Response of indicator species to changes in food web and ocean dynamics of the Ross Sea, Antarctica

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Abstract: Most of the Ross Sea has been designated a marine protected area (MPA), proposed 'to protect ecosystem structure and function'. To assess effectiveness, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) selected Adélie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) penguins, Weddell seals (*Leptonychotes weddellii*) and Antarctic toothfish (*Dissostichus mawsoni*) as ecosystem change 'indicator species'. Stable for decades, penguin and seal populations increased during 1998–2018 to surpass historical levels, indicating that change in ecosystem structure and function is underway. We review historical impacts to population trends, decadal datasets of ocean climate and fishing pressure on toothfish. Statistical modelling for Adélie penguins and Weddell seals indicates that variability in climate factors and cumulative extraction of adult toothfish may explain these trends. These mesopredators, and adult toothfish, all prey heavily on Antarctic silverfish (*Pleuragramma antarcticum*). Toothfish removal may be altering intraguild predation dynamics, leading to competitive release of silverfish and contributing to penguin and seal population changes. Despite decades of ocean/weather change, increases in indicator species numbers around Ross Island only began once the toothfish fishery commenced. The rational-use, ecosystem-based viewpoint promoted by CCAMLR regarding toothfish management needs re-evaluation, including in the context of the Ross Sea Region MPA.

Introduction

Human impacts extend back at least to the wide-scale practice of agriculture and extraction of marine biotic resources but have accelerated since the start of the Industrial Age at *c.* 1800 (e.g. Waters *et al.* 2016). While global in many respects, anthropogenic influence is more apparent in some areas than in others. In the context of the world oceans, coastal waters have been most affected by human activity (Halpern *et al.* 2008, Stock *et al.*
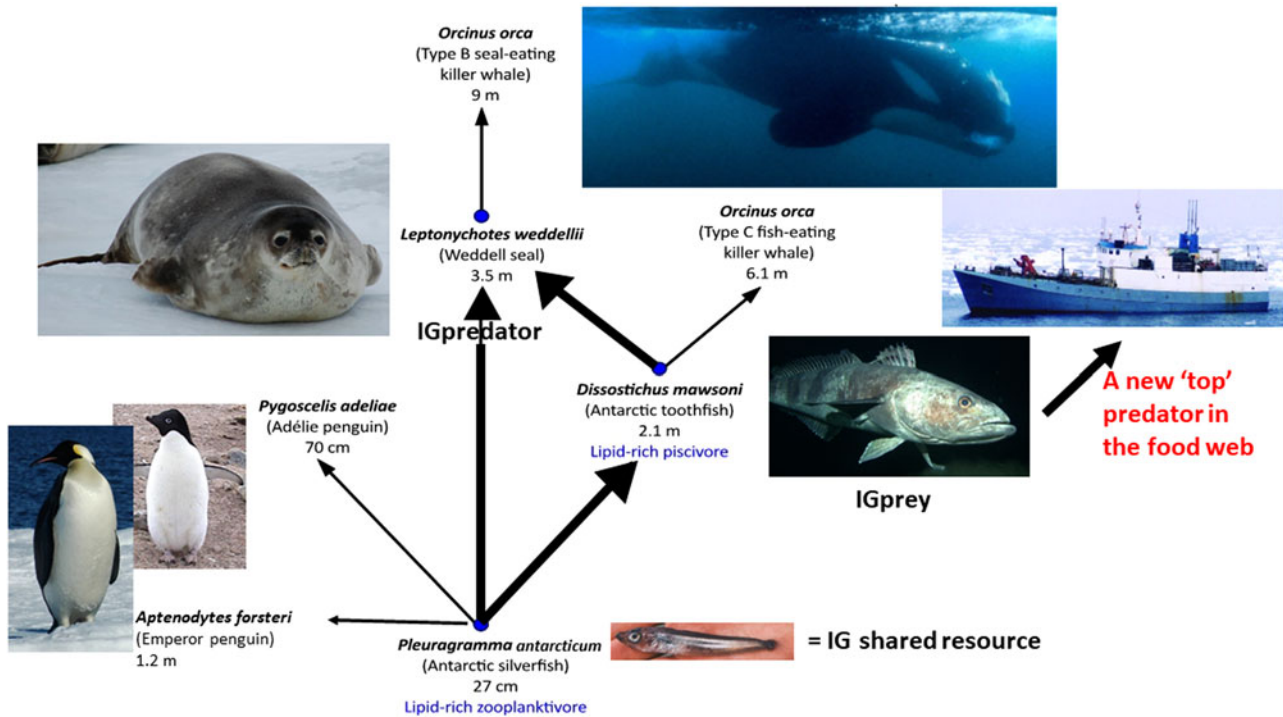
Figure 1. Species and relationships involved in the intraguild (IG) predation of Antarctic silverfish that characterize the water column food web of the Ross Sea (see details of dietary overlap in Ballard *et al.* 2012, La Mesa & Eastman 2012, Goetz *et al.* 2017). Measurements indicate average size; thicknesses of arrows indicate the strength of the primary IG relationship: that between the seal, toothfish and silverfish.

2018). From the mid-1990s to 2003, Halpern *et al.* (2008) mapped 232 sectors of the world oceans using 17 anthropogenic factors that affect marine ecosystems and found the highest levels of impact in waters over the continental shelves of Asia, Europe and north-eastern North America. They found that the Ross Sea exhibited the least total impact over that time period as well as over the following 5 years, although extensive sea-ice cover precluded full assessment (Halpern *et al.* 2015). The low impact scores for this region were partly because Halpern *et al.* (2008) considered only the then-most-recent decade (up to *c.* 2003) in their analysis and did not include historical factors (Blight & Ainley 2008) such as the near extirpation of some seals, penguins, large whales and ground fish from many coastal continental and island habitats (Koch 1992, Ballance *et al.* 2006, Blight & Ainley 2008, Ainley & Blight 2009, Hofman 2017).

As an update to Halpern *et al.*'s analysis, we utilize the Commission for the Conservation of Antarctic Marine Living Resources' (CCAMLR) perspective on 'indicator species' - Adélie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) penguins, Weddell seals (*Leptonychotes weddellii*) and Antarctic toothfish (*Dissostichus mawsoni*; Dunn *et al.* 2017, CCAMLR 2018a,b; http://archive.ccamlr.org/pu/E/sc/cemp/intro.htm) -

to review factors, such as environmental change and direct exploitation, that might have affected the Ross Sea ecosystem through the early 1990s, as well as the eventual exploitation halt and recovery for some of these species. We believe that the scenarios involving these factors serve as 'experiments' in which the responses of various species had been documented, and this documentation indicated a closely coupled food web (Ainley 2007, 2010). It is important to be familiar with these experimental results in order to better understand more recent changes.

We then turn to more recent times and review when the same 'indicator species' began to show that noticeable ecosystem change had resumed, providing additional 'experiments' against a backdrop of changing oceanographic and meteorologic conditions. Considering the early twenty-first century, or more specifically 1998–2018, our modelling analysis attempts to identify the environmental factors leading to changing population trajectories of 'indicator species'. Finally, we discuss how the identified factors are ecologically involved, how these relate to human-caused alterations and what our recommendations are for possible mitigations.

Regarding 'indicator species', a general consensus among researchers is that upper-trophic-level species can

demonstrate variation in marine ecosystems and their trophic processes, which is an especially useful strategy if there are major logistical challenges, as in the Ross Sea, to measuring trophic resources directly (e.g. Piatt *et al.* 2007, Einoder 2009, Rajpar *et al.* 2018, Velarde *et al.* 2019). Eventually, using the above-listed set of indicator species to measure effectiveness, CCAMLR in 2016 adopted the Ross Sea Region Marine Protected Area (RSRMPA; CCAMLR 2016, Brooks 2017, Brooks *et al.* 2021), which came into force in 2017. The RSRMPA covers ~1.55 M km^2 (excluding waters under the ice shelves), of which 1.12 M km^2 (~72%) are fully protected, although fishing is allowed within its boundaries to assess toothfish recruitment (Parker *et al.* 2019). 'Ecosystem structure and function' are what the RSRMPA was designed to protect (although the baselines for those terms were not identified; CCAMLR 2016). To determine effectiveness, a formal research and monitoring plan (RMP) has been proposed but has yet to be adopted; central to the RMP is the use of indicator species, as noted (Dunn *et al.* 2017, CCAMLR 2018a,b). An evaluation of MPA effectiveness is scheduled at 10 year intervals (first in 2027). A critical question is whether the recent changes among the 'indicator' seal and penguin populations in the southern Ross Sea (as reviewed below) have been/are being influenced by a decreased prevalence of large toothfish, the target of commercial fishing now mostly relegated to the edges of the RSRMPA.

Historical impacts (*to 1998*) and trends among mesopredator indicator species

The Ross Sea food web has been greatly affected by humans, although by the time frame considered by Halpern *et al.* (2008; beginning in the late 1990s) some of the impacts had abated or disappeared. Here we catalogue the most important effects of human activities on this area, some of which were expressed by changes in certain co-occurring (and competing) populations of mesopredator and supposed 'indicator species' (see above and next section). Considering that the maximum lifespan of the species included in this study is ~25 years, with a generation time of ~9 years (Clarke *et al.* 2003, Curtis 2009, Lescroël *et al.* 2023), we identified 'historical impacts' as before 1998 and 'recent' as 1998 to the end of the time series.

Important in this review is the Antarctic silverfish (*Pleuragramma antarcticum*), which is among the few neutrally buoyant Antarctic fish of continental shelf waters, along with adult toothfish (Koch 1992, Eastman 1993, 2024). That is important as both can occupy the entire water column, and so silverfish become a principal prey shared by all upper-trophic-level mesopredators. This can lead to inter- and intraspecific trophic

competition in the form of intraguild predation; in some cases, this has been demonstrated in the Ross Sea (as presented in greater detail below; Fig. 1; Ballard *et al.* 2012; La Mesa & Eastman 2012).

Historically, commercial whaling along the Ross Sea continental slope extirpated blue whales (*Balaenoptera musculus*) during the 1920s, followed by a major reduction of minke whales (*Balaenoptera bonaeren*sis) in the early 1980s (Tønnessen & Johnsen 1982, Ainley 2010). Subsequent changes in indicator species suggest that these depletions probably changed the structure and function of the Ross Sea food web. For example, the removal of minke whales probably led to competitive release of prey important also to penguins (krill, fish) and a coincident increase in numbers of trophically competing Adélie penguins (shown in Ballance *et al.* 2006, Ainley *et al.* 2007). The International Whaling Commission enacted a moratorium on commercial whaling in 1985–1986, and since then only a few blue whales have been sighted in the Ross Sea region (Matsuoka *et al.* 2006, Branch *et al.* 2007, Miller *et al.* 2019). The number of minke whales in the Ross Sea and larger region, however, recovered by the 1990s (Branch 2006, Ainley 2010), despite a much lower 'scientific catch' that was allowed several years beyond the moratorium (since ceased). Counterpart to the (re)growing minke whale population in the region, the penguin population's upward growth trend of the 1980s–1990s decreased and then levelled out instead of indicating that minke whales had replaced the penguins (Ainley *et al.* 2007). A contributing factor that operated in opposition to the effects of the whale increase was increasing winds (see below). These brought more persistent open water adjacent to colonies, making it easier to forage and increasing breeding productivity, thus compensating for the renewed trophic competition (Ainley *et al.* 2005; note that prior to 1979 only wind data had a long enough time series to overlap the penguins' time series, which began in 1959). More recent investigations have found a basis for suspected trophic competition (relaxing and then intensifying) by directly revealing the substantial spatial and trophic overlap among the penguins and whales (Ainley 1985, Karnovsky *et al.* 2007, Ballard *et al.* 2012). That is, with the seasonal arrival of minke whales, it was found that the diet of penguins shifts away from krill, as well as penguin foraging trips requiring more time and distance (Ainley *et al.* 2006, 2015b).

A second historical impact involved the numerous expeditions to the Ross Sea, especially those of the early explorers, during which Weddell seals were taken as food for humans and dogs (O'Connor 2019). This activity eventually culminated in the slaughter of ~2000 seals in southern McMurdo Sound from the mid-1950s to the early 1980s (Ainley *et al.* 2015a). Being K-selected (low reproductive rate, long lifespan; Pianka 1970), seals are
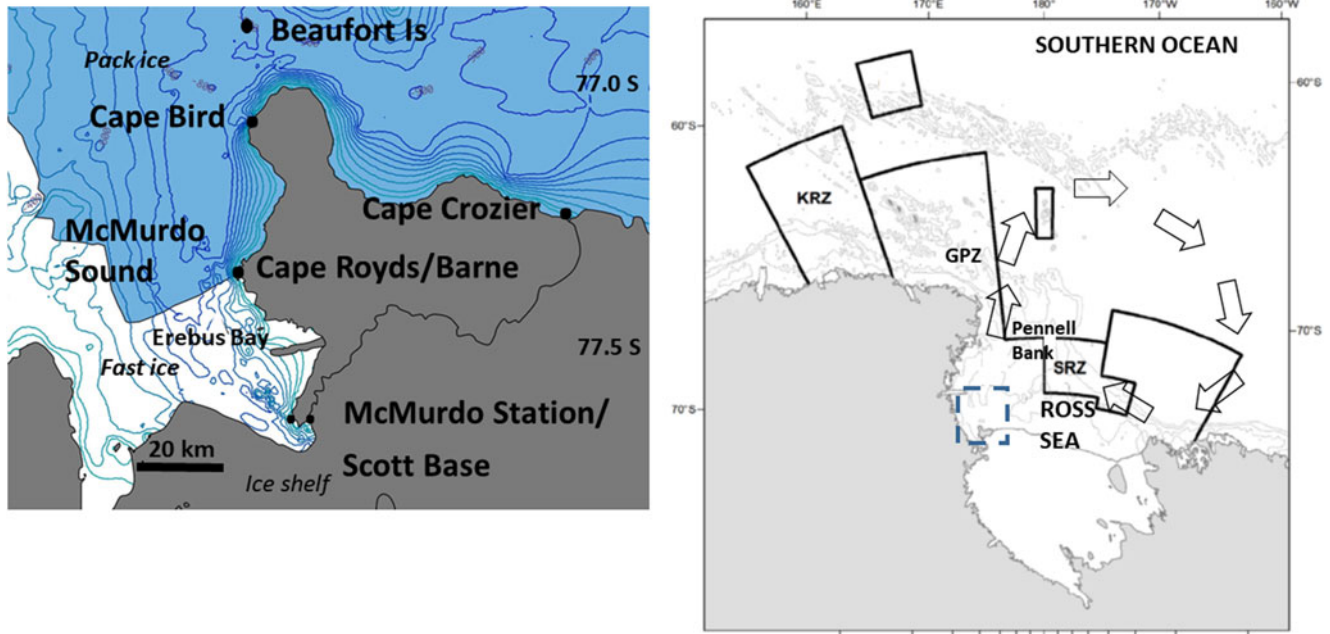
Figure 2. Locations mentioned in the text that refer to south-western Ross Sea (left panel, dotted box in right panel) and Ross Sea Region Marine Protected Area. Arrows indicate the location and movement of the Ross Gyre. GPZ = general protection zone; KRZ = krill research zone; SRZ = special research zone.

not easily replaced. The take probably affected the spatial distributions of seals (Goetz *et al.* 2023), penguins (LaRue *et al.* 2019, 2021) and fish (Ainley *et al.* 2020, Saenz *et al.* 2020). In partial response to this slaughter, the Convention for the Conservation of Antarctic Seals was entered into force in 1978 (Hofman 2017, 2019). One article encouraged the establishment of seal sanctuaries, one of which was McMurdo Sound, as well as the equally well-studied Moubray Bay/Edisto Inlet farther north along the Victoria Land coast. Beginning in 1996, in order to add further protection, nine Ross Sea sites that include seal and penguin breeding areas have been designated, under the Antarctic Treaty, as Antarctic Specially Protected Areas (see https://www.ats.aq/devph/en/apa-database). Any human activity, including entering or flying over these protected areas, is prohibited without a permit.

Recent research has found that the McMurdo Sound population of Weddell seals (the largest aggregation in the Antarctic, > 1000 breeding females; LaRue *et al.* 2021; see below) forages throughout waters of the western Ross Sea shelf (Harcourt *et al.* 2021, Goetz *et al.* 2023), an area important to foraging for other mesopredators (Ainley 1985, Karnovsky *et al.* 2007, Ballard *et al.* 2012), thus facilitating potential trophic competition. Also possibly indicating this competition among seals and penguins for Antarctic silverfish (Saenz *et al.* 2020) is the inverse relationship between local seal and penguin numbers in the Ross Sea (LaRue *et al.*

2019). Indeed, silverfish prevalence in penguin diets increases after the seasonal retreat of seals from the immediate vicinity of penguins' foraging area along the fast-ice edge in McMurdo Sound (Fig. 1; Ainley *et al.* 2020, Saenz *et al.* 2020), indicating trophic release of silverfish relative to seal numbers.

Manifesting this competition and a change in prey availability may also be changes in the moulting populations of seals along the Victoria Land coast (including McMurdo Sound), as assessed in 2008–2012: numbers of Weddell seals are now significantly lower in the western Ross Sea than in the 1950s and early 1960s (Ainley *et al.* 2015a). The long period between early and recent counts means it is not known when or why the decrease occurred or whether there were related, broader ecosystem effects. While silverfish availability could well be the most direct factor in trophic competition between penguins and seals, complicating the interaction is the seals' take of a competitor: the Antarctic toothfish (Fig. 1; Goetz *et al.* 2017, Salas *et al.* 2017, Ainley *et al.* 2020; more detail below). Within McMurdo Sound, catch per unit effort (CPUE; a measure of abundance) of Antarctic toothfish in a scientific effort using a vertical set line decreased beginning in *c.* 2000 by > 50% as seal numbers grew, the CPUE previously having been higher and near constant since the early 1970s (Ainley *et al.* 2013). Further confirming the seals' predation pressure, scientific CPUE of toothfish is also low seasonally during the annual peak of breeding seal

numbers (Ainley *et al.* 2020). Whether the recovery of seals in McMurdo Sound is having effects on penguins is the subject of a companion paper (Ainley *et al.* 2024).

A third historical impact was the near-coast marine disposal of garbage and sewage from research bases, as well as fuel spills. Coastal benthic communities were affected, with certain macrofauna becoming favoured over others (Fig. 2; Conlan *et al.* 2010, Palmer *et al.* 2021). Winter Quarters Bay/Cape Armitage (McMurdo/Scott), the 'type locality' of ~140 invertebrate and fish species (summarized in Ainley *et al.* 2010a), became severely degraded, with many of these species disappearing altogether (Palmer *et al.* 2021). The Protocol on Environmental Protection to the Antarctic Treaty (i.e. the Madrid Protocol) was signed in 1991 and entered into force by 1998. Nations agreed to the cessation of the marine disposal of refuse as well as tertiary treatment of sewage at all bases Antarctic-wide. At McMurdo Station and Scott Base, infrastructure and procedures were completely revised. Contamination or enrichment from pollutants, for example, no longer favoured some species over others, and the structure of benthic communities is once again guided largely by natural processes (Kim *et al.* 2010). Only a few human-generated micropollutants that escape treatment still find their way into the ecosystem, though their effects remain unknown (Williams 2012,

Emnet 2013, 2015, Palmer *et al.* 2021). Whether this pollution, by its localized nature (i.e. concentrated near to research bases), had any effect on seals, penguins or toothfish is not known.

Finally, unlike other seas, neither invasive organisms (at least macro-organisms) nor plastic pollution plague the Ross Sea, and there is no commercial drilling (banned under the Environmental Protocol; Ainley *et al.* 2010a). Microplastics have been detected but at levels far below those detected in other oceans (Cincinelli *et al.* 2017, Aves *et al.* 2022). Mercury has been found in Antarctic toothfish (Queirós *et al.* 2020), and some pesticides have been detected, but in very low concentrations (George & Frear 1966, Chen *et al.* 2015). Therefore, Halpern *et al.* (2008, 2015) were largely correct in deeming the Ross Sea as the least impacted marine ecosystem on the planet (at the time of the study), as it had largely recovered from earlier exploitation and pollution.

Recent trends (1998–2018) in populations of Ross Sea mesopredator indicator species

The above review explored how mesopredator 'indicator species' have helped to understand how human activity appears to have affected or will affect the Ross Sea. We depend greatly on indicator species to reflect any
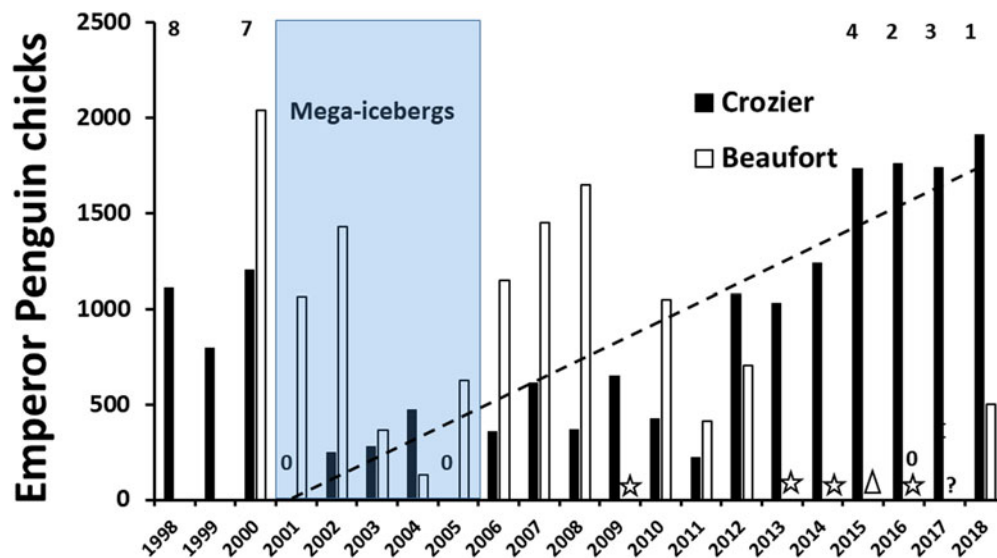

Figure 3. Annual counts of emperor penguin chicks in December (just before fledging) as an index of breeding pairs at Beaufort Island and Cape Crozier, Ross Island, 1998–2018 (one chick represents one pair). The shaded area is the period when two mega-icebergs rested against the coast at the colony location, making travel difficult (Kooyman *et al.* 2007). The dashed line depicts the Cape Crozier trend since 2001, with adjusted $R^2 = 0.796$, SE = 2.411, $P < 0.001$; since 2006, thus disregarding the B-15/C-19 era, adjusted $R^2 = 0.809$, SE = 1.073, $P < 0.001$. For Beaufort, stars represent satellite imagery estimates (1700–1900 m^2 of 'penguin pixels'), equivalent to ~1600 adults estimated by Fretwell *et al.* (2012) for 2009; the triangle indicates half that estimate (Foster-Dyer, unpublished data 2018–2019). At Crozier in 2001 and 2005, no chicks were produced (but some were present at Beaufort); at Beaufort in 2016, chicks were lost before the early December chick count, and no colony (or chicks) was evident in 2017. Numbers along the top indicate the historical rank of the Crozier count (1 = highest count), with the time series beginning in 1960 (rank 5; see Schmidt & Ballard 2020).
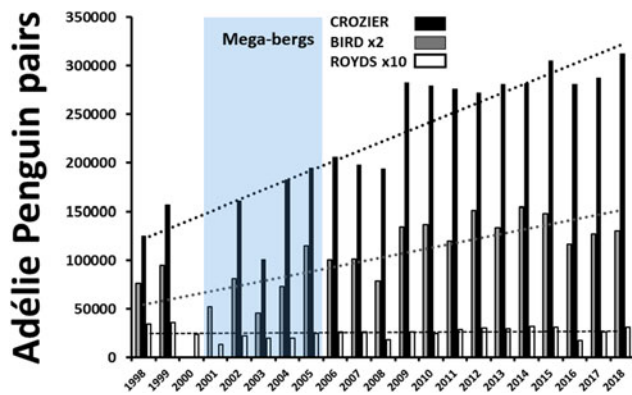
Figure 4. Annual numbers of Adélie penguin breeding pairs at capes Crozier, Bird and Royds/Barne on Ross Island, 1998–2018. Shading indicates when mega-icebergs rested against the coast. Data derived from counts of occupied nests in aerial photographs taken during the first week of December (end of incubation, when only one adult is present to represent each pair; Lyver *et al.* 2014). To give a sense of the trends (dashed lines), respective adjusted $R^2 = 0.8418$, 0.5932 and 0.0279 for capes Crozier (SE $= 940.3$, $P < 0.001$), Bird (SE $= 748.9$, $P < 0.002$) and Royds (SE $= 213.2$, $P < 0.507$). To aid comparison, Cape Bird counts are doubled and Cape Royds counts are ×10.

changes underway owing to the region's remoteness and challenging logistics, leading to inadequate surveys of middle-trophic-level species (Ainley *et al.* 2010b, Davis *et al.* 2017). This is also the strategy used by CCAMLR to assess the effectiveness of the RSRMPA (CCAMLR 2018a,b). Here we summarize more recent population trends for emperor penguins, Adélie penguins and Weddell seals.

Emperor penguin. This species breeds at seven locations in the Ross Sea (~70 000 breeding adults in the early 2000s), accounting for 28% of the world population (Barber-Meyer *et al.* 2008, Fretwell *et al.* 2012, Kooyman & Ponganis 2016). In the south-western Ross Sea, two colonies - Cape Crozier (Ross Island) and Beaufort Island - though 80 km apart, act like a meta-colony (Fig. 2). In years when fast ice failed to remain in place at Beaufort Island, there was an increase in the Cape Crozier population (Fig. 3). Similar complementary changes among closely spaced colonies occur elsewhere in the western Ross Sea (Kooyman & Ponganis 2016). That is not surprising since foraging grounds of emperor penguins from these two Ross/ Beaufort Island colonies more than likely overlap (see Kooyman *et al.* 2020, Santora *et al.* 2020, Ainley & Wilson 2023). Total emperor penguin numbers have been growing (Fig. 3) despite the negative influences of the B-15A/C-19 iceberg grounding event (hereafter, the B-15A or mega-iceberg event) that blocked access to

these colonies during 2001–2005 (Kooyman *et al.* 2007, Dugger *et al.* 2014; see below for further details about the mega-iceberg event).

Unfortunately, few recent direct counts of emperor penguins are available for Beaufort Island owing to logistical challenges preventing aerial surveys. However, the proxy data on colony 'footprint' (guano in satellite imagery), when considered qualitatively, indicate a large total for the Beaufort and Crozier colonies together. Indexed by counts of chicks in December (assuming one chick equals a breeding pair but not factoring in breeding success, thus representing a minimum), the population is now larger than at any other time in recent history and continues to grow (cf. Schmidt & Ballard 2020; including to 2021, Ballard & Schmidt, unpublished data to 2021). The satellite footprint confirms these patterns (Foster-Dyer & LaRue, unpublished data to 2019).

Adélie penguin. This species nests in 19 colonies in the Ross Sea (> 1.1 M pairs in 2011), accounting for ~35% of the world total (Lynch & LaRue 2014, Smith *et al.* 2014). A complex of four colonies - one on Beaufort Island and capes Crozier, Bird, and Royds/Barne on Ross Island - constitutes a meta-population (Dugger *et al.* 2010) that represents ~10% of the world total (Lynch & LaRue 2014). The complex has generally been growing steeply since *c.* 2000 (including through the 2001–2005 mega-iceberg episode; Fig. 4; Ainley *et al.* 2005, Lyver *et al.* 2014). Growth has continued at least for Crozier through 2019 (K. Barton, unpublished data to 2019). The Royds/Barne colony, which was most severely impacted by the B-15A mega-iceberg episode, exhibited reduced breeding success, leading to emigration of breeding adults and reduced recruitment (Dugger *et al.* 2014). Lower breeding success and recruitment are factors that continue to limit colony recovery. As discussed in more detail elsewhere (Ainley *et al.* 2024), major factors affecting breeding success at Royds are the high predation of eggs and chicks by an unusual number of south polar skuas (*Stercorarious maccormicki*; skua:penguin ratio twice that of other colonies; Wilson *et al.* 2016, Schmidt *et al.* 2021) and perhaps competition for silverfish with the world's largest Weddell seal breeding colony a few kilometres away (LaRue *et al.* 2019, 2021, Ainley *et al.* 2024).

The other Adélie penguin colonies at Ross and Beaufort islands are larger than they have ever been in the historical record (see Taylor & Wilson 1990, Taylor *et al.* 1990, Wilson *et al.* 2001, for earlier data). The Crozier colony has become the third largest for the species (cf. Lynch & LaRue 2014, Borowicz *et al.* 2018). The extent of their foraging, covering a major portion of the western and central Ross Sea continental shelf, probably affects
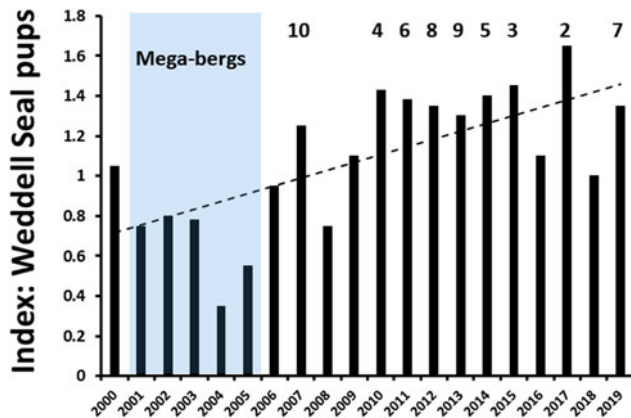
Figure 5. Index of Weddell seal population size in Erebus Bay, McMurdo Sound, during October–November 2000–2019 - pup counts are relative to the average count for 1963–2019 (one pup per female; data from Ainley *et al.* 2015a; Rotella, unpublished data to 2019). Shading represents the period when mega-icebergs prevented sea ice from escaping McMurdo Sound, with the fast ice thickening into multi-year mode, making it difficult for seals to haul out (Siniff *et al.* 2008). For the 10 most productive years (since 1963), numbers above points represent the rank of that year's production (1 = highest level, in 1967). For the seal trend for 1978–2019 (period when all pups were marked each year) and excluding 2001–2005 to avoid the mega-iceberg era, to give a sense of the trend, adjusted $R^2 = 0.5090$ (SE = 0.086, $P < 0.001$). The reduced indices for 2016 and 2018 were due to local fast-ice conditions that affected ice-crack prevalence (Ainley *et al.* 2020).

populations elsewhere in Victoria Land (Ainley *et al.* 2015b, Ballard *et al.* 2019, Santora *et al.* 2020).

Weddell seal. During the pupping/breeding period, ~22 000 Weddell seals (detected in 2011 satellite images), or 26% of the global total, haul out at sites of persistent fast ice along Ross Sea terrestrial and glacial coasts (LaRue *et al.* 2019, 2021). As judged from a multi-decadal mark-recapture study, the number of pups born in Erebus Bay and its vicinity, recorded each year (Rotella *et al.* 2016) and monitored in nearby locations, indicates that numbers of female Weddell seals giving birth to pups at this colony, and within nearby sight of the Cape Royds/Barne Adélie penguin colony (Fig. 2), have reached their highest level in the last 60 years (Fig. 5; Ainley *et al.* 2015a, 2020). Indeed, from 2010 to 2019, annual pup production exceeded the long-term average (1963–2019) in every year. Furthermore, seven of the 10 highest levels of annual pup production recorded since 1963 occurred in the most recent decade; the remaining three highest values were recorded in 1967, 1970 and 2007. The 1967 and 1970 counts are thought to be temporary demographic compensation responding to the slaughter of Weddell seals in southern McMurdo Sound during the 1950s to early 1960s (see
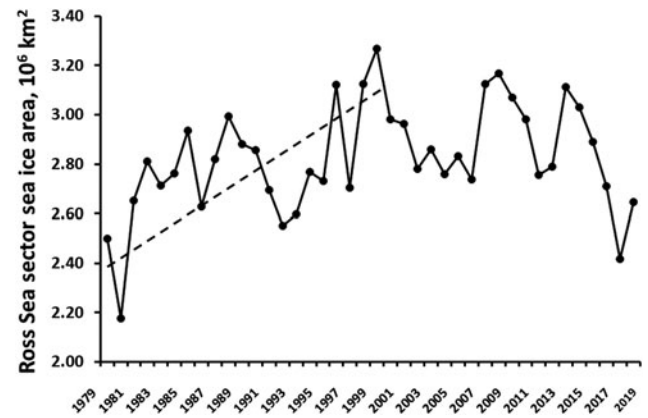

Figure 6. Annual average sea-ice extent (area) in the Ross Sea sector of the Southern Ocean as derived from satellite microwave data, 1979–2019. The dashed line indicates the increasing trend for 1979–1999 (adjusted $R^2 = 0.2904$, SE = 0.20, $P = 0.007$). Data from Parkinson (2019).

above; Testa & Siniff 1987). Whether or not the recent growth, mostly just in the breeding population (concentrated in Erebus Bay), is a culmination of population recovery from the 1950s'–1960's slaughter or a response to more prey is explored later in this paper. During December–January, following the pupping season and before the moult, individuals from this population forage over the same portion of the Ross Sea continental shelf used by penguins (see above; Beltran *et al.* 2017, 2021, Goetz *et al.* 2023), thus potentially enhancing competition.

Recent trends in the Ross Sea oceanographic climate

Habitat change related to climate. As stated above, the Ross Sea has been largely free from recent anthropogenic effects except for human-caused climate change (Halpern *et al.* 2015), which is a global factor, manifested in different ways in different regions. In the Ross Sea region, climate change has driven changes in several ocean properties, which we review here as relevant to our modelling attempts to explain penguin and seal population changes.

In contrast to the dramatic changes evident elsewhere in the Southern Ocean, especially along the western Antarctic Peninsula (Zwally *et al.* 2002, Stammerjohn *et al.* 2008, 2012, Scofield *et al.* 2010, Parkinson 2019), sea-ice extent (SIE; area of sea ice with a concentration of at least 15%, units of km^2) in the Ross Sea region increased by $6.7 \pm 1.1\%$/decade, leading to sea ice being present for most of the year (Parkinson 2019). SIE in the Ross Sea peaked in 1999 and has been variable but with a downward trend since then (Fig. 6; Parkinson 2019 for the record through 2018; Parkinson (NASA), unpublished data for the subsequent years to 2019),
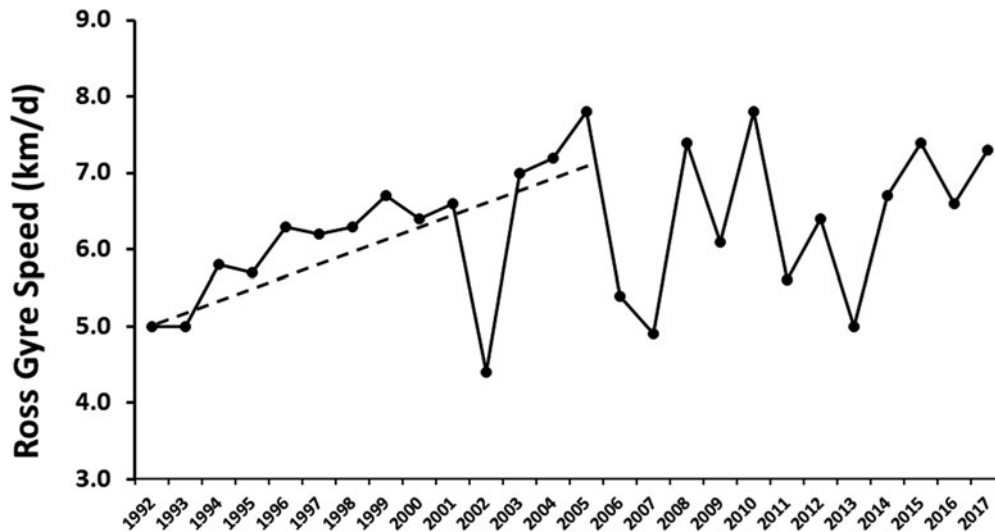
Figure 7. Annual mean speed of the Ross Gyre, July–October 1992–2017. The dashed line indicates the increasing trend for 1992–2005 ($R^2 = 0.4124$, SE = 0.049, $P < 0.02$); thereafter, it varied along a statistical plateau. Data from Comiso *et al.* (2011), Kwok *et al.* (2016, 2017) and R. Kwok (NASA; unpublished data to 2019).

although it remains far more extensive than elsewhere in the Southern Ocean. The increasing and then levelling pattern, with more variability Antarctic-wide, is consistent with the regime shift described by Hobbs *et al.* (2024). The earlier SIE increase was facilitated by stronger westerly winds over the Southern Ocean that intensified the Coriolis effect and northward Ekman transport, which in turn forced sea ice farther offshore into the easterly flowing Antarctic Circumpolar Current (ACC) and, by increased bowing of the polar jet stream, southward in the Ross Sea sector and northward in the Antarctic Peninsula sector (Stammerjohn *et al.* 2008). Like the increased westerly winds, the bowing of the jet stream was probably a response to an increasing regional atmospheric pressure differential resulting from the Antarctic Ozone Hole and warming of the middle-latitude Southern Hemisphere ocean (Thompson & Solomon 2002, Turner *et al.* 2007, 2009, Stammerjohn *et al.* 2008).

The increasing westerly winds accelerated the Ross Gyre, the large-scale clockwise rotation whose southern boundary lies along the outer Ross Sea continental shelf break and whose northern extent is the southern boundary of the ACC (Fig. 2; Jacobs *et al.* 2022, Comiso *et al.* 2011, Dotto *et al.* 2018). More specifically, annual variation in these winds reflects the Antarctic Oscillation and atmospheric pressure systems in the Ross and Amundsen sea regions (see above). Based on the flow of sea ice associated with the gyre, average July–October gyre speed increased from ∼5.0 km/day in 1992 to ∼8.0 km/day in 2005, after which it exhibited considerable interannual variation (Fig. 7); that levelling is consistent, too, with the regime shift described by

Hobbs *et al.* (2024). SIE in the Ross Sea sector varies in accord with gyre speed - with greater gyre speed, SIE reaches the southern boundary of the ACC (Comiso *et al.* 2011, Kwok *et al.* 2016, 2017). This circulation appears to affect the winter movements of Ross Sea Adélie penguins, which sometime use the flow to facilitate travel and other times cope with it when migrating against the flow (Ballard *et al.* 2010, Jongsomjit *et al.* 2024).

Other aspects of the Ross Sea physiography possibly pertinent to mesopredator trends have also changed, although not so dramatically for the Ross Sea as in the changes detailed above. The increased infusion of warm
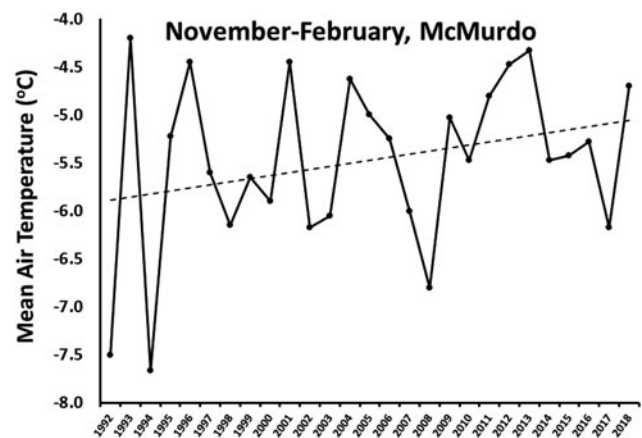

Figure 8. Average annual air temperature, November–February 1998–2018, as recorded at McMurdo Station; indicated by the dashed trend line, adjusted $R^2 = 0.0120$ (SE = 0.025, $P = 0.2500$). Data from the University of Wisconsin (http://amrc.ssec.wisc.edu/usap/mcmurdo/).
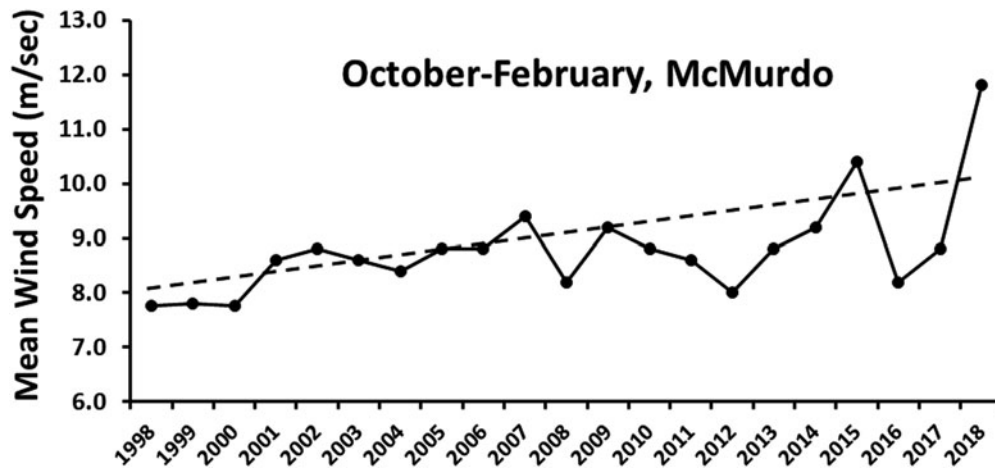
Figure 9. The annual wind speed recorded at McMurdo Station, October–February average, 1998–2018; indicated by the dashed trend line, adjusted $R^2 = 0.3023$ (SE = 0.028, $P = 0.006$). Data from the University of Wisconsin (http://amrc.ssec.wisc.edu/usap/mcmurdo/).

Circumpolar Deep Water (CDW) farther into shelf canyons/troughs (Dinniman *et al.* 2003, 2011), a result of the Coriolis effect and Ekman transport (deep water replacing surface water being advected offshore), has led to subsurface melting of ice shelves upstream to the east of the Ross Sea. Consequently, Ross Sea Surface Water (RSSW), not long ago the most saline in the Southern Ocean, has grown more dilute (-0.027/decade; Jacobs *et al.* 2022). This had been impacting the formation of Antarctic Bottom Water but has in recent years shown recovery (Silvano *et al.* 2020). Increased meltwater also may have deepened surface stratification (Jones & Smith

2017), as observed for the period from ~2000 to 2014 (34.54 isopycnal from 100 to 400 m) before returning to previous depths (Castagno *et al.* 2019, Castagno 2023). Increased stratification of the water column could significantly affect prey availability in the shallower depths, which is well known in other portions of the world ocean; it certainly affects phytoplankton dynamics in the Ross Sea (Smith *et al.* 2012), but more research is needed to detect the consequences of this within the food web. Despite the dilution and stratification of surface water, sea-surface temperature (SST) has not changed significantly (Fig. 8). The factor that might
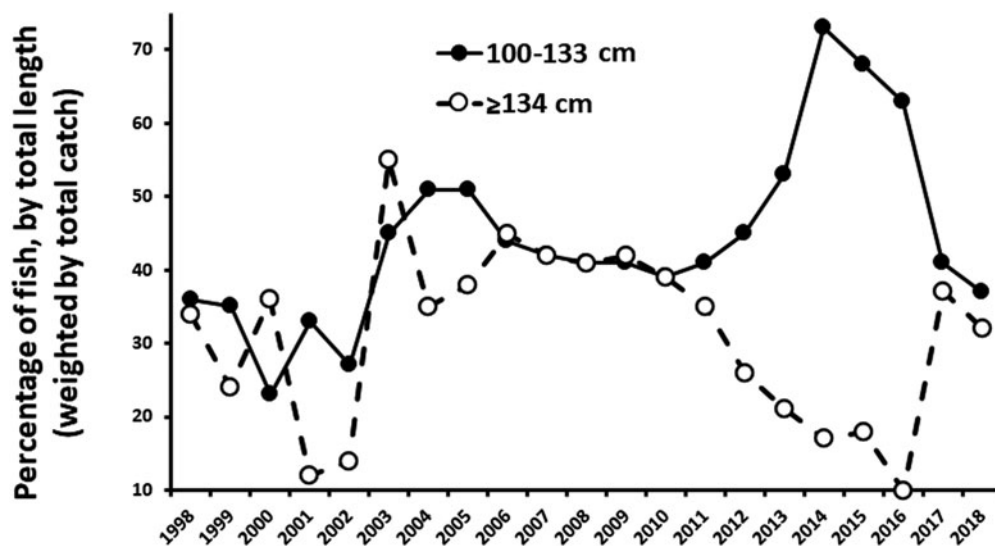

Figure 10. Annual change in percentage of large individuals in the catch of the Antarctic toothfish fishery for waters overlying the continental shelf and slope (Area 88.1), 1998–2018; data from catch-length frequency presented in graphs within CCAMLR fishery reports (CCAMLR 2008, 2018); data estimated using *Fiji* image analysis software. During the established fishery (2003–2018): for 100–133 cm total length fishes, adjusted $R^2 = 0.458$ (regression $P < 0.001$); for ≥134 cm total length fishes, $R^2 = 0.133$ (regression $P < 0.001$).

have contributed to increasing SIE per season, at least into the 2010s (Stammerjohn *et al.* 2012, Parkinson 2019), may be the less saline RSSW, which freezes at a higher temperature than more saline waters (Bronselaer *et al.* 2018).

By 2020, as noted, SIE in the Ross Sea region had recovered close to its long-term average but since had decreased again in the eastern half of the Ross Sea region (160 E–130 W; Parkinson, unpublished data to 2019). However, in the south-western Ross Sea, there has been no significant trend in the seasonal dynamics of sea ice, especially fast ice (important to both the seals and the emperor penguins). Fast-ice formation and breakout have shown no trends in McMurdo Sound (Kim *et al.* 2018), nor farther north along Victoria Land (Ainley *et al.* 2015a). Fast-ice persistence, although inconclusively decreasing in the western McMurdo Sound (Fraser *et al.* 2021), remains extensive. The extensive fast ice inhibits the formation of penguin colonies as well as significant seal aggregations (owing to multi-year ice, lack of access to open water and no protection from atmospheric elements; Siniff & Ainley 2008, Lyver *et al.* 2014).

The winds responsible for increasing large-scale SIE and gyre speed have led to more persistent (small-scale) coastal polynyas (or at least not a lengthening of the sea-ice season; Ross Sea, Terra Nova Bay and McMurdo Sound polynyas), contrary to the larger-scale change (as indicated in Parkinson 2002, Stammerjohn *et al.* 2012; see also Ainley *et al.* 2005). Primary production and chlorophyll concentration in the polynyas have changed little, with the exception of during the B-15A (Arrigo *et al.* 2002) and C-19 (Arrigo *et al.* 2003) mega-iceberg events of 2000–2005. The small change resulted in

increased prevalence of *Phaeocystis antarctica*, but being a non-diatom, colonial alga provides little opportunity for grazing within krill-based upper trophic levels (Fig. 8; Smith *et al.* 2012, Arrigo *et al.* 2015). Finally, after increasing in the late 1980s in accord with a regime shift (Ainley *et al.* 2005), air temperatures and wind speeds have remained higher than historical levels in the southern Ross Sea (Figs 9 & 10; LaRue *et al.* 2013).

Below, after considering food web changes, we propose and statistically test hypotheses regarding how these physiographic changes might be affecting the penguins and seals. An important consideration is that the climatic changes observed are relatively small but are operating at the scale of the entire Ross Sea and at a relatively slow pace compared to some of the population changes observed in our data. However, the impacts of these climate-induced changes on the indicator species' populations may not be linear or may operate through complex and yet-to-be-understood scaling mechanisms that manifest in the magnitudes of change apparent in the population data.

Recent food web change. If it proves to be the case that physical and biogeochemical changes in ocean properties are not or are only partially responsible for the increase in the three mesopredator (penguin, seal) populations of the southern Ross Sea, what other processes might have an effect? That is, what biological factors might be added to the physiographic variable mix? Offering a clue are the biological factors that, based on previous studies, are known to affect the distribution and abundance of the three mesopredators. From December to February, all three species, as noted, forage extensively over the western and central portions of the Ross Sea continental
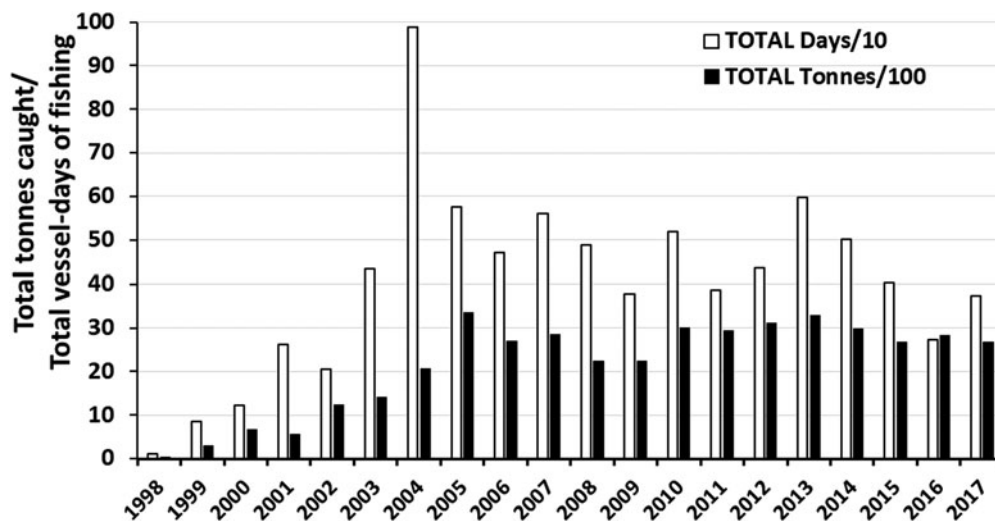

Figure 11. Annual fishing effort (in vessel-days) and annual total catch of the Antarctic toothfish fishery of the Ross Sea, Area 88.1, 1998–2017. Data from annual fishery reports (CCAMLR 2008, 2018).
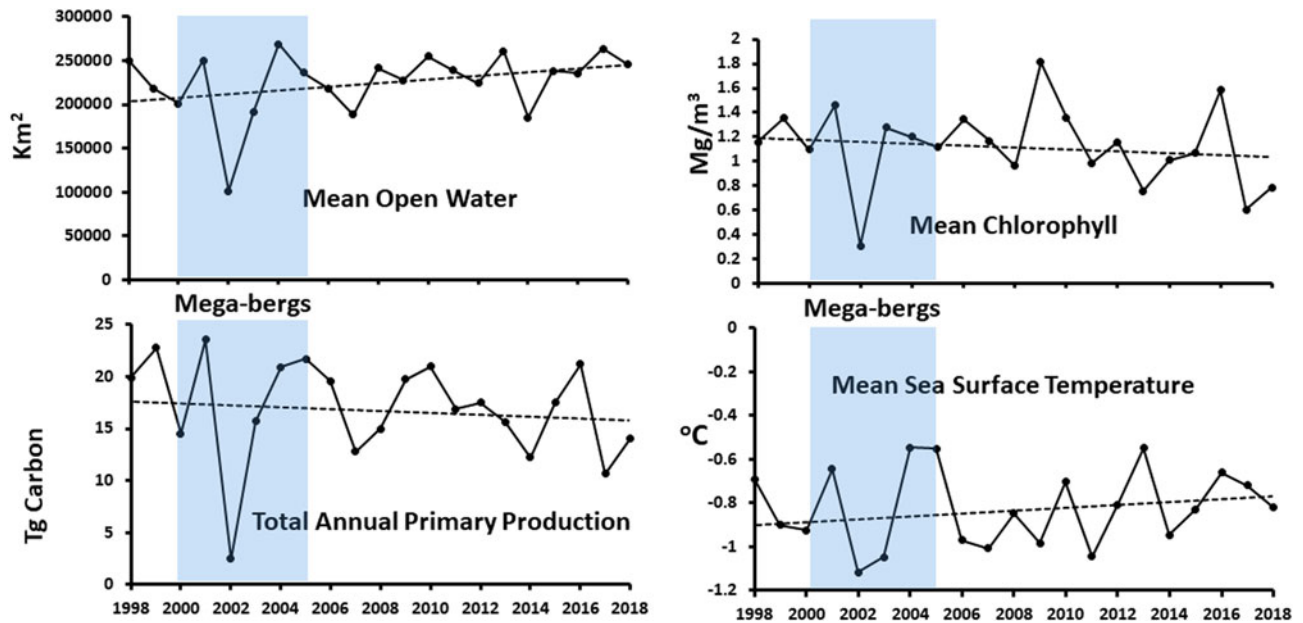
Figure 12. Annual variation (1998–2018) in Ross Sea polynya size (km² of open water, adjusted $R^2 = 0.168$, SE = 4.60, $P = 0.057$), amount of chlorophyll (mg/m³; $R^2 = -0.027$, SE = 6.58, $P = 0.514$; SeaWiFS and MODIS/Aqua), net primary productivity (Tg carbon; $R^2 = -0.064$, SE = 5.209, regression significance $F = 0.848$, $P = 0.848$; see Arrigo *et al.* 2015) and annual sea-surface temperature (°C; $R^2 = 0.0068$, SE = 0.0006, $P = 0.298$). Data from Arrigo *et al.* (2015) and Arrigo & van Djiken (unpublished data to 2018).

shelf, out to the continental shelf break (Ballard *et al.* 2019, Kooyman *et al.* 2020, Santora *et al.* 2020, Goetz *et al.* 2023). Moreover, each has a summer diet dominated by Antarctic silverfish, with the frequency of occurrence being 70–90% (Cherel & Kooyman 1998, Ballard *et al.* 2012, Goetz *et al.* 2017, Beltran *et al.* 2021, Foster-Dyer, unpublished data 2018–2019). Silverfish are by far the most abundant fish in the Ross Sea (Dewitt 1970), but little is known about the annual variation in abundance or distribution of subadults and adults (e.g. Davis *et al.* 2017). The latter age groups are key to mesopredator diets and play a crucial role in potential competition within the intraguild system (Fig. 1; Eastman 1985, Ballard *et al.* 2012).

If silverfish prove to be the key, two mechanisms might explain a rapid increase in silverfish abundance, thus altering intraguild dynamics: 1) a demographic response by silverfish to increased availability of their prey (bottom up) or 2) a release from predation (top down). Regarding the first possibility, subadult and adult silverfish in the Ross Sea feed mainly on Antarctic krill (*Euphausia superba*) in waters of the outer continental shelf and crystal krill (*Euphausia crystallorophias*) on the inner shelf; a secondary prey is copepods (La Mesa & Eastman 2012). Krill (both species) are also a main prey of penguins and baleen whales (Ballard *et al.* 2012). Silverfish become cannibalistic in the late season (Eastman 1985, La Mesa & Eastman 2012) in response to reduced krill availability owing to predation (Ainley

2007). Although some studies identified environmental factors that could change krill abundance and availability in the context of future climate change (e.g. Piñones *et al.* 2016, Davis *et al.* 2017), a very broad analysis indicated no change from the 1930s into the 2000s (Yang *et al.* 2021) Thus, bottom-up forcing is unlikely to be influencing increased silverfish abundance.

What about top-down forcing? There has been a significant decrease in prevalence of a major silverfish predator, namely the large Antarctic toothfish (Figs 11 & 12). Silverfish constitute a large component of the Antarctic toothfish diet, at ~70% frequency of occurrence among individuals occurring high in the water column (Fig. 1; Eastman 1985, La Mesa & Eastman 2012). Toothfish dwell on the bottom until reaching several years of age and ~100 cm total length (TL), whereupon they begin to accumulate interstitial fat to achieve neutral buoyancy (Near *et al.* 2003). They then increasingly rise above the bottom with little effort to access silverfish as the toothfish continue to grow. Silverfish are one of the few other neutrally buoyant notothenioids (Eastman 2024). Toothfish, especially those smaller toothfish confined to the bottom, do not prey much on silverfish (summarized in Stevens *et al.* 2014).

The size/age structure of Antarctic toothfish populations in the Ross Sea has been changing, with a decrease in large fish (see below). We argue that the disappearance of these large toothfish has led to

competitive release, providing more silverfish to the penguins and seals. The official CCAMLR-sponsored fishery for Antarctic toothfish in the Ross Sea was initiated during the 1996–1997 summer (Fig. 11), although perhaps beforehand but certainly in its early years illegal, unregulated and unreported (IUU) fishing occurred (Österblom & Sumaila 2011). Vessels required several years to locate and catch the large fish. Catch tonnage rose through the 2003–2004 seasons, stabilizing thereafter at ~2500–3000 tonnes, with some fluctuation in annual total allowable catch based on stock assessments (Fig. 11; CCAMLR 2019). Also decreasing and then stabilizing were vessel days of fishing, as better locations were discovered and the number of vessels that countries could admit became limited by CCAMLR. Fishing continued over the Ross Sea continental shelf until 2009, after which waters < 550 m in depth were closed to toothfish fishing anywhere around Antarctica, as well as in the deeper waters along the Victoria Land coast (CCAMLR Conservation Measure 22-08). Enactment of the RSRMPA also closed shelf waters to long-line fishing, with the exception of research fishing (e.g. for monitoring the prevalence of pre-recruit toothfish; Parker et al. 2015, 2019). The main fishing area now lies mostly along the continental slope (outer Pennell and Iselin banks) bordering the RSRMPA (which is < 70% off-limits to fishing), and fishing is generally from late December to early February (CCAMLR 2019).

The fishery is managed according to rules laid out by Constable et al. (2000) and allows reduction in spawning biomass to 50% of pre-fished levels over a 35 year period. According to maximum sustainable yield (MSY) theory (Barber 1988), reducing the large fish should allow an increase in younger fish taking advantage of reduced trophic intraspecific competition. As of 2014, ~20 years after the initiation of fishing (1997–1998), models indicate that spawning biomass had decreased by > 25% (Parker et al. 2015), while more recent models indicate a decrease almost to 50% by the early 2000s (CCAMLR 2019). One result of decreased spawning biomass is decreased prevalence of the large, neutrally buoyant fish (i.e. the spawners) as judged both by the commercial catch (Fig. 12) and the fishery modelling (CCAMLR 2019). This is also indicated in a much longer time series based on a scientific effort in McMurdo Sound (Ainley et al. 2013, 2016). The trend shown in Fig. 12 closely follows what CCAMLR believes, through its models, to be the pattern for declining spawning biomass (CCAMLR 2019, fig. A1.2). These fish mature only after 13–17 years of age at 120–134 cm TL (males and females, respectively; Parker & Grimes 2010, Hanchet et al. 2015), taking at least that long to be replaced in the population, and so removing them is cumulative. These are the fish that, being neutrally buoyant, compete with seals and penguins for silverfish and other prey higher in the water column, especially under sea ice (Fuiman et al. 2002). Their removal does not lead to more, smaller fish high in the water column (i.e. MSY theory) because the smaller fish are not neutrally buoyant. In the dynamics of intraguild predation, fewer large toothfish means that within the water column more silverfish potentially are available to other mesopredators (Fig. 1). Few toothfish of this size class could have been replaced since initiation of the fishery.

Hypotheses to explain recent change among indicator species populations

In the preceding sections we reviewed the historical and current exploitation of biotic components of the Ross Sea food web and the physical and biophysical changes in the Ross Sea region. During the historical period, increasing wind - the only variable concurrent with the 1959 start of the penguin population time series - was found to correlate with penguin population change in the 1980s–1990s, with the hypothesis being that increased wind led to more reliable polynyas and increased access to prey (Ainley et al. 2005).

Next, we turn to seal and penguin change in the first decades of the twenty-first century and present modelling results to assess which variables, both physical and biotic, might be responsible. Here are the hypotheses tested:

1) As large toothfish are removed, more silverfish occur in the upper water column where penguins and seals forage. Reviewed in detail above, there is significant 3D and temporal overlap in the prevalence of the indicator species considered in the present analysis. Both penguins and seals reduce local prevalence of silverfish where these predators forage intensively (Testa et al. 1985, Ainley et al. 2015a, Saenz et al. 2020). Increased abundance of silverfish in the upper water column facilitates penguin and seal foraging efficiency (lower effort and energy needed). This is especially important during post-breeding (Salas et al. 2017) and post-fledging, thus increasing the potential for subsequent recruitment and population growth. In addition, adult penguins are able to provide higher-quality food to their young, thus increasing chick growth and subsequent survival (Chapman et al. 2011, Jennings et al. 2022). More silverfish in the diet also improves adult penguin survival (Ainley et al. 2018). As we will note, we explored different temporal lags to cumulative fish taken (Box 1).

2) Variation in large-scale SIE affects the eventual recruitment of Adélie penguins. A previous study of

Box 1. Summary of variables used to explain Ross Sea mesopredator population trends.

Indicator species' annual population change

We modelled, as the dependent variable, the annual change in penguin and seal population size. The time series for emperor penguins had too many gaps in the Beaufort portion of the 'meta-colony', and thus further analysis was not possible. Adélie penguin populations for the Cape Crozier and Cape Bird colonies were sufficiently complete and were taken from Lyver *et al.* (2014), supplemented by data from Antarctica NZ (https://doi.org/10.7931/kf06-x745). Counts were made *c.* 1 December, which is when all eggs have been laid and many non-breeders or early failed breeders (lost eggs to skuas) have departed; there is just one incubating bird per nest, with each nest having undergone at least one mate exchange (Ainley 2002).

Weddell seal population size in Erebus Bay was an index of numbers of pupping females (Ainley *et al.* 2015a, 2020, Rotella *et al.*, unpublished data to 2019). Tallies represent the total of pups tagged, with a concerted effort, which began in 1973 and continues annually (Cameron & Siniff 2004, Garrott *et al.* 2012, Rotella *et al.* 2016), to tag all pups born in the area each year.

Biophysical covariate data (monthly or seasonal averages)

Sea-ice extent: km^2 total area of all ∼25 km × ∼25 km pixels of the Ross Sea containing ice of concentration at least 15% (Parkinson 2019; updates from Parkinson (NASA), unpublished data to 2019).

Fast-ice extent: in McMurdo Sound, distance (km) between McMurdo Station and fast-ice edge on 1 January (Siniff *et al.* 2008, Kim *et al.* 2018; Ainley, unpublished data to 2018, c/o US Coast Guard).

Gyre speed (km/day of ice movement), July–October, in Ross Sea sector of the Southern Ocean (Comiso *et al.* 2011, Kwok *et al.* 2016, 2017, updates from Kwok (NASA), unpublished data to 2019).

Wind speed: measured at McMurdo Station (m/s), November (http://amrc.ssec.wisc.edu/usap/mcmurdo/).

Air temperature: measured at McMurdo Station (°C), November (http://amrc.ssec.wisc.edu/usap/mcmurdo/).

Open-water extent: average annual daily km^2, in Ross Sea and McMurdo Sound polynyas, 15–31 December (Arrigo *et al.* 2015, Arrigo & van Dijken, unpublished data to 2018, SeaWiFS/MODIS). We included the 10^6 version of this variable to fit our analyses.

Open-water date: first day in spring when the open water of the Ross Sea or McMurdo Sound polynya is > 50% of the maximum open-water area (see open-water extent above; Arrigo & van Dijken, unpublished data to 2018). The earliest date recorded for any year was considered day 0, and the subsequent dates were calculated with respect to that date.

Sea-surface temperature: °C (same source as for open-water extent)

Primary productivity: Tg carbon (same source as for open-water extent)

Chlorophyll concentration: mg/m^3 (same source as for open-water extent)

Toothfish data

Cumulative fish: weight of toothfish > 134 cm total length caught in each year, calculated by knowing the total tonnes of toothfish extracted in a given year and the percentage contributed by fish > 134 cm total length. Fish take precedes indicator population counts for a given year by several months (e.g. an October–November seal count or 1 December penguin count in, say, 2005 is preceded by the fishing of 2004–2005). Considering various combinations, we obtained the best results by calculating the previous 3 fishing years of weight (cumulative) of these spawning-size fish in the catch during the period 1998–2018 (toothfish > 134 cm total length; FAO/CCAMLR Area 88.1; CCAMLR 2008, 2019). To allow for this accumulation to begin, we used predator time series beginning in 2001. We used *Fiji* image analysis software to parse the size frequency of the catch from the graphs contained in those reports. We explored different percentage weights among the 3 year cumulative values (specifically, e.g. 80% 1st year-20% 2nd year; 60% 1st year-40% 2nd year; 50% 1st year-50% 2nd year).

annual variation in size of Ross Island colonies from 1979 to 1997 showed a negative correlation of population change with SIE, with a 5 year lag, which corresponded to average age of recruitment of Adélie penguins (Wilson *et al.* 2001; see also Southwell *et al.* 2015). It was thought that variation in the extent of ice affects where the penguins spend the winter, impacting the numbers returning the following spring.

3) A year of much more extensive McMurdo Sound fast-ice extent (FIE) than the previous year has a positive effect on annual seal population growth. Under such conditions, a good deal of the fast ice will have formed in the current year (i.e. it is annual) and will provide conditions favourable for a higher number of pupping females. Those conditions include thinner ice, with lower free-board, compared to multi-year ice, and many cracks through which seals can more easily haul out (Siniff *et al.* 2008).

4) Ross Gyre speed affects the arrival of penguins at the colony in spring, either facilitating or hindering it. The Ross Gyre plays a role in penguin over-winter movement (Ballard *et al.* 2012, Jongsomjit *et al.* 2024).

For those wintering in the eastern portion of the gyre, spring arrival is sooner (higher gyre speed) and more adults will breed (Ainley 2002). A multi-year lag could be involved depending on the age classes affected, with most Adélie penguins spending their first few years at sea before their first return to their colonies (Ainley 2002). Earlier return leads to inclusion in the 1 December count. For penguins wintering in the western portion of the gyre (e.g. perhaps those from Cape Bird), higher gyre speed has a negative effect, as the penguins must travel contrary to ice movement (shown in Ainley *et al.* 2024).

5) Wind speed plays an important role, as it modulates almost every other geophysical variable. Wind speed has a positive effect on polynya opening but a negative effect on phytoplankton dynamics (Jones & Smith 2017), causing vertical mixing of phytoplankton and deepening of the surface mixed layer (i.e. halocline/thermocline). Efficiency of grazers (penguin prey) may be compromised in years with high winds, leading to poorer mesopredator foraging and population decrease (see Hypothesis 1 above).

6) Air temperature has a positive effect on seals and penguins and could possibly be a proxy variable for general weather conditions. How it would affect mesopredator population variation is uncertain. It could certainly influence persistence of sea ice and sea-ice cover depending on whether temperature decreased (more ice, longer presence) or increased (less ice, shorter presence) (see other hypotheses). It apparently correlates with Adélie penguin population growth at Beaufort Island, but this is just a result of more habitat as ice fields retreat (LaRue *et al.* 2013). Other colonies are not habitat limited. Air temperature has been implicated in penguin trends elsewhere (summarized in Ainley *et al.* 2024).

7) An early open-water date has a positive effect on the likelihood that penguins will arrive in time to breed (earlier date, earlier arrival), and large open-water extent (less walking) has a positive effect on the likelihood that females will return in time to relieve their fasting mates of their incubation duties (Ainley 2002). With earlier arrival and less subsequent desertion, more nests would be occupied when aerial photos are taken (1 December).

8) High primary production and chlorophyll concentration lead to better feeding conditions for seabirds (i.e. increased spawning and growth of prey due to high primary production leads to better feeding conditions for seabirds and seals; e.g. Pinaud & Weimerskirch 2005, Hoskins *et al.* 2008). If grazer (= prey) reproduction (especially larval survival) was altered, thus changing availability to predators, at least a few years of lag would be needed given that penguins' prey are typically > 1 year old for krill and 2–3 years old for silverfish; seals prey on 3–4-year-old silverfish (Burns *et al.* 1998, Ainley *et al.* 2003). However, exploring lags, Dugger *et al.* (2014) found no correlation between chlorophyll concentration and penguin reproductive parameters (cf. Chen *et al.* 2020, Morandini *et al.* 2022). Paterson *et al.* (2015) found a positive relationship between seal production and McMurdo Sound primary production, although this relationship is weakened if the years 2001–2005 are not included; these were years when multi-year ice excluded seals from Erebus Bay (Siniff *et al.* 2008).

SST can play a role and is frequently used in correlations to explain mesopredator natural history variation around the world. In fact, Chen *et al.* (2020) included SST in their regional exploration of important factors explaining Adélie penguin population change in the Ross Sea (using Lyver *et al.* 2014 data) and found that it was significant for extreme northern Victoria Land. Morandini *et al.* (2022), in turn, pointed out that such a result made sense because those colonies depend on a 'sensible heat polynya', derived from upwelling of warm

CDW, adjacent to Cape Adare. However, several factors, such as sea-ice prevalence, wind, air temperature, solar heating and others, greatly complicate any interpretation of SST's role in Ross Sea food web dynamics or predators' access to food, and consequently we did not include it in our analysis.

Methods

Using the above-listed variables/hypotheses and associated time series (reviewed below), we started with a saturated model (including all of the variables in the same model), testing both lags and quadratic effects of those variables, before proceeding to refine the model selection process.

Time series used in the modelling

Most of the data presented herein and included in our analysis have been published previously, as evidenced in our review above. In some cases, the published time series have been updated with additional years of data (Box 1). Therefore, we refer to existing publications for the full methods to acquire and organize the data (referred to below). The time series of our subsequent modelling is constrained by data availability. For instance, start date depended on the launch dates of appropriate satellites (1998), and end dates depend on such factors as the Ross Gyre data coming from a NASA programme that was discontinued after 2018.

Counts of penguins and seals. Most of the time series for Adélie penguin colonies at capes Bird, Crozier and Royds/Barne on Ross Island (Fig. 2) were derived from Lyver *et al.* (2014), with updates of counts from aerial photos provided by Antarctica New Zealand (https://doi.org/10.7931/kf06-x745). The Weddell seal time series of females pupping in Erebus Bay was derived from Ainley *et al.* (2015a, 2020) and Rotella (unpublished data to 2019). The time series for emperor penguins had too many gaps for analysis, especially for the Beaufort portion of the Crozier-Beaufort 'meta-colony'. Therefore, we did not further analyse emperor penguin population trends. We also did not include analysis of the Cape Royds Adélie penguin colony. After the mega-iceberg event, the Royds colony became overly affected by predation from skuas. As noted by Wilson *et al.* (2016), the skua:penguin ratio at Royds became too lopsided, resulting in lower reproductive success (Schmidt *et al.* 2021). That is, skua predation, perhaps more so than other environmental factors, has probably been the major regulatory effect on Royds colony growth during the past 20 years. We will be dealing with the Royds trend elsewhere (Ainley *et al.* 2024). The only published dataset of counts of Adélie penguins at Cape Crozier (Lyver *et al.* 2014) shows an

increase of ~40% between the years 2008 and 2009, which may not reflect the true change in number of breeding adults. We fit our model to this dataset to evaluate covariate effects explaining the observed growth (see details below). To increase confidence in our results, we also used an unpublished dataset consisting of ground counts of reference subcolonies (Ballard *et al.*, unpublished data to 2020). We fit the same statistical model to the latter dataset and compared slope estimates of model covariates from the two datasets (see Supplemental Material).

Antarctic toothfish catch. All toothfish catch information was derived from fishery reports made public by CCAMLR (2008, 2019) for FAO/CCAMLR Fishery Area 88.1 (summary of subareas S70, N70 and SRZ). In the latter summary, the proportions of the catch assigned to different size groupings (100–133 cm TL, ≥ 134 cm TL) were derived from graphs of the frequency distribution by size in the catch. *Fiji* image analysis software was used to partition the graphs according to size classes. We had to do this because the data are not available to the public.

Environmental variables. Spring–summer averages of wind speed and air temperature measured at McMurdo Station, which is at the southern edge of the study area, were derived from daily data provided by the University of Wisconsin (http://amrc.ssec.wisc.edu/usap/mcmurdo/). Annual averages of the amount of open water in Ross Sea polynyas, annual integrated primary productivity, chlorophyll concentration and SST (optimum interpolation SST) were derived from the Sea-viewing Wide-Field-of-View Sensor (SeaWiFS) and the Aqua satellite's Moderate Resolution Imaging Spectroradiometer (MODIS) using techniques described in Arrigo *et al.* (2015), where the early part of the time series was published (see also https://nsidc.org/data/g02202 and https://www.ncdc.noaa.gov/oisst; Reynolds *et al.* 2007, Meier *et al.* 2017). Annual average SIEs in the Ross Sea sector of the Southern Ocean were derived from passive-microwave data from the Scanning Multichannel Microwave Radiometer (SMMR), Special Sensor Microwave Imager (SSMI) and SSMI Sounder (SSMIS) instruments on a series of NASA and Department of Defense satellites, as described in Parkinson (2019).

Statistical methods

We calculated the year-to-year (annual) change for the Cape Crozier and Cape Bird Adélie penguin colonies, as well as for the Erebus Bay Weddell seal population from 1998 to 2018 (using the data shown in Figs 3–5). We used the natural log of the ratio N_t/N_{t-1} as our growth metric. There are several advantages to using this metric. Lack of year-to-year growth (i.e. $N_t = N_{t-1}$) results in a 0 value ($\log(1) = 0$). In addition, the log of the ratio of counts is relatively insensitive to substantial error in the estimation of the counts.

The annual growth data for the penguins and seals were analysed using an autoregressive integrated moving average (ARIMA) model; this method is widely used in the forecasting of time series data (Box *et al.* 2015). Details of how this modelling works are presented in the Supplemental Material.

The Weddell seal data were tested and did not warrant the use of an ARIMA model (i.e. ARIMA of (0,0,0) was preferred). Therefore, we explored the fit of competing linear multivariable models. We illustrate the effects of all significant covariates on population growth rates through partial dependence plots by varying the covariate of interest while keeping all other model covariates at their mean value and then predicting to this new dataset.

Model set construction and model selection. Models for both penguin colonies were fitted using the *ARIMA* function of the *forecast* package in *R* (http://www.r-project.org/). We built one model set for each colony, relating change in population size (i.e. $\ln(N_t/N_{t-1})$) to environmental (atmospheric and ocean) and fishing variables (Box 1). The three annual growth values for each mesopredator from 1998/1999 to 2000/2001 were excluded from the values analysed in order to allow at least a 3 year lag for all the variables and 3 years of cumulative data for the total toothfish of > 134 cm TL caught. Competing models for the Weddell seal dataset were fitted using the base linear model fitting function in *R*, *lm*. Per our hypotheses above, 3 year lags in effects were explored for primary production and 3–5 year lags were explored not just for toothfish removal effects but also for SIE, gyre speed and open-water extent. For all three datasets, a first model was built including all of the ocean, atmosphere and fishing variables (saturated

Table I. Results from first-order autocorrelation autoregressive integrated moving average modelling to evaluate annual growth of the Cape Crozier Adélie penguin colony, showing the autoregressive component and highest-ranked model components (Akaike information criterion ranking shown in Supplemental Material). Likelihood ratio test results are shown (df = 1).

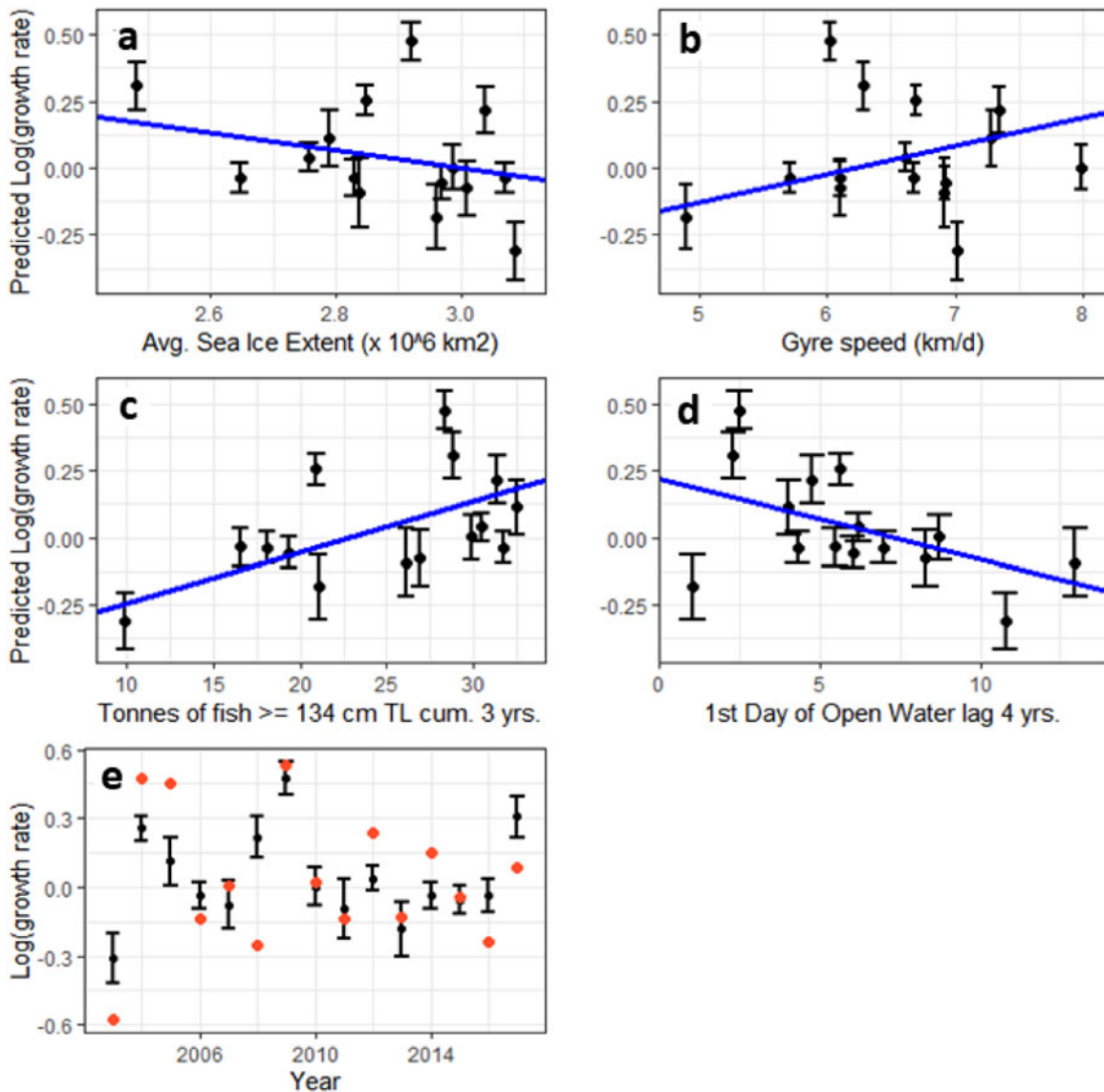| Variable	Estimate	SE	LRS (1)	*P*-value
1st-order autocorr.	-0.8014	0.2072	14.95	0.0001
Sea-Ice Ext. lag 4y	-0.2606	0.0812	-7.90	0.005
Gyre Speed, lag 4y	0.1161	0.0326	7.24	0.007
Air Temp., lag 5y	-0.0634	0.0316	-3.78	0.052
Open-Water Date Ross Sea polynya	-0.0182	0.0051	8.32	0.004
Cum. Fish_3y	0.0051	0.0028	2.62	0.106

Figure 13. Partial dependence plots for the Cape Bird Adélie penguin population growth model, showing the predicted influence on predicted log(growth rate) of: **a.** sea-ice extent ($\times 10^6$ km^2) Ross Sea sector, July–October average; **b.** Ross Sea gyre speed, July–October average; **c.** toothfish biomass removed, cumulative over 3 years; and **d.** first day that the Ross Sea polynya reaches 50% of maximum for that year. Bars show 80% confidence intervals. **e.** Predicted *vs* observed values: red dots are observed log(growth rate); black dots and bars are predicted log(growth rate) and 95% confidence intervals; blue lines indicate significant trends.

model) for which we had previous consistent hypotheses. Because the geophysical variables are to varying degrees correlated with one another, we inspected and included only the set of variables whose degree of collinearity did not result in a variance inflation factor (VIF) > 10 (Kutner *et al.* 2004). Thus, all variables included had VIF < 10, with a maximum VIF of 4.43.

Then, we used an information-theoretic approach (Burnham & Anderson 2002), with Akaike information criterion (AIC), inspection of effect sizes and likelihood ratio (LR) tests conducted by removing one variable at a

time to determine the best model(s). We started from models including all main effects and proceeded iteratively backwards, deleting non-significant terms, checking for improvement in the AIC values. The non-significance of the removed terms was further confirmed by adding them back into the final model one by one. During the selection process, when addressing Hypotheses 2 and 4 (above), 4 and 5 year lags for SIE and gyre speed and quadratic effects were included to check for significance and improvement in the model score. For Weddell seals we tested 6 year lags as well,

including for open water. Lastly, for all three datasets we compared results to a model with only the autocorrelation (for the penguin datasets) or intercept (for the seal dataset) as a null model. We selected the model with the lowest AIC value as our best model. However, when evaluating competitive models, we examined the maximized log-likelihood by fitting the reduced (by one variable at a time) model to ensure that small ΔAIC values were not solely the result of adding an additional, uninformative covariate to a preferred, more parsimonious model (Arnold 2010). Our final selected models were significant at or near $P = 0.05$, as determined by the LR test - a statistical test preferred to the Wald test, especially with small sample size (Hosmer *et al.* 2013).

All analysis code and data, including Jupyter Notebooks showing all of the above work (and also including what is included in the Supplemental Material), are available at https://zenodo.org/doi/10.5281/zenodo.10602315.

Results

ARIMA models present the data, along with autocorrelation functions (ACFs) and partial autocorrelation functions (PACFs). The detrended data were best fit by an ARIMA(2,1). The resulting residual plots indicate that an ARIMA(1,0,0) model (first-order autoregressive) without drift was needed to correct autocorrelation for the annual growth of both Adélie penguin colonies. The resulting residual plots for both colonies show that there was no obvious pattern or significant autocorrelation in the residuals, assuming first-order autoregression, and that they were normally distributed (Supplemental Material). The Ljung-Box test returned a P-value of 0.0968 for both Cape Crozier and Cape Bird.

Model selection

Adélie penguins. The best model relating annual growth of the Cape Crozier Adélie penguin colony includes SIE with a 4 year lag, gyre speed with a 4 year lag, 3 year cumulative fish (toothfish), air temperature with a 5 year lag and open-water date (AIC = -8.42; Table I & Supplemental Table 1). The slopes of the effects of these covariates are depicted in Fig. 13 & Table I. When cumulative fish weight increased (more larger, older fish removed from the food web), penguin population size increased ($\beta^\wedge_{fish} = 0.0051$, standard error (SE) = 0.0028). Similarly, annual colony growth showed a positive correlation with gyre speed with a 4 year lag ($\beta^\wedge_{gyreSPD} = 0.116$, SE = 0.033). Conversely, air temperature with a 5 year lag, SIE with a 4 year lag and

Table II. Results from first-order autocorrelation autoregressive integrated moving average modelling to evaluate annual growth of the Cape Bird Adélie penguin colony, showing the autoregressive component and highest-ranked model components (Akaike information criterion ranking shown in Supplemental Material). Likelihood ratio test results are shown (df = 1).

Variable	Estimate	SE	LRS (1)	*P*-value
1st-order autocorr.	-0.6012	0.2140	7.90	0.005
Sea-Ice Ext. Avg.	-0.3283	0.1504	3.80	0.051
Gyre Speed	0.1059	0.0503	5.10	0.024
Cumulative Fish 3 yrs	0.0191	0.0066	6.28	0.012
Open-Water Date Ross Sea polynya lag 4 yrs	-0.0304	0.0121	5.00	0.025

open-water date showed negative associations. When temperature or SIE increased or the open-water date was later in the season, the annual growth of the Cape Crozier colony decreased ($\beta^\wedge_{airtemp} = -0.0634$, SE = 0.0316; $\beta^\wedge_{OWdate} = -0.0182$, SE = 0.0051; $\beta^\wedge_{SeaIceExt} = -0.261$, SE = 0.081). The preferred model minimized AIC. LR tests leaving out one variable at a time showed that all included variables were significant at $P < 0.052$ or better, except for 3 year cumulative fish ($P = 0.106$; Table I). Excluding this variable increased AIC by 0.61 units (Supplemental Table 1), and therefore we included it in the selected model.

In Supplemental Table 4, we include the resulting slopes when fitting this model to the growth rates estimated from active nest density surveys (Ballard, unpublished data to 2020). Although only the autocorrelation component slope is significantly larger than 0, the P-values for the slopes are generally low (0.13–0.32), and their direction is the same - except for 3 year cumulative fish, for which the slope is very close to 0. Furthermore, slope values are relatively similar and confidence intervals notably overlap when comparing model outputs from the two datasets.

The results best explaining Cape Bird Adélie penguin colony growth come from models that contain average SIE, gyre speed, 3 year cumulative fish and open-water date with a 4 year lag (AIC = 7.78; see Table II, Fig. 14 & Supplemental Table 2 for details and slopes). Average SIE and open-water date with 4 year lag showed a negative correlation ($\beta^\wedge_{SIE} = -0.328$, SE = 0.150; $\beta^\wedge_{OWdate} = -0.0304$, SE = 0.0121). Thus, in years with a greater SIE during the preceding winter, annual growth of the colony was lower. In addition, Cape Crozier annual colony growth increased further when the open-water date occurred earlier in the spring. Finally, as is also true for Cape Crozier, cumulative fish had a positive effect on Cape Bird colony growth ($\beta^\wedge_{fish} = 0.0191$, SE = 0.0066). However, similar to Crozier, gyre speed had a positive effect on annual growth ($\beta^\wedge_{gyreSPD} = 0.106$, SE = 0.050). Excluding any
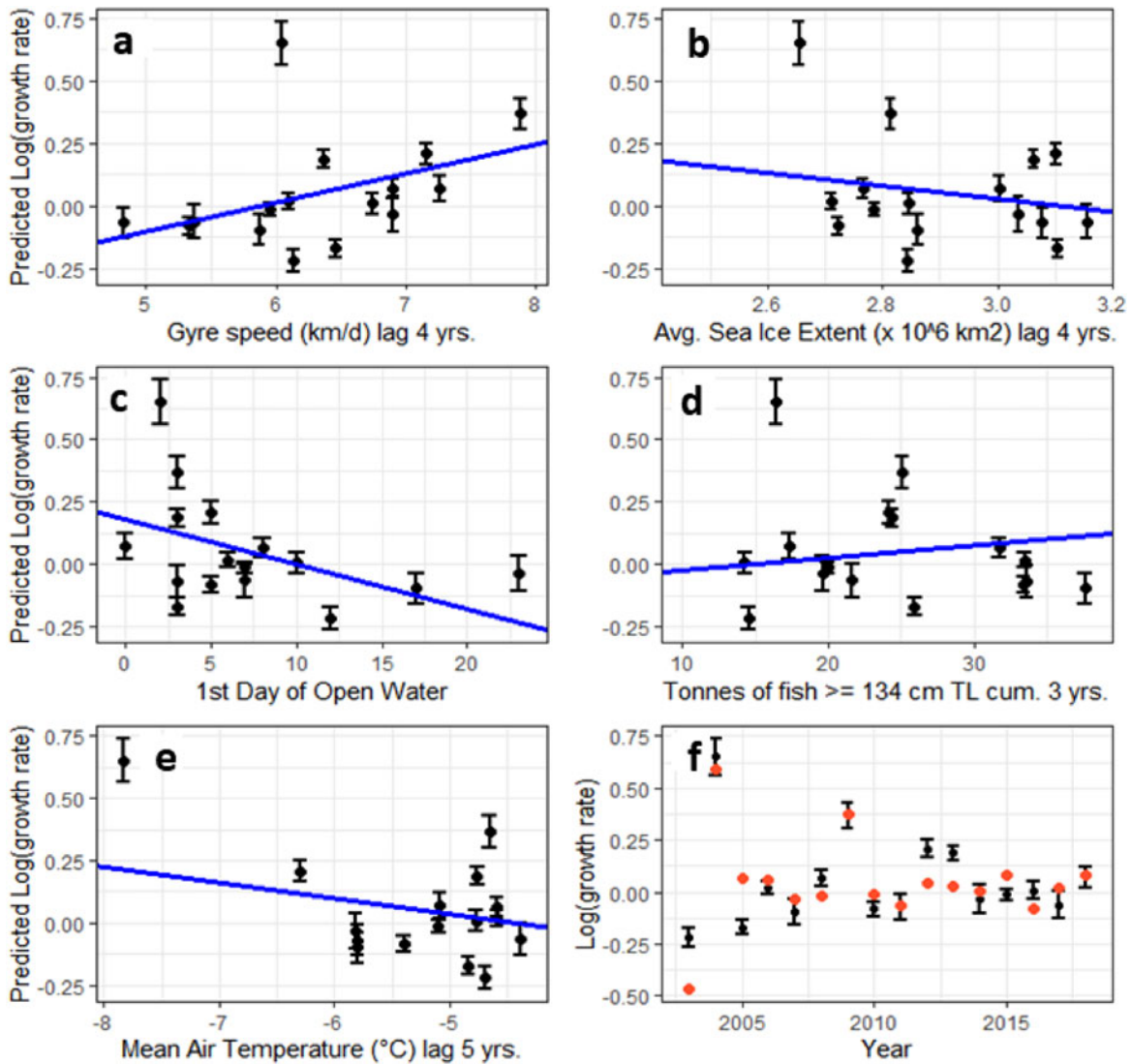
Figure 14. Partial dependence plots for the Cape Crozier Adélie penguin growth model, showing predicted influence on predicted log (growth rate) of: **a.** Ross Sea gyre speed, July–October averages, lag 4 years; **b.** sea-ice extent (x10^6 km^2) Ross Sea sector, July–October average, lag 4 years; **c.** first day that Ross Sea Polynya reaches 50% of maximum for that year; **d.** toothfish biomass removed, cumulative over 3 years; and **e.** air temperature at McMurdo Station, November–February average. Bars show 80% confidence intervals. **f.** Predicted *vs* observed values: red dots are observed log(growth rate); black dots and bars are predicted log(growth rate) and 95% confidence intervals; blue lines indicate significant trends.

one of the variables increased ΔAIC by > 2 units, except for average SIE. Excluding average SIE increased ΔAIC by 1.79 units, and thus we included all four variables in the final model. The coefficients for each of the four variables were significant at $P = 0.051$ or better (Table II). We note that the model with only the first-order temporal autocorrelation is a competitive alternative.

Weddell seals. The highest-ranking model relates annual growth of the Erebus Bay pupping aggregation to McMurdo Sound FIE, 3 year cumulative fish,

Table III. Results from the multivariable linear model for evaluating the Erebus Bay Weddell seal annual population growth rate, showing the highest-ranked model (Akaike information criterion ranking shown in Supplemental Material). Likelihood ratio test results are shown (df = 1).

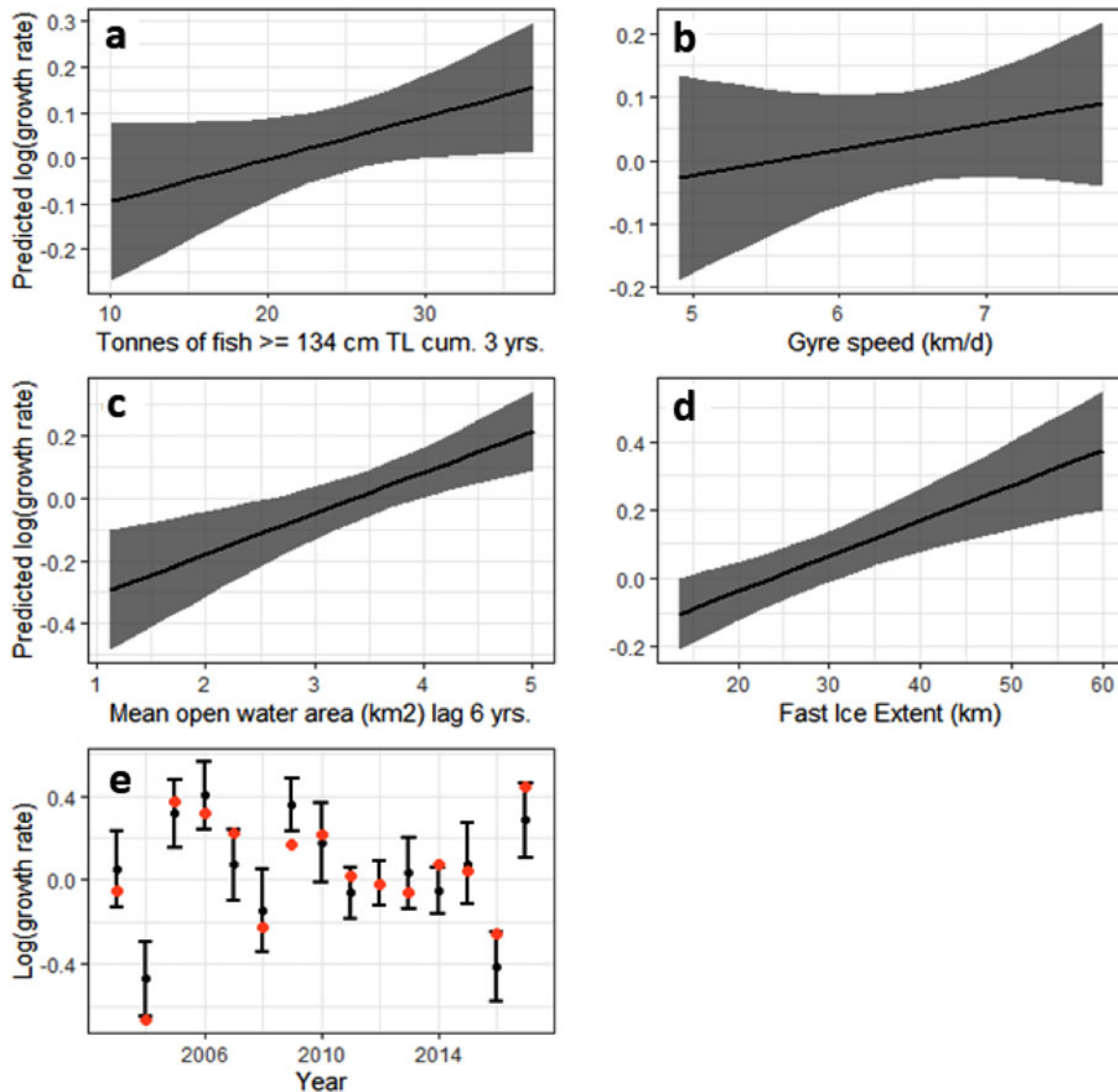| Variable	Estimate	SE	LRS (1)	*P*-value
Intercept	-1.2187	0.3845	-	-
Fast-Ice Extent	0.0103	0.0026	14.40	0.0001
Cumulative Fish 3 yrs	0.0094	0.0054	4.00	0.046
Open-Water Extent, *McMurdo Sound polynya lag 6 yrs*	0.1307	0.0370	12.16	0.004
Gyre Speed	0.0403	0.0444	8.66	0.003

Figure 15. Partial dependence plots for the Weddell seal population growth model, showing the predicted influence on predicted log (growth rate) of: **a.** toothfish biomass removed, cumulative over 3 years; **b.** Ross Sea gyre speed, July–October average; **c.** mean open water area when the Ross Sea polynya is > 50% of its maximum; and **d.** fast-ice extent (distance from McMurdo Station to the ice edge on 1 January). Shaded areas show 95% confidence intervals around black trend lines. **e.** Predicted *vs* observed values: red dots are observed log(growth rate); black dots and bars show predicted log(growth rate) and 95% confidence intervals.

open-water area (McMurdo Sound polynya) with a 6 year lag and gyre speed (AIC = -13.327). Model details are provided in Table III & Supplemental Table 3, and partial dependencies are depicted in Fig. 15. All of these covariates related positively to seal population growth. When gyre speed increased ($\beta\hat{}_{gyreSPD} = 0.0403$, SE = 0.0444), annual growth in seal numbers increased. The same is true for increases in FIE, open-water area with a 6 year lag and 3 year cumulative fish ($\beta\hat{}_{FIE} = 0.0103$, SE = 0.0026; $\beta\hat{}_{OW} = 0.131$, SE = 0.037; $\beta\hat{}_{fish} = 0.0094$, SE = 0.0054). LR tests demonstrated that each of the four variables was significant ($P = 0.046$ or better) in the final model (Table III).

Discussion

Potential effects of physical variables on population trends

A combination of physical and biotic factors appears to have facilitated increased population growth among penguins and seals in the south-western Ross Sea during the first decades of the twenty-first century. To what degree the observed changes are more the result of one *vs* the other remains an open question, but here we present some evidence that anthropogenic influences, indirectly from global-scale climate factors and directly from system-scale fishery extraction, may be behind the observed trends. Exhibiting limited population change

during the 1–2 preceding decades of climate-related change, around the year 2000 populations began to increase, reaching levels higher than when first assessed in the mid-twentieth century. Seal numbers exhibited dramatic growth, after extended stability at a lower number, and reached pre-exploitation levels. Due to sampling gaps, we were not able to model growth in emperor penguin colonies, but some of the factors affecting growth in the seal and Adélie penguin populations should apply to emperor penguins as well. All of these mesopredator species benefit from adjacent open water (giving greater access to prey, even if simply due to the need for less walking; Massom *et al.* 1998, Santora *et al.* 2020) and presumably from increased availability of high-quality prey (silverfish; Cherel & Kooyman 1998, Ainley *et al.* 2015b, 2018, Saenz *et al.* 2020).

Mean annual summer air temperature was positively correlated with annual growth of the Cape Crozier Adélie penguin colony, but the ecological or physiological reason behind this relationship is obscure. It could be related to thermoregulation, although we have no data for further evaluation. At the Antarctic Peninsula, humidity and snow/rainfall levels are high. Thus, penguins, and especially down-covered chicks, can get wet, which, if it is cold, could lead to thermoregulation issues; energy-sapping shivering results in lower chick mass at fledging (Salihoglu *et al.* 2001, Chapman *et al.* 2010, 2011). However, humidity is very low at Ross Island, and any periods inducing thermoregulatory issues, if any occur at all, would be brief (1–2 days) and thus would not compromise chicks over the duration of their growth period (as in the Antarctic Peninsula). Emmerson & Southwell (2022) presented analyses indicating that altered wind chill may explain trends in East Antarctic populations. Given their huddling during winter, emperor penguins could be affected by changes in air temperature (again, wind chill), but data on this are lacking. While rising air temperatures have resulted in retreating ice fields on nearby Beaufort Island, thus leading to Adélie Penguin colony increases (LaRue *et al.* 2013), neither Cape Crozier nor Cape Bird has lacked nesting space at least for the last 70 years.

The remaining physical oceanographic factors that we considered as possibly explaining seal and penguin population growth are related to wind strength. Wind plays an important role in variation in annual large-scale SIE (Turner *et al.* 2009), gyre speed (Comiso *et al.* 2011) and polynya behaviour (patterns such as size, development, etc.), especially coastal latent heat polynyas (Williams *et al.* 2007) within the Ross Sea. More wind promotes greater SIE, more rapid gyre speed and earlier development and faster expansion of latent heat polynyas. Wind also affects FIE in McMurdo Sound, with FIE becoming greater in winters having less

wind (Kim *et al.* 2018). The current modelling detected links to mesopredator population change regarding access to food supply. Increased wind facilitated Adélie penguin population-level increases during the 1950s–1990s (ostensibly through polynya action; Ainley *et al.* 2005, 2007). With easier prey access in nearby polynyas, penguins could compensate for competition from the recovering whale populations (Ainley *et al.* 2005, 2007). Wind data provided the most consistent and long-measured physical time series. In contrast, penguin populations also exhibited annual decreases - with a 4–5 year lag - with increased wind and thus large-scale SIE (Wilson *et al.* 2001). As noted elsewhere, a 4–5 year lag represents age of recruitment: more or fewer chicks in a year leads to a changed population 4–5 years later. Our analysis indicates that variation in large-scale SIE was probably a proxy for the more local effects of wind variation affecting polynya size and persistence. Polynya size and timing are critical to productivity and the chlorophyll signature, and wind plays a role in those factors as well (Arrigo 2007, Arrigo *et al.* 2015).

Adélie and most emperor penguin colonies are associated with polynyas (Massom *et al.* 1998, Santora *et al.* 2020), and thus it follows that an earlier opening and enlargement of the Ross Sea polynya could lead to penguin population growth (Ainley 2002). Our results showed a 4 year lag to polynya variation, with 4 years being the average age of recruitment in Adélie penguins (Ainley *et al.* 1983, Kappes *et al.* 2021). The lag might express juvenile survival (Wilson *et al.* 2001) and, in conjunction with local factors, might explain the effects of covarying large-scale SIE. More extensive ice was thought to compromise post-fledging survival as well as shifting individuals to winter farther from Ross Island, interfering with their eventual return. On the other hand, a year of high fledgling production would result in more recruits 4 years later; this is a more probable explanation.

The overall upward trend in SIE, evident into the 1990s (Wilson *et al.* 2001), plateaued in *c.* 1999. It had reached the southern boundary of the ACC, across which warmer water inhibited further expansion of the sea-ice field; annual variation could only be negative. Perhaps due to it no longer increasing, SIE lost some of its impact on penguin colony growth. Interestingly, Ross Island colonies subsequently exhibited their most dramatic growth, with most physical factors identified in our model (SIE, gyre speed and air temperature) exhibiting the 4–5 year lag effect. This substantiates the idea that population growth was largely mediated through higher recruitment of juveniles and not through higher survival of over-wintering penguins. At Cape Bird, which did not experience a similarly high growth, the analogous effect was evident only through a 4 year lag in the open-water date. No other physical factor had a lag effect.

Gyre speed, which positively affects SIE (Kwok et al. 2016, 2017), correlated positively with annual growth of Adélie penguin colonies at capes Crozier and Bird. Ice movement can aid or hinder penguin arrival at the colony in spring depending on the direction of ice movement, the route that penguins are traveling and how far away the sea-ice movement might have shifted the penguins from Ross Island during winter (Ballard et al. 2010). Jongsomjit et al. (2024) found that greater gyre speed assists penguin annual movement north during the winter, possibly resulting in greater energy conservation and higher survival rates, especially for fledglings. Returning to the colonies, a delay of a few days in arrival can be important, especially in the short summer period available to penguins at high latitudes. A strong gyre delays arrival at Cape Royds, just to the south of Cape Bird, causing the penguins to have to cope with more sea ice than the other Ross Island colonies (Ainley et al. 2024). The situation at Cape Bird and Cape Crozier seems to be the opposite. Apparently, moving ice helped the penguins in these colonies to arrive early.

The annual growth model of the Weddell seal pupping population in Erebus Bay shared some of the physical variables contained in the penguin models, although with some correlations in the opposite direction (SIE and open water). Both FIE and sea-ice cover (including pack ice) in McMurdo Sound were found to be important. FIE showed a positive relationship, which, because of its variation, we interpret to involve annual fast ice rather than multi-year ice (which failed to break out after the pupping season). Annual fast ice, with its more frequent and shallower cracks, allows more females to give birth successfully (Siniff et al. 2008). The extent of open water seemingly would signal the extent of fast ice to be sufficient to protect the seals and their pups from predatory killer whales (Orcinus orca; LaRue et al. 2019). Gyre speed is probably connected to ice movement during the winter preceding the pupping season. More movement of ice northwards in the western Ross Sea might affect seal dispersal and return (Beltran et al. 2017, 2021, Goetz et al. 2023).

Potential effects of changes in prey availability on population trends

One variable common to the models explaining trends in both Adélie penguins and Weddell seals is the cumulative take of toothfish > 134 cm TL that have been extracted from the Ross Sea over preceding 3 year periods (the effect is greater for the seals than the Cape Crozier penguins). The results are consistent with our hypothesis that removing large, neutrally buoyant toothfish would increase the availability of silverfish to the penguins and seals via competitive release (cf. Lyver et al. 2014, Pinkerton et al. 2016, Ainley et al. 2017).

Given their diet, emperor penguins might also benefit from the presence of more silverfish, which, owing to their high energy density, represent a major element of their diet (summarized in Ainley & Wilson 2023).

During the early 2000s, the commercial fishery had resolved how to catch the large toothfish; thereafter, the location of fishing effort was repeated annually, and take at ~3000 tonnes/year stabilized (with some annual variation; Fig. 9). Vessels repeatedly exploited the ideal habitat and its resident fish. Tag returns indicate that large toothfish appear to undertake limited movement (Hanchet et al. 2015). The anomalous changes in size class in 2017 and 2018 (Fig. 10) relate to the sparse sea ice in the fishing area, which removed the constraints on fishing location that affected fishing in most previous years (CCAMLR 2018a,b). The results are consistent with our hypothesis that removing large, neutrally buoyant toothfish, which occupy the upper water column, would increase the availability of upper-water-column silverfish to penguins and seals via competitive release. This is an arguably contentious proposition because there is no direct physical proof of such competitive release given the lack of any direct research and monitoring of subadult/adult silverfish (cf. Lyver et al. 2014, Pinkerton et al. 2016, Ainley et al. 2017). Although it is unrealistic to think that extractions of large adult toothfish would have no effect on the Ross Sea food web, the total biomass of observed Adélie penguin growth is far above that of the fish extracted, even a cumulative 3 year fish biomass (Pinkerton et al. 2016). Therefore, the mechanism whereby the release may be affecting penguin and seal growth could involve a complex shift in the Ross Sea food web as well as in the natural history patterns of toothfish.

Yet to be determined is the response of the emperor penguins to changes in prey availability, especially that of silverfish, which has not been directly studied. However, for the Adélie penguins, more silverfish fed to chicks leads to higher fledging mass and higher probability of survival and subsequent recruitment (Ainley et al. 2017, 2018). Foraging efficiency for the penguins, which increased with more energy-dense fish being available, would also contribute to survival in the post-fledging/post-breeding period. The importance of changes in those factors and the full demographic dynamics that have led to the population increase have yet to be ascertained.

For the Weddell seals, it appears that strong recruitment of females from several large birth cohorts (Garrott et al. 2012), combined with consistently high breeding probabilities since the end of the mega-iceberg event, may be responsible, at least in part, for the recent increases in numbers of pupping females (Rotella et al., unpublished data to 2019). Presumably, enhanced physiological condition among females would be

involved in this. Coping with 40% of body mass being lost during the pupping/breeding season (Wheatley *et al.* 2006) is helped by consuming large, energy-dense toothfish. For the seals to compensate for the loss of toothfish, silverfish would have to become much more abundant (Salas *et al.* 2017). As it is, silverfish are also energy dense, but they are many times smaller than the large toothfish taken by the seals (on the order of 0.05 *vs* 25 kg per fish dressed weight; Salas *et al.* 2017). The degree to which Weddell seals would have to alter their foraging behaviour (e.g. capturing a single large toothfish *vs* dozens of silverfish on each dive or making more dives) remains to be determined. Of course, the seals prey on other fish as well (Goetz *et al.* 2017, Beltran *et al.* 2021, Foster-Dyer *et al.* 2023), as do toothfish, especially benthic-dwelling fish species (Stevens *et al.* 2014, Parker *et al.* 2019).

Above the sea bottom, the penguins and seals mostly take near-adult and adult silverfish (≥ 12–13 cm for penguins and 20–25 cm for seals; Burns *et al.* 1998, Fuiman *et al.* 2002, Ainley *et al.* 2003). Due to their lower energy content, smaller silverfish are much less preferred (Hagen & Kattner 2017). The silverfish occur in loose schools as viewed by animal-born cameras under the ice, a situation in which they are harried by seals and other predators (Fuiman *et al.* 2002, Foster-Dyer, unpublished data 2018–2019). Thus, whether loose shoals are their usual pattern in the absence of seals is yet to be determined.

Temporal and spatial variability in the abundance of near-adult and adult silverfish, as noted above, is a critical unknown, other than the fact that they have been found to exhibit diel vertical migration (Fuiman *et al.* 2002, O'Driscoll *et al.* 2017). The annual variation in silverfish prevalence has never been examined in the Ross Sea nor anywhere else, to the best of our knowledge. Such an effort would require repeated use of an ice-strengthened ship and acoustic assessment on an established grid (O'Driscoll *et al.* 2017). This has been done only for krill in the Antarctic Peninsula region (https://pallter.marine.rutgers.edu/research-groups/research/). Acoustic surveys (O'Driscoll *et al.* 2017) as well as modelling based on environmental variables (Davis *et al.* 2017) indicate that adult silverfish are widely distributed in shelf waters (see also DeWitt 1970). Adult silverfish range from near the surface to 900 m in depth, with the larger life stages occurring deeper (La Mesa & Eastman 2012). Based on a food web model, Pinkerton *et al.* (2010) estimated ~410 000 tonnes of silverfish in the shelf waters of the entire Ross Sea (all age classes). Using acoustics and cruise tracks, O'Driscoll *et al.* (2011) estimated ~600 000 tonnes of silverfish, concentrated at 200–600 m deep; O'Driscoll *et al.* (2017) concluded that ~206 000 tonnes of that biomass should be adults (>15 cm TL; La Mesa & Eastman 2012).

Available adult silverfish biomass is important for mesopredators and a number of other predators (Eastman 1985, Hagen & Kattner 2017). How this biomass is eventually consumed by mesopredators depends on their ability to dive relative to silverfish presence (cf. Pinkerton *et al.* 2016, Ainley *et al.* 2017). As revealed by studies in McMurdo Sound, as the prevalence of large toothfish decreases, fewer occur in shallower depths. This could be an intraspecific density-dependent response (fewer competing fish leads to less incentive to rise from the bottom (i.e. to spread out) in search of food) and/or a result of depletion at shallow depths by predators (Ainley *et al.* 2020). Without toothfish predation, especially in ice-covered seas, silverfish should be more available in upper portions of the water column exploited by competitors and other predators. This is an aspect of intraguild predation, with the seals depleting the presence of and thus competition with the most easily accessible toothfish (Fig. 1; Ainley *et al.* 2020).

Some proportion of the near-adult and adult silverfish that occur over the Ross Sea shelf is available to Weddell seals and emperor penguins, both of which forage mostly to 400 m (although they do forage as deep as 800 m; Burns & Kooyman 2001, Kooyman *et al.* 2020, Beltran *et al.* 2021, Goetz *et al.* 2023, Foster-Dyer, unpublished data 2018–2019). Even foraging as deep as 400 m increases energy expenditure and so is not the preferred strategy (Beltran *et al.* 2017). Weddell seals forage at shallowest depths (80–100 m) during December–January, when the annual phytoplankton bloom appears to entice zooplankton and fishes near to the surface (Salas *et al.* 2017, Beltran *et al.* 2021, Foster-Dyer *et al.* 2023). In the upper 400 m of the water column, the silverfish biomass (< ~100 000 tonnes) would be contested among the seal, penguin and toothfish populations. Adélie penguins forage typically at 50–80 m (but they can forage as deep as 180 m). Thus, ~30 000 tonnes of Ross Sea silverfish would be accessible to them (Ainley *et al.* 2017). While these penguins are foraging to feed chicks (December–January), they appear to compete most with Weddell seals.

Given the importance of adult and near-adult silverfish to the Ross Sea food web (La Mesa *et al.* 2004, 2012) and especially to globally significant numbers of Weddell seals, the two penguin species and Antarctic toothfish (> 84 000 Weddell seals, 250 000 emperor penguins and 3 000 000 Adélie penguins, inferred from breeding population numbers given above), silverfish abundance at depths < 400 m may be sufficiently low to facilitate intense competition among these mesopredators. Seals and penguins can reduce the availability of their prey within respective colony-based central-place foraging ranges (see some of the 'experiments' detailed above), lending support to this contention (see Testa *et al.* 1985, Ainley *et al.* 2015a, Ballard *et al.* 2019). In particular, Saenz

et al. (2020) showed that when seals vacate the McMurdo Sound fast-ice edge, the penguins foraging there increase their take of silverfish. Intraguild predation (see Ainley *et al.* 2020), exacerbated by the addition of commercial fishing as another predator (Fig. 1), and increasing numbers of seals may be important. Such would be the basis for the increased availability of silverfish to the three mesopredators hypothesized in the present paper as a response to major reductions in the prevalence of competing, upper-water-column-dwelling toothfish.

Conclusions

Although correlation does not necessarily imply causation, the patterns revealed herein are worthy of consideration. On the basis of these patterns, it appears that in the Ross Sea the structure and function of the water column food web, which the RSRMPA is designed to protect, have been changing. Ocean properties and sea ice had been changing, as chronicled over several decades, are probably impacting mesopredator populations and will continue to do so in the future. However, it was not until the turn of the twenty-first century with commencement of the toothfish fishery (including a rise in IUU fishing, since removed) that seal and penguin populations began to change significantly, suggesting cumulative impacts. This concurrence in timing is what is particularly intriguing. A major trophic competitor of seals and penguins - toothfish - began to be removed, and, owing to their slow maturation in accord with a K-selected life history strategy, few have since been replaced, especially in the water column. We suggest on the basis of our results that the fishery has had a significant negative impact on the ecosystem. While the pelagic portion of the Ross Sea food web has not been monitored directly, change in structure and function is apparently occurring, as revealed by trends in indicator species.

Increasing numbers of penguins and seals are usually viewed to be the results of positive management actions, but in the context of the RSRMPA's goals these could be deemed negative. These changes could be affecting the availability of crystal krill, a main prey species of silverfish, thus also affecting competition between silverfish and other notothenioid fish. While the RSRMPA is a first step towards maintaining the 'structure and function' of the Ross Sea food web (or ecosystem), stronger fisheries management for the waters bordering the MPA is also needed. Fishing for toothfish needs to be evaluated relative to its apparent impacts on the Ross Sea ecosystem and water column food web, especially under conditions of environmental change (as mandated under Article II of the Convention for the Conservation of Antarctic Marine Living Resources (CAMLR Convention)). By itself, reducing by 50% the prevalence of a major water column predator is a change in food web structure. If a 50% reduction in spawning biomass catch by humans remains the goal, achieving it might not fulfil CCAMLR's attempt at ecosystem-based management and preservation of the current Ross Sea ecosystem's 'structure and function'. The initial justification for CCAMLR's fishing rules for toothfish in the Ross Sea was that they are not the prey of seals or penguins and so can be significantly depleted - much more than krill (see Constable *et al.* 2000). That assumption has since been proved incorrect, as detailed in a number of studies, and deserves timely re-evaluation. That would best be undertaken coincident with the planned, first 10 year evaluation of whether the RSRMPA is effectively meeting its objectives (2027).

Disclaimer

The findings and conclusions in this paper are those of the authors and do not necessarily represent the views of the National Marine Fisheries Service, NOAA. Mention of trade names and commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

Author contributions

Following discussions among coauthors about the phenomenon (increasing seals and penguins) leading to a 'need' for this analysis, virtually all coauthors contributed data, either of population or environmental trends, both published and unpublished. The analysis was completed by VM, LS and NN, with help from DGA. The main writing was done by these persons, although all other coauthors reviewed the various drafts and offered detailed suggestions for alterations.

Competing interests

The authors declare none.

Supplemental material

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