35 \cdot 10^{-5}$
Chaenocephalus aceratus	$5.71 \cdot 10^{-7}$	5.25	$1.09 \cdot 10^{-5}$
Notothenia rossii	$4.71 \cdot 10^{-7}$	0.14	$3.42 \cdot 10^{-4}$
Chionodraco rastrospinosus	$6.68 \cdot 10^{-7}$	5.25	$1.27 \cdot 10^{-5}$
Gobionotothen gibberifrons	$2.35 \cdot 10^{-7}$	5.25	$4.48 \cdot 10^{-6}$

Supplementary Table 4. Functional groups traits required to calculate the ecosystem indicators. VI: Vulnerability Index.

Functional group	**Organism**	**Ecology**	**IUCN status**	**Exploitation status**	**VI**	**Mean length (cm)**	**Max length (cm)**	**Mean weight (kg)**	**Mean life span (year)**	**Reference**
Killer Whale	Mammal	Pelagic	Data deficient	Not exploited		550	980	3500	50	1, 15, 21,23, 31
Leopard Seal	Mammal	Pelagic	Least concern	Not exploited		300	350	400	26	15, 21, 22,23, 31
Weddell Seal	Mammal	Pelagic-Neritic	Least concern	Not exploited		330	350	500	30	15, 21, 24, 31
Crabeater Seal	Mammal	Pelagic-Neritic	Least concern	Not exploited		230	260	206	25	15, 243 24, 31
Antarctic Fur Seal	Mammal	Pelagic-Neritic	Least concern	Not exploited		170	200	84	20	15, 23, 24, 31
S Elephant Seal	Mammal	Pelagic-Oceanic	Least concern	Not exploited		400	580	1700	21	15, 21, 24, 31
Sperm Whale	Mammal	Pelagic	Vulnerable	Not exploited		1600	2400	30000	69	15,21, 23,25, 31
Blue Whale	Mammal	Pelagic	Endangered	Not exploited		2500	3000	102736.5	85	15, 21,25, 31
Fin-Whale	Mammal	Pelagic	Vulnerable	Not exploited		1900	2590	55590	85	15,24,25, 31
Minke Whale	Mammal	Pelagic	Near threatened	Underexploited		800	1020	6566	47	15, 25, 26, 31
Humpback Whale	Mammal	Pelagic	Least concern	Not exploited		1450	1600	30408	85	15, 21,23,25, 31
Emperor Penguin	Birds	Land-based	Least concern	Not exploited		114	125	29.5	17.5	21, 23,24,27, 31
Gentoo Penguin	Birds	Land-based	Least concern	Not exploited		75	95	5.5	13	21, 23,24,27, 31
Chinstrap Penguin	Birds	Land-based	Least concern	Not exploited		70	76	4	17.5	21, 23,24,27, 31
Adelie Penguin	Birds	Land-based	Least concern	Not exploited		70	73	4.6	14	21, 23,24,27, 31
Macaroni Penguin	Birds	Land-based	Vulnerable	Not exploited		70	75	5.5	13	21, 23,24,27, 31
Flying Birds	Birds	Land-based	Least concern	Not exploited		46.45	52.7	1.12	18.7	23, 27, 30, 31
Cephalopod	Invertebrates	Benthopelagic	Least concern	Underexploited		40	100	3	2.5	10,19,28, 31
Myctophid	Fish	Bathydemersal	Least concern	Not exploited	31	7	12	0.003	4	16,28, 29, 31, 33
On-shelf fish	Fish	Pelagic-neritic	Not evaluated	Depleted	62	54	112	8	17	2,4, 16, 28, 29, 31, 33
N. rossi	Fish	Demersal	Not evaluated	Recovering	64	50	92	5.5	10	2,4,11, 13, 29, 31, 33
C. gunnari	Fish	Benthopelagic	Not evaluated	Depleted	64	35	66	1.5	5	2,4,5, 16, 29, 31, 33
G. gibberifrons	Fish	Demersal	Not evaluated	Depleted	70	32	55	1.5	10	2, 13, 29, 31, 33
Salp	Invertebrates	Pelagic	Not evaluated	Not exploited		5.3	10	0.001	0.08	6, 31
Benthic invertebrates	Invertebrates	Benthic	Not evaluated	Not exploited		5	20	0.03	25	3,5,7,9, 20, 31
Krill	Invertebrates	Pelagic	Least concern	Underexploited		5	7	0.002	5	7, 18, 31
Other Euphausiids	Invertebrates	Pelagic	Not evaluated	Not exploited		3	4.2	0.001	4.5	7, 17, 18, 31
Microzooplankton	Invertebrates	Pelagic	Not evaluated	Not exploited		0.001	0.002	1.00E-14	0.016	7, 31
Mesozooplankton	Invertebrates	Pelagic	Not evaluated	Not exploited		0.5	0.93	5.00E-06	1.75	7,8, 31
Macrozooplankton	Invertebrates	Pelagic	Not evaluated	Not exploited		0.9	2.2	4.00E-05	2	7, 31
Small phytoplankton	Algae	Pelagic	Not evaluated	Not exploited		0.0008	0.002	1.00E-16	0.0082	12, 31, 32
Large phytoplankton	Algae	Pelagic	Not evaluated	Not exploited		0.0025	0.027	4.00E-16	0.016	12, 14, 31, 32
Ice algae	Algae	Pelagic-Neritic	Not evaluated	Not exploited		0.001	0.005	1.00E-10	0.016	31, 34

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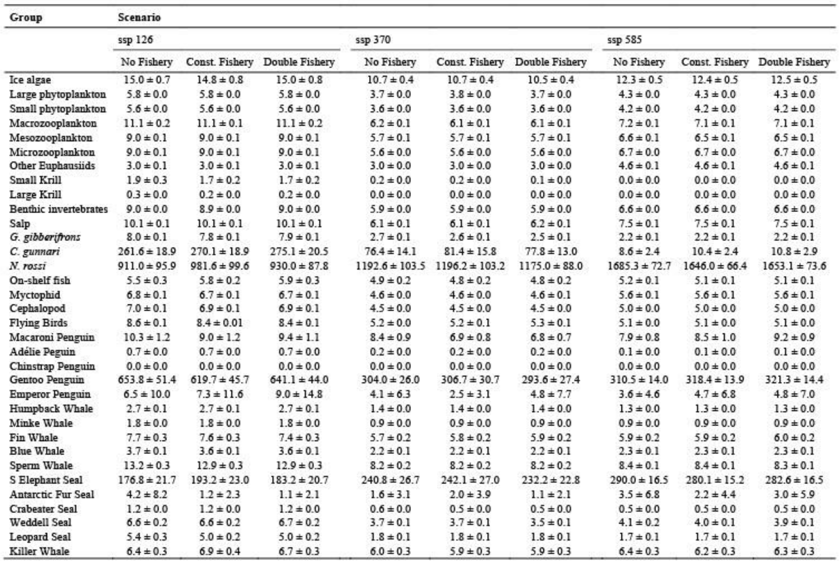
Supplementary Table 5. Sensitivity analysis for all functional groups with values representing the percentage variability with respect to control scenario (n°11). Scenario's characteristics are displayed in Table 2.

Group	Variable and Scenario (n)											
	Sea Ice			Open Water			Chlorophyll-a			Fishery		
	1	2	3	4	5	6	7	8	9	10	11	12
Ice algae	78.55	97.90	94.89	26.93	32.89	27.87	125.74	39.97	66.43	-0.62	0.00	-1.33
Large phytoplankton	-0.22	0.11	0.45	0.69	0.86	0.14	152.52	63.55	91.56	0.15	0.00	-0.45
Small phytoplankton	0.34	0.44	0.55	0.48	-0.06	-0.38	149.46	62.02	90.16	0.61	0.00	-0.21
Macrozooplankton	-0.45	-0.17	-0.02	13.62	10.50	4.53	210.72	86.27	128.93	1.02	0.00	-0.65
Mesozooplankton	0.97	1.27	1.72	7.93	6.66	2.90	156.24	65.71	98.61	0.89	0.00	-0.67
Microzooplankton	0.58	0.90	1.85	0.35	0.43	0.49	177.26	70.97	106.34	0.26	0.00	-0.40
Other Euphausiids	1.54	1.86	2.57	-37.08	-30.25	-18.79	179.76	76.76	112.67	0.57	0.00	-0.01
Small Krill	-61.03	-82.08	-90.96	-36.50	-39.34	-36.16	288.12	165.47	216.81	1.18	0.00	1.22
Large Krill	-61.95	-77.69	-89.20	-77.55	-83.20	-77.28	240.25	162.72	212.55	1.71	0.00	3.33
Benthic invertebrates	1.80	2.03	2.49	5.37	4.96	3.52	183.11	87.01	112.81	0.67	0.00	0.11
Salp	0.10	0.55	0.78	1.41	1.34	0.47	187.83	76.68	118.64	0.64	0.00	-0.37
G. gibberifrons	-69.17	-77.24	-90.28	11493.21	11424.46	7102.39	$567.36 \cdot 10^8$	$160.71 \cdot 10^8$	$161.51 \cdot 10^8$	-63.90	0.00	-67.25
C. gunnari	-9.46	-17.78	-17.23	-23.39	-76.10	-98.88	164.59	107.90	115.98	-6.08	0.00	-12.07
N. rossi	-36.83	-44.24	-53.78	1621.09	1988.46	1734.00	1207.24	405.44	463.38	1.68	0.00	3.03
On-shelf fish	-1.72	-2.22	-2.83	-33.09	-29.91	-26.21	243.01	134.78	147.14	1.19	0.00	-0.95
Myctophid	-4.93	-5.51	-5.91	-22.82	-22.04	-16.64	200.54	110.51	141.78	1.08	0.00	0.37
Cephalopod	-10.57	-13.21	-14.82	-18.80	-19.99	-17.79	209.26	117.68	139.16	1.03	0.00	0.64
Flying Birds	-14.10	-16.90	-21.57	-21.29	-24.63	-23.79	230.56	135.92	138.13	1.36	0.00	0.73
Macaroni Penguin	-56.31	-56.74	-58.39	-76.87	-73.94	-73.24	278.50	233.42	232.11	13.57	0.00	16.94
Adélie Peguin	-77.58	-83.12	-87.45	-84.19	-90.42	-91.97	232.08	223.88	243.52	2.31	0.00	5.17
Chinstrap Penguin	-94.61	-97.08	-98.83	-90.72	-89.34	-83.04	-51.15	-3.01	-6.98	-0.42	0.00	1.75
Gentoo Penguin	-84.66	-91.24	-93.36	110.64	56.41	10.53	85.77	100.90	122.82	1.08	0.00	0.30
Emperor Penguin	-21.82	-28.60	-36.43	-61.11	-31.44	-51.49	219.24	171.76	201.40	17.10	0.00	15.42
Humpback Whale	-48.28	-55.39	-61.26	-66.62	-68.27	-68.21	240.84	167.35	167.17	2.12	0.00	2.72
Minke Whale	-49.78	-58.73	-66.02	-83.69	-83.64	-81.88	231.38	163.99	175.60	2.02	0.00	2.91
Fin Whale	-20.02	-22.58	-23.98	-40.16	-37.96	-38.57	106.35	78.77	83.10	4.18	0.00	2.88
Blue Whale	-30.18	-36.37	-40.29	-55.84	-53.84	-51.56	229.09	149.75	150.99	1.87	0.00	1.79
Sperm Whale	-8.99	-9.55	-11.45	-7.95	-12.08	-9.93	231.65	132.11	141.43	0.93	0.00	0.57
S Elephant Seal	-24.13	-30.98	-39.88	1092.30	1444.61	1208.29	1639.20	536.97	584.22	1.65	0.00	2.11
Antarctic Fur Seal	113.57	75.22	84.38	693.96	732.27	603.93	201.53	28.40	33.90	1.68	0.00	-18.39
Crabeater Seal	-56.31	-66.37	-73.50	-90.63	-90.96	-88.51	234.48	178.08	182.14	1.72	0.00	2.57
Weddell Seal	7.71	8.85	7.66	-47.35	-39.61	-31.13	387.23	179.93	177.87	2.46	0.00	-1.87
Leopard Seal	-58.58	-58.91	-65.42	-76.07	-88.90	-89.76	448.39	294.33	321.93	2.52	0.00	4.35
Killer Whale	-29.83	-35.43	-34.05	50.07	53.26	50.67	85.87	40.91	44.70	1.24	0.00	1.99

Supplementary Table 6. Impact of climatic variability and fisheries by year 2100. Mean values ± 95% confidence interval. The climatic and fishery-related characteristics of each scenario are shown in Table 2. B: Biomass. The temporal evolution of the ecosystem indicators and groups is displayed in the **Supplementary Figures 6**-7.

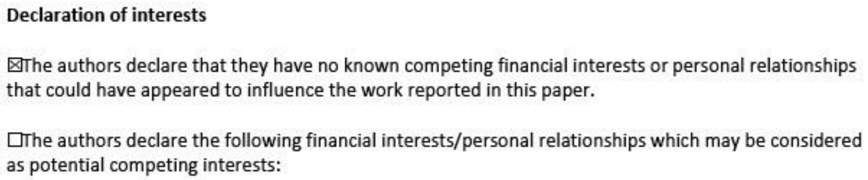


Group	**Scenario**								
	ssp 126			ssp 370			ssp 585		
	No Fishery	Const. Fishery	Double Fishery	No Fishery	Const. Fishery	Double Fishery	No Fishery	Const. Fishery	Double Fishery
Ice algae	15.0 ± 0.7	14.8 ± 0.8	15.0 ± 0.8	10.7 ± 0.4	10.7 ± 0.4	10.5 ± 0.4	12.3 ± 0.5	12.4 ± 0.5	12.5 ± 0.5
Large phytoplankton	5.8 ± 0.0	5.8 ± 0.0	5.8 ± 0.0	3.7 ± 0.0	3.8 ± 0.0	3.7 ± 0.0	4.3 ± 0.0	4.3 ± 0.0	4.3 ± 0.0
Small phytoplankton	5.6 ± 0.0	5.6 ± 0.0	5.6 ± 0.0	3.6 ± 0.0	3.6 ± 0.0	3.6 ± 0.0	4.2 ± 0.0	4.2 ± 0.0	4.2 ± 0.0
Macrozooplankton	11.1 ± 0.2	11.1 ± 0.1	11.1 ± 0.2	6.2 ± 0.1	6.1 ± 0.1	6.1 ± 0.1	7.2 ± 0.1	7.1 ± 0.1	7.1 ± 0.1
Mesozooplankton	9.0 ± 0.1	9.0 ± 0.1	9.0 ± 0.1	5.7 ± 0.1	5.7 ± 0.1	5.7 ± 0.1	6.6 ± 0.1	6.5 ± 0.1	6.5 ± 0.1
Microzooplankton	9.0 ± 0.1	9.0 ± 0.1	9.0 ± 0.1	5.6 ± 0.0	5.6 ± 0.0	5.6 ± 0.0	6.7 ± 0.0	6.7 ± 0.0	6.7 ± 0.0
Other Euphausiids	3.0 ± 0.1	3.0 ± 0.1	3.0 ± 0.1	3.0 ± 0.0	3.0 ± 0.0	3.0 ± 0.0	4.6 ± 0.1	4.6 ± 0.1	4.6 ± 0.1
Small Krill	1.9 ± 0.3	1.7 ± 0.2	1.7 ± 0.2	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Large Krill	0.3 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Benthic invertebrates	9.0 ± 0.0	8.9 ± 0.0	9.0 ± 0.0	5.9 ± 0.0	5.9 ± 0.0	5.9 ± 0.0	6.6 ± 0.0	6.6 ± 0.0	6.6 ± 0.0
Salp	10.1 ± 0.1	10.1 ± 0.1	10.1 ± 0.1	6.1 ± 0.1	6.1 ± 0.1	6.2 ± 0.1	7.5 ± 0.1	7.5 ± 0.1	7.5 ± 0.1
G. gibberifrons	8.0 ± 0.1	7.8 ± 0.1	7.9 ± 0.1	2.7 ± 0.1	2.6 ± 0.1	2.5 ± 0.1	2.2 ± 0.1	2.2 ± 0.1	2.2 ± 0.1
C. gunnari	261.6 ± 18.9	270.1 ± 18.9	275.1 ± 20.5	76.4 ± 14.1	81.4 ± 15.8	77.8 ± 13.0	8.6 ± 2.4	10.4 ± 2.4	10.8 ± 2.9
N. rossi	911.0 ± 95.9	981.6 ± 99.6	930.0 ± 87.8	1192.6 ± 103.5	1196.2 ± 103.2	1175.0 ± 88.0	1685.3 ± 72.7	1646.0 ± 66.4	1653.1 ± 73.6
On-shelf fish	5.5 ± 0.3	5.8 ± 0.2	5.9 ± 0.3	4.9 ± 0.2	4.8 ± 0.2	4.8 ± 0.2	5.2 ± 0.1	5.1 ± 0.1	5.1 ± 0.1
Myctophid	6.8 ± 0.1	6.7 ± 0.1	6.7 ± 0.1	4.6 ± 0.0	4.6 ± 0.0	4.6 ± 0.1	5.6 ± 0.1	5.6 ± 0.1	5.6 ± 0.1
Cephalopod	7.0 ± 0.1	6.9 ± 0.1	6.9 ± 0.1	4.5 ± 0.0	4.5 ± 0.0	4.5 ± 0.0	5.0 ± 0.0	5.0 ± 0.0	5.0 ± 0.0
Flying Birds	8.6 ± 0.1	8.4 ± 0.01	8.4 ± 0.1	5.2 ± 0.0	5.2 ± 0.1	5.3 ± 0.1	5.1 ± 0.0	5.1 ± 0.0	5.1 ± 0.0
Macaroni Penguin	10.3 ± 1.2	9.0 ± 1.2	9.4 ± 1.1	8.4 ± 0.9	6.9 ± 0.8	6.8 ± 0.7	7.9 ± 0.8	8.5 ± 1.0	9.2 ± 0.9
Adélie Peguin	0.7 ± 0.0	0.7 ± 0.0	0.7 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0	0.1 ± 0.0	0.1 ± 0.0	0.1 ± 0.0
Chinstrap Penguin	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Gentoo Penguin	653.8 ± 51.4	619.7 ± 45.7	641.1 ± 44.0	304.0 ± 26.0	306.7 ± 30.7	293.6 ± 27.4	310.5 ± 14.0	318.4 ± 13.9	321.3 ± 14.4
Emperor Penguin	6.5 ± 10.0	7.3 ± 11.6	9.0 ± 14.8	4.1 ± 6.3	2.5 ± 3.1	4.8 ± 7.7	3.6 ± 4.6	4.7 ± 6.8	4.8 ± 7.0
Humpback Whale	2.7 ± 0.1	2.7 ± 0.1	2.7 ± 0.1	1.4 ± 0.0	1.4 ± 0.0	1.4 ± 0.0	1.3 ± 0.0	1.3 ± 0.0	1.3 ± 0.0
Minke Whale	1.8 ± 0.0	1.8 ± 0.0	1.8 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0
Fin Whale	7.7 ± 0.3	7.6 ± 0.3	7.4 ± 0.3	5.7 ± 0.2	5.8 ± 0.2	5.9 ± 0.2	5.9 ± 0.2	5.9 ± 0.2	6.0 ± 0.2
Blue Whale	3.7 ± 0.1	3.6 ± 0.1	3.6 ± 0.1	2.2 ± 0.1	2.2 ± 0.1	2.2 ± 0.1	2.3 ± 0.1	2.3 ± 0.1	2.3 ± 0.1
Sperm Whale	13.2 ± 0.3	12.9 ± 0.3	12.9 ± 0.3	8.2 ± 0.2	8.2 ± 0.2	8.2 ± 0.2	8.4 ± 0.1	8.4 ± 0.1	8.3 ± 0.1
S Elephant Seal	176.8 ± 21.7	193.2 ± 23.0	183.2 ± 20.7	240.8 ± 26.7	242.1 ± 27.0	232.2 ± 22.8	290.0 ± 16.5	280.1 ± 15.2	282.6 ± 16.5
Antarctic Fur Seal	4.2 ± 8.2	1.2 ± 2.3	1.1 ± 2.1	1.6 ± 3.1	2.0 ± 3.9	1.1 ± 2.1	3.5 ± 6.8	2.2 ± 4.4	3.0 ± 5.9
Crabeater Seal	1.2 ± 0.0	1.2 ± 0.0	1.2 ± 0.0	0.6 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0	0.5 ± 0.0
Weddell Seal	6.6 ± 0.2	6.6 ± 0.2	6.7 ± 0.2	3.7 ± 0.1	3.7 ± 0.1	3.5 ± 0.1	4.1 ± 0.2	4.0 ± 0.1	3.9 ± 0.1
Leopard Seal	5.4 ± 0.3	5.0 ± 0.2	5.0 ± 0.2	1.8 ± 0.1	1.8 ± 0.1	1.8 ± 0.1	1.7 ± 0.1	1.7 ± 0.1	1.7 ± 0.1
Killer Whale	6.4 ± 0.3	6.9 ± 0.4	6.7 ± 0.3	6.0 ± 0.3	5.9 ± 0.3	5.9 ± 0.3	6.4 ± 0.3	6.2 ± 0.3	6.3 ± 0.3

Supplementary Table 7. Mean value for the relative biomass of all the model functional groups during the period 2095-2100 compared with the timeframe 1996-2001. Values are expressed as percentage.

Group	**Scenario**		
	ssp126	ssp370	ssp585
Ice algae	695.7	465.7	555.7
Large phytoplankton	387.0	212.2	260.9
Small phytoplankton	350.0	191.7	241.8
Macrozooplankton	1251.5	644.1	762.1
Mesozooplankton	672.9	389.4	461.7
Microzooplankton	537.9	298.1	376.8
Other Euphausiids	293.3	295.0	504.9
Small Krill	211.3	-72.6	-100.0
Large Krill	-51.4	-94.6	-100.0
Benthic invertebrates	871.2	536.9	617.6
Salp	1103.2	631.5	793.3
G. gibberifrons	2419.1	731.8	604.4
C. gunnari	13548.3	4022.0	410.2
N. rossi	61084.2	77488.3	108213.2
On-shelf fish	532.2	432.2	464.4
Myctophid	759.7	481.9	606.5
Cephalopod	890.1	537.7	606.1
Flying Birds	785.7	450.9	435.4
Macaroni Penguin	946.9	709.0	831.7
Adélie Peguin	-24.5	-73.9	-83.4
Chinstrap Penguin	-100.0	-99.1	-99.5
Gentoo Penguin	61902.6	29228.0	30663.4
Emperor Penguin	727.4	315.0	376.9
Humpback Whale	149.5	29.6	18.9
Minke Whale	95.2	-1.2	-4.2
Fin Whale	614.9	447.6	459.0
Blue Whale	274.3	130.3	136.1
Sperm Whale	1322.1	795.0	813.9
S Elephant Seal	19240.6	24909.2	29705.1
Antarctic Fur Seal	91.2	38.5	160.2
Crabeater Seal	28.6	-40.7	-47.8
Weddell Seal	565.0	264.9	303.6
Leopard Seal	539.1	120.9	107.7
Killer Whale	566.0	492.5	527.2

Declaration of competing interest



Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

5. DISCUSIÓN

5.1. Comparación con estudios previos de ecorregionalización

Este estudio permitió la identificación de nuevas regiones físicas y biogeoquímicas en el OA. Además, al establecer el límite norte para el OA en 50°S el estudio permitió realizar comparaciones de las similitudes y diferencias entre el ambiente antártico y el subantártico. Este análisis reveló un mayor número de regiones biogeoquímicas significativas con respecto a las zonas físicas. El número de regiones del OA (12 y 18 según criterios físicos y biogeoquímicos, respectivamente) fue comparable con otros estudios de ecorregionalización. El estudio de Grant et al. (2006) dividió el OA en 14 regiones diferentes según la batimetría, la temperatura superficial del mar (TSM) y la concentración de nutrientes, mientras que Raymond (2014) estableció 20 regiones utilizando batimetría, TSM y cobertura de hielo. Por otro lado, el estudio de regionalización para la zona CCAMLR 48.1 es el primero de mi conocimiento e identifica un número sorprendentemente alto de zonas significativas (14 regiones físicas y 16 biogeoquímicas), probablemente debido a la ausencia *a priori* de una agrupación no jerárquica inducida por el reducido tamaño de muestra. La distribución circumpolar observada para las regiones físicas oceánicas fue similar a los hallazgos de estudios previos de regionalización (Grant et al. 2006; Spalding et al. 2012; Raymond 2014). Adicionalmente, las Islas

Malvinas y la zona costera de la Patagonia Sur se agruparon en una sola región física, acorde con trabajos previos. Este trabajo dividió la zona costera antártica en siete *clusters* diferentes, lo cual coincidió con Raymond (2014) y discrepó con la regionalización de Grant et al. (2006) que agrupó toda la zona costera de la Antártida en una sola región. Adicionalmente, Grant et al. (2006) identificaron el área oceánica del giro de Weddell como un grupo separado, en contraste con la división de esta área en cuatro regiones diferentes de la presente investigación y respaldada por los resultados de Raymond (2014). La inclusión de la variabilidad espacial del hielo marino (Raymond 2014; este estudio) podría originar una mayor heterogeneidad física con respecto a una regionalización (Grant et al. 2006) que incorporó la concentración de nitratos y silicatos, ya que concentraciones elevadas y homogéneas de macronutrientes generalmente se observan al sur de 50°S y a lo largo de la zona costera antártica (Pollard et al. 2006; Sigman y Hain 2012).

5.2. Similitudes y diferencias entre la regionalización física y biogeoquímica

La heterogeneidad espacial de los frentes oceánicos influyó en la regionalización física del OA causando un patrón circumpolar, mientras que esto no se vio reflejado en la regionalización biogeoquímica ya que se identificaron regiones biogeoquímicas cruzando los frentes en el Océano Índico y Pacífico.

Las bajas estimaciones de Productividad Primaria Neta (PPN) a ambos lados de los frentes podrían ser explicadas por una combinación entre limitación al crecimiento fitoplanctónico por luz (Venables y Moore 2010), pastoreo por zooplancton (Le Quéré et al. 2016) y agotamiento de hierro disuelto (Tagliabue et al. 2014; Wadley et al. 2014). Las zonas costeras alrededor de América del Sur y las Islas Malvinas se fusionaron en un grupo físico significativamente diferente a todos los demás en el OA mientras que la región costera alrededor de la Patagonia fue dividida en dos regiones de acuerdo a las variables biogeoquímicas y una de estas también apareció en zonas costeras antárticas. Esto sugirió que las zonas costeras de la Patagonia y algunas zonas antárticas comparten ciertas características biogeoquímicas (*i.e.*, altas estimaciones de PPN y concentración de diatomeas), pero no dinámica física similares. La alta productividad costera Antártica podría verse impulsada por el derretimiento del hielo marino durante el periodo estival austral, inyectando micronutrientes (Lannuzel et al. 2016) y aumentando la estabilidad de la capa fótica (Taylor et al. 2013). Por otro lado, la alta PPN en ambientes subantárticos podría verse sustentada por la alta mezcla causada por las mareas sobre la plataforma continental (Romero et al. 2006), descargas continentales de agua dulce (Cuevas et al. 2019) y el suministro de hierro por transporte sobre la plataforma o polvo atmosférico (Jickells et al. 2005; García et al. 2008). Además, las aguas que rodean las islas oceánicas (*e.g.*, Auckland, Kerguelen y Georgia del Sur) se agruparon en una región biogeoquímica separada, mientras que esta distinción no fue revelada por la regionalización física. Las elevadas tasas de PPN alrededor de las islas oceánicas pueden explicarse por un “efecto masa de isla" causado por la fertilización con hierro vía advección (Boyd et al. 2004; Robinson et al. 2016).

La distribución espacial de los frentes polares influyó en la regionalización física de la zona noroeste de la zona CCAMLR 48.1, mientras que esta división no se detectó claramente en la regionalización biogeoquímica. Por otro lado, la regionalización física de la zona CCAMLR 48.1 no identificó una diferencia entre la parte oriental y occidental del Estrecho de Bransfield que, por el contrario, fue observada durante la regionalización biogeoquímica. La entrada de agua de deshielo continental y la influencia de la corriente que trae aguas del Mar de Weddell (Sangrà et al. 2011; Moffat y Meredith 2018) podrían causar el gradiente biogeoquímico observado en el Estrecho de Bransfield. La Bahía Margarita y la plataforma sur de la PA Oriental presentaron condiciones físicas y biogeoquímicas similares (las estimaciones de capa de mezcla más someras y las más altas de PPN y concentración de diatomeas), probablemente debido a la elevada presencia de hielo marino durante el verano austral y su influencia en los ciclos biogeoquímicos (Hyatt et al. 2011; Siegert et al. 2019).

No se observó una fuerte consistencia entre la regionalización física y biogeoquímica del OA, mientras que esta correlación fue mayor para la zona CCAMLR 48.1. La mayor correspondencia para la zona 48.1 podría ser explicada por el menor tamaño de muestra en comparación con el OA y/o la respuesta de las regiones biogeoquímicas y físicas a los patrones espaciales de la pendiente de la plataforma (Heywood et al. 2014). La inconsistencia detectada para el OA podría atribuirse a la menor variabilidad espacial de las variables biogeoquímicas explicadas por factores físicos en comparación con la zona CCAMLR 48.1 (60 y 77%, respectivamente). De hecho, se demostró como ciertas regiones del OA con diferentes condiciones físicas pueden presentar las mismas características biogeoquímicas, como por ejemplo en las áreas oceánicas a ambos lados de los frentes subantártico y polar. Esta diferencia podría inducir un número más comparable de regiones físicas y biogeoquímicas para la zona CCAMLR 48.1 (14 y 16, respectivamente) con respecto al OA (12 y 18).

5.3. Principales factores físicos que explican la variabilidad espacial biogeoquímica

El análisis BIO-ENV reveló que la combinación de batimetría y concentración de hielo marino controló principalmente la variabilidad espacial biogeoquímica en el OA. Tanto el gradiente nerítico-pelágico como la variabilidad del hielo marino afectan los ciclos y la estequiometría de macro y micronutrientes

(García et al. 2008; Torres et al. 2014; Annett et al. 2017; Cuevas et al. 2019; Henley et al. 2020), estabilidad de la columna de agua (Hellmer 2004; Romero et al. 2006; Cuevas et al. 2019) y la irradiación lumínica (Smith y Comiso 2008). Además, la batimetría afecta directamente el tiempo de exposición del COP al oxígeno durante la remineralización (Dunne et al. 2007), mientras que se han descubierto pulsos de partículas fecales de kril que contribuyen fuertemente a las exportaciones de COP cerca de la zona marginal de hielo (Belcher et al. 2019; Henley et al. 2020). Por lo tanto, la variabilidad del hielo marino es un mecanismo sensible que puede influir en las tasas de PPN, las exportaciones de COP, la composición de las especies de fitoplancton y la producción de sulfuro de dimetilo, un gas climáticamente activo con alta concentración en la zona de hielo marginal (Deppeler y Davidson 2017; Meredith et al. 2017; Hendry et al. 2018; Henley et al. 2019). La fuerte interdependencia entre el hielo marino y el espectro de abundancia y tamaño del fitoplancton implica que su variabilidad también puede afectar los niveles tróficos más altos de la red trófica, cambiando la estructura y el funcionamiento de todo el ecosistema (Kerr et al. 2018). Por otro lado, la batimetría fue identificada como la variable física que describió mayormente la variabilidad espacial biogeoquímica en la zona CCAMLR 48.1. La exclusión de la variabilidad del hielo marino como factor determinante a la hora de influenciar los patrones biogeoquímicos podría ser explicada por su baja heterogeneidad espacial durante el verano austral en la región, ya que la mayor parte de la PA exhibió bajas concentraciones de hielo marino con la excepción de la Bahía Margarita y la parte meridional de la costa este de la PA.

El número y la extensión de las regiones biogeoquímicas podrían variar en el futuro, ya que tanto el hielo marino como la batimetría experimentarán cambios (en diferentes escalas de tiempo). Los cambios en el ancho de la plataforma continental y la batimetría pueden ocurrir en escalas de tiempo de décadas a siglos debido al equilibrio entre el ajuste isostático glacial y el aumento del nivel del mar (King et al. 2012; Barletta et al. 2018). Por otro lado, la variabilidad espacial de la tendencia interanual del hielo marino para el OA mostró una marcada heterogeneidad a lo largo de las principales zonas de hielo marino marginal y en la zona CCAMLR 48.1. La heterogeneidad y tendencias parecen ser explicadas principalmente por los patrones de circulación atmosférica superficial (Eayrs et al. 2019) y el calentamiento de aguas profundas (Meredith et al. 2017). A pesar de la tendencia negativa del hielo marino detectada en la PA Occidental se ha registrado una pausa en el incremento de la temperatura atmosférica y la tendencia del hielo marino en esta área durante las últimas dos décadas, probablemente debido a la variabilidad climática interdecadal (Meredith et al. 2017; Henley et al. 2019). No obstante, Reygondeau et al. (2020) proyectaron una expansión hacia los polos de las aguas subantárticas y una contracción en las regiones biogeoquímicas más cercanas al continente antártico para 2100.

5.4. Estudios de regionalización como herramienta para el desarrollo de modelos ecosistémicos

El estudio de regionalización puede ayudar en la interpretación y construcción de modelos ecosistémicos locales asociados a las condiciones particulares de cada región. La regionalización física del OA proporciona valiosa información para la parametrización de varias condiciones ambientales (*i.e.*, cobertura de hielo marino, temperatura superficial del mar, batimetría, profundidad de la capa de mezcla e irradiación lumínica) que impactan el ecosistema y generan una alta heterogeneidad en las características biogeoquímicas del hábitat (Murphy et al. 2012, 2013, 2016). Por ejemplo, la información generada en la regionalización física podría ser utilizada como condición inicial en futuros modelos ecosistémicos que estudien la variabilidad espacial de las dinámicas de diferentes grupos fitoplanctónicos (*e.g.*, diatomeas y nanofitoplancton) en función de las condiciones ambientales. Además, la regionalización biogeoquímica permite identificar las regiones de alta productividad importantes para mantener la biodiversidad antártica y proporciona información útil para el desarrollo de futuros modelos ecosistémicos que estudien en profundidad procesos críticos del ciclo del carbono en ambientes antárticos y subantárticos. En específico, el estudio de las diferentes condiciones de capa de mezcla, cobertura de hielo marino y abundancias de grupos fitoplanctónicos podrían contribuir a crear modelos que estudien el reciclaje del hierro y las exportaciones hacia las profundidades. La información generada en este estudio puede proporcionar datos útiles para la realización y comparación de modelos ecosistémicos locales en el OA y en la zona CCAMLR 48.1.

5.5. Factores principales que modulan la trama trófica antártica

El análisis de sensibilidad mostró cómo varios grupos funcionales fueron influenciados tanto por el hielo marino como por la dinámica del área libre de hielo, aunque la mayor variabilidad se atribuyó a las fluctuaciones en la clorofila-a, sugiriendo un control *bottom-up* en la trama trófica. El estudio de Suprenand y Ainsworth (2017) destacó la importancia del fitoplancton y de las algas asociadas al hielo marino en el nivel trófico promedio del ecosistema de la PA, así como en la biomasa de sus grupos funcionales y en los indicadores de diversidad durante las proyecciones para 2050. El control *bottom*-up para la trama trófica de la PA fue también identificado por el modelo EwE de Hoover et al. (2012). Por otro lado, la pesquería de kril no pareció ser un factor crucial en la dinámica temporal de los grupos funcionales y los indicadores ecológicos. La actual tasa de explotación se estableció en un nivel preventivo apropiado para mantener la población de kril y sustentar a sus depredadores (Nicol et al. 2012; Hill et al. 2016; Watters et al.

2020). La magnitud del aumento en la pesquería de kril proyectada en este estudio estuvo por debajo del rendimiento máximo sostenible identificado en el 25-50% de la biomasa no explotada (Hill et al. 2016). Además, el presente trabajo no consideró la variabilidad espacial y estacional de la pesquería de kril. El Estrecho de Bransfield fue la ubicación principal de las capturas de kril en la 48.1 (62%), seguido por el área pelágica occidental del Paso Drake (15%; CCAMLR 2020). Las pesquerías de kril han cambiado su periodo de actividad desde el verano al otoño e invierno debido a una reducción en la cobertura de hielo marino (Smetacek y Nicol 2005; Nicol et al. 2012; Brooks et al. 2018), causando una posible superposición entre las pesquerías, el desove exitoso de kril (Meyer et al. 2020) y los depredadores dependientes del kril en pequeñas escalas espacio-temporales (Hinke et al. 2017; Atkinson et al. 2019). La falta de parametrización de la variabilidad espacial y estacional en la abundancia, el ciclo de vida y la pesquería de kril podría inducir una subestimación del impacto de la pesca en los resultados, ya que Watters et al. (2020) identificaron el impacto de la pesquería de kril en sus depredadores similar al de fenómenos climáticos como el El Niño Oscilación del Sur y el Modo Anular del Sur.

5.6. Escenarios y tendencias para la población de kril

La variabilidad del kril se asocia principalmente con la producción primaria y la dinámica del hielo marino (Smetacek 2008; Piñones y Fedorov 2016). La cobertura de hielo marino invernal es crucial para el desove exitoso de kril, la supervivencia de las larvas y el reclutamiento después del verano (Smetacek y Nicol 2005; Saba et al. 2014; Henley et al. 2019; Rogers et al. 2020), mientras que la abundancia, distribución y composición de especies del zooplancton dependen de la disponibilidad y de la comunidad de fitoplancton y de la estructura de la columna de agua (Henley et al. 2019). El efecto de los grandes mamíferos marinos sobre las dinámicas de la población de kril todavía no está aclarado debido a su doble efecto en la depredación y, al mismo tiempo, en la estimulación de la producción primaria a través del reciclaje de micronutrientes (Smetacek 2008; Surma et al. 2014; Maldonado et al. 2016; Cavan et al. 2019). Este estudio evidenció una fuerte disminución en la biomasa de kril, con una casi extinción de *E. superba* durante los escenarios ssp370 y ssp585 y una disminución en su biomasa del 51% con las condiciones ambientales encontradas en las proyecciones ssp126. De similar manera, el estudio de Meredith et al. (2019) identificó una reducción en la biomasa de kril tanto en el "mejor" escenario climático como en el "peor de los casos" utilizando diferentes proyecciones de emisiones de gases de efecto invernadero. Recientemente surgió un debate sobre la magnitud y veracidad de la disminución del kril (Hill et al. 2016; Cox et al. 2018; Meyer et al. 2020), aunque el trabajo de Hill et al. (2019) pareció reafirmar la disminución de la densidad de kril antártico, al menos en la región suroeste del sector atlántico del OA (Atkinson et al. 2019). La variabilidad climática está provocando una transición hacia los polos de las condiciones óptimas para el desove, el crecimiento y una contracción general del hábitat de kril en el OA (Piñones y Fedorov 2016; Atkinson et al. 2019; Perry et al. 2019; Sylvester et al. 2021). Además, se esperan cambios en el comportamiento, fisiología y distribución del kril con el aumento de la temperatura (Piñones y Fedorov 2014; Murphy et al. 2017; Siegert et al. 2019; Veytia et al. 2020).

5.7. La trama trófica antártica en 2100

Un cambio en la comunidad fitoplanctónica antártica hacia una mayor dominancia de nanofitoplancton ha sido predicho para el futuro (Deppeler y Davidson 2017; Antoni et al. 2020), aunque recientes mediciones *in situ* no revelaron tendencias significativas para los diferentes grupos de microalgas (Schofield et al. 2017). El modelo no fue capaz de predecir cambios en la dominancia de grupos entre los productores primarios debido a una falta de parametrización específica. La alteración del espectro de tamaño del fitoplancton podría cambiar la estructura y el funcionamiento de todo el ecosistema (Saba et al. 2014; Deppeler y Davidson 2017; Kerr et al. 2018) y favorecer la proliferación de salpas (Atkinson et al. 2004, 2019; Moline et al. 2004; Ferreira et al. 2020). Las proyecciones ambientales simuladas en este estudio dieron como resultado una modificación de la comunidad de zooplancton, con una disminución (aumento) de kril (salpas y otros grupos de zooplancton), de acorde con las evidencias de Suprenand y Ainsworth (2017) bajo diferentes escenarios de producción primaria en 2050. El aumento de las partículas fecales de copépodos, salpas y fitodetritos (causado por una disminución del pastoreo de kril) podría contrarrestar la pérdida de exportaciones de COP asociadas al kril, aunque es probable que los ciclos biogeoquímicos se vean alterados (Cavan et al. 2019).

El modelo mostró un fuerte aumento en la biomasa de peces asumiendo la ausencia de pesquerías para estas especies de aquí a 2100. Por lo tanto, se predijo una recuperación en las poblaciones de peces después de la fuerte extracción que diezmó las poblaciones de peces de la Antártida durante el período 1960-1980 (Ainley y Pauly 2014; McBride et al. 2014). La mayor parte de las poblaciones de peces se encuentra actualmente por debajo de su nivel pre-explotación y no se ha recuperado por completo (O'Brien y Crockett 2013). Según Klein et al. (2018) los peces y las ballenas no se verán fuertemente afectados por los efectos del calentamiento en el crecimiento del kril, mientras que los pingüinos parecieron ser los más afectados por estos cambios con una disminución del 30%. Se ha observado una disminución significativa en los pingüinos Adelia y Barbijo dependientes del kril en la PA (Ducklow et al. 2013; Saba et al. 2014), de acorde a las simulaciones que predijeron una disminución (casi agotamiento) para la biomasa de los pingüinos Adelia (Barbijo) en 2100. La pérdida de los pingüinos Adelia y Barbijo, incluso en ausencia de presión pesquera, también fue indicada por otros resultados de modelación (Watters et al. 2013). Por el contrario, la población de pingüinos Papúa, más tolerantes a las dinámicas del hielo, ha aumentado en los últimos años (Ducklow et al. 2013; Henley et al. 2019), lo que también fue indicado por la presente investigación. Otras especies dependientes del hielo y del kril, como la foca cangrejera y la ballena Minke, podrían experimentar una contracción de su hábitat con una transición hacia un clima más marítimo para la PA (Henley et al. 2019). Se predijo un aumento en la biomasa de estas especies durante el escenario más optimista, mientras que se registró una disminución con las proyecciones ssp370 y 585. Las especies tolerantes al hielo y al kril como la ballena jorobada y el lobo fino antártico podrían verse menos afectadas por el cambio climático (Ducklow et al. 2013) y un aumento en su biomasa fue observado bajo todos los escenarios climáticos y pesqueros (Figura 4 de la sección 4.2).

Se espera que la reducción de la cobertura de hielo marino favorezca la productividad de los ecosistemas bentónicos (Henley et al. 2019), lo que podría explicar el aumento en la biomasa de organismos demersales, la relación entra la biomasa demersal y pelágica y favorecer el acoplamiento bentopelágico de la trama trófica. Se observó una disminución en el índice de biodiversidad de Kempton durante todos los escenarios ambientales, mientras que el índice de Shannon reveló un descenso solo con las proyecciones ssp585. Suprenand y

Ainsworth (2017) también evidenciaron una disminución similar en el índice de Kempton para el ecosistema antártico en 2050. A pesar del aislamiento de la Antártida de otros continentes, los patrones de biodiversidad son similares a los del resto del planeta (Chown et al. 2017; Pecl et al. 2017). La variabilidad climática puede afectar la biodiversidad tanto pelágica como bentónica (Griffiths 2010; Chown et al. 2015), aunque se atribuyó una mayor vulnerabilidad a las aguas someras y al ecosistema costero (Rogers et al. 2020).

5.8. Limitaciones del modelo trófico

La ubicación de las fuentes de datos utilizadas para calibrar y desarrollar el modelo trófico sugirió que los resultados obtenidos en este estudio podrían ser representativos solo para el ecosistema costero de la zona 48.1. La zona CCAMLR 48.1 se caracteriza por una fuerte variabilidad espacial en patrones físicos (Stammerjohn et al. 2008; Comiso et al. 2017; Kumar et al. 2021; Santamaría-del-Ángel et al. 2021), biogeoquímicos (Ducklow et al. 2007; Marrani et al. 2008; Schofield et al. 2017; Hendry et al. 2018; Testa et al. 2021) y de niveles tróficos superiores (Weimerskirch et al. 2003; Thiele et al. 2004; Trivelpiece et al. 2011; Ducklow et al. 2013; Murphy et al. 2013).

Se estima que la magnitud del aumento en la biomasa de varios grupos funcionales entre 1996 y 2100 proporcionada por el modelo podría ser exagerada, probablemente debido a una sobreestimación en las proyecciones de clorofila-a. A pesar de la incertidumbre en la magnitud de los incrementos de biomasa, las tendencias de clorofila-a de las proyecciones para 2100 siguen siendo válidas y la evolución temporal observada para diversos grupos funcionales coincide con estudios previamente publicados (Ducklow et al. 2013; Saba et al. 2014; Henley et al. 2019).

La mortalidad causada por la contaminación no se incluyó en el modelo ya que sus efectos en el ecosistema antártico aún no se comprenden completamente. Se han detectado micro, mesoplásticos y partículas de pintura en sedimentos profundos y en la capa superficial del OA (Waller et al. 2017; Lacerda et al. 2019). El zooplancton filtrador podría verse afectado por la ingestión de microplásticos (Li et al. 2016), aunque Dawson et al. (2018) demostraron la capacidad del kril de convertir microplásticos en nanoplásticos a través de la fragmentación digestiva. Esto podría afectar el ecosistema pelágico antártico y los ciclos biogeoquímicos globales debido a un impacto en las mudas del kril y en la exportación de sus partículas fecales (Bergami et al. 2020). Además, el impacto antrópico causado por la acidificación del OA no se incluyó en el presente modelo porque, a pesar de la influencia de la acidificación en los niveles tróficos inferiores (Hancock et al. 2020), su impacto en el ecosistema antártico es estimado ser menor en comparación con aquello causado por el aumento de temperatura (Convey y Peck 2019).

5.9. Retos futuros

Este trabajo proporciona información útil para la futura calibración de modelos biogeoquímicos tanto para el OA como para la zona CCAMLR 48.1. Los resultados de la regionalización biogeoquímica sugirieron la división de la zona 48.1 en dos provincias (la zona de la plataforma continental y el océano profundo) durante futuras parametrizaciones, con la excepción de la parte septentrional de la PA Oriental y la Bahía Margarita debido a las diferentes dinámicas físicas y biogeoquímicas que caracterizan estas regiones (Hyatt et al. 2011; Moffat y Meredith 2018; Siegert et al. 2019). Este estudio identificó las regiones biogeoquímicas más productivas tanto para el OA como para la zona CCMAR 48.1. Esta valiosa información será útil a la hora de desarrollar propuestas para instituir áreas marinas protegidas, aunque se subraya la necesidad de obtener mayor información sobre la variabilidad espacial de niveles tróficos superiores (*i.e.*, zooplancton, zoobentos, peces, aves y mamíferos marinos) para avanzar una propuesta más sólida. Una primera aproximación reveló la existencia de regiones extendidas sin información para estos grupos, remarcando la necesidad de completar esas bases de datos.

Teniendo en cuenta la relevancia de los productos pesqueros entre los servicios ecosistémicos del OA (Nicol et al. 2012; Rogers et al. 2020; Cavanagh et al. 2021), la incertidumbre con respecto a la dinámica del kril en un clima cambiante sugiere imponer un período de veda para las pesquerías de kril como medida de protección (Cheung 2018). Una decisión similar ya ha sido adoptada en 2017 para el ecosistema polar del hemisferio norte (Brooks et al. 2018) y podría ayudar la comprensión de las dinámicas del kril en la PA sin la influencia de las pesquerías. Se considera esta medida política como necesaria debido a que la sobreexplotación secuencial de ballenas, focas y peces durante los últimos 200 años impactó fuertemente la trama trófica antártica e impidió diferenciar el efecto de las pesquerías de la influencia climática (Trivelpiece et al. 2011). Esta medida podría ayudar a contrarrestar los riesgos relacionados con el cambio climático para varias áreas antárticas y reducir la probabilidad de extinción para varios grupos funcionales (Klein et al. 2018; Dahood et al. 2020). El control *bottom-up* de la trama alimentaria antártica evidenciada durante este estudio insta al desarrollo de proyecciones locales de clorofila más precisas, ya que las proyecciones actuales del CMIP6 podrían ser inadecuadas. Además, el control *top-down* sobre la dinámica del ecosistema antártico debería investigarse más a fondo durante futuros estudios de modelación. Para finalizar, se destaca la necesidad de recopilar más datos *in situ* de estaciones permanentes para mejor parametrizar y comprender la variabilidad espaciotemporal de los principales grupos funcionales que constituyen la trama trófica antártica.

6. CONCLUSIONES

Este estudio permitió la identificación de nuevas regiones físicas y biogeoquímicas en el Océano Austral (OA) y en la zona CCAMLR 481 y favoreció la comparación entre ellas. El número de regiones físicas y biogeoquímicas del OA identificadas (12 y 18, respectivamente) fue comparable con estudios previos de ecorregionalización. Las áreas costeras de la Patagonia se fusionaron en un grupo físico significativamente diferente de todos los demás en el OA, mientras que los patrones biogeoquímicos se compartieron con algunas áreas costeras del continente antártico. La combinación entra la batimetría y la cobertura de hielo marino fue la componente que explicó principalmente la variabilidad biogeoquímica en el OA (coeficiente de correlación de rango de Spearman: 0,68). Se identificaron 14 regiones físicas y 16 biogeoquímicas significativas para la zona 48.1 de la CCAMLR y la batimetría fue el principal factor que explicó la variabilidad espacial biogeoquímica (0,81). Los resultados obtenidos sugirieron la división de la zona 48.1 en dos provincias principales separadas por la pendiente de la plataforma durante futuras parametrizaciones del ecosistema, con la exclusión de la parte septentrional de la PA Oriental y la Bahía Margarita debido a la afluencia de aguas del Mar de Weddell y la mayor presencia de hielo marino, respectivamente. La correspondencia entre las regiones físicas y biogeoquímicas fue mayor para la zona CCAMLR 48.1 con respecto al OA, probablemente debido a la menor variabilidad espacial de las variables biogeoquímicas explicada por factores físicos en el OA en comparación con el área CCAMLR 48.1 (60 y 77 %, respectivamente). La regionalización física y biogeoquímica del OA no logró identificar la zona CCAMLR 48.1 como una región estadísticamente diferente, sugiriendo que los límites de la zona 48.1 deberían revisarse siguiendo criterios biogeoquímicos.

Por otro lado, la variabilidad ambiental tuvo un mayor impacto en la trama trófica antártica en 2100 en comparación con la pesquería de kril. A pesar de esto, la falta de parametrización en la variabilidad espacial y estacional de la pesquería de kril podría causar una subestimación de su impacto. Entre las diferentes variables ambientales (*i.e.*, hielo marino, área de aguas libres de hielo y clorofila-a), las fluctuaciones de la clorofila-a parecieron tener el mayor impacto en la variabilidad temporal de la biomasa de los grupos funcionales e indicadores ecosistémicos, sugiriendo un control *bottom-up* en la trama trófica antártica. En 2100 se observó una reestructuración trófica, con una marcada disminución en la población de kril y un aumento de salpas y otros grupos zooplanctónicos. Se detectó también una reducción en los depredadores dependientes del kril y del hielo, como los pingüinos Adelia y Barbijo y la foca cangrejera. A la hora de desarrollar futuras parametrizaciones del ecosistema antártico se estimaron necesarias nuevas proyecciones locales de clorofila-a debido a que las actuales presentan un bajo nivel de confiabilidad.

Esta Tesis proporciona datos útiles para propósitos de parametrización de ecosistemas y manejo de recursos vivos tanto para el OA como para la zona CCAMLR 48.1. Se contribuyó al conocimiento científico identificando los factores físicos que controlan mayormente la variabilidad biogeoquímica en los ecosistemas antárticos y analizando diferencias y similitudes entre los patrones físicos y biogeoquímicos en el OA. Además, se evaluó la sensibilidad de las tramas tróficas antárticas a la variabilidad ambiental y a las pesquerías de kril, indicando los factores que más impactaron la variabilidad temporal de varios grupos funcionales e indicadores ecosistémicos. Para finalizar, se sugirieron posibles escenarios para la trama trófica antártica en el año 2100, identificando las especies más vulnerables y aquellas que se verán favorecidas.

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