

REVIEW

Southern Ocean food-webs and climate change: A short review and future directions

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Abstract

Food-webs are a critical feature of ecosystems and help us understand how communities will respond to climate change. The Southern Ocean is facing rapid and accelerating changes due to climate change. Though having evolved in an isolated and somewhat extreme environment, Southern Ocean biodiversity and food-webs are among the most vulnerable. Here, we review 1) current knowledge on Southern Ocean food-webs; 2) methods to study food-webs; 3) assessment of current and future impacts of climate change on Southern Ocean food-webs; 4) knowledge gaps; and 5) the role of Early Career Researchers (ECRs) in future studies. Most knowledge on Southern Ocean food-webs come from the pelagic environment, both at macro- and microbial levels. Modelling and diet studies of individual species are major contributors to the food-web knowledge. These studies revealed a short food-web, predominantly sustained by Antarctic Krill (*Euphausia superba*). Additionally, alternative pathways exist, involving other krill species, fish, and squid, which play equally important roles in connecting primary producers with top predators. Advantages and disadvantages of several techniques used to study Southern Ocean food-webs were identified, from the classical analyses of stomach contents, scats, or boluses to the most recent approaches such as metabarcoding and trophic-biomarkers. Observations show that climate change can impact the food-web in different ways. As an example, changes to smaller phytoplankton species can lengthen the food-web, increasing assimilation losses and/or changing nutrient cycles. Future studies need to focus on the benthic-dominated food-webs and the benthopelagic coupling. Furthermore, research during the winter season and below the ice-shelves is needed as these areas may play a crucial role in the functioning of this ecosystem. ECRs can play a significant role in advancing the study of Southern Ocean food-webs due to their willingness for interdisciplinary collaboration and proficiency in employing various methodologies, contributing to the construction of high-resolution food-webs.

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Introduction

Food-webs consist of a network of biological interactions that reflect predator-prey interactions in an ecosystem [1]. Food-webs are primarily composed of several food chains, i.e. pathways of energy transfer from primary producers to top predators [2]. These networks are the primary drivers of structure and function in ecosystems [3–5] and do not only influence the population sizes and distributions of organisms [6], but regulate the stability and resilience of the ecosystem. Such regulation can originate from top predators influencing lower trophic levels (i.e. “top-down” [7]), from primary producers (i.e. “bottom-up” [6]), or from mid-trophic level species when an intermediate level of the food-web is dominated by a single species (i.e. “waist-wasp” [8]). Disturbances or alterations targeting a particular species can trigger cascading effects, impacting multiple trophic levels and potentially leading to imbalances that disrupt the entire system [6, 9]. Food-webs provide information on energy flux, nutrient cycling, and the responses of communities to external stressors such as climate change [3, 10]. How a community will cope with these stressors depends on the food-web structure.

The structure of food-webs has been a major focus of ecological studies [11–13]. The number of species, number of links, connectance, modularity, and food chain length (FCL) are important characteristics in determining the structure of food-webs [1, 11, 12, 14, 15]. Among these, FCL is recognized to largely influence community and ecosystem processes, and hence how communities will respond to changes in the environment [10, 12]. Some studies also suggest that the structure of food-webs can be determined only by the predators’ functional traits, such as body size or type of locomotion, and with very few traits, e.g. predator-prey size ratio, it is possible to determine potential predators and preys in a community [16–18]. Under both approaches, the structure of a food-web is highly dependent on biodiversity [5].

The biodiversity of a region is strongly influenced by abiotic and biotic factors [19]. In marine ecosystems, species distributions are mainly defined by water temperature but, on a smaller scale, other habitat characteristics such as productivity, salinity, or substrate, may play a role in determining the presence and abundance of species [5, 20, 21]. Within the distributional range of species, environmental conditions are not homogeneous [22]. Oceanic fronts exemplify this: temperature abruptly decreases southwards of the Antarctic Polar Front, and where the Weddell Front cross the South Sandwich Islands. Consequently, communities in the northern part of the archipelago are typically composed by subantarctic species while those in the south are typically Antarctic species [23–26]. Conditions at border regions are less favourable for the survival and proliferation of species, with individuals inhabiting these areas being more susceptible to environmental change [27, 28]. This influence of abiotic factors indicates that both species and food-webs are vulnerable to climate change [3, 29, 30]. For instance, the poleward movement of temperate generalist predators is redefining predator-prey interactions in Arctic food-webs [14].

Climate change serves as a primary catalyst for changes in marine ecosystems with shifts in environmental conditions having profound repercussions on biodiversity and food-webs [31–33]. From the surface to the deep-sea, warming, freshening, acidification, and alterations in productivity and circulation patterns are being observed throughout the world’s oceans [31, 34, 35]. Predicting the effects of climate change on individual species is relatively simpler compared to projecting consequences on the entire structure of a food-web [29, 36]. The complexity arises from the involvement of a broader array of variables, encompassing multi-trophic level effects, species-species interactions, and responses to changes in habitat, all of which collectively shape the overarching response of the community [3, 14, 37]. Changes in prey energetic value, predator-prey ratios, or phytoplankton communities that alter the FCL (e.g. changes to smaller phytoplankton species increase the FLC due to the introduction of

heterotrophic phytoplankton) are examples of shifts in food-webs due to climate change [34, 38, 39]. However, climate change impacts are not uniform in all food-webs. Those with higher connectance and low modularity are more resistant than those with lower connectance and high modularity [5, 14, 30]. For example, the loss of one prey in a food-web with high modularity can lead to cascade effects but these are contained to a specific module where that prey species is; if a first consumer species is prey of just one predator that is consequently prey of a top predator (low connectance), the loss of the first consumer species will only affect that predator and its respective top predator; in contrast, if a species is a prey of different predators and one predator has different prey species (especially mesoconsumers; high connectance), if the prey species is impacted by climate change this will cascade through several food chains in that food-web and impact a wider number of top predators [5, 14, 30]. The Southern Ocean is one of the regions changing faster due to climate change and impacts on ecosystems within this region have already been documented [40–42].

Early Career Researchers (ECRs), defined here as researchers within five years of completing their last degree, can play a major role in marine science, including the Southern Ocean [43, 44]. Incorporating ECRs in research teams and involving them in large international initiatives can benefit both the ECRs (e.g. providing unique opportunities to network, develop communication skills, and foster wider collaborations) and the teams and initiatives themselves [43]. The involvement of ECRs in scientific projects increases, for example, the diversity of teams, new ideas, and perspectives, which are important to increase the work quality [43, 45–47]. Recently, ECRs have been involved in polar and climate change science at several levels, for example, the Marine Ecosystem Assessment for the Southern Ocean (MEASO) had the involvement of 203 scientists of which 30% were ECRs [43, 48]; ECRs participated in the review of the Intergovernmental Panel on Climate Change (IPPC) Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC; [49]) and the Sixth Assessment Report (AR6; [50]) as a group review [51, 52]. More recently, a delegation of ECRs from the Association of Polar Early Career Scientists (APECS) participated in the United Nations Climate Change Conference (COP 28). Besides these contributions, ECRs have the capacity to deliver the best possible science, including in food-web studies, as they have, among others, the potential for cross-disciplinary, cross-generational, and international collaboration necessary in this research topic.

This review aims to: 1) assess the state of knowledge on Southern Ocean food-webs; 2) discuss available techniques that can improve our understanding of Southern Ocean predator-prey interactions and the structure of Southern Ocean food-webs; 3) assess possible impacts of climate change in Southern Ocean food-webs; 4) discuss possible future directions of food-web research in the Southern Ocean; and 5) explore the roles of ECRs in this discipline.

Southern Ocean food-webs

Southern Ocean (here considered as south of the Antarctic Polar Front (Fig 1)) food-webs were traditionally presented as short and dominated by an Antarctic krill (*Euphausia superba*) surplus that supports the predators of the region (Fig 1) [53, 54]. However, this long-standing hypothesis has been deconstructed over the last decades, with several studies showing alternative pathways where other krill species, fish, and cephalopods play a major role in linking primary producers to higher trophic levels (Fig 1) [e.g. 55–60]. Furthermore, studies suggest that Salps (*Salpa thompsoni*) constitute an alternative prey to Antarctic krill, but likely in different locations of the Southern Ocean [61]. Despite the existence of these alternative pathways, Antarctic krill remain widely accepted as an essential species in Southern Ocean ecosystems, with

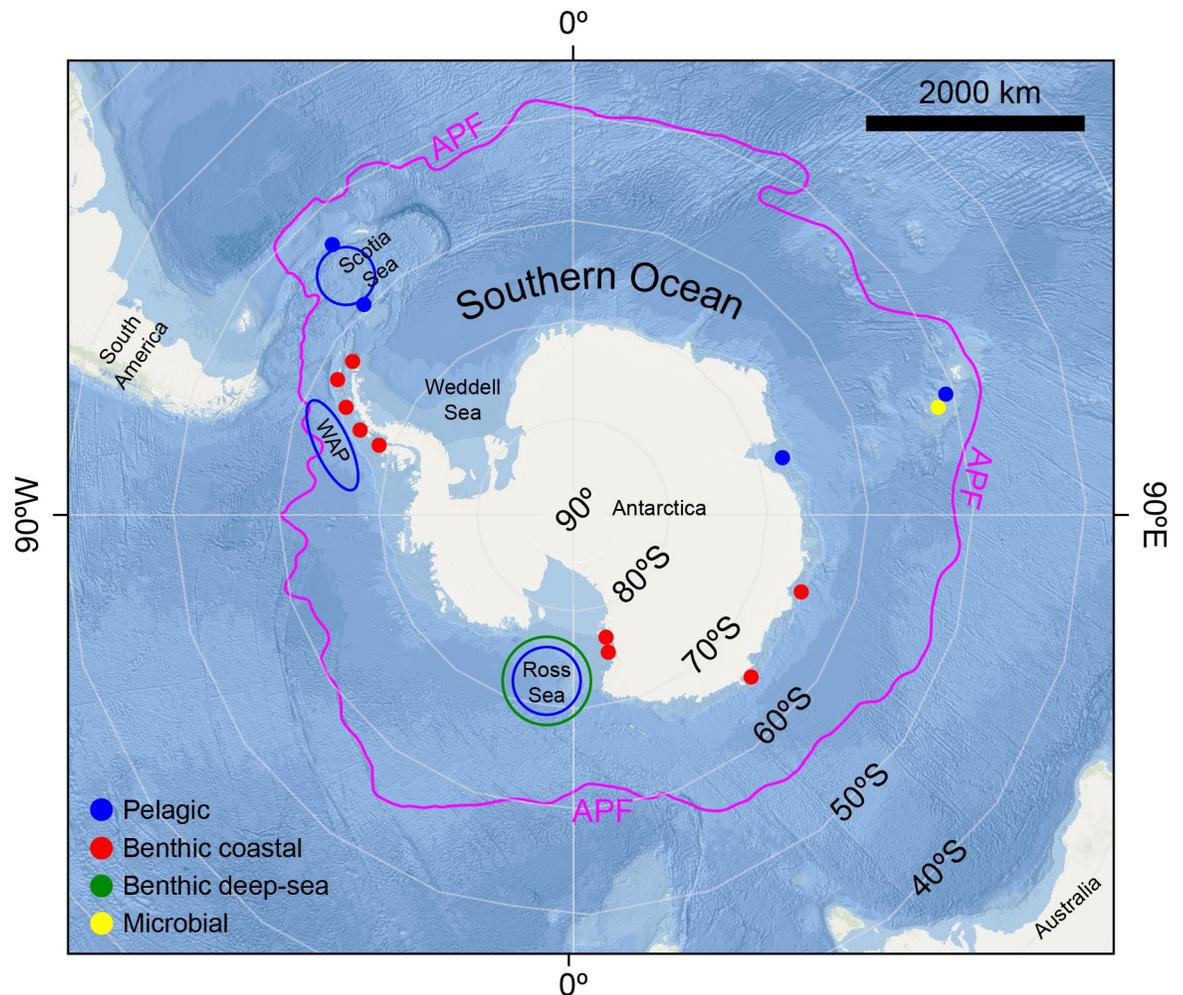


Fig 1. Southern Ocean and the Antarctic Polar Front (APF). Full circles show locations where previous studies analysed the food-web (e.g. Fildes Bay); Empty circles show the location of general studies, i.e. studies analysing the food-web of an entire region (e.g. Ross Sea). Colour code shows the different types of food-webs. WAP: Western Antarctic Peninsula. Map was produced using QGIS 3.20 Odense. Basemap is the “ESRI Ocean Basemap” [65].

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changes in its dynamics and/or biomass having profound impacts on the functioning of these ecosystems [62–64].

Santana et al. [66] showed that Southern Ocean food-webs follow a pyramid shape with higher numbers of basal species than top predators. Approximately 40% of species in these food-webs are omnivorous, spanning up to three trophic levels [66]. However, percentage of omnivory can vary between food-webs in the Southern Ocean, e.g. the East Antarctic food-web presents lower omnivory ($\approx 26\%$) than the food-web in the West Antarctic ($\approx 48\%$) [66]. In addition, several prey species have the same predators, and *vice-versa*, i.e. high connectance, suggesting high vulnerability and generality of the food-web [5, 14, 30, 66]. Southern Ocean food-webs are structured by both top-down and bottom-up effects [39, 63, 67], and display seasonal effects, such as decreased connectance in response to yearly thawing [59, 60, 68]. However, *in-situ* studies examining the entire food-webs and their structure remain scarce. The few existing studies mostly focus on the West Antarctic Peninsula, Scotia Sea and

Subantarctic Islands [e.g. 69–72]. Furthermore, with few exceptions [e.g. 66, 71, 72], the topological features, e.g. connectance, modularity, of the Southern Ocean food-webs remain poorly studied.

Most studies of the Southern Ocean food-web have focused on the pelagic environment (Fig 1). For example, Murphy et al. [73] compared the West Antarctic Peninsula and South Georgia ecosystems, focusing on the pelagic food-web and its interaction with land-based predators. This study showed that, despite the contrasting biodiversity and seasonality, the structure of food-webs at both locations is similar, with Antarctic krill playing a pivotal role in both ecosystems. However, the presence of different predators and plankton species (linked to the winter sea-ice in the Western Antarctic Peninsula) support varying energy pathways between both systems [73]. Stowasser et al. [69], using stable isotopes, studied the pelagic food-web of the Scotia Sea. This study revealed a short food-web, but the presence of tertiary consumers such as myctophids *Gymnoscopelus nicholsi* and *Protomyctophum bolini* provides evidence of alternative pathways [69]. Also at the Scotia Sea, López-López et al. [72] compiled a database of trophic interactions to study the pelagic food-web in the northern (near South Georgia) and southern (near South Orkney) areas of this sea. This study identified multiple pathways in the food-web, with differences between both areas, i.e. the North has a more complex food-web than the South, with higher number of species, connectance, and clusters. Furthermore, it shows an influence of depth in the food-web, with the mean trophic position being higher in species inhabiting deeper areas [72].

Coastal benthic food-webs have been studied in different locations through the Southern Ocean but primarily focusing on the Western Antarctic Peninsula [74–80]. Marina et al. [71] studied the food-web structure of Potter Cove at King George Island, showing a short food-web, and low link density, connectance, percentage of omnivores and clustering coefficient. Using stable isotopes, Rossi et al. [74] showed that the sea-ice has an influence on the structure of food-webs at Terra Nova Bay (Ross Sea) due to the release of sympagic material. After the seasonal sea-ice breakup, food-webs become less complex, with lower number of species and link density [74]. A similar influence of sea-ice was found for Tethys Bay (Ross Sea) by Caputi et al. [79], with a shortening of food-web after the seasonal sea-ice breakup. Michel et al. [77] had the opportunity to study food-web structure at Adélie Land during two anomalous years when the sea-ice did not break. Invertebrates would change their diet in response to the continuous sea-ice cover and the consequent non-release of sympagic material [77]. Cardona et al. [75] studied coastal benthic food-webs at five locations along the Western Antarctic Peninsula and found that sea-ice partially determine the differences on food-web structures across the five locations, though the main influence came from the intensity of the phytoplankton bloom in the spring/summer. This study also found that, despite the great latitudinal range (from 62 to 67 °S), food-web structure was similar between locations [75]. Gillies et al. [76] at Windmill Islands (East Antarctica) and Zenteno et al. [78] at Fildes Bay (King George Island) showed that Antarctic coastal benthic food-webs can have different carbon pathways such as pelagic particulate organic matter, benthic organic matter and macroalgae. All these coastal benthic food-webs presented three to four trophic levels, with food-webs not including fish being shorter (three trophic levels) than those including, at least, one fish species showing that fish is the top predator of these food-webs [75–80]. Some of these results, i.e. both pelagic and coastal benthic food-webs, contrast with those of Santana et al. [66] and support variability across different Southern Ocean food-webs.

The microbial food-web is mainly controlled by top-down regulation, with dinoflagellate production driving the dynamics of smaller phytoplankton and heterotrophic nanoflagellates, which ultimately influence the bacterial community [81–83]. These studies also showed that microbial communities respond to bottom-up effects such as iron inputs, and present strong

seasonal patterns being less efficient in the spring (higher respiration rates) and summer (higher viral lysis in warmer waters) [82, 83]. These variations influence the response of higher trophic levels. Regarding the demersal/benthic-dominated food-webs in the deep-sea, very little information exists. Pinkerton and Bradford-Grieve [84] modelled a food-web for the Ross Sea which includes a benthic/demersal component, showing a connection with the pelagic component *via* demersal fish feeding on pelagic organisms like squid. This study showed that large demersal fish can occupy trophic levels as high as toothed whales [84]. Furthermore, studies on the diet of demersal top predators such as the Antarctic toothfish (*Dissostichus mawsoni*) gave us some information on trophic interactions near the bottom of the ocean [e.g. 85–87], though a lot of information is still needed for deep-sea ecosystems (Fig 2). Similarly, a total lack of knowledge exists about the food-web below ice-shelves (Fig 2). Aside from studies analysing the entire food-web, knowledge on Southern Ocean food-webs and trophic interactions is advancing through studies analysing the diet and trophic relations (using a wide variety of techniques) of specific species, e.g. seabirds [e.g. 88, 89], marine mammals [e.g. 90–93], fish [e.g. 86, 87], cephalopods [e.g. 94–96], crustaceans [e.g. 97, 98], and others.

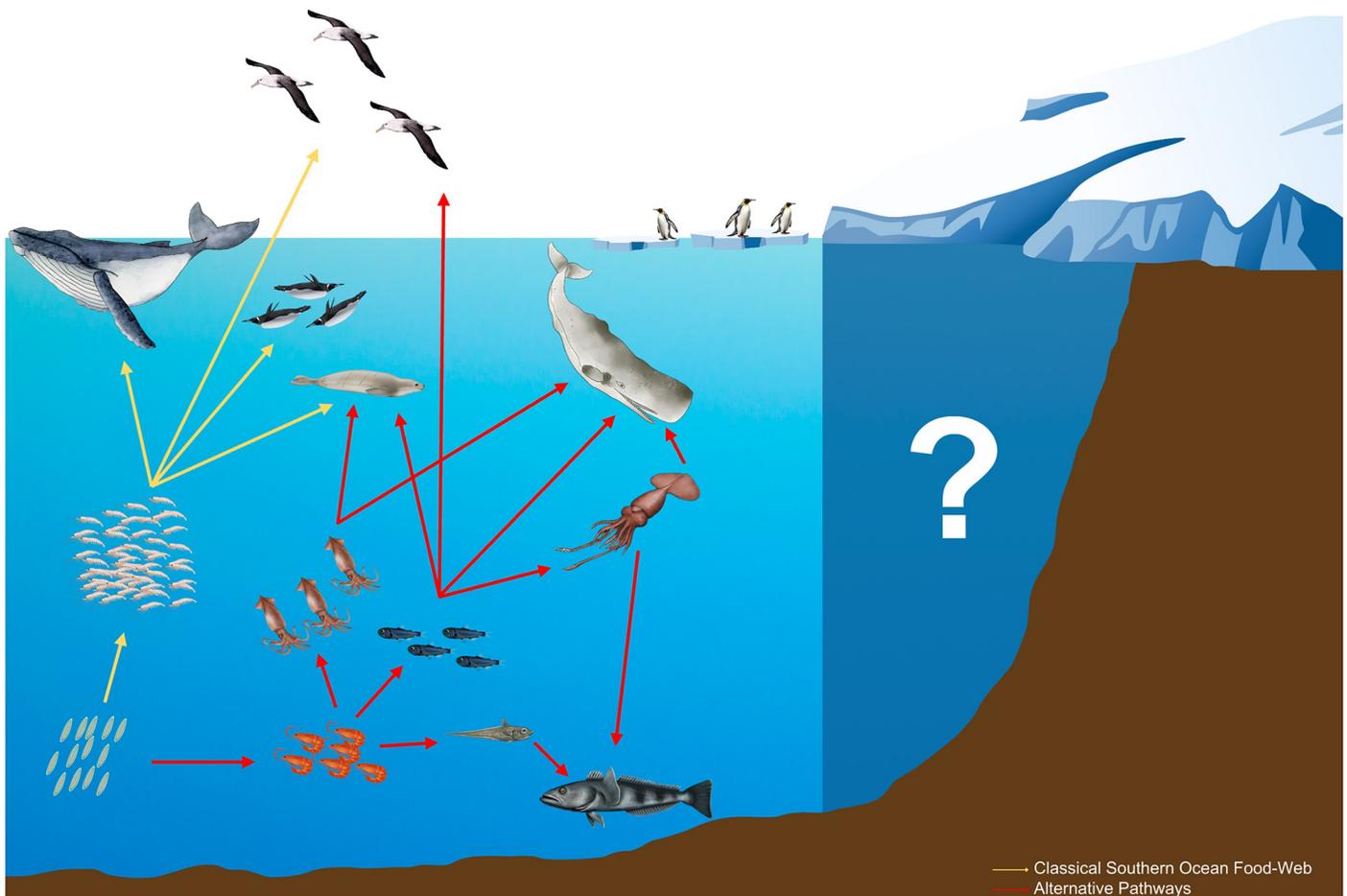


Fig 2. Illustration of Southern Ocean food-web different pathways. Yellow arrows show the long standing short, krill-dominated pathway while red arrows show alternative, but equally important, pathways with other krill, fish, and squid as major links between primary producers and higher-level predators. Myctophid and toothfish drew by Tom Langbehn.

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How to study Southern Ocean food-webs

There are several methodologies for studying marine food-webs worldwide, including those of the Southern Ocean. Advantages and limitations arise when considering each methodology (Table 1). Their advantages and limitations are, with few exceptions like the barometric associated trauma in deep-sea organisms that do not apply to coastal and surface ecosystems, common to all marine ecosystems. However, the remoteness of Southern Ocean implies bigger constraints and specific limitations to the use of some methodologies compared to other regions of the world, especially during the winter due to sea-ice [24]. Furthermore, despite recent efforts [99, 100], knowledge on the Southern Ocean biodiversity (especially in the deep-sea) remains scarce, thus classical taxonomic identification to define trophic interactions may not be sufficient [101–103]. Therefore, alternative methodologies to study trophic interactions such as DNA metabarcoding, trophic biomarkers or biologging present higher usefulness for Southern Ocean food-web studies in comparison to other regions of the World's Ocean.

Historically, research on food-webs and trophic ecology of Southern Ocean species has primarily relied on the examination of stomach contents of predators [e.g. 104, 105]. This methodology has the advantage of being a direct observation of the predator-prey interaction and often allows for the identification of prey species [106, 107]. However, it only gives a snapshot

Table 1. Summary of the advantages and limitations of different methodologies used to study Southern Ocean food-webs. Studies presented are examples of applying the different methodology to study the entire food-web, the diet and/or trophic ecology of Southern Ocean ecosystems and species (and in some cases from the Patagonian shelf).

| Methodology | Advantages | Limitations | Studies applying the methodology |
|--|--|--|--|
| Stomach contents/Scats/ Boluses | <ul style="list-style-type: none"> • Allow prey identification • Low cost (except for sample collection) • Non-invasive methodology (scats and boluses) • Allow to determine the numerical and mass importance of prey | <ul style="list-style-type: none"> • Snapshot of last feeding event • Digestion state influence the prey identification • Results biased towards taxa with hard structures • Requires high number of samples | [85, 86, 89, 90, 97, 104, 105, 109, 110, 174] |
| Metabarcoding | <ul style="list-style-type: none"> • Allow identification of soft body prey, cryptic interactions, and minor prey group • Can be applied into non-invasive diet samples (scats and boluses) | <ul style="list-style-type: none"> • Dependent on the primer choice and design • Relatively expensive | [87, 88, 114, 116, 121–124] |
| Bulk Stable Isotopic Analyses (SIA) | <ul style="list-style-type: none"> • Provide information on the foraging area and trophic level • Requires low amount of sample (<1 mg) | <ul style="list-style-type: none"> • Preclude identification of prey to species level • Requires baseline information • Trophic enrichment factor required to properly access trophic level | [69, 74–78, 86, 91, 93, 95, 96, 98, 132, 133, 175] |
| Fatty Acids (FA) | <ul style="list-style-type: none"> • Qualitative and quantitative information on the diet • High number of variables that increase likelihood of describing prey-specific diet and trophic level | <ul style="list-style-type: none"> • Requires prey fatty acid profile | [136, 141, 176–179] |
| Compound Specific SIA in Amino Acids (CSIA-AA) and Fatty Acids (CSIA-FA) | <ul style="list-style-type: none"> • Similar information to bulk SIA and FA • Does not require baseline information | <ul style="list-style-type: none"> • Trophic discrimination factor is necessary and depend on the species and location • More expensive than bulk analysis | [96, 148, 152, 153] |
| Biologging | <ul style="list-style-type: none"> • Allow description of feeding behaviour and habitat • Detect prey capture moments • Can be used to detect trophic interactions during the winter | <ul style="list-style-type: none"> • Requires extra devices to determine the prey species (e.g. video cameras) • Some technologies are still under development • Limited by the size of the animal | [90, 92, 162–169] |

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of the recent feeding events, the digestion state may preclude the prey's identification, results are biased towards prey with hard indigestible structures, e.g. fish otoliths or cephalopod beaks, and it requires a high number of samples, especially if the predator tends to regurgitate upon capture [107, 108]. Furthermore, it demands, for some predators such as fish, the capture and sacrifice of the animal. Alternative, less invasive techniques such as the visual analyses of scats (mammals) or boluses (birds) are still used as a direct observation of the diet of high-trophic level predators [e.g. 109, 110].

Metabarcoding is another method commonly used to study the diet of organisms and can overcome the bias towards prey with hard structures from stomach content analyses [111, 112]. It has been successfully applied to many species such as seabirds and marine mammals with a wide range of dietary habits [113–116]. This method combines the use of Next Generation Sequencing (NGS) with DNA metabarcoding and can be used in different types of samples, e.g. faeces, cloacal swab, intestinal fluid etc. [117, 118]. This process performs selective amplification of small target regions from genomes that contain a combination of highly conserved and highly variable elements [119]. Metabarcoding allows the detection of highly resolved food-web linkages, having the capacity to detect soft-bodied and cryptic interactions [120], overlooked by other methods relying on hard part remains. DNA metabarcoding is becoming an increasingly prevalent method for identifying species interactions in the Southern Ocean [e.g. 88, 116, 121–125]. However, the level of resolution and accuracy of data obtained from DNA metabarcoding is highly dependent on primer choice and design [113]. Certain markers provide high taxonomic coverage but low resolution (e.g. universal marker targeting the 18S rRNA gene), whilst group-specific markers can identify targeted prey to species level (e.g. marker targeting a 12S rRNA, 16S rRNA, or cytochrome *c* oxidase *I* genes) [126–130]. A combination of both universal and group-specific markers can provide a comprehensive overview of a species' diet [125]. This approach allows for the preservation of species resolution for targeted prey, whilst also identifying minor prey groups [129].

Trophic biomarkers have been used to overcome some of the disadvantages found in conventional techniques and have the advantage of integrating dietary information over longer time scales, dependent on tissue turnover rate [131]. In recent decades, bulk stable isotope analyses (SIA) have been widely used in species-specific dietary studies, and more broadly to glean insights into trophic structures and food-webs [e.g. 69, 132, 133]. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopes are the most used and provide information on the source of the food-web and the trophic level of an organism, respectively [134, 135]. Similarly, fatty acid composition analyses provide valuable information of a species' diet [136–138]. Synthesis of some fatty acids is restricted to lower trophic levels and are minimally modified when transferred to higher trophic levels [138]. This allows both qualitative and quantitative prey assessment by directly analysing the predators' fatty acids [136, 139–141]. When compared to SIA, the advantage of fatty acid analyses is the number of variables used to predict the prey captured. To describe diet, SIA is usually based on two variables, i.e. carbon and nitrogen. This often limits the analysis to a certain number of food sources that can be considered for diet tracing or to a description of the trophic position rather than determining the exact prey species [142, 143]. In contrast, the wide number of fatty acids that are transferred from prey to predators increases the probability of identifying the specific prey and even quantifying the proportion of each prey more accurately [141, 144]. Regardless of their use, both SIA and fatty acids are limited by the baseline prey information available. SIA requires the baseline value for the isotope in the study area (i.e. by analysing organic matter), and in both SIA and fatty acid the correct assessment of prey species is not possible without the preys' isotopic or fatty acid signature [141, 145, 146].

Some of these caveats can be overcome by Compound Specific Stable Isotopes Analysis of Amino Acids (CSIA-AA) or Fatty Acids (CSIA-FA), which allows the assessment of more complex food-webs. Compared with SIA, a larger number of markers can be used in CSIA, increasing the tracing power [147]. Succinctly, in CSIA-AA, some amino acids are incorporated directly from the food into an animal's tissue without undergoing metabolic changes (e.g. source amino acids), while others undergo biochemical transformations after consumption (e.g. trophic amino acids), thereby simultaneously providing insights into the isotopic baseline, an animal's physiology, and its diet [148–150]. This method enables the disentanglement of the effects of primary production sources from trophic effects without the need to sample the food-web's baseline, and the tracking of nutrient and energy flow, providing more accurate trophic position estimation [149–151]. CSIA-AA is particularly valuable for studying the trophic ecology of organisms and food-web structure at broad spatial and temporal scales in the Southern Ocean, making it especially relevant for migratory species like birds, seals, and whales, and when comparing communities from different Southern Ocean basins [96, 152, 153].

CSIA-FA is commonly used in aquatic systems to quantify consumers' reliance on food sources from different habitats (e.g. ice algae [154]). Similar to amino acids, fatty acids also undergo modifications with trophic transfer, but specific fatty acids cannot be synthesised by marine predators and can hence be used as biomarkers of their source [155]. These group-specific biomarkers can be measured in mixed samples without physical separation [155]. One limitation of CSIA-AA, CSIA-FA, and bulk SIA to assess the trophic level of an organism is the determination of the Trophic Discrimination Factor (TDF for CSIA) and Trophic Enrichment Factor (TEF for SIA), which refers to the difference of $\delta^{15}\text{N}$ values between a predator and its prey. For SIA the most accepted, and commonly used, TEF is $\sim 3.4\text{‰}$ [69, 156–158], though recent studies suggest that this value changes according to the trophic position (the higher the trophic position, the lower the TEF) and the study region [159]. The most used TDF value is 7.6‰ though no studies have evaluated if this value changes with trophic position, region, or taxa [150].

Furthermore, newly developed technologies give us the possibility of tracking, describing, and quantifying the foraging ecology of marine megafauna (i.e. Biologging), providing a unique opportunity to identify predator-prey interactions in remote and isolated regions like the Southern Ocean [reviewed in 160]. Because biologgers can be deployed and record data for several months, this technique can be useful to characterize trophic interactions also during Winter [161]. Devices such as Time Depth Recorders (TDRs) and accelerometers allow for the description of the diving behaviour of many Antarctic predators as well as the identification of prey items by recording capture events [e.g. 92, 162]. However, identifying and validating the actual prey species remains a challenge. Nowadays, behavioural descriptive devices are often used with additional instruments that provide direct information about the prey consumed, such as stomach sensors [e.g. 163, 164], beak openings characteristics [e.g. 165], sonar tags [e.g. 166], and/or video cameras [e.g. 167–169]. Although each instrument has its own limitations, the rapid development of more accurate, self-sufficient, and long-lasting technologies will certainly prove to be advantageous in refining our understanding of predator roles in Southern Ocean food-webs.

Food-web modelling

Food-web modelling is another valuable tool for studying Southern Ocean food-webs and assessing the effects of climate change [59, 61, 66, 68, 71]. Different modelling approaches exist such as qualitative models that represent the current knowledge on food-webs and can focus on a specific predator, directly evaluating the predator-prey interactions, e.g. if prey

populations change how the predators are affected [e.g. 170]); ecological network models that can evaluate impacts of external stressors such as climate change in the food-web, e.g. evaluate the impact of local extinctions in the structure of the food-web [e.g. 171]; modelling key species and trophic interactions which have been used to test regional and seasonal differences in food-webs across the Southern Ocean [e.g. 68]; and whole food-web models which models the entire food-web, from primary producers to top predators and can be used to study, for example, cascading effects arising from climate change or other external stressors such as fisheries [e.g. 84]. Despite a powerful methodology, models demand sufficient and reliable data on the diet of the different species, the structure and functioning of the food-web, but also the dynamics of the entire ecosystem [172, 173].

Climate change: A threat to Southern Ocean food-webs

The Southern Ocean is characterised by extreme oceanographic features such as cold temperatures, strong seasonality (e.g. formation of winter sea-ice), and distinct thermal fronts which act as boundary zones, including the strongest and fastest current in the world, the Antarctic Circumpolar Current [180–182]. These unique features have largely isolated the Southern Ocean and its biota, with species evolving unique phenotypes and physiological adaptations [183, 184]. This relatively isolated evolutionary process is reflected in the high levels of endemism ($\approx 97\%$ of all species) [24, 184, 185]. However, being highly adapted to this environment, Southern Ocean species are among the most vulnerable to climate change [41, 186, 187]. Consequently, Southern Ocean food-webs are also vulnerable to climate change [66, 184].

The Southern Ocean is rapidly changing in response to climate change [188]. This ocean dominates the global ocean uptake of anthropogenic CO_2 and heat [41, 189, 190]. This buffer role is leading to profound physical changes, including, *inter alia*, rapidly increasing sea temperatures, decreasing salinity and pH, spatial and temporal variability in sea-ice thickness and extent, changes in ocean circulation and even a poleward shift of oceanic fronts [41, 181, 186, 191]. These oceanographic changes increase the probability of invasion by non-native species and affect the primary production across the Southern Ocean [48, 49, 190, 192, 193]. However, the impacts of climate change differ among regions, with some areas being more affected than others, for example, the Western Antarctic Peninsula and the Scotia Sea are changing faster than elsewhere in the Southern Ocean [42, 48, 49, 194–197].

Although Southern Ocean ecosystems are unique in many aspects, the impact of climate change on the structure of food-webs may be similar to those in other regions, e.g. redistribution of species leading to novel interactions [32]; changes in phytoplankton diversity, densities and phenology will affect the structure of the food-webs [38, 198]; and the loss of species in a community can alter food-web structures [30].

In the Southern Ocean, there is a notable shift in phytoplankton communities, characterized by the replacement of large diatoms with smaller species such as cryptophytes, nanoflagellates, and other varieties of phytoplankton [82, 199]. Furthermore, shifts in the life cycle of phytoplankton, such as changes in the seasonality of phytoplankton blooms due to the early-sea ice retreat, may generate desynchrony with the dependent species which will highly influence the food-web [198]. For example, Antarctic krill larvae rely on sea-ice algae to survive and reach adult life-stages; changes in the seasonality of sea-ice affect the life cycle of algae which will, consequently, impact Antarctic krill survival and all trophic levels above [200]. Aside from changes in the phytoplankton diversity and phenology, enhancement of primary production due to increasing temperatures, reduction of sea-ice cover, iron fertilisation from glacier melting, and changes in water stratification and wind patterns [29, 201, 202] are some of the clear developments attributed to climate change during the last 20 years [165, 167]. For

example, the number of large icebergs releasing from the Antarctic ice sheet is increasing [203]; while melting these icebergs release into the water nutrients and trace elements, including iron, that enhance productivity in the Southern Ocean [201, 204]. These shifts will cascade through food-webs, changing the carbon supply to higher trophic levels, the amount of carbon reaching the deep-sea which will affect benthic-dominated food-webs and the benthopelagic coupling (e.g. changes in the amount of particulate organic matter reaching the seafloor due to changes in the phytoplankton community at the surface will affect benthic species that depend on this food source and, consequently, impact pelagic predators feeding on these benthic organisms), and increasing assimilation losses (e.g. on average, only 10% of the energy of a prey is transferred to its predator, and thus increasing the length of the food chain with more intermediate consumers will decrease the amount of energy transferred to the top predator) [34, 205].

In some Southern Ocean regions, sea warming is driving an important shift in the Antarctic pelagic community composition from Antarctic krill to Salps, potentially affecting pelagic food-webs and especially Antarctic krill predators [62, 206]. In response to this phenomenon, some predators can change their diet in years of poor Antarctic krill availability. This is the case for Antarctic fur seals (*Arctocephalus gazella*) at South Georgia that feed on *Slosarczykovia circumantarctica* when krill is not abundant [109]. Indeed, modelling studies suggest that because of climate change, the keystone value of cephalopods and fish might be higher than Antarctic krill in ecosystems where krill is currently the keystone species [59]. The existence of these alternative pathways may buffer ecosystems from the impacts of climate change [59]. However, these alternative pathways result in longer food chains in comparison to the typical three trophic-level, krill-dominated food-webs [e.g. 55, 56, 69, 207]. This can, ultimately, affect entire ecosystems by altering major ecosystem processes like nutrient and carbon cycles [12]. Nonetheless, further research is needed to assess the long-term effect of transitioning to these alternative pathways over species typically involved in the short, krill-dominated pathway [42, 48].

Another common climate change-related threat is the increasing frequency and intensity of extreme weather events in the Southern Ocean during the last few decades [208]. This includes, *inter alia*, marine heat waves, years of extremely low sea-ice extent, and accelerated loss of ice shelves (through more frequent loss of larger icebergs), all of which are anticipated to affect the Southern Ocean biodiversity and food-webs [208]. Large icebergs scour benthic habitats, decimating respective communities, and melt in the open ocean, fertilising these areas with nutrients [208, 209]. Food-webs are influenced by iceberg scouring in two principal ways: (1) proliferation of species with rapid colonisation rates; and (2) introduction of nutrients like iron from melting icebergs resulting in phytoplankton blooms [201, 208, 210]. On the other hand, marine heat waves lead to breeding failures of some predators, e.g. Adelie penguin (*Pygoscelis adeliae*), but they also impact the structure of phytoplankton communities [208, 211]. A previous study noted an increase in productivity during a marine heat wave in Potter Cove (King George Island), with increased mortality of diatoms, changes in the phytoplankton community, and physiological consequences, damage, and changes in their lipid composition [211]. Changes in the lipid composition of primary producers likely influence grazer communities, which cascade to higher trophic levels [186, 211].

The reduction of sea-ice and ice-shelves due to ocean warming can also alter the structure of food-webs. Newly ice-free areas and the shrinking of ice-shelves will increase inter-species competition for penguins as they switch from Ice krill (*E. cristallorophias*) to Antarctic silverfish (*Pleuragramma antarcticum*) which is a major prey of seals, fish, and seabirds [212, 213]. Furthermore, the reduction of sea-ice will impact the early life-stages of Antarctic krill and Antarctic silverfish, which through their major role as mid-trophic level species, will impact top predators in the region by changes in prey density, increasing competition for fewer

resources, resulting in changes in their foraging area and, to some extent, altering their diets [63, 109, 214]. In addition, early sea-ice loss is linked to an earlier sea-ice algae bloom which can result in a desynchronization of species-dependent processes. For instance, penguins and seals that rely on ice for reproduction, and several krill species, which depend on early seasonal sea-ice algae biomass, are being affected [215]. This desynchronization can trigger cascading effects throughout entire food-webs [200].

While climate change is anticipated to have significant detrimental impacts on many Southern Ocean species (i.e. “the losers”), it is important to bear in mind that some species and/or populations are likely to benefit from climate change (i.e. “the winners”) [216, 217]. For example, the poleward shift of the Antarctic Circumpolar Current may be detrimental for populations of King penguins (*Aptenodytes patagonicus*) at the Crozet Islands but benefit those at South Georgia [218]. Similarly, the number of Adelie penguins on Beaufort Island has increased in response to the expansion of available breeding habitat by an increase in ice-free areas due to glacier-retreat [219]. At the Antarctic Peninsula, populations of both Adelie and Chinstrap (*P. antarctica*) penguins are decreasing because of either lower availability of Antarctic krill and Antarctic silverfish or snow accumulation and increased melt-water run-off [216]. In contrast, Gentoo penguins (*Pygoscelis papua*) seem to benefit from the changing environment at the Antarctic Peninsula [216]. Population growth and range expansion of climate “winners” will affect food-webs differently depending on their trophic level. For example, increased availability or introduction of new prey species, i.e. non-native species dispersing southwards, will likely benefit generalist predators with broad ecological niches or, at least, mitigate the effects of declines in their traditional prey, because generalist predators feed on what is available thus new prey will increase the range of prey, whilst range expansions of generalist predators into new areas may be detrimental to lower trophic levels [182, 205].

These and other impacts of climate change in food-webs, directly or indirectly through impacts on individual species, will magnify the consequences of climate change on Southern Ocean biota [41, 186, 205]. Southward range expansions of species from northern territories may act as a vector of new diseases like the high pathogenic Avian Influenza H5N1 [220]. Changes in the structure of food-webs towards a longer food chain length will increase the concentration, bioavailability and biomagnification of metals [207], and increase the assimilation loss with top predators needing to feed on more prey to obtain the same amount of energy [38]. Novel interactions and the disappearance of some species can ultimately lead to a decrease in abundance and changes in the distribution of some species [186, 190, 218]. The cumulative impacts of climate change on organisms and changes in the structure of communities will ultimately increase the vulnerability of Southern Ocean biodiversity [186, 218, 221, 222]. Therefore, we may expect that Southern Ocean food-webs will differ in the future from what we know now.

Future directions for the study of Southern Ocean food-webs

Our knowledge of Southern Ocean food-webs has significantly improved over the last decade. However, several knowledge gaps, such as the topological features of these food-webs, persist. Topological features influence the response of communities to climate change [1, 13], therefore it is crucial that future studies, using visual predator-prey interactions or stomach contents (when possible), analyse these characteristics. Furthermore, previous studies analysing both macro- and microbial food-webs, have mostly focused on pelagic and coastal environments [e.g. 58, 69, 73, 74, 79, 80, 82, 84]. Consequently, there is a paucity of information on the structure of deep-sea benthic-dominated food-webs, including the important benthopelagic coupling [223, 224]. Future research should also focus on these deep-sea benthic food-web structures given their role in structuring deep-sea ecosystems and in the nutrient and carbon

cycles. The lack of understanding of these food-web structures limits our ability to predict the response of deep-sea communities to climate change [34, 224]. Furthermore, there is a paucity of information on food-webs below ice-shelves and during winter (including the pelagic). This assumes greater importance when new habitats, e.g. hard-substrate communities under the ice [225], or communities/aggregates, e.g. icefish colonies beneath the ice [226], are discovered. Many of these gaps exist because of the inaccessibility to some areas of the Southern Ocean, e.g. below ice-shelves or winter sea-ice, but also by high logistical operational costs [24]. The development of new technologies that allow sampling in these areas, e.g. autonomous underwater vehicles that collect samples and data for several months without the need to return to the surface and can thus operate below the sea-ice during the winter months, may be a crucial step forward to improve our knowledge on Southern Ocean food-webs.

Previous studies also showed that food-web structures vary seasonally, with different food-web structures during the sea-ice period and post sea-ice breakup [e.g. 74, 79], and regionally [59, 60, 68]. These studies showed that the Antarctic krill-dominated food-web is the predominant pathway in the Atlantic and East Pacific sectors, as well as in the Antarctic region of the East Indian and Indian sectors, while in the West Pacific sector a mesopelagic fish pathway dominates, and a cephalopod and mesopelagic fish pathways are the most common in the subantarctic islands of the East Indian and Indian sectors [59, 61, 68, 69, 73, 172]. Seasonal variation of food-web structures, mostly in response to changes in environmental conditions like sea-ice, highlights the importance of studies to understand how food-web structures are influenced by the environment. Furthermore, it is important to study if the different regional structures of the food-web are driven by different environmental conditions in different locations and evaluate if interannual environmental changes in one location may influence the structure of food-webs [227].

The phytoplankton community has a direct influence on structuring marine food-webs, e.g. smaller phytoplankton are present in longer food chains [12, 38]. Previous studies showed that climate change will impact Southern Ocean phytoplankton communities [186, 228], therefore it is important to study the effects of changes in phytoplankton communities and how they will cascade through the food-web [40, 199, 211]. Previous studies have shown that different species across different trophic levels—from benthic invertebrates to top predators—can change their diet in response to atypical years [77, 109]. Despite no evidence existing of impacts on predators due to this short-term dietary shift, a long-term change due to climate change was not assessed. Furthermore, some changes in food-webs cannot be evaluated over a short-term period, thus long-term studies are also needed to better capture the impacts of climate change in the food-webs [48].

A useful tool for the future of food-web research is the existence of databases that combine diet and trophic biomarkers for different Southern Ocean species, e.g. the Southern Ocean Diet and Energetics Database (SO-Diet) [229]. Data sharing through open-access databases generates opportunities for dietary studies on individual species to be integrated into larger food-web research [e.g. 66]. However, publishing data, either being databases targeting a specific topic (e.g. SO-Diet) or public repositories (e.g. Dryad, GenBank, TreeBASE, Zenodo, etc), requires that authors shape the data to be published and make it understandable to everyone. The preparation of the data consumes time and, on many occasions, there is no recognition by funding agencies and/or universities which may discourage authors from publishing their data (if not mandatory by scientific journals). Consequently, it is possible to see several diet and/or trophic studies without associated data nor a DOI of a public repository. To encourage more data sharing we suggest that the publication of databases should be fully recognised as scientific work by authors. Besides databases, the development or extension of, for example, qualitative models that can be used to estimate the abundance of lower trophic level

organisms or whole food-web models that allow the impact of changes in the entire food-web to be studied, offers great promise for the future [230, 231].

The role of early career researchers in the study of Southern Ocean food-webs

ECRs can play an important role in the study of Southern Ocean food-webs [43]. One of the most crucial aspects to study these complex networks is time, e.g. to collect and analyse large amounts of data or develop new technologies. Professors and senior researchers usually have, among others, lecturing duties, coordinate working groups and/or institutes, and write project proposals and reports, while researchers at the beginning of their career can usually focus on research. Though, we must be aware that focusing on large-scale, transdisciplinary food-web studies is not always possible for ECRs. Previous studies identified that because of, but not limited to, pressure to publish, uncertainty regarding the future, lack of support from institutions, and demanding workloads may act as a barrier for ECRs and create severe time limitations to engage in such studies [44, 232]. If these obstacles can be overcome, ECRs could have time to work on more complex data and explore, for example, existing databases. Furthermore, ECRs have more potential and time for interdisciplinary collaborations. This willingness to break disciplinary boundaries and work with researchers and/or datasets from various backgrounds, and sourced from different methodologies, breaking away from traditional academic silos, lead to innovative research surrounding species interactions, and thus the construction of multi-layered, high-resolution (i.e. networks including different types of interactions at different size-, spatial, and temporal-scales that interact among them) food-webs [233].

To study deep-sea food-webs, as well as those in winter and/or below ice-shelves, new and innovative technologies are needed, and here ECRs can play a major role as younger scientists are more prone to develop and test new tools [234]. In earlier stages of a researcher's academic career, e.g. Master thesis, studying the diet or trophic ecology of a single species, which is achievable within the time frame of this academic work, can play an important role to the study of Southern Ocean food-webs as it delivers information that can be integrated, for example, into food-web models. Moreover, the ECR community is more diverse regarding gender, ethnicity, and background. However, we need to be aware that we are still far from the ideal, with recognized barriers to ECRs from underrepresented, marginalised, and overburdened groups including, but not limited to, women, LGBTQI+, black, indigenous and people of colour (BIPOC) [43, 47, 235, 236]. Higher diversity results in broader perspectives and novel insights into research problems, enhancing innovation, e.g. development of new technologies, which ultimately result in novel findings [45, 46].

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