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Workshop report and synthesis: United States research and monitoring in support of the Ross Sea region Marine Protected Area

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WORKSHOP REPORT AND SYNTHESIS: UNITED STATES RESEARCH AND MONITORING IN SUPPORT OF THE ROSS SEA REGION MARINE PROTECTED AREA

26-27 April 2021

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The Ross Sea region Marine Protected Area (RSRMPA), after several years of deliberations, was designated by CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) in 2016, coming into force in 2017 (via CCAMLR Conservation Measure 91-05). Helpful was Halpern et al. (2008, Science), who summarized global information up to 2003, and showed independently that the Ross Sea was the least anthropogenically affected stretch of ocean on the planet. Certainly, it deserved protection. In a 2008 'bioregionalization,' exercise, CCAMLR also identified the Ross Sea shelf and slope as being important for inclusion in a network of MPAs (SC-CAMLR XXVII). CCAMLR has subsequently agreed to adopt a system of MPAs, which now includes the RSRMPA and the South Orkney Islands Southern Shelf MPA (designated in 2009). The RSRMPA was established to be consistent with CCAMLR's own articles of incorporation, having the goals of conserving marine living resources, maintaining ecosystem structure and function, protecting vital ecosystem processes and areas of ecological significance, and promoting scientific research (for full list of 11 objectives, see Conservation Measure 91-05, paragraph 3).

Soon after the RSRMPA came into force, a Research and Monitoring Plan (RMP) was developed (SC-CAMLR-XXXVI/20) and endorsed by CCAMLR's Scientific Committee (CCAMLR-XXXVI, para 5.45). The RSRMPA RMP lists 38 research and monitoring topics (SC-CAMLR-XXXVI/20, Table 1), and outlines priority elements (SC-CAMLR-XXXVI/20, Table 4), relevant to the objectives of the MPA. The RMP identifies key indicators (and 'indicator species') for evaluating ecosystem change and ultimately effectiveness of the RSRMPA. These indicators are: (i) Numbers of nesting pairs of Adélie (Pygoscelis adelieae) and emperor penguins (*Aptenodytes forsteri*); (ii) Numbers of Weddell seals (*Leptonychotes weddellii*) and type C killer whales (*Orcinus orca*); (iii) Biomasses of Antarctic krill, crystal krill (*E. crystallorophias*), Antarctic silverfish (*Pleuragramma antarcticum*), and Antarctic toothfish (*Dissostichus mawsoni*); and (iv) Densities of benthic taxa that constitute vulnerable marine ecosystems. The two primary threats that might change ecosystem structure and function in the Ross Sea region are climate change and fishing. In this vein, overall, the goal of research and monitoring is to detect the effects of fisheries, and separate them from climate change, in any alteration of the Ross Sea food webs and ecosystem. Candidate baseline data for these indicators, including zone-specific estimates, were gathered, presented to SC-CAMLR, and added to the CCAMLR GIS database (SC-CAMLR-XXXVII/11, SC-XXXVII-BG-13). Since the RSRMPA came into force, several Member States have been actively pursuing research and monitoring in support of the MPA (see e.g., SC-CAMLR-39/BG/32, SC-CAMLR-39/BG/53), including the United States (see e.g., SC-CAMLR-39/BG/17).

With the goal of collating, synthesizing, and working towards coordination of U.S. research and monitoring in the RSRMPA, the U.S. Ross Sea science community convened a virtual workshop on 26-27 April 2021. The workshop included 51 participants (see Appendix A) representing active U.S. Ross Sea scientists as well as representatives of major U.S. science funding institutions (National Science Foundation - Office of Polar Programs, OPP, NASA, NOAA, Pew Charitable Trusts, and Schmidt Ocean

Institute). The array of participants was multi-disciplinary, with Ross Sea expertise spanning biophysical (weather, sea ice, physical oceanography, polynyas, primary productivity, climate effects and variability), forage species (silverfish, krill), mesopredators (toothfish, seals, penguins, whales), benthos, pollution and wildlife health (see Appendix A). The workshop goals were to identify, collate, assess, and synthesize research conducted by U.S. researchers in the Ross Sea since 2010, and seen to be relevant to the goals of the MPA (defined in CCAMLR Conservation Measure 91-05). This was done via participants' summary presentations of research in their areas of expertise (see Appendix A) and gathering all published U.S. Ross Sea region research since 2010 (see Appendix C), as well as currently funded research (see Appendix D). Further goals were to discuss and identify gaps in RSRMPA research and monitoring, determine ways to fill those gaps, elucidate critical uncertainties regarding the Ross Sea ecosystem structure and dynamics (see Appendix B), and develop ideas for coordination between ongoing and future research in the RSRMPA. Below we provide a summary of ongoing and, since 2010, peer-reviewed U.S. Ross Sea research of relevance to meeting the objectives and possible future updates of the RSRMPA and RMP. We also note critical uncertainties, data gaps and actions the workshop participants consider necessary to address them.

SUMMARY OF UNITED STATES ROSS SEA RESEARCH

The U.S has a long history of marine research in the Ross Sea and surrounding waters akin to a *de facto* Long-Term Ecological Research project (two of which OPP already funds), particularly for McMurdo Sound and the adjacent waters (see Appendix C; for a directed literature review, see CCAMLR 2010a, CCAMLR 2010b, CCAMLR 2010c; also Smith et al. 2012, 2014). Oceanographic structure of the Ross Sea was elucidated in the 1960-70s by surveys conducted by the *USNS Eltanin*, and continued by ocean sampling from U.S. Coast Guard icebreakers, important research platforms for a region covered extensively by sea ice for 9-10 months of the year (see, e.g., Jacobs 2006, Phil Trans R Soc). The pace of U.S. ocean science in the Ross Sea increased with the acquisition of the *R/V N.B. Palmer* in 1992 and increased international collaborations that made use of additional vessels. Subsequent and ongoing U.S. research identified decreasing Ross Sea salinity caused by upstream melt of ice shelves feeding into the adjacent Amundsen Sea and subsequently delivered to the Ross Sea via the coastal current. But recently, ocean salinity decreases have (perhaps temporally) abated or even reversed (c.f., Jacobs et al. 2002, Science; Castagno et al. 2019, Nature Communications; Silvano et al. 2020, Nature Geosciences). Investigations have documented the intrusion of warm Circumpolar Deep Water into the Ross Sea's several submarine canyons (Dinniman et al. 2011). Finally, deployment of probes through holes drilled through the Ross Ice Shelf, as well as instrumented seals, have extended the spatial breadth of Ross Sea sampling, including both its physics and biota under the shelf (e.g., Kim 2019).

The Ross Sea and adjacent offshore ocean is one of the most heavily ice-covered areas in the Southern Ocean (Comiso et al. 2011, Kwok et al. 2017). Sea-ice dynamics are complex, and this area also shows the strongest increase in sea ice with time (1979-present), even despite considerable seasonal to decadal variability, including recently several years of relative decreased sea ice (Parkinson 2019). Therefore, the physical dynamics of the Ross Sea region have been of central interest. Since the late 1970s, with the development of microwave and visual sensors deployed on satellites, mostly by the U.S. National Aeronautics and Space Administration (NASA), associated researchers have monitored the changing sea-ice regime of the Ross Sea and surrounding ocean. The relationship of annual and seasonal sea-ice variability to fluctuations in decadal and long-term climate modes, such as the Southern Annular Mode, has been emphasized (e.g., Kwok et al. 2016). Due to increasing winds – which U.S. researchers have monitored – sea-ice extent, and also sea-ice season, have been increasing in the Ross Sea region, unlike what is occurring in lower latitude portions of the Southern Ocean (e.g., Thompson & Solomon 2002, Science; Stammerjohn et al. 2012). These sea-ice trends have important implications for altering the structure and dynamics of the Ross Sea ecosystem, including ocean access, primary productivity, and the numerical and functional relationships among higher trophic level species and populations (e.g., Massom

& Stammerjohn 2010, Arrigo et al. 2015). Fast ice prevalence shows no discernable trend, though, at least in McMurdo Sound, the date of minimum fast ice extent occurs later and date of fast ice advance occurs earlier (Ainley et al. 2015, Kim et al. 2019).

Although dominated by sea ice (often snow-covered) that shields the ocean from sunlight, the Ross Sea is spectacularly productive, due largely to its latent and sensible heat polynyas (Jacobs & Comiso 1989, JGR; Arrigo et al. 2015). U.S. research identified the processes that enhance the heightened productivity of polynya marginal ice zones (MIZ), a finding applicable to both polar regions (Smith & Nelson 1985, Science). Through water column sampling and remote sensing from satellites, the phytoplankton dynamics and productivity of the Ross Sea, which contribute as much as 28% to total Southern Ocean production (Arrigo et al. 1998, JGR), have been well studied by U.S. researchers (e.g., summary in Smith et al. 2014). This effort included decades of research on sea-ice microbial communities (SIMCO), mostly within McMurdo Sound fast ice (e.g., Soohoo et al. 1987, MEPS), an understanding especially important to the sympagic portion of the Ross Sea ecosystem, as well as other directed programs (e.g., ROAVERRS, Ditullio & Dunbar 2003, ARS 78).

The Ross Sea neritic biota is represented by both benthic and water column communities. While U.S. research first mapped, by camera, the characteristics and diversity of benthic communities throughout the southwestern Ross Sea (Barry et al. 2003, ARS 78), most researchers concentrated on the benthic communities of McMurdo Sound, accessible from McMurdo Station, by using the fast ice as a platform without vessel support. That biotic community's response to ocean-climate regime shifts, now a well-researched subject the world over, was first discovered during these efforts, and continues to be important in ongoing research (e.g., Dayton 1989, Nature; Dayton et al. 2019). Extensive effort also has been made to investigate effects of pollutants emanating from McMurdo Station, and biotic responses to its recent amelioration (Kim et al. 2010).

In general, the water column biota, apart from phytoplankton, is not well researched in the Ross Sea. U.S. researchers characterized the Ross Sea fish fauna early on and investigated interspecific interactions within the food web (e.g., DeWitt 1970, in Antarctic Ecology (Holdgate, ed.); Eastman 1985, PB**)**. Subsequently, most U.S. fish research has focused on physiology and genetics, which have only indirect relevance to differentiating climate-change effects from those of fishing in the alteration of food web structure and dynamics in the Ross Sea. A spin-off of the physiological research is the longest record of catch per unit effort of an Antarctic fish (toothfish), as a measure of prevalence, and subsequently the main target of Ross Sea fisheries (Ainley et al. 2013). Most recent U.S. research on Ross Sea fish, and zooplankton, besides describing new species (e.g., Dayton & Hammerstrom 2018), has come from multiple-year studies of the diets of upper level predators. On some occasions these efforts have been accompanied with acoustically equipped ocean buoyancy gliders to quantify the preyscape, and an acoustic survey of zooplankton, krill, and fish in McMurdo Sound using a remotely operated vehicle (ROV) deployed through the fast ice (e.g., Saenz et al. 2020).

The main upper trophic level predators of the Ross Sea – Weddell seals, killer whales, minke whales (*Balaenoptera bonaerensis*), Adélie penguins and emperor penguins – are the best known of anywhere south of the Antarctic Polar Front, with the U.S. contributing centrally to the effort. The only demographic studies – using marked, known-age, known-history individuals, extending for ~50 years for Weddell seals and ~25 years for Adélie penguins – were conducted at Ross Island and led by U.S. researchers (see Appendix C). Changes in demographic variables, as well as foraging dynamics, have been measured against bio-physical processes in the surrounding ocean, as well as interspecific, competitive interactions, involving toothfish, penguins, seals and whales. Included are activities throughout the polar year thanks to the advent of microtechnology and the science of biologging (see Appendix C & D).

As indicated above, the populations of Weddell seals, and the two penguin species, have been tracked closely by U.S. researchers for several decades (in collaboration with New Zealand scientists) using aerial surveys when possible (Lyver et al. 2014, Kooyman & Ponganis 2017). In the case of the seals, many surveys have been conducted using snowmobiles (Ainley et al. 2015, 2020). Recently, this effort has been made easier through the use of high-resolution satellite imagery and aerial vehicle (e.g., drones) techniques pioneered and instituted by U.S. scientists (LaRue et al. 2014, 2019; Shah et al. 2020). The importance of such population monitoring is enhanced by coincident demographic and foraging behavior studies that indicate the possible causes and effects of observed changes in the sizes, age/sex compositions and productivity of these indicators of systemic changes (e.g., Kappes et al. 2021).

During the last two years, several initiatives have continued into 2021 largely unaffected by the Covid-19 pandemic (see Appendix D). At least 10 NSF-/NASA-supported, satellite studies have been investigating sea-ice dynamics and oceanographic factors affecting the Ross Sea, including four investigations of the Ross Gyre and three of Circumpolar Deep Water intrusions into canyons of the continental shelf. These broader areas of ocean research have had and will continue to have important implications for the Ross Sea biota. Monitoring of meteorological conditions, using remote stations, is also on-going. Three projects are investigating the productivity 'hotspot' in the Ross Sea across scales, including polynyas and primary productivity. Integrating into those efforts are seven projects focused on the demography and foraging ecology of the 'indicator' Adélie penguin, emperor penguin, and Weddell seal, including direct linkage to spatial aspects of their preyscape in the southern Ross Sea.

WORKSHOP SUMMARY

From the synthesis and workshop discussions, several things stand out.

First, the sheer quantity and breadth of U.S. Ross Sea research compares in scope to a large, complex, and long-running Long Term Ecological Research (LTER) program (as funded by the NSF OPP for McMurdo Dry Valleys and Palmer Station), especially in and adjacent to McMurdo Sound. These studies will continue to be, foundational in: (1) assessing and monitoring the effectiveness of the RSRMPA in differentiating the effects of climate change and fishing on the structure and dynamics of the Ross Sea regional food webs; and (2) determining how management of regional fisheries may need to be adapted to account for the population and ecosystem effects of climate change. The southwestern Ross Sea is especially well studied, though critical uncertainties and gaps remain in understanding both fished and forage species – especially the distributions, interannual variations in abundance, and interactions of toothfish, krill and silverfish, which are important to penguins and seals. The eastern Ross Sea is much less studied, yet based on movement and spatial utilization of key 'indicator' species (e.g., Goetz et al. 2018), is emerging as a critical location for future research (see Ainley et al. 1984, AOU Monograph; Ballard et al. 2012). Future field-based studies, and annual monitoring, of forage species are critically needed across the Ross Sea. Far more than the well-studied seals and penguins, critical uncertainties remain regarding the life history of Antarctic toothfish, another 'indicator' species. These include: actual abundance; location, timing and frequency of spawning; and dispersal of eggs, including the role of Ross Gyre; location of post-larval and juvenile fish; proportions of adult fish migrating; spawning ground residence time; and population genetics. The impacts of climate change on the toothfish population remain largely unquantified. Without this kind of information, separating the ecosystem, effects of fishing from those of climate will remain challenging.

Second, the two factors most critical to changing ecosystem structure and function in the Ross Sea are climate change and fishing. While there can be no doubt that, if there is adequate baseline information and appropriately structured monitoring, Adelie and emperor penguins, Weddell seals, and killer whales can provide indications of possible adverse ecosystem changes caused by ongoing climate changes and/or fishing (see for instance, Lyver et al. 2014, Ainley et al. 2017). The aforementioned long-term U.S.

supported penguin and seal studies in the southwestern Ross Sea meet both these conditions and, if continued, will provide useful information about the nature and possible causes of changes in population sizes and composition. Moreover, high-resolution satellite imagery will mitigate lack of research vessels, but more importantly provide a larger scale context of population change. However, baseline and monitoring studies in sites elsewhere will be of great value. These study sites should be included in CEMP, similar to elsewhere in Antarctica (e.g. Scotia Sea, East Antarctica) where monitoring representative colonies of krill-dependent penguins and fur seals (*Arctocephalus gazella*) is prevalent. This would help in informing if (and how) climate change and/or fishing is changing ecosystem structure and function in the Ross Sea. Fishing, in the context of climate change, needs to be better studied and monitored for its ecosystem impacts. Additional field and monitoring studies on forage species (as noted above), benthic communities, and toothfish need to be conducted. Importantly, while the MPA has no capacity to protect the Ross Sea ecosystem from climate change, a well-executed RMP can separate fishing from climate effects, thus providing the scientific information needed to enhance the ecosystem's resilience to anthropogenic influence.

Third, workshop participants highlighted a critical need for studies that integrate ecological processes with physical oceanographic change to facilitate a better understanding of alterations of Ross Sea ecology. For example, physical processes are hypothesized to heavily influence biological processes (e.g., how Ross Sea toothfish utilize or cope with currents, e.g. Ross Gyre, during their spawning migrations), yet these are not well understood, nor are these connections defined in the RSRMPA RMP priority elements. In this vein, workshop participants believe the development of an integrated biophysical model that feeds into a comprehensive ecosystem model for the Ross Sea would help determine research and monitoring needs and priorities as well as help interpret sparse observations and biophysical linkages. Such a coupled modelling system could then be used not only to better inform how the integrated system is currently functioning, but also how fishing and climate change may impact the Ross Sea ecosystem and how the MPA might better meet its objectives.

Finally, while LTER-equivalent research has been underway in McMurdo Sound and southwestern Ross Sea for decades (covering sea ice, weather, physical oceanography, biological oceanography, seal and penguin population change, toothfish prevalence, and changes to the shallow benthos), the funding for this research is not stable, nor has the planning and execution of the various components been coordinated. Research in the U.S. Antarctic Program regarding the Ross Sea depends almost entirely on funding of peer-reviewed unsolicited proposals by the NSF-OPP, supplemented with additional funding by NASA and other agencies. Workshop participants noted the need for more stable and long-term funding, including funding specifically aimed at determining whether the objectives of the RSRMPA are being met and, if not, what in the RMP or the MPA itself may improve RSRMPA outcomes. Multi-agency contributions and coordination will be essential. Participants also noted the need for more coordination among projects – which the workshop directly facilitated – as well as continued and more collaboration and coordination between other Member States doing research and monitoring in the RSRMPA. Overall, the U.S. Ross Sea science community was enthusiastic to contribute to research and monitoring of the RSRMPA, including contributing to the forthcoming MPA review.

References Cited

Ainley, D.G., E.F. O'Connor, and R.J. Boekelheide. 1984. The Marine Ecology of Birds in the Ross Sea, Antarctica. *Ornithological Monographs No. 32.* The American Ornithologists' Union. Washington D.C.

Ainley, D.G., N. Nur, J.T. Eastman, G. Ballard, C.L. Parkinson, C.W. Evans, and A.L. DeVries. 2013. Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo Sound, Antarctica, 1972-2011. Fish and Fisheries 14: 343-363, doi:10.1111/j.1467-2979.2012.00474.x.

Ainley, D.G., G. Ballard, R.M. Jones, D. Jongsomjit, S.D. Pierce, W.O. Smith, Jr., and S. Veloz. 2015. Trophic cascades in the western Ross Sea, Antarctica: revisited. Marine Ecology Progress Series 534: 1–16, doi:10.3354/meps11394.

Ainley, D. G., M.A. LaRue, I. Stirling, S. Stammerjohn, and D.B. Siniff. 2015. An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast. Marine Mammal Science, doi:10.1111/mms.12220.

Ainley, D.G., E.L. Crockett, J.T. Eastman, W.R. Fraser, N. Nur, K. O'Brien, L.A. Salas, and D.B. Siniff. 2017. How overfishing a large piscine mesopredator explains growth in Ross Sea penguin populations: a framework to better understand impacts of a controversial fishery. Ecological Modelling 349: 69-75.

Ainley, D.G., P.A. Cziko, N. Nur, J.J. Rotella, J.T. Eastman, M. LaRue, I. Stirling, and P.A. Abrams. 2020. Further evidence that Antarctic toothfish are important in Weddell seal diet. Antarctic Science, doi:10.1017/S0954102020000437.

Arrigo, K.R., et al., Primary production in Southern Ocean waters. Journal of Geophysical Research: Oceans, 1998. 103(C8): p. 15587-15600.

Arrigo, K.R., G.L. van Dijken, and A.L. Strong. 2015. Environmental controls of marine productivity hot spots around Antarctica. Journal of Geophysical Research 120: 5545–5565, doi:10.1002/2015JC010888.

Ballard, G., D. Jongsomjit, S.D. Veloz, and D.G. Ainley 2012. Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. Biological Conservation 156: 72-82.

Barry, J.P., J.M. Grebmeier, J. Smith and R.B. Dunbar. 2003. Oceanographic Versus Seafloor- Habitat Control of Benthic Megafaunal Communities in the S.W. Ross Sea, Antarctica. American Geophysical Union, Antarctic Research Series, Volume 78.

CCAMLR. 2010a. Ross Sea Bioregionalization, Part I: Validation of the 2007 CCAMLR Bioregionalization Workshop Results Towards Including the Ross Sea in a Representative Network of Marine Protected Areas in the Southern Ocean. WG-EMM-10/11

CCAMLR. 2010b. Ross Sea Bioregionalization, Part II: Patterns of Co-Occurrence of Mesopredators in an Intact Polar Ocean Ecosystem. WG-EMM-10/12

CCAMLR. 2010c. Bioregionalisation and Spatial Ecosystem Processes in the Ross Sea Region. WG-EMM-10/30.

CCAMLR. 2016. Conservation Measure 91-05, Ross Sea Region Marine Protected Area.

Dayton, P.K., and K. Hammerstrom. 2018. A hagfish at Salmon Bay, McMurdo Sound, Antarctica? Antarctic Science 30: 243–244.

Dayton, P.K., S.C. Jarrell, S. Kim, E. Parnell, S.F. Thrush, K. Hammerstrom, and J.J. Leichter. 2019. Benthic responses to an Antarctic regime shift: food particle size and recruitment biology. Ecological Applications 29(1), p.e01823.

DeWitt, H.H. 1970. The character of the midwater fish fauna of the Ross Sea, Antarctica. In: Holgate MW (ed) Antarctic ecology, vol 1. Academic Press, London, pp 305–314.

Dinniman, M.S., J.M. Klinck, and W.O. Smith, Jr. 2011. A model study of Circumpolar Deep Water on the West Antarctic Peninsula and Ross Sea continental shelves. Deep-Sea Research II 58: 1508–1523.

Castagno, P., Capozzi, V., DiTullio, G.R. et al. 2019. Rebound of shelf water salinity in the Ross Sea. Nat Commun 10, 5441. https://doi.org/10.1038/s41467-019-13083-8

Comiso, J. C., R. Kwok, S. Martin, and A. L. Gordon. 2011. Variability and trends in sea ice extent and ice production in the Ross Sea. Journal of Geophysical Research 116, C04021, doi:10.1029/2010JC006391

Dayton, P.K. 1989. Interdecadal Variation in an Antarctic Sponge and Its Predators from Oceanographic Climate Shifts. Science 245 (4925): 1484 – 1486.

Ditullio, G.R. and R.B. Dunbar. 2003. Biogeochemistry of the Ross Sea. American Geophysical Union. Antarctic Research Series, volume 78.

Eastman, J. 1985. *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. Polar Biology 4, 155-160.

Goetz, K., G.L Kooyman, and B.I. McDonald. 2018. Post-molt movement and dive behavior of non-breeding emperor penguins in the eastern Ross Sea, Antarctica. Marine Ecology Progress Series 593: 155-171.

Halpern, B. et al. 2008. A global map of human impact on marine ecosystems, Science, 319: 948-52.

Jacobs, S.S. and J.C. Comiso. 1989. Sea ice and oceanic processes on the Ross Sea continental shelf. Journal of Geophysical Research 94: 18195-18211.

Jacobs, S.S., C.F. Giulivi and P.A. Mele. 2002. Freshening of the Ross Sea During the Late 20th Century. Science 297 (5580): 386-389.

Jacobs, S. 2006. Observations of change in the Southern Ocean. Philos Trans R Soc A 364: 1657-1681.

Kappes, P.J., K.M. Dugger, A. Lescroël, D.G. Ainley, G. Ballard, K.J. Barton, P.O'B. Lyver, and P.R. Wilson. 2021. Age-related reproductive performance of the Adélie penguin, a long-lived seabird exhibiting similar outcomes regardless of individual life-history strategy. Journal of Animal Ecology, doi:10.1111/1365-2656.13422.

Kim, S., K. Hammerstrom, K.W. Conlan, and A.R. Thurber. 2010. Polar ecosystem dynamics: recovery of communities from organic enrichment in McMurdo Sound, Antarctica. Integrative and Comparative Biology 50: 1031–1040, doi:10.1093/icb/icq058.

Kim, S. 2019. Complex life under the McMurdo Ice Shelf, and some speculations on food webs. Antarctic Science 31: 80-88, doi:10.1017/S0954102018000561.

Kim, S., K. Hammerstrom, and P. Dayton. 2019. Epifaunal community response to iceberg-mediated environmental change in McMurdo Sound, Antarctica. Marine Ecology Progress Series 613, doi:10.3354/meps12899.

Kooyman, G. L. and P.J. Ponganis. 2017. Rise and fall of Ross Sea emperor penguin colony populations: 2000 to 2012. Antarctic Science 29: 201-208, doi:10.1017/S0954102016000559.

Kwok, R., J.C. Comiso, T. Lee, and P.R. Holland. 2016. Linked trends in the South Pacific sea ice edge and Southern Oscillation Index. Geophysical Research Letters 43, doi:10.1002/2016GL070655.

Kwok, R., S.S. Pang, and S. Kacimi. 2017. Sea ice drift in the Southern Ocean: Regional patterns, variability, and trends. Elementa: Science of the Anthropocene 5: 32, doi.org/10.1525/elementa.226

Massom, R.A., and S.E. Stammerjohn. 2010. Antarctic sea ice change and variability – physical and ecological implications. Polar Science 4: 149-186, doi:10.1016/j.polar.2010.05.001.

LaRue, M.A., H.J. Lynch, P.O'B Lyver, K. Barton, D.G Ainley, A. Pollard, W.R. Fraser, and G. Ballard. 2014. A method for estimating population colony sizes of Adélie penguins using remote sensing imagery. Polar Biology, doi 10.1007/s00300-014-1451-8.

LaRue, M., D. Iles, S. Labrousse, L. Salas, G. Ballard, D. Ainley, and B. Saenz. 2019. A possible Adélie penguin sub-colony on fast ice by Cape Crozier, Antarctica. Antarctic Science, doi:10.1017/S095410201900018X.

Lyver, P.O'B, M. Barron, K.J. Barton, D.G. Ainley, A. Pollard, S. Gordon, S. McNeill, G. Ballard, and P.R. Wilson. 2014. Trends in the breeding population of Adélie Penguins in the Ross Sea, 1981–2012: A Coincidence of Climate and Resource Extraction Effects. PLoS ONE 9(3): e91188, doi:10.1371/journal.pone.0091188

Parkinson, C.L. 2019. A 40-y record reveals gradual Antarctic sea ice increases followed by decreases at rates far exceeding the rates seen in the Arctic. Proceedings of the National Academy of Sciences 116 (29): 14,414-14,423, doi/10.1073/pnas.1906556116.

Saenz, B.T., D.G. Ainley, K.L. Daly, G. Ballard, E. Conlisk, M.L. Elrod, and S.L. Kim. 2020. Drivers of concentrated predation in an Antarctic marginal-ice-zone food web. Scientific Reports 10: 7282, https://doi.org/10.1038/s41598-020-63875-y.

SC-CAMLR. 2008. Report of the XXVII Meeting of the CAMLR Scientific Committee.

SC-CAMLR. 2017. Report of the XXXVI Meeting of the CAMLR Scientific Committee.

SC-CAMLR-XXXVI/20. 2017. Dunn, A., M. Vacchi, and G. Watters. The Ross Sea region Marine Protected Area Research and Monitoring Plan.

SC-CCAMLR-XXXVII/11. 2018. USA Delegation. Candidate baseline data for ecosystem indicators in the Ross Sea region. Part A: Brief presentation of data.

SC-CCAMLR-XXXVII/BG/13. 2018. USA Delegation. Candidate baseline data for ecosystem indicators in the Ross Sea region. Part B: Discussion of the data.

SC-CAMLR-39/BG/17. 2020. Report on the United States research and monitoring in support of the Ross Sea region Marine Protected Area.

SC-CAMLR-39/BG/32. 2020. New Zealand research and monitoring in the Ross Sea region in support of the Ross Sea region Marine Protected Area: 2020 update.

SC-CAMLR-39/BG/53. 2020. Italy research and monitoring in the Ross Sea region in support of the Ross Sea region Marine Protected Area: 2020 update.

Shah, K., G. Ballard, A. Schmidt, and M. Schwager. 2020. Multidrone aerial surveys of penguin colonies in Antarctica. Science Robotics 5, eabc3000.

Silvano, A., A. Foppert, S.R. Rintoul, P.R. Holland, T. Tamura, N. Kimura, P. Castagno, P. Falco, G. Budillon, F.A. Haumann, A.C. Naveira Garabato, and A.M. Macdonald. 2020. Recent recovery of Antarctic Bottom Water formation in the Ross Sea driven by climate anomalies. Nature Geoscience, https://doi.org/10.1038/s41561-020-00655-3

Smith, W.O. and D.M. Nelson. 1985. Phytoplankton Bloom Produced by a Receding Ice Edge in the Ross Sea: Spatial Coherence with the Density Field. Science 227 (4683): 163-166.

Smith, W.O. Jr., P.N. Sedwick, K.R. Arrigo, D.G. Ainley, and A.H. Orsi. 2012. The Ross Sea in a sea of change. Oceanography 25: 44-57.

Smith, W.O. Jr., D.G. Ainley, K.R. Arrigo, and M.S. Dinniman. 2014a. The oceanography and ecology of the Ross Sea. Annual Review of Marine Science 6: 469–487.

Smith, W.O., Jr., K.T. Goetz, D.E. Kaufman, B.Y. Queste, V. Asper, D.P. Costa, M.S. Dinniman, M.A.M. Friedrichs, E.E. Hofmann, K.J. Heywood, J.M. Klinck, J.T. Kohut, and C.M. Lee. 2014b. Multi-platform, multi-disciplinary investigations of the Ross Sea, Antarctica. Oceanography 27: 180-185.

SooHoo, J. B.,Palmisano, A. C.,Kottmeier, S.T .,Lizotte, M. P., SooHoo, S. L., S u h v a n , C. W. (1987). Spectral light absorption and quantum yield of photosynthesis in sea ice microalgae and a bloom of *Phaeocystis pouchetii* from McMurdo Sound, Antarctica. Mar. Ecol. Prog. Ser. 39: 175-189

Stammerjohn, S., R. Massom, D. Rind, and D. Martinson. 2012. Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophysical Research Letters 39, L06501, doi:10.1029/2012GL050874

Thompson, D.W.J. and S. Solomon. 2002. Interpretation of Recent Southern Hemisphere Climate Change. Science 296 (5569): 895-899.

APPENDIX A

Ross Sea Region Marine Protected Area Research and Monitoring U.S. Workshop: Agenda, Schedule & Participants

Agenda

1. Overview of workshop goals (Day 1)
2. Introduction to Ross Sea region MPA & research and monitoring plan (Day 1)
3. Summary of Ross Sea science (draft document prepared by conveners) in context of Ross Sea region MPA research and monitoring (Day 1 & 2)
4. Urgent questions related to understanding the Ross Sea ecosystem structure and function
5. Additional research and monitoring gaps (Day 2)
6. Ways to potentially answer urgent questions & fill research and monitoring gaps (Day 2)
7. Potential plan for coordination (U.S. & International) (Day 2)
8. CCAMLR MPA Information Repository (Day 2)
9. AOB (Day 2)

Workshop Schedule (April 26-27, 2021)

DAY 1 (times in Pacific)		
12:00	Greetings, zoom tutorial, workshop goals	D. Ainley, C. Brooks
12:10	Introduction to Ross Sea region MPA and research & monitoring plan	G. Watters
12:25	Q&A	All
Lightning talks start		
Biophysical Context		
12:35	Weather	M. Lazzara
12:40	Large scale sea ice	S. Stammerjohn
12:45	Physical ocean patterns	E. Hofmann, M. Dinniman
12:50	Polynyas	K. Arrigo, S. Stammerjohn
12:55	Primary Productivity	K. Arrigo
1:00	Marginal ice zone productivity	R. Dunbar
Forage Species		
1:05	Silverfish natural history	C. Brooks, J. Eastman
1:10	Trophic role of silverfish	J. Eastman
1:15	Krill	B. Davis, K. Daly
1:20	Relationship of predator populations to preyscape	D. Ainley
1:25-1:40	BREAK	
Indicator Species		
1:40	Toothfish movement	C. Brooks
1:45	Decadal change in toothfish prevalence	D. Ainley
1:50	Weddell seal abundance/distribution	M. LaRue
1:55	Weddell seal demography	J. Rotella
2:00	Weddell seal population change	D. Ainley, M. LaRue
2:05	Weddell seal diet and foraging	J. Burns, K. Goetz
2:10	Relationship seals and toothfish	L. Salas, D.Ainley et al.
2:15	Adélie penguin demography and population change	K. Dugger, M. LaRue

2:20	Adélie penguin diet and foraging	G. Ballard, D. Ainley
2:25	Emperor penguin population change	M. LaRue, G. Kooyman
2:30	Emperor penguin diet and foraging	K. Goetz, G. Kooyman
2:35	Benthic community variation and distribution	S. Kim
2:40	Benthic community decadal change	S. Kim
2:45	Pollution and Wildlife Health: Viruses	A. Varsani
2:50	Cetaceans, especially killer whales	B. Pitman
Climate Effects		
2:55	Bio-physical synthesis and climate projections	J. Russell
DAY 2		
1:30	Summary from Day 1, goals for Day 2	C. Brooks
1:35	Outstanding Q&A from Day 1	All
1:40	Introduce CCAMLR MPA Information Repository	C. Brooks
1:55	**Break out groups session 1:** Discuss how previous, current, and future work relates to Ross Sea MPA research and monitoring, specifically	All
2:15	Report back from groups	All
2:25	**Break out groups session 2:** Discuss and identify gaps in Ross Sea research and monitoring. Discuss outstanding urgent questions regarding the Ross Sea ecosystem.	All
2:45	Report back from groups	All
2:55	BREAK	
3:10	**Break out groups session 3:** Brainstorm ways to fill research and monitoring gaps.	All
3:30	Report back from groups	All
3:40	Large group discussion on further research and monitoring.	All
4:00	Agency and funders summaries	NSF, Pew, NOAA
4:15	Outstanding questions, ideas, discussion	All
4:25	Closing remarks	D. Ainley, C. Brooks

Participants

David Ainley, H.T. Harvey & Associates; Kevin Arrigo, Stanford University; Grant Ballard, Point Blue Conservation Science; Sarah Becker, University of Colorado Boulder; Cassandra Brooks, University of Colorado Boulder; Jen Burns, Texas Tech University; Vasco Chavez-Molina, University of Colorado Boulder; Kendra Daly, University of South Florida; Brynn Davis, Old Dominion University; Mike Dinniman, Old Dominion University; Ryan Dolan, Pew Charitable Trusts; Katie Dugger, Oregon State University; Rob Dunbar, Stanford University; Alice DuVivier, National Center for Atmospheric Research; Joe Eastman, Ohio University; Lauren Fields, NOAA; Kim Goetz, NOAA; Karla Heidelberg, NSF; Bob Hofman, Marine Mammal Commission; Eileen Hofmann, Old Dominion University; Stephanie Jenouvrier, Woods Hole Oceanographic Institute; Christopher Jones, NOAA; Andrea Kavanagh, Pew Charitable Trusts; Mi Ae Kim, NOAA; Stacy Kim, California State University; Jerry Kooyman, University of California San Diego; Dennis Jongsomjit, Point Blue Conservation Science; Michelle LaRue, University of Minnesota; Matthew Lazzara, Madison College; Nature McGinn, NSF; Peter Milne, NSF; Emily Nocito, University of Colorado Boulder; Kim Ohnemus, NSF; Polly Penhale, NSF; Bob Pitman, Oregon State University; Jay Rotella, University of Montana

Joellen Russell, University of Arizona; Leo Salas, Point Blue Conservation Science; Jarrod Santora, NOAA; Annie Schmidt, Point Blue Conservation Science; Sharon Stammerjohn, University of Colorado Boulder; Nancy Sung, NSF; David Sutherland, NSF; Zephyr Sylvester, University of Colorado Boulder; Hannah Synder, Madison College; Woody Turner, NASA;
Arvind Varsani, Arizona State University; Maria Vernet, NSF; George Watters, NOAA; John Weller, Sea Legacy; Carlie Wiener, Schmidt Ocean Institute.

APPENDIX B

Central questions that have emerged from the Appendix C and D reviews, related to understanding, and thus facilitating the protection, of Ross Sea ecosystem structure and function; most are inter-related:

1. Have katabatic winds changed in intensity and frequency over past 30 years in RS region? What are prospects for the future? RE: latent heat polynya generation/persistence?
2. How is variability in the SAM index related to the size of the Ross Sea polynya and the distribution of ice both on the shelf and in offshore waters? How might this change in the future?
3. Has/is the increased intrusion of CDW into Ross Sea troughs, or changing characteristics of AABW, affecting(ed) benthic and demersal communities?
4. What is relative contribution of diatoms to overall RS productivity, and how might that vary annually with width of polynya marginal ice zones and depth of mixed layer?
5. Is there annual variation in the 3D presence (abundance, distribution) of crystal krill and silverfish in the SW Ross Sea (region of most intense indicator species investigation)? Has increased intrusion of CDW brought Antarctic krill farther south in Ross Sea troughs?
6. Are there distinctive year-class strengths in Antarctic toothfish, and if so what factors contribute to weak vs strong year classes?
7. The Ross Gyre varies annually in intensity but has been generally increasing over the past 30 years. What are the implications for transport of Antarctic toothfish eggs/larvae from sea mounts onto the RS shelf, or out of the system?
8. How have long-lines altered the abundance and species composition of benthic communities along Ross Sea slope? Or have they? If so, recoverable within 20-30 years as per CCAMLR Article II(3)(c)?
9. As southern Ross Sea Adélie penguin colonies grow in size, foraging areas increase and food provisioning of chicks decreases (lower feeding frequency with longer parental trips). Chicks fledge at increasingly smaller mass, theoretically compromising post-fledging survival. What demographic mechanisms, then, explain why southern colonies have continued to increase in size?
10. What are the demographic relationships among emperor penguin colonies, i.e. a species that has no territory and increased propensity to change colonies depending on conditions? Specifically, what's the connection between Beaufort, Franklin and Crozier EMPE colonies, if any? And what about cluster of colonies in NW Victoria Land?
11. Why do EMPE and WESE choose to forage during winter over RS banks or their shoulders, as opposed to other habitat? During summer waters above those banks are covered by thick Phaeocystis bloom, which few upper level predators frequent.
12. Is there overlap in the foraging areas of Cape Colbeck breeding Weddell seals and emperor penguins with western Ross Sea colonies of these species?
13. Why have Weddell seals decreased dramatically in abundance in northern Victoria Land during last few decades?

14. What are the demographic mechanisms, and biophysical covariates, that explain Weddell seal population increase in McMurdo Sound during pupping in the most recent two decades?

APPENDIX C

PUBLISHED RESULTS FROM RESEARCH GENERATED BY UNITED STATES SCIENTISTS RELEVANT TO THE ROSS SEA MARINE ECOSYSTEM, 2010 TO THE PRESENT (2021)

TABLE OF CONTENTS

PHYSICAL PROCESSES RELATED TO SEA ICE AND WATER COLUMN STUCTURE/HABITAT

Ackley, S.F., S. Stammerjohn, T. Maksym, M. Smith, J. Cassano, P. Guest, J-L. Tison, B. Delille, B. Loose, P. Sedwick, L. DePace, L. Roach, and J. Parno. 2020. Sea-ice production and air/ice/ocean/biogeochemistry interactions in the Ross Sea during the PIPERS 2017 autumn field campaign. *Annals of Glaciology* 1-15, https://doi.org/10.1017/aog.2020.31.

The Ross Sea is known for showing the greatest sea-ice increase, as observed globally, particularly from 1979 to 2015. However, corresponding changes in sea-ice thickness and production in the Ross Sea are not known, nor how these changes have impacted water masses, carbon fluxes, biogeochemical processes and availability of micronutrients. The PIPERS project sought to address these questions during an autumn ship campaign in 2017 and two spring airborne campaigns in 2016 and 2017. PIPERS used a multidisciplinary approach of manned and autonomous platforms to study the coupled air/ice/ocean/biogeochemical interactions during autumn and related those to spring conditions. Unexpectedly, the Ross Sea experienced record low sea ice in spring 2016 and autumn 2017. The delayed ice advance in 2017 contributed to (1) increased ice production and export in coastal polynyas, (2) thinner snow and ice cover in the central pack, (3) lower sea ice Chl-*a* burdens and differences in sympagic communities, (4) sustained ocean heat flux delaying ice thickening and (5) a melting, anomalously southward ice edge persisting into winter. Despite these impacts, airborne observations in spring 2017 suggest that winter ice production over the continental shelf was likely not anomalous.

Arzeno, I.B., R.C. Beardsley, R. Limeburner, B. Owens, L. Padman, S.R. Springer, C.L. Stewart, and M.J.M. Williams. 2014. Ocean variability contributing to basal melt rate near the ice front of Ross Ice Shelf, Antarctica. *Journal of Geophysical Research* 119: 4214-4233, doi:10.1002/2014JC009792.

Basal melting of ice shelves is an important, but poorly understood, cause of Antarctic ice sheet mass loss and freshwater production. We use data from two moorings deployed through Ross Ice Shelf, ~6 and ~16 km south of the ice front east of Ross Island, and numerical models to show how the basal melting rate near the ice front depends on sub-ice-shelf ocean variability. The moorings measured water velocity, conductivity, and temperature for ~2 months starting in late November 2010. About half of the current velocity variance was due to tides, predominantly diurnal components, with the remainder due to subtidal oscillations with periods of a few days. Subtidal variability was dominated by barotropic currents that were large until mid-December and significantly reduced afterward. Subtidal currents were correlated between moorings but uncorrelated with local winds, suggesting the presence of waves or eddies that may be associated with the abrupt change in water column thickness and strong hydrographic gradients at the ice front. Estimated melt rate was $\sim 1.2 \pm 0.5$ m a^{-1} at each site during the deployment period, consistent with measured trends in ice surface elevation from GPS time series. The models predicted similar annual-averaged melt rates with a strong annual cycle related to seasonal provision of warm water to the ice base. These results show that accurately modeling the high spatial and temporal ocean variability close to the

ice-shelf front is critical to predicting time-dependent and mean values of meltwater production and ice-shelf thinning.

Bebieva, Y. and K. Speer, 2019. The regulation of sea ice thickness by double-diffusive processes in the Ross Gyre. *Journal of Geophysical Research: Oceans*, https://doi.org/10.1029/2019JC015247

New fine-scale observations from the central Ross Gyre reveal the presence of double-diffusive staircase structures underlying the surface mixed layer. These structures are persistent over seasons, with more developed mixed layers within the double-diffusive staircase in winter months. The sensitivity of the ice formation rate with respect to mixing processes within the main pycnocline (double-diffusive versus purely turbulent mixing) is investigated with the 1-D model. A scenario with purely turbulent mixing results in significant underestimates of sea ice thickness. However, a scenario when double-diffusive mixing operates in the presence of weak shear yields plausible ranges for sea ice thickness that agrees well with the observations. The model results and observations suggest a peculiar feedback mechanism that promotes the self-maintenance of double-diffusive staircases. Suppression of the vertical heat fluxes due to the presence of a double-diffusive staircase, compared to purely turbulent case, allows Upper Circumpolar Deep Water to be more exposed to surface buoyancy fluxes. Our results shed light on the process—double diffusion—that might account for estimated rates of winter water mass transformation in the central Ross Gyre.

Bronselaer, B., M. Winton, S.M. Griffies, W.J. Hurlin, K.B. Rodgers, O.V. Sergienko, R.J. Stouffer, and J.L. Russell. 2018. Change in future climate due to Antarctic meltwater. *Nature*, https://doi.org/10.1038/s41586-018-0712-z

Meltwater from the Antarctic Ice Sheet is projected to cause up to one metre of sea-level rise by 2100 under the highest greenhouse gas concentration trajectory (RCP8.5) considered by the Intergovernmental Panel on Climate Change (IPCC). However, the effects of meltwater from the ice sheets and ice shelves of Antarctica are not included in the widely used CMIP5 climate models, which introduces bias into IPCC climate projections. Here we assess a large ensemble simulation of the CMIP5 model 'GFDL ESM2M' that accounts for RCP8.5-projected Antarctic Ice Sheet meltwater. We find that, relative to the standard RCP8.5 scenario, accounting for meltwater delays the exceedance of the maximum global-mean atmospheric warming targets of 1.5 and 2 degrees Celsius by more than a decade, enhances drying of the Southern Hemisphere and reduces drying of the Northern Hemisphere, increases the formation of Antarctic sea ice (consistent with recent observations of increasing Antarctic sea-ice area) and warms the subsurface ocean around the Antarctic coast. Moreover, the meltwater-induced subsurface ocean warming could lead to further ice-sheet and ice-shelf melting through a positive feedback mechanism, highlighting the importance of including meltwater effects in simulations of future climate.

Castagno, P., P. Falco, M.S. Dinniman, G. Spezie, and G. Budillon, 2017. Temporal variability of the Circumpolar Deep Water inflow onto the Ross Sea continental shelf. *Journal of Marine Systems* 166: 37-49, doi:10.1016/j.jmarsys.2016.05.006.

The intrusion of Circumpolar Deep Water (CDW) is the primary source of heat, salt and nutrients onto Antarctica's continental shelves and plays a major role in the shelf physical and biological processes. Different studies have analyzed the processes responsible for the transport of CDW across the Ross Sea shelf break, but until now, there are no continuous observations that investigate the timing of the intrusions. Also, few works have focused on the effect of the tides that control these intrusions. In the Ross Sea, the CDW intrudes onto the shelf in several locations, but mostly along the troughs. We use hydrographic observations and a mooring placed on the outer shelf in the middle of the Drygalski Trough

in order to characterize the spatial and temporal variability of CDW inflow onto the shelf. Our data span from 2004 to the beginning of 2014. In the Drygalski Trough, the CDW enters as a 150 m thick layer between 250 and 400 m, and moves upward towards the south. At the mooring location, about 50 km from the shelf break, two main CDW cores can be observed: one on the east side of the trough spreading along the west slope of Mawson Bank from about 200 m to the bottom and the other one in the central-west side from 200 m to about 350 m depth. A signature of this lighter and relatively warm water is detected by the instruments on the mooring at bottom of the Drygalski Trough. High frequency periodic CDW intrusion at the bottom of the trough is related to the diurnal and spring/neap tidal cycles. At lower frequency, a seasonal variability of the CDW intrusion is noticed. A strong inflow of CDW is observed every year at the end of December, while the CDW inflow is at its seasonal minimum during the beginning of the austral fall. In addition an interannual variability is also evident. A change of the CDW intrusion before and after 2010 is observed.

Cerovecki, I., A.J.S. Meijers, M.R. Mazloff, S.T. Gille, V.M. Tamsitt, and P.R. Holland 2019. The Effects of Enhanced Sea Ice Export from the Ross Sea on Recent Cooling and Freshening of the Southeast Pacific. *Journal of Climate* 32, https://doi.org/10.1175/JCLI-D-18-0205.1

The top 2000 m of the Southern Ocean has freshened and warmed over recent decades. However, the high latitude (south of 508S) southeast Pacific was observed to be cooler and fresher in the years 2008–10 compared to 2005–07 over a wide depth range including surface, mode, and intermediate waters. The causes and impacts of this event are analyzed using the ocean–sea ice data-assimilating Southern Ocean State Estimate (SOSE) and observationally based products. In 2008–10, a strong positive southern annular mode coincided with a negative El Niño– Southern Oscillation and a deep Amundsen Sea low. Enhanced meridional winds drove strong sea ice export from the eastern Ross Sea, bringing large amounts of ice to the Amundsen Sea ice edge. In 2008, together with increased precipitation, this introduced a strong freshwater anomaly that was advected eastward by the Antarctic Circumpolar Current (ACC), mixing along the way. This anomaly entered the ocean interior not only as Antarctic Intermediate Water, but also as lighter Southeast Pacific Subantarctic Mode Water (SEPSAMW). A numerical particle release experiment carried out in SOSE showed that the Ross Sea sector was the dominant source of particles reaching the SEPSAMW formation region. This suggests that large-scale climate fluctuations can induce strong interannual variability of volume and properties of SEPSAMW. These fluctuations act at different time scales: instantaneously via direct forcing and also lagged over advective time scales of several years from upstream regions.

Comiso, J. C., R. Kwok, S. Martin, and A. L. Gordon. 2011. Variability and trends in sea ice extent and ice production in the Ross Sea. *Journal of Geophysical Research* 116, C04021, doi:10.1029/2010JC006391

Salt release during sea ice formation in the Ross Sea coastal regions is regarded as a primary forcing for the regional generation of Antarctic Bottom Water. Passive microwave data from November 1978 through 2008 are used to examine the detailed seasonal and interannual characteristics of the sea ice cover of the Ross Sea and the adjacent Bellingshausen and Amundsen seas. For this period the sea ice extent in the Ross Sea shows the greatest increase of all the Antarctic seas. Variability in the ice cover in these regions is linked to changes in the Southern Annular Mode and secondarily to the Antarctic Circumpolar Wave. Over the Ross Sea shelf, analysis of sea ice drift data from 1992 to 2008 yields a positive rate of increase in the net ice export of about 30,000 km2 yr−1. For a characteristic ice thickness of 0.6 m, this yields a volume transport of about 20 km3 yr−1, which is almost identical, within error bars, to our estimate of the trend in ice production. The increase in brine rejection in the Ross Shelf Polynya associated with the estimated increase with the ice production, however, is not consistent with

the reported Ross Sea salinity decrease. The locally generated sea ice enhancement of Ross Sea salinity may be offset by an increase of relatively low salinity of the water advected into the region from the Amundsen Sea, a consequence of increased precipitation and regional glacial ice melt.

Cunningham, C.A., and Bonatti, J.P. 2011. Local and remote responses to opposite Ross Sea ice anomalies: a numerical experiment with the CPTEC/INPE AGCM. *Theoretical and Applied Climatology* 106: 23- 44, doi:10.1007/s00704-011-0407-y.

This work examines the near-surface responses, in the Southern Hemisphere atmosphere, to a reduction and an excess of sea ice cover in the Ross Sea. Large ensembles (60 members) of the Atmospheric General Circulation Model of the Center for Weather Forecast and Climate Studies (AGCM-CPTEC) are used for this purpose. Locally, when the sea ice cover decreases (increases), heat fluxes, temperature, and pressure increase (decreases). A principal component analysis of temperature and geopotential height identifies the potential remote connections. We have found three main results: first, an association between the sea ice cover in the Ross Sea and a wave train that resembles the Pacific South American (PSA) pattern; second, a relationship between temperatures in the Ross Sea and in the southern South America; and third, an apparent correspondence between reduced sea ice cover in the Ross Sea and the subtropical jet over Australia.

Dinniman, M.S., J.M. Klinck, E.E. Hofmann, and W.O. Smith, Jr. 2018. Effects of projected changes in wind, atmospheric temperature and freshwater inflow on the Ross Sea. *Journal of Climate* 31: 1619-1635.

A 5-km horizontal resolution regional ocean–sea ice–ice shelf model of the Ross Sea is used to examine the effects of changes in wind strength, air temperature, and increased meltwater input on the formation of high salinity shelf water (HSSW), on-shelf transport and vertical mixing of Circumpolar Deep Water (CDW) and its transformation into modified CDW (MCDW), and basal melt of the Ross Ice Shelf (RIS). A 20% increase in wind speed, with no other atmospheric changes, reduced summer sea ice minimum area by 20%, opposite the observed trend of the past three decades. Increased winds with spatially uniform, reduced atmospheric temperatures increased summer sea ice concentrations, on-shelf transport of CDW, vertical mixing of MCDW, HSSW volume, and (albeit small) RIS basal melt. Winds and atmospheric temperatures from the SRES A1B scenario forcing of the MPI ECHAM5 model decreased on-shelf transport of CDW and vertical mixing of MCDW for 2046–61 and 2085–2100 relative to the end of the twentieth century. The RIS basal melt increased slightly by 2046–61 (9%) and 2085–2100 (13%). Advection of lower-salinity water onto the continental shelf did not significantly affect sea ice extent for the 2046–61 or 2085–2100 simulations. However, freshening reduces on-shelf transport of CDW, vertical mixing of MCDW, and the volume of HSSW produced. The reduced vertical mixing of MCDW, while partially balanced by the reduced on-shelf transport of CDW, enhances the RIS basal melt rate relative to the twentieth-century simulation for 2046–61 (13%) and 2085–2100 (17%).

Dinniman, M.S., J.M. Klinck, and W.O. Smith, Jr. 2011. A model study of Circumpolar Deep Water on the West Antarctic Peninsula and Ross Sea continental shelves. *Deep-Sea Research II* 58: 1508–1523.

Transport of relatively warm, nutrient-rich Circumpolar Deep Water (CDW) onto continental shelves around Antarctica has important effects on physical and biological processes. However, the characteristics of the CDW along the shelf break, as well as what happens to it once it has been advected onto the continental shelf, differ spatially. In the present study high resolution (4–5 km) regional models of the Ross Sea and the West Antarctic Peninsula coastal ocean are used to compare differences in CDW transport. The models compared very well with observations from both regions. Examining the fluxes not

only of heat, but also of a simulated ‘‘dye’’ representing CDW, shows that in both cases CDW crosses the shelf break in specific locations primarily determined by the bathymetry, but eventually floods much of the shelf. The frequency of intrusions in Marguerite Trough was ca. 2–3 per month, similar to recent mooring observations. A significant correlation between the along shelf break wind stress and the cross shelf break dye flux through Marguerite Trough was observed, suggesting that intrusions are at least partially related to short duration wind events. The primary difference between the CDW intrusions on the Ross and west Antarctic Peninsula shelves is that there is more vigorous mixing of the CDW with the surface waters in the Ross Sea, especially in the west where High Salinity Shelf Water is created. The models show that the CDW moving across the Antarctic Peninsula continental shelf towards the base of the ice shelves not only is warmer initially and travels a shorter distance than that advected towards the base of the Ross Ice Shelf, but it is also subjected to less vertical mixing with surface waters, which conserves the heat available to be advected under the ice shelves. This difference in vertical mixing also likely leads to differences in the supply of nutrients from the CDW into the upper water column, and thus modulates the impacts on surface biogeochemical processes

Dinniman, M.S., J.M. Klinck, L.-S. Bai, D.H. Bromwich, K.M. Hines, and D.M. Holland. 2015. The effect of atmospheric forcing resolution on delivery of ocean heat to the Antarctic floating ice shelves. *Journal of Climate* 68: 6067-6085, doi:10.1175/JCLI-D-14-00374.1

Oceanic melting at the base of the floating Antarctic ice shelves is now thought to be a more significant cause of mass loss for the Antarctic ice sheet than iceberg calving. In this study, a 10-km horizontal-resolution circum-Antarctic ocean–sea ice–ice shelf model [based on the Regional Ocean Modeling System (ROMS)] is used to study the delivery of ocean heat to the base of the ice shelves. The atmospheric forcing comes from the ERA-Interim reanalysis (;80-km resolution) and from simulations using the polar-optimized Weather Research and Forecasting Model (30-km resolution), where the upper atmosphere was relaxed to the ERAInterim reanalysis. The modeled total basal ice shelf melt is low compared to observational estimates but increases by 14% with the higher-resolution winds and just 3% with both the higher-resolution winds and atmospheric surface temperatures. The higher-resolution winds lead to more heat being delivered to the ice shelf cavities from the adjacent ocean and an increase in the efficiency of heat transfer between the water and the ice. The higher-resolution winds also lead to changes in the heat delivered from the open ocean to the continental shelves as well as changes in the heat lost to the atmosphere over the shelves, and the sign of these changes varies regionally. Addition of the higher-resolution temperatures to the winds results in lowering, primarily during summer, the wind-driven increase in heat advected into the ice shelf cavities due to colder summer air temperatures near the coast.

Drucker, R., S. Martin, and R. Kwok. 2011. Sea ice production and export from coastal polynyas in the Weddell and Ross Seas. *Geophysical Research Letters* 38, L17502, doi:10.1029/2011GL048668.

For 1992–2008, we use data from the Special Sensor Microwave/Imager (SSM/I) and the Advanced Microwave Scanning Radiometer-EOS (AMSR-E) to examine differences in ice production and export in the Weddell and Ross Seas. We find that the Ross production is three times that in the Weddell; the Ross export, twice that in the Weddell. In the Ross, the ice production has a statistically significant positive trend of about 21 km3 y−1 and approximately equals the export, while in the Weddell, the production trend is statistically flat and provides only about 60% of the export. For each sea, comparison of the ice production with the total winter sea ice volume shows that the Weddell polynyas produce 5–10% of the total; the Ross polynyas, 20–50%. The explanation for these differences is that in the Ross, the low-pressure system is better situated for generation of large polynyas than in the Weddell.

Fogt, R.L., A.J. Wovrosh, R.A. Langen, and I. Simmonds. 2012. The characteristic variability and connection to the underlying synoptic activity of the Amundsen-Bellingshausen Seas Low. *Journal of Geophysical Research: Atmospheres* 117:D7

Recent studies have noted an asymmetrical climate change across Antarctica, with significant warming in West Antarctica and the Antarctica Peninsula, and primarily insignificant trends in East Antarctica. Due to its proximity, variations in the position and intensity of the Amundsen-Bellingshausen Seas Low (ABSL) are a suspected atmospheric mechanism. Here, we investigate the ABSL to understand its characteristic variability and underlying synoptic-scale influences, based on three reanalysis data sets. The ABSL is defined as the minimum monthly pressure in the 45°–75°S, 180°–60°W domain. Using this criterion, a significant north-south and east-west progression is noted in the climatological (1979–2001 average) ABSL, which is strongly tied to the location of the maximum cyclone system density and minimum cyclone central pressures. More than 550 cyclones a year were identified in the vicinity of the ABSL; during spring, significant trends in their central pressures are noted in the Ross Sea. The implied changes in temperature advection by these stronger systems are consistent with the warming in West Antarctica. The strongest cyclone events (i.e., the ten with the deepest central pressures) also demonstrate a connection to the climatological ABSL, albeit weaker. Moreover, these strong cyclone events are significantly linked to the Southern Annular Mode (SAM), particularly in their annual frequency and location/steering in the summer. This shows that large-scale forcing, such as from the SAM, may influence the strongest cyclones in the region and could allow for the prediction of such events.

Gordon, A.L., B.A. Huber,and J. Busecke. 2015. Bottom water export from the western Ross Sea, 2007 through 2010. *Geophysical Research Letters* 42: 5387-5394, doi:10.1002/2015GL064457.

Bottom water export from the Ross Sea, February 2007 to January 2011, exhibits seasonal and interannual variability. Temperature minima coupled to salinity maxima in late austral summer, into the fall, indicate input from High-Salinity Shelf Water (HSSW). Secondary temperature minima lacking the high-salinity trait, characteristic of Low-Salinity Shelf Water (LSSW), appear in the spring. Warmer bottom water similar to modified Circumpolar Deep Water (mCDW) is observed in winter and in early summer. The LSSW and mCDW may be drawn from the Drygalski Basin, as the HSSW pool retreats poleward from the shelf break in response to increased winter polar easterlies allowing these less dense overlying waters to spill into the deep ocean within the benthic layer. Bottom salinity decreased from 2007 to 2011 by 0.007 $year^{-1}$ significantly higher than regional decadal trends, which we propose is a result of HSSW retreat induced by strengthening polar easterlies.

Hobbs, W. R., Massom, R., Stammerjohn, S., Reid, P., Williams, G., and Meier, W. (2016). A review of recent changes in Southern Ocean sea ice, their drivers and forcings. *Global and Planetary Change* 143: 228-250, doi:10.1016/j.gloplacha.2016.06.008.

Over the past 37 years, satellite records show an increase in Antarctic sea ice cover that is most pronounced in the period of sea ice growth. This trend is dominated by increased sea ice coverage in the western Ross Sea, and is mitigated by a strong decrease in the Bellingshausen and Amundsen seas. The trends in sea ice areal coverage are accompanied by related trends in yearly duration. These changes have implications for ecosystems, as well as global and regional climate. In this review, we summarise the research to date on observing these trends, identifying their drivers, and assessing the role of anthropogenic climate change. Whilst the atmosphere is thought to be the primary driver, the ocean is also essential in explaining the seasonality of the trend patterns. Detecting an anthropogenic signal in Antarctic sea ice is particularly challenging for a number of reasons: the expected response is small compared to the very high natural variability of the system; the observational record is relatively short;

and the ability of global coupled climate models to faithfully represent the complex Antarctic climate system is in doubt.

Holland, P.R., and R. Kwok. 2012. Wind-driven trends in Antarctic sea-ice drift. ***Nature Geoscience,*** **http://www.nature.com/doifinder/10.1038/ngeo1627**

The sea-ice cover around Antarctica has experienced a slight expansion in area over the past decade. This small overall increase is the sum of much larger opposing trends in different sectors that have been proposed to result from changes in atmospheric temperature or wind stress3–5, precipitation, ocean temperature8, and atmosphere or ocean feedbacks. However, climate models have failed to reproduce the overall increase in sea ice11. Here we present a data set of satellite tracked sea-ice motion for the period of 1992–2010 that reveals large and statistically significant trends in Antarctic ice drift, which, in most sectors, can be linked to local winds. We quantify dynamic and thermodynamic processes in the internal ice pack and show that wind-driven changes in ice advection are the dominant driver of ice-concentration trends around much of West Antarctica, whereas wind-driven thermodynamic changes dominate elsewhere. The ice-drift trends also imply large changes in the surface stress that drives the Antarctic ocean gyres, and in the fluxes of heat and salt responsible for the production of Antarctic bottom and intermediate waters.

Holland, M. M., L. Landrum, M. Raphael, and S. Stammerjohn. 2017. Springtime winds drive Ross Sea ice variability and change in the following autumn. ***Nature Communications 8*****(731), doi:10.1038/s41467-017-00820-0.**

Autumn sea ice trends in the western Ross Sea dominate increases in Antarctic sea ice and are outside the range simulated by climate models. Here we use a number of independent data sets to show that variability in western Ross Sea autumn ice conditions is largely driven by springtime zonal winds in the high latitude South Pacific, with a lead-time of 5 months. Enhanced zonal winds dynamically thin the ice, allowing an earlier melt out, enhanced solar absorption, and reduced ice cover the next autumn. This seasonal lag relationship has implications for sea ice prediction. Given a weakening trend in springtime zonal winds, this lagged relationship can also explain an important fraction of the observed sea ice increase. An analysis of climate models indicates that they simulate weaker relationships and wind trends than observed. This contributes to weak western Ross Sea ice trends in climate model simulations.

Kim, S., B. Saenz, J. Scanniello, K. Daly, and D. Ainley. 2018. Local climatology of fast ice in McMurdo Sound, Antarctica. ***Antarctic Science*** **30: 1-18, doi:10.1017/S0954102017000578.**

Fast ice plays important physical and ecological roles: as a barrier to wind, waves and radiation, as both barrier and safe resting place for air-breathing animals, and as substrate for microbial communities. While sea ice has been monitored for decades using satellite imagery, high-resolution imagery sufficient to distinguish fast ice from mobile pack ice extends only back to c. 2000. Fast ice trends may differ from previously identified changes in regional sea ice distributions. To investigate effects of climate and human activities on fast ice dynamics in McMurdo Sound, Ross Sea, the sea and fast ice seasonal events (1978–2015), ice thicknesses and temperatures (1986–2014), wind velocities (1973–2015) and dates that an icebreaker annually opens a channel to McMurdo Station (1956–2015) are reported. A significant relationship exists between sea ice concentration and fast ice extent in the Sound. While fast/sea ice retreat dates have not changed, fast/sea ice reaches a minimum later and begins to advance earlier, in partial agreement with changes in Ross Sea regional pack ice dynamics. Fast ice minimum extent within McMurdo Sound is significantly correlated with icebreaker arrival date as well as wind velocity. The potential impacts of changes in fast ice climatology on the local marine ecosystem are discussed.

Knuth, S.L., G.J. Tripoli, J.E. Thom, and G.A. Weidner. 2010. The influence of blowing snow and precipitation on snow depth change across the Ross Ice Shelf and Ross Sea regions of Antarctica. *Journal of Applied Meteorology and Climatology* 49: 1306-3121, doi:10.1175/2010JAMC2245.1.

Measuring snowfall in the polar regions is an issue met with many complications. Across the Antarctic, ground-based precipitation measurements are only available from a sparse network of manned stations or field studies. Measurements from satellites promise to fill in gaps in time and space but are still in the early stages of development and require surface measurements for proper validation. Currently, measurements of accumulation from automated reporting stations are the only available means of tracking snow depth change over a broad area of the continent. The challenge remains in determining the cause of depth change by partitioning the impacts of blowing snow and precipitation. While a methodology for separating these two factors has yet to be developed, by comparing accumulation measurements with meteorological measurements, an assessment of whether these terms were a factor in snow depth change during an event can be made. This paper describes a field study undertaken between January 2005 and October 2006 designed to identify the influences of precipitation and horizontal snow transport on surface accumulation. Seven acoustic depth gauges were deployed at automatic weather stations (AWS) across the Ross Ice Shelf and Ross Sea regions of Antarctica to measure net accumulation changes. From these measurements, episodic events were identified and were compared with data from the AWS to determine the primary cause of depth change—precipitation or horizontal snow transport. Information regarding the local impacts of these two terms, as well as climatological information regarding snow depth change across this region, is also provided.

Kohut, J., E. Hunter, and B. Huber, 2013. Small-scale variability of the cross-shelf flow over the outer shelf of the Ross Sea. *Journal of Geophysical Research* 118: 1863-1876, doi:10.1002/jgrc.20090.

The importance of cross-shelf transport across the Ross Sea on local and remote processes has been well documented. In the Ross Sea, mid-water intrusions of Circumpolar Deep Water (CDW) are modified by shelf water near the shelf break to form Modified Circumpolar Deep Water (MCDW). In 2010–2011, we deployed multi-platform technologies focused on this MCDW intrusion in the vicinity of Mawson and Pennell Banks to better understand its role in ecosystem processes across the shelf. The high-resolution time and space sampling provided by an underwater glider, a short-term mooring, and a ship-based survey highlight the scales over which these critical cross-shelf transport processes occur. MCDW cores were observed as small-scale well-defined features over the western slopes of Pennell and Mawson Banks. The mean transport along Pennell Bank was estimated to be about 0.24 *Sv* but was highly variable in time (hours to days). The observations suggest that the core of MCDW is transported by a predominately barotropic flow that follows topography around the banks toward the south until the slope of the bank flattens and the warmer water moves up and over the bank. This pathway is shown to link the source MCDW with an area of high productivity over the shallows of Pennell Bank.

Kwok, R., S.S. Pang, and S. Kacimi. 2017. Sea ice drift in the Southern Ocean: Regional patterns, variability, and trends. *Elementa: Science of the Anthropocene* 5: 32, doi.org/10.1525/elementa.226

Understanding long-term changes in large-scale sea ice drift in the Southern Ocean is of considerable interest given its contribution to ice extent, to ice production in open waters, with associated dense water formation and heat flux to the atmosphere, and thus to the climate system. In this paper, we examine the trends and variability of this ice drift in a 34-year record (1982–2015) derived from satellite observations. Uncertainties in drift (~3 to 4 km day–1) were assessed with higher resolution observations. In a linear model, drift speeds were ~1.4% of the geostrophic wind from reanalyzed sea-level pressure, nearly 50% higher than that of the Arctic. This result suggests an ice cover in the Southern Ocean that is thinner, weaker, and less compact. Geostrophic winds explained all but ~40% of the variance in ice drift.

Three spatially distinct drift patterns were shown to be controlled by the location and depth of atmospheric lows centered over the Amundsen, Riiser-Larsen, and Davis seas. Positively correlated changes in sea-level pressures at the three centers (up to 0.64) suggest correlated changes in the wind-driven drift patterns. Seasonal trends in ice edge are linked to trends in meridional winds and also to on-ice/off-ice trends in zonal winds, due to zonal asymmetry of the Antarctic ice cover. Sea ice area export at flux gates that parallel the 1000-m isobath were extended to cover the 34-year record. Interannual variability in ice export in the Ross and Weddell seas linked to the depth and location of the Amundsen Sea and Riiser-Larsen Sea lows to their east. Compared to shorter records, where there was a significant positive trend in Ross Sea ice area flux, the longer 34-year trends of outflow from both seas are now statistically insignificant.

Kwok, R., J.C. Comiso, T. Lee, and P.R. Holland. 2016. Linked trends in the South Pacific sea ice edge and Southern Oscillation Index. *Geophysical Research Letters* 43, doi:10.1002/2016GL070655.

Previous work have shown that seaice variability in the South Pacific is associated with extratropical atmospheric anomalies linked to the Southern Oscillation (SO). Over a 32 year period (1982–2013), our study shows that the trend in Southern Oscillation Index (SOI) is also able to quantitatively explain the trends in sea ice edge, drift, and surface winds in this region. On average two thirds of the winter ice edge trend in this sector, linked to ice drift and surface winds, could be explained by the positive SOI trend, thus subjecting the ice edge to strong decadal SO variability. If this relationship holds, the negative SOI trend prior to the recent satellite era suggests that ice edge trends opposite to that of the recent record over a similar time scale. Significant low-frequency ice edge trends, linked to the natural variability of SO, are superimposed upon any trends expected of anthropogenic forcing.

Mack, S., L. Padman, and J. Klinck, 2013. Extracting tidal variability of sea ice concentration from AMSR-E passive microwave single-swath data: a case study of the Ross Sea. *Geophysical Research Letters*, 40: 547-552, doi:10.1002/grl.50128.

The periodic divergence of stress applied by ocean tidal currents to sea ice affects the time-averaged ice concentration (C_{ice}) and heat and freshwater fluxes at the ocean surface. We demonstrate that, at sufficiently high latitudes, tidal variability in C_{ice} can be extracted from single-swath data from the Advanced Microwave Scanning Radiometer–EOS (AMSR-E) satellite passive microwave sensor, although time intervals between swaths are irregular. For the northwest Ross Sea where tidal currents are large, tidal divergence is the dominant cause of C_{ice} variability in winter, with a range of ±0.2 about a mean of ~0.8. Daily-averaged C_{ice} values vary from >0.9 at neap tides to ~0.7 at spring tides. Variability at the fundamental tidal periods is about half that expected from an inverse barotropic tide model for the Ross Sea, suggesting that the measured tidal signal in C_{ice} may be used to diagnose sea ice mechanical properties and ice/ocean coupling.

Mack, S.L., M.S. Dinniman, J.M. Klinck, D.J. McGillicuddy, Jr., and L. Padman, 2019. Modeling ocean eddies on Antarctica's cold water continental shelves and their effects on ice shelf basal melting. *Journal of Geophysical Research* 124: 5067-5084, doi:10.1029/2018JC014688.

Changes in the rate of ocean-driven basal melting of Antarctica's ice shelves can alter the rate at which the grounded ice sheet loses mass and contributes to sea level change. Melt rates depend on the inflow of ocean heat, which occurs through steady circulation and eddy fluxes. Previous studies have demonstrated the importance of eddy fluxes for ice shelves affected by relatively warm intrusions of Circumpolar Deep Water. However, ice shelves on cold water continental shelves primarily melt from dense shelf water near the grounding line and from light surface water at the ice shelf front. Eddy effects on basal melt of these ice shelves have not been studied. We investigate where and when a regional ocean

model of the Ross Sea resolves eddies and determine the effect of eddy processes on basal melt. The size of the eddies formed depends on water column stratification and latitude. We use simulations at horizontal grid resolutions of 5 and 1.5 km and, in the 1.5-km model, vary the degree of topography smoothing. The higher-resolution models generate about 2–2.5 times as many eddies as the low-resolution model. In all simulations, eddies cross the ice shelf front in both directions. However, there is no significant change in basal melt between low- and high-resolution simulations. We conclude that higher-resolution models (<1 km) are required to better represent eddies in the Ross Sea but hypothesize that basal melt of the Ross Ice Shelf is relatively insensitive to our ability to fully resolve the eddy field.

Maksym, T., S.E. Stammerjohn, S. Ackley, and R. Massom. 2012. Antarctic sea ice -- a polar opposite? *Oceanography* 25: 140–151, doi:10.5670/oceanog.2012.88.

As the world's ice diminishes in the face of climate change—from the dramatic decline in Arctic sea ice, to thinning at the margins of both the Greenland and Antarctic ice sheets, to retreating mountain glaciers the world over—Antarctic sea ice presents something of a paradox. The trend in total sea ice extent in the Antarctic has remained steady, or even increased slightly, over the past three decades, confounding climate model predictions showing moderate to strong declines. This apparent intransigence masks dramatic regional trends; declines in sea ice in the Bellingshausen Sea region that rival the high-profile decline in the Arctic have been matched by opposing increases in the Ross Sea. Much of the explanation lies in the unique nature of the Antarctic sea ice zone. Its position surrounding the continent and exposure to the high-energy wind and wave fields of the open Southern Ocean shape both its properties and its connection to the atmosphere and ocean in ways very different from the Arctic. Sea ice extent and variability are strongly driven by large-scale climate variability patterns such as the El Niño-Southern Oscillation and the Southern Annular Mode. Because many of these patterns have opposing effects in different regions around the continent, decreases in one region are often accompanied by similar, opposing increases in another. Yet, the failure of climate models to capture either the overall or regional behavior also reflects, in part, a poor understanding of sea ice processes. Considerable insight has been gained into the nature of these processes over the past several decades through field expeditions aboard icebreakers. However, much remains to be discovered about the nature of Antarctic sea ice; its connections with the ocean, atmosphere, and ecosystem; and its complex response to present and future climate change.

Meehl, G.A., J.M. Arblaster, C.M. Bitz, C.T.Y. Chung, and H. Teng. 2016. Antarctic sea-ice expansion between 2000 and 2014 driven by tropical Pacific decadal climate variability. *Nature Geoscience*, http://dx.doi.org/10.1038/ngeo2751

Antarctic sea-ice extent has been slowly increasing in the satellite record that began in 1979. Since the late 1990s, the increase has accelerated, but the average of all climate models shows a decline. Meanwhile, the Interdecadal Pacific Oscillation, an internally generated mode of climate variability, transitioned from positive to negative5, with an average cooling of tropical Pacific sea surface temperatures, a slowdown of the global warming trend6–8 and a deepening of the Amundsen Sea Low near Antarctica that has contributed to regional circulation changes in the Ross Sea region and expansion of sea ice10. Here we show that the negative phase of the Interdecadal Pacific Oscillation in global coupled climate models is characterized by anomalies similar to the observed sea-level pressure and near-surface 850 hPa wind changes near Antarctica since 2000 that are conducive to expanding Antarctic sea-ice extent, particularly in the Ross Sea region in all seasons, involving a deepening of the Amundsen Sea Low. These atmospheric circulation changes are shown to be mainly driven by precipitation and convective heating anomalies related to the Interdecadal Pacific Oscillation in the equatorial eastern Pacific, with additional contributions from convective heating anomalies in the South Pacific convergence zone and tropical Atlantic regions.

Parkinson, C.L. 2019. A 40-y record reveals gradual Antarctic sea ice increases followed by decreases at rates far exceeding the rates seen in the Arctic. *Proceedings of the National Academy of Sciences* 116 (29): 14,414-14,423, doi/10.1073/pnas.1906556116.

Following over 3 decades of gradual but uneven increases in sea ice coverage, the yearly average Antarctic sea ice extents reached a record high of 12.8 million km2 in 2014, followed by a decline so precipitous that they reached their lowest value in the 40-y 1979–2018 satellite multichannel passive-microwave record, 10.7 million km2, in 2017. In contrast, it took the Arctic sea ice cover a full 3 decades to register a loss that great in yearly average ice extents. Still, when considering the 40-y record as a whole, the Antarctic sea ice continues to have a positive overall trend in yearly average ice extents, although at 11,300 ± 5,300 km2·y−1, this trend is only 50% of the trend for 1979–2014, before the precipitous decline. Four of the 5 sectors into which the Antarctic sea ice cover is divided all also have 40-y positive trends that are well reduced from their 2014–2017 values. The one anomalous sector in this regard, the Bellingshausen/Amundsen Seas, has a 40-y negative trend, with the yearly average ice extents decreasing overall in the first 3 decades, reaching a minimum in 2007, and exhibiting an overall upward trend since 2007 (i.e., reflecting a reversal in the opposite direction from the other 4 sectors and the Antarctic sea ice cover as a whole).

Parkinson, C.L., and D.J. Cavalieri. 2012. Antarctic sea ice variability and trends, 1979-2010. *The Cryosphere* 6: 871-880, doi:10.5194/tc-6-871-2012.

In sharp contrast to the decreasing sea ice coverage of the Arctic, in the Antarctic the sea ice cover has, on average, expanded since the late 1970s. More specifically, satellite passive-microwave data for the period November 1978–December 2010 reveal an overall positive trend in ice extents of 17 100 ± 2300 km2 yr−1. Much of the increase, at 13 700 ± 1500 km2 yr−1, has occurred in the region of the Ross Sea, with lesser contributions from the Weddell Sea and Indian Ocean. One region, that of the Bellingshausen/Amundsen Seas, has (like the Arctic) instead experienced significant sea ice decreases, with an overall ice extent trend of −8200 ± 1200 km2 yr−1. When examined through the annual cycle over the 32-yr period 1979–2010, the Southern Hemisphere sea ice cover as a whole experienced positive ice extent trends in every month, ranging in magnitude from a low of 9100 ± 6300 km2 yr−1 in February to a high of 24 700 ± 10 000 km2 yr−1 in May. The Ross Sea and Indian Ocean also had positive trends in each month, while the Bellingshausen/Amundsen Seas had negative trends in each month, and the Weddell Sea and western Pacific Ocean had a mixture of positive and negative trends. Comparing ice-area results to ice-extent results, in each case the ice-area trend has the same sign as the ice-extent trend, but the magnitudes of the two trends differ, and in some cases these differences allow inferences about the corresponding changes in sea ice concentrations. The strong pattern of decreasing ice coverage in the Bellingshausen/Amundsen Seas region and increasing ice coverage in the Ross Sea region is suggestive of changes in atmospheric circulation. This is a key topic for future research.

Piñones, A., E.E. Hofmann, D.P. Costa, K. Goetz, J.M. Burns, F. Roquet, M.S. Dinniman, and J.M. Klinck, 2019. Hydrographic variability along the inner and mid-shelf region of the western Ross Sea obtained using instrumented seals. *Progress in Oceanography* 174: 131-142, doi:10.1016/j.pocean.2019.01.003.

Temperature and salinity measurements obtained from sensors deployed on Weddell seals (*Leptonychotes weddellii*) between late austral summer and the following spring for 2010–2012 were used to describe the temporal and spatial variability of hydrographic conditions in the western Ross Sea, with particular emphasis on the inner-shelf region off Victoria Land and McMurdo Sound. Potential temperature-salinity diagrams constructed for regions where the seals remained for extended periods showed four water masses on the continental shelf: Modified Circumpolar Deep Water, Antarctic Surface Water, Shelf Water and Modified Shelf Water. Depth-time distributions of potential density and

buoyancy frequency showed the erosion of the upper water column stratification associated with the transition from summer to fall/winter conditions. The within-year and interannual variability associated with this transition was related to wind speed. Changes in upper water column density were positively correlated with cross-shelf wind speeds >5.5 m s^{-1} with a 3–4 day lag. A range of wind speeds was required to erode the density structure because of different levels of stratification in each year. A comparison of wind mixing potential versus stratification (Wedderburn number) showed that synoptic scale wind events during 2012 with speeds of 5.5 and 6.5 m s^{-1} were needed to erode the summer stratification for Ross Island and Victoria Land regions, respectively. Stronger winds (>8.5 m s^{-1}) were required during 2010 and 2011. The interannual variability in total heat content accumulated during summer (about 20%) was related to the duration of open water, with the largest heat content occurring in 2012, which was characterized by a summer sea ice minimum stronger than other years and relatively higher mCDW influence over the mid and outer-shelf regions. The heat content was lost after mid-April and reached a minimum in winter as a result of deep winter convection. The quantitative analysis of hydrographic variability of the inner-shelf region of the western Ross Sea obtained from the seal-derived measurements provides a baseline for assessing future changes.

Porter, D.F., S.R. Springer, L. Padman, H.A. Fricker, K.J. Tinto, S.C. Riser, R.E. Bell, and the ROSETTA-Ice Team. 2019. Evolution of the Seasonal Surface Mixed Layer of the Ross Sea, Antarctica, Observed With Autonomous Profiling Floats. *Journal of Geophysical Research* 124: 4934-4953, doi:10.1029/2018JC014683.

Oceanographic conditions on the continental shelf of the Ross Sea, Antarctica, affect sea ice production, Antarctic Bottom Water formation, mass loss from the Ross Ice Shelf, and ecosystems. Since ship access to the Ross Sea is restricted by sea ice in winter, most upper ocean measurements have been acquired in summer. We report the first multiyear time series of temperature and salinity throughout the water column, obtained with autonomous profiling floats. Seven Apex floats were deployed in 2013 on the midcontinental shelf, and six Air-Launched Autonomous Micro Observer floats were deployed in late 2016, mostly near the ice shelf front. Between profiles, most floats were parked on the seabed to minimize lateral motion. Surface mixed layer temperatures, salinities, and depths, in winter were −1.8 °C, 34.34, and 250–500 m, respectively. Freshwater from sea ice melt in early December formed a shallow (20 m) surface mixed layer, which deepened to 50–80 m and usually warmed to above −0.5 °C by late January. Upper-ocean freshening continued throughout the summer, especially in the eastern Ross Sea and along the ice shelf front. This freshening requires substantial lateral advection that is dominated by inflow from melting of sea ice and ice shelves in the Amundsen Sea and by inputs from the Ross Ice Shelf. Changes in upper-ocean freshwater and heat content along the ice shelf front in summer affect cross-ice front advection, ice shelf melting, and calving processes that determine the rate of mass loss from the grounded Antarctic Ice Sheet in this sector.

Raphael, MN, M.M. Holland, L. Landrum, and W.R. Hobbs. 2019. Links between the Amundsen Sea Low and sea ice in the Ross Sea: seasonal and interannual relationships. *Climate Dynamics* 52: 2333- 2349, doi:10.1007/s00382-018-4258-4

Previous studies have shown that sea ice extent in the Southern Ocean is influenced by the intensity and location of the Amundsen Sea Low (ASL), through their effect on the meridional winds. However, the inhomogeneous nature of the influence of the ASL on sea ice as well as its influence during critical periods of the sea ice annual cycle is not clear. In this study, we do a spatio-temporal analysis of links between the ASL and the sea ice during the advance and retreat periods of the ice over the period 1979–2013 focusing on the role of the meridional and zonal winds. We use the ERA-Interim monthly-averaged 500 mb geopotential height and 10 m wind data along with monthly Passive Microwave Sea Ice

Concentrations (SIC) to examine the seasonal and interannual relationships between the ASL and SIC in the Ross–Amundsen sea ice sector. To characterize the state of the ASL we use indices that describe its location and its intensity. We show that the ASL has preferred locations and intensities during ice advance and retreat seasons. The strength and direction of the influence of the ASL are not spatially homogeneous and can change from advance to retreat season and there are strong significant relationships between the characteristics of the ASL and SIC, within and across seasons and interannually.

Reid P, Stammerjohn S, Massom R, Scambos T, and Lieser J. 2015. The record 2013 Southern Hemisphere sea-ice extent maximum. *Annals of Glaciology* 56: 99-106.

Observations of Southern Hemisphere sea ice from passive microwave satellite measurements show that a new record maximum extent of 19.58 × 106km2 was reached on 30 September 2013; the extent is just over two standard deviations above the 1979-2012 mean and follows a similar record (19.48 × 106km2) in 2012. On the record day in 2013, sea-ice extent was greater than the 30 year average (1981-2010) in nearly all Southern Ocean regions. For the year as a whole, Southern Hemisphere sea-ice area and extent were well above average, and numerous monthly and daily records were broken. Analysis of anomaly patterns and the atmospheric and oceanic events suggests that a sequence of regional wind and cold-freshened surface waters is likely responsible for the record maximum and the generally high 2013 extent. In particular, the Ross Sea sector experienced a combination of cold southerly winds associated with the position and depth of the Amundsen Sea low, and lower than normal sea surface temperatures (up to 2°C below normal). The resulting very high anomaly in ice extent in this region was a major component of the overall record maximum.

Roach, C.J. and K. Speer, 2019. Exchange of water between the Ross Gyre and ACC assessed by Lagrangian particle tracking. *Journal of Geophysical Research: Oceans*, https://doi.org/10.1029/2018JC014845

To reach upwelling and downwelling zones deep within the Southern Ocean seasonal sea ice cover, water masses must move across the Antarctic Circumpolar Current and through current systems including the Ross Gyre, Weddell Gyre, and Antarctic Slope Current. In this study we focus our attention on the Lagrangian exchange between the Ross Gyre and surrounding current systems. We conducted numerical experiments using five-day 3-D velocity fields from the Southern Ocean State Estimate with a particle tracking package to identify pathways by which waters move from near the Antarctic coastal margins or Antarctic Circumpolar Current into the interior of the Ross Gyre, and to identify the time scales of variability associated with these pathways. Waters from near the Antarctic margins enter the Ross Gyre along the western and northern boundaries of gyre until the gyre separates from the Pacific-Antarctic Ridge near fracture zones. At this juncture, Antarctic Circumpolar Current-derived inflow dominates the across-gyre transport up to the Antarctic margin. Transport and exchange associated with different time-average components of flow are calculated to determine the relative contributions of high- and low-frequency and time-mean components.

Schlosser, E., F.A. Haumann, and M.N. Raphael. 2018. Atmospheric influences on the anomalous 2016 Antarctic sea ice decay. *The Cryosphere* 12: 1103–1119, doi:org/10.5194/tc-12-1103-2018

In contrast to the Arctic, where total sea ice extent (SIE) has been decreasing for the last three decades, Antarctic SIE has shown a small, but significant, increase during the same time period. However, in 2016, an unusually early onset of the melt season was observed; the maximum Antarctic SIE was already reached as early as August rather than the end of September, and was followed by a rapid decrease. The decay was particularly strong in November, when Antarctic SIE exhibited a negative anomaly (compared to the 1979–2015 average) of approximately 2 million km2. ECMWF Interim

reanalysis data showed that the early onset of the melt and the rapid decrease in sea ice area (SIA) and SIE were associated with atmospheric flow patterns related to a positive zonal wave number three (ZW3) index, i.e., synoptic situations leading to strong meridional flow and anomalously strong southward heat advection in the regions of strongest sea ice decline. A persistently positive ZW3 index from May to August suggests that SIE decrease was preconditioned by SIA decrease. In particular, in the first third of November northerly flow conditions in the Weddell Sea and the Western Pacific triggered accelerated sea ice decay, which was continued in the following weeks due to positive feedback effects, leading to the unusually low November SIE. In 2016, the monthly mean Southern Annular Mode (SAM) index reached its second lowest November value since the beginning of the satellite observations. A better spatial and temporal coverage of reliable ice thickness data is needed to assess the change in ice mass rather than ice area.

Silvano, A., A. Foppert, S.R. Rintoul, P.R. Holland, T. Tamura, N. Kimura, P. Castagno, P. Falco, G. Budillon, F.A. Haumann, A.C. Naveira Garabato, and A.M. Macdonald. 2020. Recent recovery of Antarctic Bottom Water formation in the Ross Sea driven by climate anomalies. ***Nature Geoscience*****, https://doi.org/10.1038/s41561-020-00655-3**

Antarctic Bottom Water (AABW) supplies the lower limb of the global overturning circulation, ventilates the abyssal ocean and sequesters heat and carbon on multidecadal to millennial timescales. AABW originates on the Antarctic continental shelf, where strong winter cooling and brine released during sea ice formation produce Dense Shelf Water, which sinks to the deep ocean. The salinity, density and volume of AABW have decreased over the last 50 years, with the most marked changes observed in the Ross Sea. These changes have been attributed to increased melting of the Antarctic Ice Sheet. Here we use in situ observations to document a recovery in the salinity, density and thickness (that is, depth range) of AABW formed in the Ross Sea, with properties in 2018–2019 similar to those observed in the 1990s. The recovery was caused by increased sea ice formation on the continental shelf. Increased sea ice formation was triggered by anomalous wind forcing associated with the unusual combination of positive Southern Annular Mode and extreme El Niño conditions between 2015 and 2018. Our study highlights the sensitivity of AABW formation to remote forcing and shows that climate anomalies can drive episodic increases in local sea ice formation that counter the tendency for increased ice-sheet melt to reduce AABW formation.

Sinclair, K.E., N.A.N. Bertler, M.M. Bowen, and K.R. Arrigo. 2014. 20th Century sea ice trends in the Ross Sea from a high resolution, coastal ice core record. ***Geophysical Research Letters*** **41: 3510-3516, doi:10.1002/2014GL059821**

We present the first proxy record of sea ice area (SIA) in the Ross Sea, Antarctica, from a 130-year coastal ice core record. High-resolution deuterium excess data show prevailing stable SIA from the 1880s until the 1950s, a 2–5% reduction from the mid-1950s to the early-1990s, and a 5% increase after 1993. Additional support for this reconstruction is derived from ice core methanesulphonic acid (MSA) concentrations and whaling records. While SIA has continued to decline around much of the West Antarctic coastline since the 1950s, concurrent with increasing air and ocean temperatures, the underlying trend is masked in the Ross Sea by a switch to positive SIA anomalies since the early-1990s. This increase is associated with a strengthening of southerly winds and the enhanced northwards advection of sea ice.

Smith, W.O., Jr., M.S. Dinniman, E.E. Hofmann, and J.M. Klinck. 2014. The effects of changing winds and temperatures on the oceanography of the Ross Sea in the 21st century. ***Geophysical Research Letters*** **41, doi:10.1002/2014GL059311.**

The Ross Sea is critically important in regulating Antarctic sea ice and is biologically productive, which makes changes in the region's physical environment of global concern. We examined the effects of projected changes in atmospheric temperatures and winds on aspects of the ocean circulation likely important to primary production using a high-resolution sea ice-ocean-ice shelf model of the Ross Sea. The modeled summer sea-ice concentrations decreased by 56% by 2050 and 78% by 2100. The duration of shallow mixed layers over the continental shelf increased by 8.5 and 19.2 days in 2050 and 2100, and the mean summer mixed layer depths decreased by 12 and 44%. These results suggest that the annual phytoplankton production in the future will increase and become more diatomaceous. Other components of the Ross Sea food web will likely be severely disrupted, creating significant but unpredictable impacts on the ocean's most pristine ecosystem.

Smith, W.O., Jr., K.T. Goetz, D.E. Kaufman, B.Y. Queste, V. Asper, D.P. Costa, M.S. Dinniman, M.A.M. Friedrichs, E.E. Hofmann, K.J. Heywood, J.M. Klinck, J.T. Kohut, and C.M. Lee. 2014. Multi-platform, multi-disciplinary investigations of the Ross Sea, Antarctica. *Oceanography* 27: 180-185.

In 2010–2011, three projects combined to characterize the temporal and spatial distributions of Modified Circumpolar Deep Water (MCDW) in the Ross Sea using icebreaker-based sampling, gliders, instrumented seals, and hindcasts from a numerical circulation model. The fieldwork clearly identified MCDW throughout the Ross Sea, and the data were used to determine its influence on potential heat and nutrient inputs and biotic distributions. Furthermore, the numerical simulations confirm its apparent trajectory and location. Substantial small-scale variability in oceanographic and biological distributions suggests that such variability may play an important role in biogeochemical cycles. Data from the three projects provide a view of hydrographic variability in the Ross Sea that is impossible to obtain using traditional sampling. Multiplatform investigations are promising approaches to future polar experiments where logistical considerations are of paramount importance.

Stammerjohn, S., R. Massom, D. Rind, and D. Martinson. 2012. Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. *Geophysical Research Letters* 39, L06501, doi:10.1029/2012GL050874

This bi-polar analysis resolves ice edge changes on space/time scales relevant for investigating seasonal ice-ocean feedbacks and focuses on spatio-temporal changes in the timing of annual sea ice retreat and advance over 1979/80 to 2010/11. Where Arctic sea ice decrease is fastest, the sea ice retreat is now nearly 2 months earlier and subsequent advance more than 1 month later (compared to 1979/80), resulting in a 3-month longer summer ice-free season. In the Antarctic Peninsula and Bellingshausen Sea region, sea ice retreat is more than 1 month earlier and advance 2 months later, resulting in a more than 3-month longer summer ice-free season. In contrast, in the western Ross Sea (Antarctica) region, sea ice retreat and advance are more than 1 month later and earlier respectively, resulting in a more than 2 month shorter summer ice-free season. Regardless of trend magnitude or direction, and at latitudes mostly poleward of 70_ (N/S), there is strong correspondence between anomalies in the timings of sea ice retreat and subsequent advance, but little correspondence between advance and subsequent retreat. These results support a strong ocean thermal feedback in autumn in response to changes in spring sea ice retreat. Further, model calculations suggest different net ocean heat changes in the Arctic versus Antarctic where autumn sea ice advance is 1 versus 2 months later. Ocean-atmosphere changes, particularly in boreal spring and austral autumn (i.e., during March-May), are discussed and compared, as well as possible inter-hemispheric climate connections.

Stern, A.A., M.S. Dinniman, V. Zagorodnov, S.W. Tyler, and D.M. Holland, 2013. Intrusion of warm surface water beneath the McMurdo Ice Shelf, Antarctica. *Journal of Geophysical Research* 118: 7036-7048, doi:10.1002/2013JC008842.

A 6 month temperature record collected below McMurdo Ice Shelf in 2011–2012 shows the temporal and spatial structure of the summertime warm water signal that penetrates beneath the ice shelf. The strength and duration of the warm water intrusion suggest an annual melt rate at Windless Bight of 0.71 m/yr. A Ross Sea numerical model demonstrates a seasonal warm water pathway leading from the west side of the Ross Sea Polynya (RSP) toward McMurdo Sound. The warm water enters McMurdo Sound, subducts beneath the ice shelf and causes accelerated summer melting. Temperature data were recorded using Distributed Temperature Sensing fiber optics, which gives a vertical temperature profile at a 1 m vertical resolution. This study constitutes one of the first successful implementations of this technology in Polar Regions.

Stuecker, M.F., C.M. Bitz, and K.C. Armour. 2018. Conditions leading to the unprecedented low Antarctic sea ice extent during the 2016 austral spring season. *Geophysical Research Letters* 44: 9008–9019, doi:10.1002/2017GL074691.

The 2016 austral spring was characterized by the lowest Southern Hemisphere (SH) sea ice extent seen in the satellite record (1979 to present) and coincided with anomalously warm surface waters surrounding most of Antarctica. We show that two distinct processes contributed to this event: First, the extreme El Niño event peaking in December–February 2015/2016 contributed to pronounced extratropical SH sea surface temperature and sea ice extent anomalies in the eastern Ross, Amundsen, and Bellingshausen Seas that persisted in part until the following 2016 austral spring. Second, internal unforced atmospheric variability of the Southern Annular Mode promoted the exceptional low sea ice extent in November–December 2016. These results suggest that a combination of tropically forced and internal SH atmospheric variability contributed to the unprecedented sea ice decline during the 2016 austral spring, on top of a background of slow changes expected from greenhouse gas and ozone forcing.

Thompson, L., M. Smith, J. Thomson, S. Stammerjohn, S. Ackley, and B. Loose, 2020. Frazil ice growth and production during katabatic wind events in the Ross Sea, Antarctica. *The Cryosphere* 14: 3329-3347, doi:10.5194/tc-14-3329-2020.

Katabatic winds in coastal polynyas expose the ocean to extreme heat loss, causing intense sea ice production and dense water formation around Antarctica throughout autumn and winter. The advancing sea ice pack, combined with high winds and low temperatures, has limited surface ocean observations of polynyas in winter, thereby impeding new insights into the evolution of these ice factories through the dark austral months. Here, we describe oceanic observations during multiple katabatic wind events during May 2017 in the Terra Nova Bay and Ross Sea polynyas. Wind speeds regularly exceeded 20 m s^{-1}, air temperatures were below −25 °C, and the oceanic mixed layer extended to 600 m. During these events, conductivity–temperature–depth (CTD) profiles revealed bulges of warm, salty water directly beneath the ocean surface and extending downwards tens of meters. These profiles reflect latent heat and salt release during unconsolidated frazil ice production, driven by atmospheric heat loss, a process that has rarely if ever been observed outside the laboratory. A simple salt budget suggests these anomalies reflect in situ frazil ice concentration that ranges from 13 to 266×10^{-3} kg m^{-3}. Contemporaneous estimates of vertical mixing reveal rapid convection in these unstable density profiles and mixing lifetimes from 7 to 12 min. The individual estimates of ice production from the salt budget reveal the intensity of short-term ice production, up to 110 cm d^{-1} during the windiest events, and a seasonal average of 29 cm d^{-1}. We further found that frazil ice production rates covary with wind speed and with location along the upstream–

downstream length of the polynya. These measurements reveal that it is possible to indirectly observe and estimate the process of unconsolidated ice production in polynyas by measuring upper-ocean water column profiles. These vigorous ice production rates suggest frazil ice may be an important component in total polynya ice production.

Wenta, M., and J.J. Cassano. 2020. The atmospheric boundary layer and surface conditions during katabatic wind events over the terra nova bay polynya. *Remote Sensing* 12:24, pages 4160.

Off the coast of Victoria Land, Antarctica an area of open water—the Terra Nova Bay Polynya (TNBP)—persists throughout the austral winter. The development of this coastal polynya is driven by extreme katabatic winds blowing down the slopes of Transantarctic Mountains. The surface-atmosphere coupling and ABL transformation during the katabatic wind events between 18 and 25 September 2012 in Terra Nova Bay are studied, using observations from Aerosonde unmanned aircraft system (UAS), numerical modeling results and Antarctic Weather Station (AWS) measurements. First, we analyze how the persistence and strength of the katabatic winds relate to sea level pressure (SLP) changes in the region throughout the studied period. Secondly, the polynya extent variations are analysed in relation to wind speed changes. We conclude that the intensity of the flow, surface conditions in the bay and regional SLP fluctuations are all interconnected and contribute to polynya development. We also analyse the Antarctic Mesoscale Prediction System (AMPS) forecast for the studied period and find out that incorrect representation of vertical ABL properties over the TNBP might be caused by overestimated sea ice concentrations (SIC) used as model input. Altogether, this research provides a unique description of TNBP development and its interactions with the atmosphere and katabatic winds.

BIO-PHYSICAL INTERACTIONS

LOWER TROPHIC LEVELS

Ackley, S.F., S. Stammerjohn, T. Maksym, M. Smith, J. Cassano, P. Guest, J.-L. Tison, B. Delille, B. Loose, P. Sedwick, L. DePace, L. Roach, and J. Parno. 2020. Sea-ice production and air/ice/ocean/biogeochemistry interactions in the Ross Sea during the PIPERS 2017 autumn field campaign. *Annals of Glaciology* 61: 181-195, doi:10.1017/aog.2020.31.

The Ross Sea is known for showing the greatest sea-ice increase, as observed globally, particularly from 1979 to 2015. However, corresponding changes in sea-ice thickness and production in the Ross Sea are not known, nor how these changes have impacted water masses, carbon fluxes, biogeochemical processes and availability of micronutrients. The PIPERS project sought to address these questions during an autumn ship campaign in 2017 and two spring airborne campaigns in 2016 and 2017. PIPERS used a multidisciplinary approach of manned and autonomous platforms to study the coupled air/ice/ocean/biogeochemical interactions during autumn and related those to spring conditions. Unexpectedly, the Ross Sea experienced record low sea ice in spring 2016 and autumn 2017. The delayed ice advance in 2017 contributed to (1) increased ice production and export in coastal polynyas, (2) thinner snow and ice cover in the central pack, (3) lower sea-ice Chl-a burdens and differences in sympagic communities, (4) sustained ocean heat flux delaying ice thickening and (5) a melting, anomalously southward ice edge persisting into winter. Despite these impacts, airborne observations in spring 2017 suggest that winter ice production over the continental shelf was likely not anomalous.

Alderkamp, A.-C., G.L. van Dijken, K.E. Lowry, K.M. Lewis, H. Joy-Warren, W. van de Poll, P. Laan, L. Gerringa, T. Delmont, B. Jenkins, and K.R. Arrigo. 2019. Effects of iron and light availability on phytoplankton photosynthetic properties in the Ross Sea. *Marine Ecology Progress Series* 621: 33–50, doi.org/10.3354/meps1300.

Waters of the Southern Ocean are characterized by high macronutrient concentrations but limited availability of trace metals and light, often making it difficult for phytoplankton to achieve maximum growth rates. One strategy employed by Southern Ocean phytoplankton in culture to cope with low light and low dissolved iron (DFe) is to enhance light absorption by increasing their antenna size, rather than the number of reaction centers, thereby reducing their Fe demand. Here we provide physiological evidence that natural populations of Southern Ocean phytoplankton employ a similar photoacclimation strategy to cope with low ambient DFe concentrations. During a research cruise to the Ross Sea in 2014, we conducted four bioassay experiments in which we manipulated light and DFe concentrations and measured changes in phytoplankton biomass, growth rate, photosynthetic parameters, fluorescence parameters, and pigment composition. Phytoplankton responded strongly to DFe additions, exhibiting significantly higher biomass, growth rates, and photosynthetic competency. At low light, the maximum photosynthetic rate (P*max) was significantly reduced and the photosynthetic efficiency (α*) was unchanged compared to the high light treatment, regardless of phytoplankton species composition or DFe concentration. Our data suggest that Southern Ocean phytoplankton have evolved an Fe-saving strategy whereby they photoacclimate to low light by increasing their photosynthetic unit size, rather than photosynthetic unit number, even when DFe is available. It appears this Fe-saving strategy is characteristic of both *P. antarctica* and diatoms, suggesting that it is a common adaptation among phytoplankton taxa that grow under Fe limitation in the Southern Ocean.

Armstrong, I., A. Asanuma, M.J. Behrenfeld, A.M. Ciotti, M. Dowell, N. Hoepffner, K.J. W. Hyde, J. Ishizaka, T. Kameda, J. Marra, F. Mélin, A. Morel, J. O'Reilly, M. Scardi, W.O. Smith Jr., T.J. Smyth, S. Tang, J. Uitz, K. Waters, and T.K. Westberry. 2011. Estimating marine primary productivity in coastal and pelagic regions across the globe: An evaluation of satellite-based ocean color models. *Biogeosciences* 8: 489-503.

Nearly half of the earth's photosynthetically fixed carbon derives from the oceans. To determine global and region specific rates, we rely on models that estimate marine net primary productivity (NPP) thus it is essential that these models are evaluated to determine their accuracy. Here we assessed the skill of 21 ocean color models by comparing their estimates of depth-integrated NPP to 1156 in situ 14C measurements encompassing ten marine regions including the Sargasso Sea, pelagic North Atlantic, coastal Northeast Atlantic, Black Sea, Mediterranean Sea, Arabian Sea, subtropical North Pacific, Ross Sea, West Antarctic Peninsula, and the Antarctic Polar Frontal Zone. Average model skill, as determined by root-mean square difference calculations, was lowest in the Black and Mediterranean Seas, highest in the pelagic North Atlantic and the Antarctic Polar Frontal Zone, and intermediate in the other six regions. The maximum fraction of model skill that may be attributable to uncertainties in both the input variables and in situ NPP measurements was nearly 72%. On average, the simplest depth/wavelength

integrated models performed no worse than the more complex depth/wavelength resolved models. Ocean color models were not highly challenged in extreme conditions of surface chlorophyll-*a* and sea surface temperature, nor in high-nitrate low-chlorophyll waters. Water column depth was the primary influence on ocean color model performance such that average skill was significantly higher at depths greater than 250 m, suggesting that ocean color models are more challenged in Case-2 waters (coastal) than in Case-1(pelagic) waters. Given that in situ chlorophyll-*a* data was used as input data, algorithm improvement is required to eliminate the poor performance of ocean color NPP models in Case-2 waters that are close to coastlines. Finally, ocean color chlorophyll-*a* algorithms are challenged by optically complex Case-2 waters, thus using satellite-derived chlorophyll-a to estimate NPP in coastal areas would likely further reduce the skill of ocean color models.

Arrigo, K.R., G.L. van Dijken, and A.L. Strong. 2015. Environmental controls of marine

productivity hot spots around Antarctica. *Journal of Geophysical Research* 120: 5545–5565, doi:10.1002/2015JC010888.

Antarctic coastal polynyas are biologically rich ecosystems that support large populations of mammals and birds and are globally significant sinks of atmospheric carbon dioxide. To support local phytoplankton blooms, these highly productive ecosystems require a large input of iron (Fe), the sources of which are poorly known. Here we assess the relative importance of six different environmental factors in controlling the amount of phytoplankton biomass and rates of net primary production (NPP) in 46 coastal polynyas around Antarctica. Data presented here suggest that melting ice shelves are a primary supplier of Fe to coastal polynyas, with basal melt rates explaining 58% of the between-polynya variance in mean chlorophyll *a* (Chl *a*) concentration. In a multiple regression analysis, which explained 78% of the variance in chlorophyll *a* (Chl *a*) between polynyas, basal melt rate explained twice as much of the variance as the next most important variable. Fe upwelled from sediments, which is partly controlled by continental shelf width, was also important in some polynyas. Of secondary importance to phytoplankton abundance and NPP were sea surface temperature and polynya size. Surprisingly, differences in light availability and the length of the open water season explained little or none of the variance in either Chl *a* or NPP between polynyas. If the productivity of coastal polynyas is indeed sensitive to the release of Fe from melting ice shelves, future changes in ice shelf melt rates could dramatically influence Antarctic coastal ecosystems and the ability of continental shelf waters to sequester atmospheric carbon dioxide.

Asper, V., and W.O. Smith, Jr. 2019. Variations in the abundance and distribution of aggregates in the Ross Sea, Antarctica. *Elementa: Science of the Anthropocene* 7: 23, https://doi.org/10.1525/elementa.355

The vertical distribution and temporal changes in aggregate abundance and sizes were measured in the Ross Sea, Antarctica between 2002 and 2005 to acquire a more complete understanding of the mechanisms and rates of carbon export from the euphotic layer. Aggregate abundance was determined by photographic techniques, and water column parameters (temperature, salinity, fluorescence, transmissometry) were assessed from CTD profiles. During the first three years the numbers of aggregates increased seasonally, being much more abundant within the upper 200 m in late summer than in early summer from 50 to 100 m (12.5 L–1 in early summer vs. 42.9 L–1 in late summer). In Year 4 aggregate numbers were substantially greater than in other years, and average aggregate abundance was maximal in early rather than late summer (177 vs. 84.5 L–1), which we attributed to the maximum biomass and aggregate formation being reached earlier than in other years. The contribution of aggregate particulate organic carbon to the total particulate carbon pool was estimated to be 20%. Ghost colonies, collapsed colonies of the haptophyte *Phaeocystis antarctica*, were observed during late summer in Year 4, with maximum numbers in the upper 100 m of ca. 40 L–1. Aggregate abundance, particulate organic carbon and ghost colonies all decreased exponentially with depth, and the rate of ghost colony disappearance suggested that their contribution to sedimentary input was small at the time of sampling. Bottom nepheloid layers were commonly observed in late summer in both transmissometer and aggregate data. Late summer nepheloid layers had fluorescent material within them, suggesting that the particles were likely generated during the same growing season. Longer studies encompassing the entire production season would be useful in further elucidating the role of these aggregates in the carbon cycle of these regions.

Bercovici, S.K., B.A. Huber, H.B. DeJong, R.B. Dunbar, and D.A. Hansell, 2017, Dissolved organic carbon in the Ross Sea: deep enrichment and export. *Limnology and Oceanography* 62: 1-11, doi:10.1002/lno.10592.

Antarctica's continental shelves generate the densest waters in the world and are responsible for the formation of Antarctic Bottom Water (AABW), a water mass with the potential to sequester carbon in the deep ocean for millennia. One such form of marine carbon is dissolved organic carbon (DOC), the ocean's largest standing stock of reduced carbon. In this study, we quantify DOC enrichment in dense shelf waters (DSW) in the Ross Sea and assess the potential for DOC to be sequestered from Antarctic shelves into AABW. We find that Ross Sea DSW is enriched in DOC by ∼7 μmol kg−1 relative to the incoming source waters (initial conditions), which is primarily caused by vertical mixing. The total DOC excess in DSW suggests that 4.0 ± 0.6 Tg DOC yr−1 is exported off the shelf. However, this exported fraction does not appear to persist in newly formed AABW and is likely remineralized, sequestering this carbon as TCO2 in the deep ocean.

Bertrand, E.M., M.A. Saito, P.A. Lee, R.B. Dunbar, and G.R. DiTullio. 2011. Iron limitation of springtime bacterial and phytoplankton community in the Ross Sea: Implications for vitamin B_{12} nutrition. *Frontiers in Microbiology* 2, doi:10.3389/fmicb.2011.00160.

The Ross Sea is home to some of the largest phytoplankton blooms in the Southern Ocean. Primary production in this system has previously been shown to be iron limited in the summer and periodically iron and vitamin B12 colimited. In this study, we examined trace metal limitation of biological activity in the Ross Sea in the austral spring and considered possible implications for vitamin B12 nutrition. Bottle incubation experiments demonstrated that iron limited phytoplankton growth in the austral spring while B12, cobalt, and zinc did not. This is the first demonstration of iron limitation in a Phaeocystis antarctica-dominated, early season Ross Sea phytoplankton community. The lack of B12 limitation in this location is consistent with previous Ross Sea studies in the austral summer, wherein vitamin additions did not stimulate P. antarctica growth and B12 was limiting only when bacterial abundance was low. Bottle incubation experiments and a bacterial regrowth experiment also revealed that iron addition directly enhanced bacterial growth. B12 uptake measurements in natural water samples and in an iron fertilized bottle incubation demonstrated that bacteria serve not only as a source for vitamin B12, but also as a significant sink, and that iron additions enhanced B12 uptake rates in phytoplankton but not bacteria. Additionally, vitamin uptake rates did not become saturated upon the addition of up to 95 pM B12. A rapid B12 uptake rate was observed after 13 min, which then decreased to a slower constant uptake rate over the next 52 h. Results from this study highlight the importance of iron availability in limiting early season Ross Sea phytoplankton growth and suggest that rates of vitamin B12 production and consumption may be impacted by iron availability.

Bochdansky, A.B., R.B. Dunbar, D.A. Hansell, and G.J. Herndl, 2019, Estimating carbon flux from optically recording total particle volume at depths below the primary pycnocline. *Frontiers in Marine Science*, https://doi.org/10.3389/fmars.2019.00778.

Optical instruments can rapidly determine numbers and characteristics of water column particles with high sensitivity. Here we show the usefulness of optically assessed total particle volume below the main pycnocline to estimate carbon export in two systems: the open subarctic North Atlantic and the Ross Sea, Antarctica. Both regions exhibit seasonally high phytoplankton production and efficient export (i.e., a strong biological pump). Total particle volumes in the mesopelagic (200–300 m) were significantly correlated with those in the overlying surface mixed layer (50–60 m), indicating that most particles at depth reflect export from the surface. This connectivity, however, is modulated by the physical structure of the water column and by particle type (e.g., the presence of colonies of the haptophyte Phaeocystis antarctica versus diatoms). Evidence from both regions show that a strong pycnocline can delay or may even prevent particles from settling to deeper layers, which then succumb to disintegration, and microbial and zooplankton consumption. Strong katabatic winds in the Ross Sea may deepen the mixed layer,

causing a rapid transfer of particles to mesopelagic depths through the mixed-layer pump. Independent estimates of seasonally integrated export production in the Ross Sea, based on upper water column carbon mass balance, were significantly correlated (in the order of shared variance) with (1) total particle volumes from images, (2) particulate organic carbon, and (3) chlorophyll fluorescence, all recorded at a depth range of 200–300 m. Carbon export was not significantly correlated with particle abundance measured by a Coulter counter at the same depth range. Measuring total particle volume below the primary pycnocline is therefore a useful approach to estimate carbon export at least in regions characterized by seasonally high particle export.

Carr, S.A., S.W. Vogel, R.B. Dunbar, J. Brandes, C.T. Mills, J.R. Spear, R. Levy, T.R. Naish, R.D. Powell, S.G. Wakeham, and K.W. Mandernack, 2013, Bacterial abundance and composition in marine sediment beneath the Ross Ice Shelf, Antarctica. *Geobiology* 11: 377-395, doi:10.1111/gbi.12042.

Marine sediments of the Ross Sea, Antarctica, harbor microbial communities that play a significant role in the decomposition, mineralization, and recycling of organic carbon (OC). In this study, the cell densities within a 153-cm sediment core from the Ross Sea were estimated based on microbial phospholipid fatty acid (PLFA) concentrations and acridine orange direct cell counts. The resulting densities were as high as 1.7 × 107 cells mL−1 in the top ten centimeters of sediments. These densities are lower than those calculated for most near-shore sites but consistent with deep-sea locations with comparable sedimentation rates. The δ13C measurements of PLFAs and sedimentary and dissolved carbon sources, in combination with ribosomal RNA (SSU rRNA) gene pyrosequencing, were used to infer microbial metabolic pathways. The δ13C values of dissolved inorganic carbon (DIC) in pore waters ranged down core from −2.5‰ to −3.7‰, while δ13C values for the corresponding sedimentary particulate OC (POC) varied from −26.2‰ to −23.1‰. The δ13C values of PLFAs ranged between −29‰ and −35‰ throughout the sediment core, consistent with a microbial community dominated by heterotrophs. The SSU rRNA gene pyrosequencing revealed that members of this microbial community were dominated by β-, δ-, and γ-Proteobacteria, Actinobacteria, Chloroflexi and Bacteroidetes. Among the sequenced organisms, many appear to be related to known heterotrophs that utilize OC sources such as amino acids, oligosaccharides, and lactose, consistent with our interpretation from δ13CPLFA analysis. Integrating phospholipids analyses with pore water chemistry, δ13CDIC and δ13CPOC values and SSU rRNA gene sequences provides a more comprehensive understanding of microbial communities and carbon cycling in marine sediments, including those of this unique ice shelf environment.

Carr, S.A, F.L. Schubotz, R.B. Dunbar, C.T. Mills, R. Dias, R.E. Summons, and K.W. Mandernack. 2018. Acetoclastic Methanosaeta are dominant methanogens in organic-rich Antarctic marine sediments. *ISME – Multidisciplinary Journal of Microbial Ecology* 12: 330-342, doi:10.1038/ismej.2017.150.

Despite accounting for the majority of sedimentary methane, the physiology and relative abundance of subsurface methanogens remain poorly understood. We combined intact polar lipid and metagenome techniques to better constrain the presence and functions of methanogens within the highly reducing, organic-rich sediments of Antarctica's Adélie Basin. The assembly of metagenomic sequence data identified phylogenic and functional marker genes of methanogens and generated the first Methanosaeta sp. genome from a deep subsurface sedimentary environment. Based on structural and isotopic measurements, glycerol dialkyl glycerol tetraethers with diglycosyl phosphatidylglycerol head groups were classified as biomarkers for active methanogens. The stable carbon isotope (δ13C) values of these biomarkers and the Methanosaeta partial genome suggest that these organisms are acetoclastic methanogens and represent a relatively small (0.2%) but active population. Metagenomic and lipid

analyses suggest that Thaumarchaeota and heterotrophic bacteria co-exist with Methanosaeta and together contribute to increasing concentrations and δ13C values of dissolved inorganic carbon with depth. This study presents the first functional insights of deep subsurface Methanosaeta organisms and highlights their role in methane production and overall carbon cycling within sedimentary environments.

DeJong, H.B., R.B. Dunbar, D.A. Mucciarone, and D. Koweek. 2015. Calcium carbonate saturation of the surface waters in the Ross Sea and Southern Ocean: controls and implications for the onset of aragonite undersaturation. *Biogeosciences* 12: 6881–6896, doi:10.5194/bg-12-6881-2015.

Predicting when surface waters of the Ross Sea and Southern Ocean will become undersaturated with respect to biogenic carbonate minerals is challenging in part due to the lack of baseline high-resolution carbon system data. Here we present ~ 1700 surface total alkalinity measurements from the Ross Sea and along a transect between the Ross Sea and southern Chile from the austral autumn (February–March 2013). We calculate the saturation state of aragonite (ΩAr) and calcite (Ω Ca) using measured total alkalinity and pCO2. In the Ross Sea and south of the Polar Front, variability in carbonate saturation state (Ω) is mainly driven by algal photosynthesis. Freshwater dilution and calcification have minimal influence on Ω variability. We estimate an early spring surface water ΩAr value of ~ 1.2 for the Ross Sea using a total alkalinity–salinity relationship and historical pCO2 measurements. Our results suggest that the Ross Sea is not likely to become undersaturated with respect to aragonite until the year 2070.

DeJong, H.B., R.B. Dunbar, D.A. Mucciarone, D.K. Koweek, S. Bercovici, and D.A. Hansell. 2017. Net community production and carbon export in the Ross Sea, Antarctica: insights from the late summer. *Global Biogeochemical Cycles* 31: 473-491, doi:10.1002/2016GB005417.

The phytoplankton bloom in the Ross Sea is the largest in spatial extent and one of the most productive in Antarctica, yet the fate of the summer bloom remains poorly understood. Here we present carbon system data from the first biogeochemical process cruise to be conducted in both the western and central Ross Sea during late summer (February–March 2013). Using one-dimensional carbon budgets, we found evidence for substantial positive net community production (425 ± 204 mmol C m−2 d−1) during the late summer in Terra Nova Bay (TNB) of the western Ross Sea, which was rapidly exported to below 200 m. In addition, seasonally integrated carbon export was higher in diatom-dominated TNB (7.3 ± 0.9 mol C m−2) compared to the Phaeocystis antarctica-dominated central Ross Sea (3.4 ± 0.8 mol C m−2). Substantial late summer productivity and export may be a widespread phenomenon in Antarctic coastal regions that is not accounted for in regional carbon models.

DeJong, H.B., and R.B. Dunbar. 2017. Air-sea CO_2 exchange in the Ross Sea, Antarctica. *Journal of Geophysical Research: Oceans* 122: 8167–8181, https://doi.org/10.1002/2017JC012853.

Although the Ross Sea is one of the most productive regions in Antarctica, it is not clear to what extent this region is an atmospheric CO2 sink. We calculate instantaneous CO2 flux rates with in situ pCO2 and wind speed data from 20 cruises in the Ross Sea. In addition, we estimate annual CO2 fluxes into the Ross Sea with nutrient budgets from a late summer cruise. We find that the Ross Sea is a lesser atmospheric CO2 sink (–7.5 ± 0.5 Tg C yr−1, −1.3 ± 0.1 mol C m−2 yr−1) than previously reported (–13 Tg C yr−1, −1.7 to −4.2 mol C m−2 yr−1). One exception is Terra Nova Bay (TNB) in the western Ross Sea, with CO2 flux rates (–4.8 ± 0.3 mol C m−2, January–March) that are 3–4 times greater than the Ross Sea mean. The majority of the CO2 flux into TNB occurs during the late summer with instantaneous CO2 flux rates up to −246 mmol C m−2 d−1. These extraordinary CO2 flux rates are caused by the unique coupling of strong katabatic winds and low surface pCO2 values. Although strong katabatic winds deepen the mixed layer and entrain CO2-rich water from below, late season net community productivity

maintains low surface water pCO2 levels. While TNB only covers ~1% (3,600 km2) of the Ross Sea continental shelf, extraordinary air-to-sea CO2 fluxes during the late summer may be regular features in many of the major sea ice production polynyas (148,000 km2 combined), including Antarctic Bottom Water formation regions.

DeJong, H.B., R.B. Dunbar, and E.A. Lyons. 2018. Late summer frazil ice-associated algal blooms around Antarctica. *Geophysical Research Letters* 45: 826-845, https://doi.org/10.1002/2017GL075472.

Antarctic continental shelf waters are the most biologically productive in the Southern Ocean. Although satellite-derived algorithms report peak productivity during the austral spring/early summer, recent studies provide evidence for substantial late summer productivity that is associated with green colored frazil ice. Here we analyze daily Moderate Resolution Imaging Spectroradiometer satellite images for February and March from 2003 to 2017 to identify green colored frazil ice hot spots. Green frazil ice is concentrated in 11 of the 13 major sea ice production polynyas, with the greenest frazil ice in the Terra Nova Bay and Cape Darnley polynyas. While there is substantial interannual variability, green frazil ice is present over greater than 300,000 km2 during March. Late summer frazil ice-associated algal productivity may be a major phenomenon around Antarctica that is not considered in regional carbon and ecosystem models.

Dinniman, M.S., P. St-Laurent, K.R. Arrigo, E.E. Hofmann, and G.L. van Dijken. 2020. Analysis of iron sources in Antarctic continental shelf waters. *Journal of Geophysical Research-Oceans* 125(5): https://doi.org/10.1029/2019JC015736.

Previous studies showed that satellite-derived estimates of chlorophyll *a* in coastal polynyas over the Antarctic continental shelf are correlated with the basal melt rate of adjacent ice shelves. A 5-km resolution ocean/sea ice/ice shelf model of the Southern Ocean is used to examine mechanisms that supply the limiting micronutrient iron to Antarctic continental shelf surface waters. Four sources of dissolved iron are simulated with independent tracers, assumptions about the source iron concentration for each tracer, and an idealized summer biological uptake. Iron from ice shelf melt provides about 6% of the total dissolved iron in surface waters. The contribution from deep sources of iron on the shelf (sediments and Circumpolar Deep Water) is much larger at 71%. The relative contribution of dissolved iron supply from basal melt driven overturning circulation within ice shelf cavities is heterogeneous around Antarctica, but at some locations, such as the Amundsen Sea, it is the primary mechanism for transporting deep dissolved iron to the surface. Correlations between satellite chlorophyll *a* in coastal polynyas around Antarctica and simulated dissolved iron confirm the previous suggestion that productivity of the polynyas is linked to the basal melt of adjacent ice shelves. This correlation is the result of upward advection or mixing of iron-rich deep waters due to circulation changes driven by ice shelf melt, rather than a direct influence of iron released from melting ice shelves. This dependence highlights the potential vulnerability of coastal Antarctic ecosystems to changes in ice shelf basal melt rates.

Fragoso, G.M., and W.O. Smith, Jr. 2012. Influence of hydrography on phytoplankton distribution in the Amundsen and Ross Seas, Antarctica. *Journal of Marine Systems* 89: 19-29.

The phytoplankton of the Ross Sea have been intensively studied, in contrast to that of the Amundsen Sea. This study focused on understanding the environmental variables that influence the spatial patterns of assemblages during late summer, 2007, and late spring–early summer, 2008 in the Amundsen and Ross Seas. Blooms of the prymnesiophyte *Phaeocystis antarctica*, and the silicoflagellate

Dictyocha speculum occurred in the southwestern to eastern parts of the Ross Sea, respectively, whereas diatoms dominated in southeastern Ross and the Amundsen Sea. Shallow mixed layers supported the growth of diatoms, but were not the only factor required for diatom bloom development. Modified Circumpolar Deep Water intruded into the subsurface waters (b200 m) in the southwestern Ross Sea during February 2007, and possibly favored the formation of *P. antarctica* blooms. Photosynthetic quantum yield data suggest that blooms from the southwestern Ross Sea were approaching stress during January 2008, likely due to iron limitation, in contrast to blooms close to the ice edge in the Amundsen Sea, where iron may be more available to the phytoplankton. A detailed comparison between the Amundsen and Ross Seas may allow a greater understanding of the environmental-induced impacts on phytoplankton distribution and regional biogeochemical cycles.

Gerringa, L., A.-C. Alderkamp, G. Van Dijken, P. Laan, R. Middag, and K. Arrigo. 2020. Dissolved trace metals in the Ross Sea. *Frontiers in Marine Science* 7: 577098. doi:10.3389/fmars.2020.577098

The dissolved (D) trace metals zinc (Zn), cadmium (Cd), cobalt (Co), copper (Cu), iron (Fe), manganese (Mn), nickel (Ni), titanium (Ti), lanthanum (La), yttrium (Y), and lead (Pb) were analyzed via ICPMS in samples from the Ross Sea obtained during a cruise between 20 December 2013 and 5 January 2014. The concentrations of DZn, DCd, DCo, DCu, DFe, DMn, DNi, and DTi were significantly lower in the Antarctic surface Water (AASW) compared to the other deeper water masses, indicating biological uptake and possibly scavenging. In the AASW, DLa and DY were higher than in Winter Water (WW). This can be explained by a spring source from ice melt followed by loss during summer and autumn, probably due to passive adsorption. Dissolved Pb was low (16 pM) and no distinction between water masses was possible. Akin to the macro-nutrients nitrate and silicate, the modified Circumpolar Deep Water (mCDW) shows elevated DCd compared to the shelf water masses. Sea ice melt and ice sheet melt released DZn, DFe, DMn, DNi, DY, DLa, and probably DPb into the Ross Sea. However, only DFe, DMn, DY and DLa are transported into the Antarctic Circumpolar Current with the outflowing High Salinity Shelf Water (HSSW). The bottom nepheloid layer (BNL) released DFe, as well as DMn and DCu, into the HSSW whereas lateral transport from land formed a source of DMn and DFe. One station in the Ross Sea Polynya was resampled after two weeks, during which time the thickness of the BNL increased, with accompanying increases in DFe and DMn near the seafloor. In the surface layer nutrients (including micro-nutrients) were depleted further. The uptake slopes/stoichiometric ratios of DZn, DCd and DCo versus phosphate indicated that the distribution of these metals is related to uptake as well as the composition of the phytoplankton community. Estimated stoichiometric ratios of Zn and Cd relative to P were higher at a station dominated by *Phaeocystis antarctica* than at diatom-dominated stations, implying a higher utilization of these metals by *P. antarctica*.

Gerringa, L.J.A., P. Laan, K. R. Arrigo, G.L. van Dijken, and A.-C. Alderkamp. 2019. The organic complexation of Fe in the Ross Sea. *Marine Chemistry* 215, 103672.

The Ross Sea Polynya (RSP) has the highest primary production of Antarctic waters. Iron (Fe) is one of the most important growth limiting factors in the Southern Ocean. Dissolved iron (DFe)-binding organic ligands play an important ecological role because they increase the residence time of the scarce Fe. Therefore, we studied the DFe-binding organic ligands in the vicinity of the Ross Sea during a cruise between 20 December 2013 and 5 January 2014. The DFe-binding organic ligands were measured using Competing Ligand Exchange Cathodic Stripping Voltammetry (CLE-CSV) with TAC as competing ligand. The DFe-binding organic ligand concentrations always exceeded the DFe concentrations except in the bottom nepheloid layer of the RSP. No relationship was found between depth and DFe-binding organic ligand concentrations in the RSP indicating that these ligands are resistant to degradation and are probably exported by high salinity shelf water into the circumpolar current. DFe-binding organic ligand

concentrations were highest in the RSP and the Antarctic Circumpolar Current (ACC) west of the Ross Sea, in association with seasonal phytoplankton blooms, although no correlation was found with parameters reflecting phytoplankton abundance or species. Phytoplankton sources and sinks of DFe-binding organic ligands are likely related to the seasonal progression of the bloom. In 39% of the samples, two DFe-binding organic ligand groups were distinguished based on the difference in binding strength. The distinction was especially clear in the RSP and in the ACC west of the RSP (54 and 77% of the samples, respectively) where blooms occurred and much less in the low biomass waters of the ACC east of the RSP and ice covered eastern part of the Ross Sea (15 and 10% of the samples, respectively). In these waters, other environmental factors, like sea ice melt, probably explain the absence of distinct relationships between primary production and ligand characteristics.

Gerringa, L.J.A., P. Laan, G.L. van Dijken, H. van Haren, H.J.W. De Baar, K.R. Arrigo, and A.-C. Alderkamp. 2015. Sources of iron in the Ross Sea polynya in late spring and summer. *Marine Chemistry* 177: 447-459.

Dissolved Fe (DFe) was measured in the Ross Sea Polynya (RSP), Antarctica, during a GEOTRACES cruise between 20 December 2013 and 5 January 2014. DFe was measured over the full water column with special emphasis on samples near the seafloor. In the upper mixed layer, DFe was very low everywhere (b0.10 nM). DFe increased with depth to values between 0.60 and 2.76 nM near the seafloor. The highest DFE concentrations were found at stations where a bottom nepheloid layer (BNL) was present (28 out of 32 stations). Deep DFe was lower 0.24–0.38 nM) at stations with no BNL. The main DFe supply to the upper mixed layer was vertical diffusive transport from the seafloor sediments, with a mean flux of 3.3 °— 10−8 mol DFe m−2 day−1. DFe fluxes showed large spatial variability of three orders of magnitude and were positively correlated to DFe concentrations near the sediment and vertical turbulent eddy diffusivity (Kz) and negatively correlated to water depth. The greatest fluxes were observed above the shallow banks such as Ross and Pennell Banks, and sediments with a BNL. We studied the horizontal diffusive transport from Franklin Island as an example of horizontal DFe transport from landmasses. No DFe transport was detected in the upper 100 m of the water column, probably due to uptake by phytoplankton. However, at 200 and 300 m depth, the DFe transport at distances between 50 and 100 km from Franklin Island was as large as the mean diffusive upward transport, indicating the potential importance of landmasses as a local source of DFe. Conversely, no horizontal transport of DFe from banks was detected. In addition, the Ross Ice Shelf (RIS)was a negligible source of DFe.Only the Ice ShelfWater (ISW), a watermass formed under the RIS, contained slightly elevated DFe (0.18–0.26 nM) compared to the surrounding waters. However, this elevated DFe did not reach into the RSP. Icebergs were not encountered and were not evaluated as a DFe source. Overall, we conclude that DFe from the seafloor and land mass sediments are the main DFe sources of DFe that support phytoplankton in the upper mixed layer of the Ross Sea Polynya in early summer.

Kaufman, D.E., M.A.M. Friedrichs, J.C.P. Hemmings, and W.O. Smith, Jr. 2018. Assimilating bio-optical glider data: time and space variability during a phytoplankton bloom in the southern Ross Sea. *Biogeosciences* 15: 73–90, https://doi.org/10.5194/bg-15-73-2018.

The Ross Sea is a region characterized by high primary productivity in comparison to other Antarctic coastal regions, and its productivity is marked by considerable variability both spatially (1–50 km) and temporally (days to weeks). This variability presents a challenge for inferring phytoplankton dynamics from observations that are limited in time or space, which is often the case due to logistical limitations of sampling. To better understand the spatiotemporal variability in Ross Sea phytoplankton dynamics and to determine how restricted sampling may skew dynamical interpretations, high-resolution bio-optical glider measurements were assimilated into a one-dimensional biogeochemical model adapted for the Ross Sea. The assimilation of data from the entire glider track using the micro-genetic and local

search algorithms in the Marine Model Optimization Testbed improves the model–data fit by ~50 %, generating rates of integrated primary production of 104 g Cm-2 yr-1 and export at 200m of 27 gCm-2 yr-1. Assimilating glider data from three different latitudinal bands and three different longitudinal bands results in minimal changes to the simulations, improves the model–data fit with respect to unassimilated data by ~35 %, and confirms that analyzing these glider observations as a time series via a one-dimensional model is reasonable on these scales. Whereas assimilating the full glider data set produces well-constrained simulations, assimilating subsampled glider data at a frequency consistent with cruise-based sampling results in a wide range of primary production and export estimates. These estimates depend strongly on the timing of the assimilated observations, due to the presence of high mesoscale variability in this region. Assimilating surface glider data subsampled at a frequency consistent with available satellite-derived data results in 40% lower carbon export, primarily resulting from optimized rates generating more slowly sinking diatoms. This analysis highlights the need for the strategic consideration of the impacts of data frequency, duration, and coverage when combining observations with biogeochemical modeling in regions with strong mesoscale variability.

Kaufman, D.E., M.A.M. Friedrichs, W.O. Smith, Jr., E.E. Hofmann, M.S. Dinniman, and J.C.P. Hennings. 2017. Climate change impacts on Ross Sea biogeochemistry: results from 1D modeling experiments. Journal of Geophysical Research 122: 2339–2359, https://doi:10.1002/2016JC012514.

The Ross Sea, a highly productive region of the Southern Ocean, is expected to experience warming during the next century along with reduced summer sea ice concentrations and shallower mixed layers. This study investigates how these climatic changes may alter phytoplankton assemblage composition, primary productivity, and export. Glider measurements are used to force a one-dimensional biogeochemical model, which includes diatoms and both solitary and colonial forms of *Phaeocystis antarctica*. Model performance is evaluated with glider observations, and experiments are conducted using projections of physical drivers for mid-21st and late-21st century. These scenarios reveal a 5% increase in primary productivity by midcentury and 14% by late-century and a proportional increase in carbon export, which remains approximately 18% of primary production. In addition, scenario results indicate diatom biomass increases while *P. antarctica* biomass decreases in the first half of the 21st century. In the second half of the century, diatom biomass remains relatively constant and *P. antarctica* biomass increases. Additional scenarios examining the independent contributions of expected future changes (temperature, mixed layer depth, irradiance, and surface iron inputs from melting ice) demonstrate that earlier availability of low light due to reduction of sea ice early in the growing season is the primary driver of productivity increases over the next century; shallower mixed layer depths additionally contribute to changes of assemblage composition and export. This study further demonstrates how glider data can be effectively used to facilitate model development and simulation, and inform interpretation of biogeochemical observations in the context of climate change.

Kaufman, D.E., M.A.M. Friedrichs, W.O. Smith, Jr., B.Y. Queste, and K.J. Heywood. 2014. Biogeochemical variability in the southern Ross Sea as observed by a glider deployment. *Deep-Sea Research* I 92: 93-106.

High-resolution autonomous glider data (including temperature, salinity, fluorescence, and optical backscatter) collectedduringthe2010–2011australsummeridentified variations in phytoplankton biomass alongtwoglidersectionsnear761400S. Sea surface temperatures were warmer during the latter, west ward section, while mixed layer depths were deeper. Substantial quantities of Modified Circumpolar Deep Water, identified by neutral density criteria, were located within both sections. Chlorophyll (Chl) concentrations computed from fluorescence exhibited daily quenching near the surface, and deep chlorophyll concentration sat200m became periodically elevated, suggesting substantial export on small

space and time scales. The concentrations of particulate organic carbon (POC) computed from backscatter increased abruptly during the latter, westward section, concurrent with a decrease in chlorophyll. These higher POC:Chl ratios were not strongly correlated with presence of MCDW or with shallower mixed layer depths, but were strongly associated with higher surface temperatures and wind speed. The observed POC:Chl increase suggests a marked spatial and temporal transition between a Phaeocystis Antarctica-dominated assemblage characterized by modest POC:Chl ratios to a diatom- dominated assemblage. Finally, a subsampling analysis highlights the capability of high-resolution glider data to resolve these biological/physical parameter correlations that are not discernible from lower frequency data typical of traditional cruise stations.

Kustka, A.B., J.T. Kohut, A.E. White, P.J. Lam, A. Milligan, M.S. Dinniman, S. Mack, E. Hunter, M.R. Hiscock, W.O. Smith, Jr., and C.I. Measures. 2015. The roles of MCDW and deep water iron supply in sustaining a recurrent phytoplankton bloom on central Pennell Bank (Ross Sea). *Deep-Sea Research I* 105: 171-185.

During January–February 2011 standing stocks of phytoplankton (chl a) in the Pennell Bank region of the Ross Sea were variable over10–100km spatial scales. One area of elevated chl a on central Pennell Bank (CPB) appeared to be a recurrent mid-summer feature. The western flank (WF) of Pennell Bank had pronounced signatures of Modified Circumpolar Deep Water (MCDW). We evaluated the spatial extent of Fe limitation and net primary production and tested whether MCDW may provide elevated amounts of Fe to the CPB region, through a combination of insitu measurements, shipboard incubations and a horizontally resolved physical model. Regional fluxes of dissolved Fe from deep to surface waters were compared to calculated Fe demands. Low in situ variable to maximum fluorescence (Fv/Fm; 0.24–0.37) and surface water dissolved Fe concentrations (0.12–0.21nM) were suggestive of wide spread limitation, corroborated by the consistent responses (Fv/Fm, growth, and nutrient removal ratios) of incubation treatments to Fe addition. MCDW from the WF region had lower dissolved Fe concentrations than that measured in CDW (Circumpolar Deep Water), which suggests on-shelf modification with Fe deplete surface waters and is consistent with the lack of stimulation due to incubation amendments with filtered MCDW. Model results and empirical data suggest MCDW from the WF region is further modified and mixed en route to the CPB region, leading to both the erosion of the canonical MCDW signature and an elevated dissolved Fe inventory of CPB region deep water. This suggests the addition of Fe possibly via diagenesis, as suggested by Marsay et al.(2014). Calculated deep water supply rates to the surface waters of CPB were _0.18–0.43 md_1, while calculated rates at the northern Pennell Bank (NPB) regions were negative. The CPB populations exhibited _4.5-fold higher net production rates compared to those in the WF and NPB regions and required 520–3200 nmol Fe m-2 d-1. The modeled vertical supply rates seem to provide 2–15% of the estimated Fe requirement. Since this flux is based on subsurface dissolved Fe inventories, it does not account for any bio available Fe from deep water particulate sources or for Fe recycling in the upper water column. These data suggest there current productivity hot spot sat CPB are not fueled by Fe-rich MCDW but are partially supported by the delivery of Fe through vertical exchange processes.

Jones, R.M., and W.O. Smith, Jr. 2017. The influence of short-term events on the hydrographic and biological structure of the southwestern Ross Sea. *Journal of Marine Systems* 166: 184-195.

The Ross Sea continental shelf supports very high productivity and phytoplankton biomass. Conventional methods, including ship-based sampling, instrumented moorings, satellite imagery, and modelling, have illustrated the typical patterns of seasonal progression of the phytoplankton blooms. While variability in the Ross Sea is substantial over relatively large scales, our understanding of smaller scales of variability (on the order of a few hours or several kilometers) is limited. Utilizing data from an

autonomous glider, we examined the mechanisms driving both the transitions between stages of the phytoplankton bloom and the short-term perturbations in chlorophyll concentrations. Three phases within the bloom were defined based on chlorophyll changes: an accumulation phase, a dissipation period, and a post-dissipation phase. Short-term perturbations in chlorophyll were repeatedly observed and correlated with wind speed. These chlorophyll perturbations were strongly influenced by the degree of temporal coupling between wind events and the depth of mixing, which varied among phases. Delays of 12–24 h between wind events and chlorophyll changes were observed during the accumulation phase, but shortened to 2–12 h in the dissipation phase. Furthermore, while physical factors contributed to the observed short-term reductions in biomass and the appearance of chlorophyll at depth throughout the study, we hypothesize that turbulence during the period of maximum biomass induced aggregate formation and led to rapid vertical flux. These results suggest that the small-scale, short-term physical perturbations may induce substantial vertical redistribution of biogenic material, which in turn can have significant biogeochemical impacts.

Kohut, J.T., A.B. Kustka, M.R. Hiscock, P.J. Lam, C. Measures, A. Milligan, A. White, F. Carvalho, M. Hatta, B.M. Jones, D.C. Ohnemus, and J.M. Swartz, 2017. Mesoscale variability of the summer bloom over the northern Ross Sea shelf: A tale of two banks. *Journal of Marine Systems* 166: 50-60, doi:10.1016/j.jmarsys.2016.06.009

Multi-year satellite records indicate an asymmetric spatial pattern in the summer bloom in the Northern Ross Sea, with the largest blooms over the shallows of Pennell Bank compared to Mawson Bank. In 2010–2011, high-resolution spatiotemporal in situ sampling focused on these two banks to better understand factors contributing to this pattern. Dissolved and particulate Fe profiles suggested similar surface water depletion of dissolved Fe on both banks. The surface sediments and velocity observations indicate a more energetic water column over Mawson Bank. Consequently, the surface mixed layer over Pennell Bank was more homogeneous and shallower. Over Mawson Bank we observed a thicker more homogeneous bottom boundary layer resulting from stronger tidal and sub-tidal currents. These stronger currents scour the seafloor resulting in sediments less likely to release additional sedimentary iron. Estimates of the quantum yield of photosynthesis and the initial slope of the photosynthesis-irradiance response were lower over Mawson Bank, indicating higher iron stress over Mawson Bank. Overall, the apparent additional sedimentary source of iron to, and longer surface residence time over Pennell Bank, as well as the reduced fluxes from the more isolated bottom mixed layer over Mawson Bank, sustain the observed asymmetric pattern across both banks.

Li, Y., R. Ji, S. Jenouvrier, M. Jin, and J. Stroeve. 2016. Synchronicity between ice retreat and phytoplankton bloom in circum-Antarctic polynyas. Geophysical Research Letters 43: 2086–2093, doi:10.1002/2016GL067937.

Phytoplankton in Antarctic coastal polynyas has a temporally short yet spatially variant growth window constrained by ice cover and day length. Using 18-year satellite measurements (1997–2015) of sea ice and chlorophyll concentrations, we assessed the synchronicity between the spring phytoplankton bloom and light availability, taking into account the ice cover and the incident solar irradiance, for 50 circum-Antarctic coastal polynyas. The synchronicity was strong (i.e., earlier ice-adjusted light onset leads to earlier bloom and vice versa) in most of the western Antarctic polynyas but weak in a majority of the eastern Antarctic polynyas. The west-east asymmetry is related to sea ice production rate: the formation of many eastern Antarctic polynyas is associated with strong katabatic wind and high sea ice production rate, leading to stronger water column mixing that could damp phytoplankton blooms and weaken the synchronicity.

Li, Y., D.J. McGillicuddy, M.S. Dinniman, and J.M. Klinck, 2017. Processes regarding formation of low-salinity high-biomass lenses near the edge of the Ross Ice Shelf. *Journal of Marine Systems* 166: 108-119, doi:10.1016/j.jmarsys.2016.07.002.

Both remotely sensed and in situ observations in austral summer of early 2012 in the Ross Sea suggest the presence of cold, low-salinity, and high-biomass eddies along the edge of the Ross Ice Shelf (RIS). Satellite measurements include sea surface temperature and ocean color, and shipboard data sets include hydrographic profiles, towed instrumentation, and underway acoustic Doppler current profilers. Idealized model simulations are utilized to examine the processes responsible for ice shelf eddy formation. 3-D model simulations produce similar cold and fresh eddies, although the simulated vertical lenses are quantitatively thinner than observed. Model sensitivity tests show that both basal melting underneath the ice shelf and irregularity of the ice shelf edge facilitate generation of cold and fresh eddies. 2-D model simulations further suggest that both basal melting and downwelling-favorable winds play crucial roles in forming a thick layer of low-salinity water observed along the edge of the RIS. These properties may have been entrained into the observed eddies, whereas that entrainment process was not captured in the specific eddy formation events studied in our 3-D model—which may explain the discrepancy between the simulated and observed eddies, at least in part. Additional sensitivity experiments imply that uncertainties associated with background stratification and wind stress may also explain why the model underestimates the thickness of the low-salinity lens in the eddy interiors. Our study highlights the importance of incorporating accurate wind forcing, basal melting, and ice shelf irregularity for simulating eddy formation near the RIS edge. The processes responsible for generating the high phytoplankton biomass inside these eddies remain to be elucidated.

Liu, X., and W.O. Smith, Jr. 2012. A statistical analysis of the controls on phytoplankton distribution in the Ross Sea, Antarctica. *Journal of Marine Systems* 94: 135-144.

The continental shelf of the Ross Sea, Antarctica, is characterized by extreme seasonal and interannual changes in atmospheric and oceanographic processes, which result in distinct temporal patterns in phytoplankton biomass and assemblage composition. However, the environmental forcing of these variations remains uncertain, especially when a series of correlated variables are considered. Hydrological profiles, dissolved nutrients, particulate matter, and phytoplankton pigments were measured in the southern Ross Sea in austral spring and summer during four years (1996–97, 2003–04, 2004–05, and 2005–06), and a series of multivariate analyses were conducted to assess the causative mechanisms in the control of phytoplankton distributions in the Ross Sea. Our results demonstrate that the significant interannual, seasonal and spatial variability that occurs in the southern Ross Sea in hydrographic and chemical properties is highly correlated with the variability in phytoplankton distributions. Although multiple controlling mechanisms were suggested, mixed layer depths did not appear to be a dominant factor regulating phytoplankton biomass or composition; conversely, we found a significant role of water column temperature in structuring phytoplankton assemblage composition in the southern Ross Sea, in that cooler water strongly selects for *Phaeocystis antarctica*, which is a dominant control of carbon flux to depth, and thus of substantial biogeochemical importance.

Long, M.C., R.B. Dunbar, P.D. Tortell, W.O. Smith, Jr., D.A. Mucciarone, and G.R. DiTullio. 2011. Vertical structure, seasonal drawdown, and net community production in the Ross Sea, Antarctica. Journal of Geophysical Research 116, C10029, doi:10.1029/2009JC005954.

We calculate net community production (NCP) during summer 2005–2006 and spring 2006 in the Ross Sea using multiple approaches to determine the magnitude and consistency of rates. Water column carbon and nutrient inventories and surface ocean O2/Ar data are compared to satellite-derived primary

productivity (PP) estimates and 14C uptake experiments. In spring, NCP was related to stratification proximal to upper ocean fronts. In summer, the most intense C drawdown was in shallow mixed layers affected by ice melt; depth-integrated C drawdown, however, increased with mixing depth. DO2/Ar-based methods, relying on gas exchange reconstructions, underestimate NCP due to seasonal variations in surface DO2/Ar and NCP rates. Mixed layer DO2/Ar requires approximately 60 days to reach steady state, starting from early spring. Additionally, cold temperatures prolong the sensitivity of gas exchange reconstructions to past NCP variability. Complex vertical structure, in addition to the seasonal cycle, affects interpretations of surface-based observations, including those made from satellites. During both spring and summer, substantial fractions of NCP were below the mixed layer. Satellite-derived estimates tended to overestimate PP relative to 14C-based estimates, most severely in locations of stronger upper water column stratification. Biases notwithstanding, NCP-PP comparisons indicated that community respiration was of similar magnitude to NCP. We observed that a substantial portion of NCP remained as suspended particulate matter in the upper water column, demonstrating a lag between production and export. Resolving the dynamic physical processes that structure variance in NCP and its fate will enhance the understanding of the carbon cycling in highly productive Antarctic environments.

Long, M.C., L.N. Thomas, and R.B. Dunbar. 2012. Control of phytoplankton bloom inception in the Ross Sea, Antarctic, by Ekman restratification. *Global Biogeochemical Cycles* 26: GB1006, doi:10.1029/2010GB003982.

Observations from November 2006 in the southwestern Ross Sea indicate that stratification developed in a localized fashion, proximal to upper ocean fronts. These regions were hotspots for biological productivity, exhibiting greater drawdown of $CO_2$and accumulation of oxygen, indicative of enhanced photosynthesis and air-sea gas exchange. While the effect of stratification is clear, the reasons for its development was not; air temperatures were unseasonably cold, sea-ice melt and sea surface warming were not significant. By comparing a one-dimensional mixed layer model with two-dimensional numerical simulations that include horizontal density gradients characteristic of the region, it is shown that Ekman advection is critical to structuring early season stratification. Where fronts are forced by winds that oppose the surface frontal current, Ekman advection displaces lighter water over dense. As biological productivity is light limited in the Ross Sea, and thus sensitive to the depth of the mixed layer, Ekman restratification plays an important role in determining the spatial distribution and development of the annual phytoplankton bloom in the region. The presence of fronts is therefore of first-order importance to the restratification and bloom dynamics of the Ross Sea in the early spring.

Mack, S.L., M.S. Dinniman, D.J. McGillicuddy, Jr., P.N. Sedwick, and J.M. Klinck, 2017. Dissolved iron transport pathways in the Ross Sea: Influence of tides and mesoscale eddies in a regional ocean model. *Journal of Marine Systems* 166: 73-86, doi:10.1016/j.jmarsys.2016.10.008.

Phytoplankton production in the Ross Sea is regulated by the availability of dissolved iron (dFe), a limiting micro-nutrient, whose sources include Circumpolar Deep Water, sea ice melt, glacial melt, and benthic sources (sediment efflux and remineralization). We employ a passive tracer dye to model the benthic dFe sources and track pathways from deep areas of the continental shelf to the surface mixed layer in simulations with and without tidal forcing, and at 5 and 1.5 km horizontal resolution. This, combined with dyes for each of the other dFe sources, provides an estimate of total dFe supply to surface waters. We find that tidal forcing increases the amount of benthic dye that covers the banks on the continental shelf. Calculations of mixed layer depth to define the surface ocean give similar average values over the shelf, but spatial patterns differ between simulations, particularly along the ice shelf front. Benthic dFe supply in simulations shows an increase with tidal forcing and a decrease with higher resolution. The changes in benthic dFe supply control the difference in total supply between simulations.

Overall, the total dFe supply from simulations varies from 5.60 to 7.95 μmol m^{-2} $year^{-1}$, with benthic supply comprising 32–50%, comparing well with recent data and model synthesis. We suggest that including tides and using high horizontal resolution is important, especially when considering spatial variability of iron supply on the Ross Sea shelf.

Marsay, C.M., P.N. Sedwick, M.S. Dinniman, P.M. Barrett, S.L. Mack, and D.J. McGillicuddy. 2014. Estimating the benthic efflux of dissolved iron on the Ross Sea continental shelf. ***Geophysical Research Letters*** **41: 7576-7583, doi:10.1002/2014GL061684.**

Continental margin sediments provide a potentially large but poorly constrained source of dissolved iron (dFe) to the upper ocean. The Ross Sea continental shelf is one region where this benthic supply is thought to play a key role in regulating the magnitude of seasonal primary production. Here we present data collected during austral summer 2012 that reveal contrasting low surface (0.08 ± 0.07 nM) and elevated near-seafloor (0.74 ± 0.47 nM) dFe concentrations. Combining these observations with results from a high-resolution physical circulation model, we estimate dFe efflux of 5.8×10^7 mol yr^{-1} from the deeper portions (>400 m) of the Ross Sea continental shelf; more than sufficient to account for the inferred "winter reserve" dFe inventory at the onset of the growing season. In addition, elevated dFe concentrations observed over shallower bathymetry suggest that such features provide additional inputs of dFe to the euphotic zone throughout the year.

McGillicuddy, D.J., P.N. Sedwick, M.S. Dinniman, K.R. Arrigo, T.S. Bibby, B.E. Greenan, E.E. Hofmann, J.M. Klinck, C.M. Marsay, W.O. Smith, Jr., B.M. Sohst, and G.L. van Dijken. 2015. Iron supply and demand in an Antarctic shelf ecosystem. ***Geophysical Research Letters*** **42: doi:10.1002/2015GL065727.**

The Ross Sea sustains a rich ecosystem and is the most productive sector of the Southern Ocean. Most of this production occurs within a polynya during the November-February period, when the availability of dissolved iron (dFe) is thought to exert the major control on phytoplankton growth. Here we combine new data on the distribution of dFe, high-resolution model simulations of ice melt and regional circulation, and satellite-based estimates of primary production to quantify iron supply and demand over the Ross Sea continental shelf. Our analysis suggests that the largest sources of dFe to the euphotic zone are wintertime mixing and melting sea ice, with a lesser input from intrusions of Circumpolar Deep Water, and a small amount from melting glacial ice. Together these sources are in approximate balance with the annual biological dFe demand inferred from satellite-based productivity algorithms, although both the supply and demand estimates have large uncertainties.

Mosby, A., and W.O. Smith, Jr. 2015. Phytoplankton growth rates in the Ross Sea, Antarctica. ***Aquatic Microbial Ecology*** **74: 157-171.**

The Ross Sea is a highly productive region of the Southern Ocean, but phytoplankton growth rates there are poorly constrained. Variability in growth rates was investigated on a January−February 2012 cruise to the Ross Sea using 37 14C isotopic tracer incubations and 11 dilution experiments. We examined the effects of extended incubations on measured growth rates in 14C incubations, quantified phytoplankton growth and grazing mortality rates through dilution experiments, and analyzed the effects of irradiance on carbon:chlorophyll ratios in dilution experiments. Growth rates in 14C incubations ranged from 0.03 to 0.85 d−1. We found that chlorophyll based phytoplankton growth rates in dilution experiments differed from measurements based on cell abundance, and concluded that chlorophyll-based growth rates may be inaccurate due to changing carbon:chlorophyll ratios during incubations. Unbalanced

phytoplankton growth among experiments was likely due to acclimation due to different mixed layer depth at stations sampled and incubation at constant irradiance. Growth rates measured in 72 h 14C incubations were not markedly different from those conducted over 24 h, indicating that loss of fixed 14C through grazing and respiration was not a significant source of error. All growth rates measured were significantly below those predicted based on temperature. As rates of grazing are low and physical conditions vary spatially, 14C incubations may be a more appropriate means of measuring growth rates than dilution experiments in the Ross Sea.

Mosby, A.F., and W.O. Smith, Jr. 2017. Structural equation modeling of the influence of environmental factors on summer phytoplankton growth in the Ross Sea. *Polar Biology* 40: 291-299.

The Ross Sea is a highly productive region of the Southern Ocean, and net phytoplankton growth varies seasonally, ranging from zero to near the temperature-limited maximum. Given that variations in growth can result from a number of factors (such as irradiance and iron concentrations), variability in net growth rate was investigated using structural equation modeling (SEM) and data collected during a January–February 2012 cruise to the Ross Sea. Structural equation modeling indicated that summer growth rates were significantly affected by iron concentrations and particulate organic carbon (POC) levels, the latter which most likely contributed to the seasonal depletion of iron by phytoplankton. Conversely, growth rates did not strongly vary with mixed layer depth (and hence irradiance). SEM indicated that if iron concentrations were increased by 1.0 standard deviation (ca. 0.12 nM), summer growth rates would increase by 0.5 standard deviation (ca. 0.07 day-1). Similarly, if POC (a measure of phytoplankton biomass in this region) was increased by 1.0 standard deviation (from 23.0 to 39.4 lmol L-1), growth rates would decrease by 0.31 standard deviations (*0.04 day-1), which we speculate is likely due to heightened iron limitation via increased total iron uptake. This modeling exercise confirms the dominant role of iron in regulating summer phytoplankton rates over the continental shelf of the Ross Sea.

Munro, D.R., R.B. Dunbar, D.A. Mucciarone, K.R. Arrigo, and M.C. Long. 2010. Stable isotope composition of dissolved inorganic carbon and particulate organic carbon in sea ice from the Ross Sea, Antarctica. *Journal of Geophysical Research* 115(C9), C09005, http://dx.doi.org/10.1029/2009JC005661.

We examined controls on the carbon isotopic composition of sea ice brines and organic matter during cruises to the Ross Sea, Antarctica in November/December 1998 and November/December 2006. Brine samples were analyzed for salinity, nutrients, total dissolved inorganic carbon ($\square CO_2$), and the $^{13}C/^{12}C$ ratio of $\square CO_2$ ($\square^{13}C_{\square CO2}$). Particulate organic matter from sea ice cores was analyzed for percent particulate organic carbon (POC), percent total particulate nitrogen (TPN), and stable carbon isotopic composition ($\square^{13}C_{POC}$). $\square CO_2$ in sea ice brines ranged from 1368 to 7149 mmol kg^{-1}, equivalent to 1483 to 2519 mmol kg^{-1} when normalized to 34.5 psu salinity ($s\square CO_2$), the average salinity of Ross Sea surface waters. Sea ice primary producers removed up to 34% of the available $\square CO_2$, an amount much higher than the maximum removal observed in sea ice free water. Carbonate precipitation and CO_2 degassing may reduce $s\square CO_2$ by a similar amount (e.g., 30%) in the most hypersaline sea ice environments, although brine volumes are low in very cold ice that supports these brines. Brine $\square^{13}C_{\square CO2}$ ranged from −2.6 to +8.0‰ while $\square^{13}C_{POC}$ ranged from −30.5 to −9.2‰. Isotopic enrichment of the ($\square CO_2$ pool via net community production accounts for some but not all carbon isotopic enrichment of sea ice POC. Comparisons of $s\square CO_2$, $\square^{13}C_{\square CO2}$, and $\square^{13}C_{POC}$ within sea ice suggest that $\square p$ (the net photosynthetic fractionation factor) for sea ice algae is ~8‰ smaller than the $\square p$ observed for phytoplankton in open water regions of the Ross Sea. These results have implications for modeling of carbon uptake and transformation in the ice-covered ocean and for reconstruction of past sea ice extent

based on stable isotopic composition of organic matter in sediment cores.

Phan-Tan, L., L. Nguyen-Ngoc, W.O. Smith, Jr., and H. Doan-Nhu. 2018. A new dinoflagellate species, *Protoperidinium smithii* H. Doan-Nhu, L. Phan-Tan et L. Nguyen-Ngoc sp. nov., and an amended description of *Protoperidinium defectum* (Balech 1965) Balech 1974 from the Ross Sea, Antarctica. *Polar Biology*, https://doi.org/10.1007/s00300-018-2262-0

The Ross Sea is one of the most well studied marginal seas in Antarctica. However, information of phytoplankton and in particular dinoflagellate diversity is limited. In this present study, samples at the surface and depth of the chlorophyll maximum at 40 stations during summer (2011–2012) were investigated for *Protoperidinium* species. A new species has described: *Protoperidinium smithii* H. Doan-Nhu, L. Phan-Tan et L. Nguyen-Ngoc sp. nov. This species belongs to subgenus Minusculum and have all of the features of this group. The new species is similar to *Protoperidinium bipes* (Paulsen) Balech 1974 and *Protoperidinium defectum* (Balech) Balech 1974. However, it is clearly differentiated from both species by its cell body shape, very short right antapical spine, a short apical horn, and the largest 1′plate among species in subgenus *Minusculum*. *Protoperidinium defectum* is also amended by several characteristics including detail plates tabulation since the first description in 1965.

Queste, B.Y., K.J. Heywood, W.O. Smith, Jr., D.E. Kaufman, T. Jickells, M.S. Dinniman, and C. Lee. 2015. Observations of dissolved oxygen dynamics during a phytoplankton bloom in the Ross Sea polynya. *Antarctic Science* 27: 362-372.

The Ross Sea polynya is one of the most productive regions in the Southern Ocean. However, limited access and high spatio-temporal variability of physical and biological processes limit the use of conventional oceanographic methods to measure early season primary productivity. High-resolution observations from two Seagliders provide insights into the timing of a bloom in the southern Ross Sea polynya in December 2010. Changes in chlorophyll and oxygen concentrations are used to assess bloom dynamics. Using a ratio of dissolved oxygen to carbon, net primary production is estimated over the duration of the bloom showing a sensitive balance between net autotrophy and heterotrophy. The two gliders, observing spatially distinct regions during the same period, found net community production rates of -0.9±0.7 and 0.7±0.4 g Cm-2 d-1. The difference highlights the spatial variability of biological processes and is probably caused by observing different stages of the bloom. The challenge of obtaining accurate primary productivity estimates highlights the need for increased observational efforts, particularly focusing on subsurface processes not resolved using surface or remote observations. Without an increased observational effort and the involvement of emerging technologies, it will not be possible to determine the seasonal trophic balance of the Ross Sea polynya and quantify the shelf's importance in carbon export.

Reddy, T.E, D.M. Holland, and K.R. Arrigo. 2010. Ross ice shelf cavity circulation, residence time, and melting: Results from a model of oceanic chlorofluorocarbons. *Continental Shelf Research* 30 (7): 733-742.

Despite their harmful effects in the upper atmosphere, anthropogenic chlorofluorocarbons dissolved in seawater are extremely useful for studying ocean circulation and ventilation, particularly in remote locations. Because they behave as a passive tracer in seawater, and their atmospheric concentrations are well-mixed, well-known, and have changed over time, they are ideal for gaining insight into the oceanographic characteristics of the isolated cavities found under Antarctic ice shelves, where direct observations are difficult to obtain. Here we present results from a modeling study of air-sea chlorofluorocarbon exchange and ocean circulation in the Ross Sea, Antarctica. We compare our model estimates of oceanic CFC-12 concentrations along an ice shelf edge transect to field data collected during

three cruises spanning 16 yr. Our model produces chlorofluorocarbon concentrations that are quite similar to those measured in the field, both in magnitude and distribution, showing high values near the surface, decreasing with depth, and increasing over time. After validating modeled circulation and air-sea gas exchange through comparison of modeled temperature, salinity, and chlorofluorocarbons with field data, we estimate that the residence time of water in the Ross Ice Shelf cavity is approximately 2.2 yr and that basal melt rates for the ice shelf average 10 cm yr $^{-1}$. The model predicts a seasonal signature to basal melting, with highest melt rates in the spring and also the fall.

Saenz, B.T., and K.R. Arrigo. 2014. Annual primary production in Antarctic sea ice during 2005–2006 from a sea ice state estimate. *Journal of Geophysical Research Oceans* 119: 3645–3678, doi:10.1002/2013JC009677.

Using the data-bounded Sea Ice Ecosystem State (SIESTA) model, we estimate total Antarctic sea ice algal primary production to be 23.7 Tg C a21 for the period July 2005–June 2006, of which 80% occurred in the bottom 0.2 m of ice. Simulated sea ice primary production would constitute 12% of total annual primary production in the Antarctic sea ice zone, and _1% of annual Southern Ocean primary production. Model sea ice algal growth was net nutrient limited, rather than light limited, for the vast majority of the sunlit season. The seasonal distribution of integrated ice algal biomass matches available observations. The vertical algal distribution was weighted toward the ice bottom compared to observations, indicating that interior ice algal communities may be under-predicted in the model, and that nutrient delivery via gravity-induced convection is not sufficient to sustain summertime algal biomass. Bottom ice algae were most productive in ice of 0.36 m thickness, whereas interior algal communities were most productive in ice of 1.10 m thickness. Sensitivity analyses that tested different atmospheric forcing inputs, sea ice parameterizations, and nutrient availability caused mean and regional shifts in sea ice state and ice algal production even when sea extent and motion was specified. The spatial heterogeneity of both ice state and algal production highlight the sensitivity of the sea ice ecosystem to physical perturbation, and demonstrate the importance of quality input data and appropriate parameterizations to models of sea ice and associated biology.

Ryan-Keogh, T.J., L.M. Delizo, W.O. Smith, Jr., P.N. Sedwick, D.J. McGillicuddy Jr., C.M. Moore, and T.S. Bibby. 2017. Temporal progression of photosynthetic strategy by phytoplankton in the Ross Sea, Antarctica. *Journal of Marine Systems* 166: 87-96.

The bioavailability of iron influences the distribution, biomass and productivity of phytoplankton in the Ross Sea, one of the most productive regions in the Southern Ocean. We mapped the spatial and temporal extent and severity of iron-limitation of the native phytoplankton assemblage using long- (N24 h) and short-term (24 h) iron-addition experiments along with physiological and molecular characterizations during a cruise to the Ross Sea in December–February 2012. Phytoplankton increased their photosynthetic efficiency in response to iron addition, suggesting proximal iron limitation throughout most of the Ross Sea during summer. Molecular and physiological data further indicate that as nitrate is removed from the surface ocean the phytoplankton community transitions to one displaying an iron-efficient photosynthetic strategy characterised by an increase in the size of photosystem II (PSII) photochemical cross section (σPSII) and a decrease in the chlorophyll-normalised PSII abundance. These results suggest that phytoplankton with the ability to reduce their photosynthetic iron requirements are selected as the growing season progresses, which may drive the well-documented progression from *Phaeocystis antarctica*- assemblages to diatom-dominated phytoplankton. Such a shift in the assemblage-level photosynthetic strategy potentially mediates further drawdown of nitrate following the development of iron deficient conditions in the Ross Sea.

Ryan-Keogh, T.R., and W.O. Smith, Jr. 2021. Temporal patterns of iron limitation in the Ross Sea as determined from chlorophyll fluorescence. *Journal of Marine Systems* 215, https://doi.org/10.1016/j.jmarsys.2020.103500.

The Ross Sea is one of the most productive regions in the Southern Ocean, with a significant role in carbon cycling as well as the massive abundance of higher trophic levels. The seasonal cycle is well established with an early summer *Phaeocystis antarctica* bloom that declines followed by a diatom bloom in late summer. This seasonal progression of the phytoplankton has been linked to the availability of iron in the mixed layer. Investigating the temporal progression of iron limitation is often limited by both the decreased sampling resolution from traditional platforms, such as ships, and the lack of regular deployments of specific sensors that can measure phytoplankton physiology. Through the use of a novel technique that uses the degree of quenching (NPQGlider), determined from a standard fluorometer deployed on a buoyancy glider, a proxy for iron limitation, αNPQ, was calculated for a glider time series in the Ross Sea from December 2011 to February 2012. Surface chlorophyll concentrations indicated that there were four stages: the first being a pre-bloom phase, the second in which phytoplankton growth was rapid, resulting in the accumulation of biomass; the third in which biomass in the surface layer decreased, and the fourth in which chlorophyll concentrations remained low but the POC:Chl ratio increased. The levels of NPQGlider in this region were much higher compared to other Southern Ocean regions, with the highest levels in the third phase. Similarly, αNPQ remained low throughout most of the time series except for the transition from the second to third phase when the surface biomass decreases. The increase in POC:Chl ratios in the final phase combined with the low values of αNPQ suggest the switch from a *Phaeocystis antarctica* bloom to a potentially non-iron limited diatom bloom. These results confirm that the application of novel methodologies to proven and reliable sensors will provide a greater understanding of biogeochemical cycles and their controls throughout the ocean.

Salmon, E., E.E. Hofmann, M.S. Dinniman, and W.O. Smith, Jr. 2020. Evaluation of iron sources in the Ross Sea. *Journal Marine Systems*, https://doi.org/10.1016/j.jmarsys.2020.103429.

A one-dimensional numerical model that includes the complex life cycle of *Phaeocystis antarctica*, diatom growth, dissolved iron (dFe) and irradiance controls, and the taxa's response to changes in these variables is used to evaluate the role of different iron sources in supporting phytoplankton blooms in the Ross Sea. Simulations indicate that sea ice melt accounts for 20% of total dFe inputs during low light conditions early in the growing season (late November-early December), which enhances blooms of *P. antarctica* in early spring. Advective inputs of dFe (60% of total inputs) maintain the *P. antarctica* bloom through early January and support a diatom bloom later in the growing season (early to mid-January). In localized regions near banks shallower than 450 m, suspension of iron-rich sediments and entrainment into the upper layers contributes dFe that supports blooms. Seasonal dFe budgets constructed from the simulations show that diatom-associated dFe accounts for the largest biological reservoir of dFe. Sensitivity studies show that surface input of dFe from sea ice melt, a transient event early in the growing season, sets up the phytoplankton sequencing and bloom magnitude, suggesting that the productivity of the Ross Sea system is vulnerable to changes in the extent and magnitude of sea ice.

Schine, C.M.S., A.-C. Alderkamp, G. van Dijken, L.J.A. Gerringa, P. Laan, H. van Haren, W.H. van de Poll, and K.R. Arrigo. 2021. Massive Southern Ocean phytoplankton bloom fed by iron of possible hydrothermal origin. *Nature Communications*, https://doi.org/10.1038/s41467-021-21339-5.

A phytoplankton bloom of substantial size, magnitude, and longevity was sampled in the high-nutrient, low-chlorophyll waters of the Antarctic Circumpolar Current in the Pacific sector of the

Southern Ocean. Visible in satellite images for three months (December 2013 - February 2014), the bloom covered an area of ~266,000 km^2. Depth-integrated chlorophyll *a* was >300 mg m^{-2} with primary production rates >1 g C m^{-2} d^{-1}, resulting in a CO_2 flux of -0.38 g C m^{-2} d^{-1}. The bloom was initially fed by elevated iron in surface waters and sustained by a high vertical flux of iron across the ferricline, which balanced depth-integrated growth rates measured *in situ*. The elevated iron supporting this bloom is likely of hydrothermal origin based on the position of the bloom relative to two active hydrothermal vent fields along the Australian Antarctic Ridge and the association of the elevated iron with a distinct water mass that is characteristic of a nonbuoyant hydrothermal vent plume.

Schine, C.M.S., G. van Dijken, and K.R. Arrigo. 2016. Spatial analysis of trends in primary production and relationship with large-scale climate variability in the Ross Sea, Antarctica (1997–2013). ***Journal of Geophysical Research*** **120, doi:10.1002/2015JC011014.**

Recent studies have documented an increase in sea ice extent and the duration of the ice season in the Ross Sea, Antarctica. We conducted a satellite-based study to quantify changes in net primary production (NPP) and chlorophyll a (Chl a) in response to the observed changes in ice dynamics in the Ross Sea south of 60°S. Our study covers a 16 year time period (1997–2013) and incorporates both the shelf and off-shelf regions of the Ross Sea. We observed significant secular changes in NPP from 1997 to 2013 in the off-shelf region, with NPP increasing on the eastern side and decreasing on the western side of our study area. The changes we observed in NPP are consistent with the changes we observed in sea surface temperature (SST) and open water days (OWDs), decreasing (increasing) on the western (eastern) side of our study area. Finally, we examined the influence of the Southern Annular Mode (SAM) and the El Nino Southern Oscillation (ENSO), on SST, OWDs, Chl a, and NPP in the Ross Sea and observed a significant relationship between the state of the SAM and ENSO and SST, OWDs, and NPP across the study region. The response of OWDs, SST, and NPP to atmospheric forcing by SAM and ENSO was opposite for the shelf and off-shelf regions, such that during a positive phase of SAM or negative phase of ENSO (La Nina), SST, OWDs, and NPP increased on the shelf and decreased in the off-shelf region.

Sedwick, P.N., C.M. Marsay, A.M. Aguilar-Islas, M.C. Lohan, B.M. Sohst, M.C. Long, K.R. Arrigo, R.B. Dunbar, M.A. Saito, W.O. Smith, and G.R. DiTullio. 2011. Early-season iron depletion in the Ross Sea polynya: Implications for iron dynamics on the Antarctic continental shelf. ***Journal of Geophysical Research*** **116, C12019, doi:10.1029/2010JC006553.**

The Ross Sea polynya is among the most productive regions in the Southern Ocean and may constitute a significant oceanic CO2 sink. Based on results from several field studies, this region has been considered seasonally iron limited, whereby a “winter reserve” of dissolved iron (dFe) is progressively depleted during the growing season to low concentrations (~0.1 nM) that limit phytoplankton growth in the austral summer (December–February). Here we report new iron data for the Ross Sea polynya during austral summer 2005–2006 (27 December–22 January) and the following austral spring 2006 (16 November–3 December). The summer 2005–2006 data show generally low dFe concentrations in polynya surface waters (0.10 ± 0.05 nM in upper 40 m, n = 175), consistent with previous observations. Surprisingly, our spring 2006 data reveal similar low surface dFe concentrations in the polynya (0.06 ± 0.04 nM in upper 40 m, n = 69), in association with relatively high rates of primary production (~170–260 mmol C m^{-2} d^{-1}). These results indicate that the winter reserve dFe may be consumed relatively early in the growing season, such that polynya surface waters can become “iron limited” as early as November; i.e., the seasonal depletion of dFe is not necessarily gradual. Satellite observations reveal significant biomass accumulation in the polynya during summer 2006–2007, implying significant sources of “new” dFe to surface waters during this period. Possible sources of this new dFe include episodic vertical exchange, lateral advection, aerosol input, and reductive dissolution of particulate iron.

Sinclair, K.E., N.A.N. Bertler, M.M. Bowen, and K.R. Arrigo. 2014. Twentieth century sea ice trends in the Ross Sea from a high resolution, coastal ice-core record. *Geophysical Research Letters* 41(10): 3510-3516, doi:10.1002/2014GL059821.

We present the first proxy record of sea-ice area (SIA) in the Ross Sea, Antarctica, from a 130 year coastal ice-core record. High-resolution deuterium excess data show prevailing stable SIA from the 1880s until the 1950s, a 2–5% reduction from the mid-1950s to the early-1990s, and a 5% increase after 1993. Additional support for this reconstruction is derived from ice-core methanesulphonic acid concentrations and whaling records. While SIA has continued to decline around much of the West Antarctic coastline since the 1950s, concurrent with increasing air and ocean temperatures, the underlying trend is masked in the Ross Sea by a switch to positive SIA anomalies since the early-1990s. This increase is associated with a strengthening of southerly winds and the enhanced northward advection of sea ice.

Smith, W.O. Jr., V. Asper, S. Tozzi, X. Liu, and S.E. Stammerjohn. 2011. Surface layer variability in the Ross Sea, Antarctica as assessed by in situ fluorescence measurements. *Progress in Oceanography* 88: 28-45, doi: 10.1016/j.pocean.2010.08.002.

Phytoplankton fluorescence, temperature and salinity were measured from December through February using in situ instruments deployed at two locations in the southern Ross Sea, Antarctica during the austral summers of three consecutive years (2003–2004, 2004–2005, and 2005–2006) to assess the short-term, seasonal and inter annual variations in phytoplankton biomass and oceanographic conditions. The seasonal climatologies of physical forcing variables were also determined from satellite measurements, and the data from the two sites compared to the 2000–2009 mean. In situ fluorometers were deployed at three depths at 77_S, 172.7_E and 77.5_S, 180_. Significant differences between the two sites were consistently observed, confirming the anticipated high level of spatial and temporal heterogeneity. Chlorophyll fluorescence was maximal in late December, and generally decreased rapidly to modest levels in January and February. However, during 1 year (2003–2004) a secondary bloom was found, with summer maxima being similar to those observed during spring. Fluorescence displayed a strong diel cycle, with strong quenching during periods of maximum irradiance. The magnitude of this reduction was large (the minimum average fluorescence was 25% of the daily mean) and decreased with depth. Fluorescence varied interannually, with the absolute levels and temporal patterns being different among years. The two sites had different temperature/salinity properties as measured at 24 m, and both variables changed with time. During 2004–2005 we were able to continuously measure the photosynthetic quantum efficiency of PSII (Fv/Fm) at 11 m, which revealed a minimum in December, and an increase in January, whereas the absolute fluorescence (Fo) decreased simultaneously. We suggest that this reflected a mixing event, whereby available irradiance increased, allowing a short period of growth in a more favorable optical environment. While substantial variations from the mean physical forcing were observed, the linkage of these physical variations with fluorescence was not always clear. Short-term (over 24-h) changes in fluorescence occurred, and were likely related to advective events. Wind events altered fluorescence in the surface layer, and these redistributed phytoplankton in the surface. The variability in chlorophyll fluorescence and physical forcing over a variety of scales in the Ross Sea provides insights into temporal– spatial coupling of phytoplankton.

Smith, W.O. Jr., M. Dinniman, G.R. DiTullio, S. Tozzi, O. Mangoni, M. Modigh, and V. Saggiomo. 2010. Phytoplankton photosynthetic pigments in the Ross Sea: Patterns and relationships among functional groups. *Journal of Marine Systems* 82: 177-185.

Phytoplankton assemblages of the Ross Sea are generally dominated by two functional groups: diatoms and haptophytes (*Phaeocystis antarctica*). Within this "normal" pattern of dominance, there is a substantial amount of temporal (over months, seasons and years) and spatial variability. Such variability has a significant impact on several biogeochemical cycles, such as the carbon and sulfur cycles, at the regional and global scales. We compiled all available accessory pigment data for the southern Ross Sea as a means to quantify the prevalence and dominance of each group, and generated a seasonal "climatology" of assemblage composition. The climatological pattern of phytoplankton pigments shows that haptophytes normally grow and accumulate early in the season, and largely in the southern Ross Sea polynya. Diatoms reach a biomass maximum later, and reach most extensive concentrations closer to the coast of Victoria Land. While the pattern of spring growth of *P. antarctica* followed by an increase in diatom abundance is found frequently, deviations from that pattern were observed. Two periods – November, 2006 and January, 2004 – illustrated that variations of up to one order of magnitude can occur relative to the climatology. These deviations may provide insights into the dominant control mechanisms of the two functional groups.

Smith, W.O., Jr., M.S. Dinniman, E.E. Hofmann, and J.M. Klinck. 2014. The effects of changing winds and temperatures on the oceanography of the Ross Sea in the 21st century. *Geophysical Research Letters* 41, doi:10.1002/2014GL059311.

The Ross Sea is critically important in regulating Antarctic sea ice and is biologically productive, which makes changes in the region's physical environment of global concern. We examined the effects of projected changes in atmospheric temperatures and winds on aspects of the ocean circulation likely important to primary production using a high-resolution sea ice-ocean-ice shelf model of the Ross Sea. The modeled summer sea-ice concentrations decreased by 56% by 2050 and 78% by 2100. The duration of shallow mixed layers over the continental shelf increased by 8.5 and 19.2 days in 2050 and 2100, and the mean summer mixed layer depths decreased by 12 and 44%. These results suggest that the annual phytoplankton production in the future will increase and become more diatomaceous. Other components of the Ross Sea food web will likely be severely disrupted, creating significant but unpredictable impacts on the ocean's most pristine ecosystem.

Smith, W.O., Jr., and K. Donaldson. 2015. Photosynthesis-irradiance responses in the Ross Sea, Antarctica: a meta-analysis. *Biogeosciences* 12: 1-11.

A meta-analysis of photosynthesis–irradiance measurements was completed using data from the Ross Sea, Antarctica, using a total of 417 independent measurements. PBm, the maximum, chlorophyll-specific, irradiance saturated rate of photosynthesis, averaged 1.1_0.06 µgC (µg Chl)1 h□1. Light-limited, chlorophyll-specific photosynthetic rates (_B/ averaged 0.030_0.023 µgC (µg Chl)1 h□1 (µmol quantam m-2 s-1/□1. Significant variations in PB m and _B were found as a function of season, with spring maximum photosynthetic rates being 60% greater than those in summer. Similarly, _ values were 48% greater in spring. There was no detectable effect of sampling location on the photosynthetic parameters, and temperature and macronutrient (NO3/ concentrations also did not have an influence. However, irradiance and carbon dioxide concentrations, when altered under controlled conditions, exerted significant influences on photosynthetic parameters. Specifically, reduced irradiance resulted in significantly decreased PBm and increased _B values, and increased CO2 concentrations resulted in significantly increased PBm and _B values. Comparison of photosynthetic parameters derived at stations where iron concentrations were above and below 0.1nM indicated that reduced iron levels were associated with significantly increased PBm values, confirming the importance of iron within the photosynthetic process. No significant difference was detected between stations dominated by diatoms and those dominated by the haptophyte *Phaeocystis antarctica*. The meta-analysis confirms the

photosynthetic rates predicted from global analyses that are based solely on temperature and irradiance availability, but suggests that, for more accurate predictions of productivity in polar systems, a more detailed model that includes temporal effects of photosynthetic parameters will be required.

Smith, W.O., Jr., and D.E. Kaufman. 2018. Particulate organic carbon climatologies in the Ross Sea: evidence for seasonal acclimations within phytoplankton. *Progress in Oceanography* 168: 182-195, https://doi.org/10.1016/j.pocean.2018.10.003

The distributions of nutrients, chlorophyll (chl), particulate organic carbon (POC), particulate organic nitrogen (PON), and biogenic silica (BSi) were compiled from 42 cruises to the Ross Sea continental shelf to generate a monthly climatology. Nutrients were elevated in spring and removal began in early spring (November) and continued through December, at which time nitrate and phosphate removal largely ceased. Silicic acid concentrations also began to decrease in November, but continued throughout the summer. Chlorophyll concentrations increased simultaneously with nitrate removal and became maximal in December, after which time they decreased. Concentrations of chlorophyll remained relatively low and constant through February, although smaller regions remained elevated and contributed to the expected substantial spatial variability. Particulate organic carbon and nitrogen concentrations paralleled chlorophyll concentrations through the spring maximum, and also decreased in early summer. However, a notable increase in particulate organic carbon occurred later in summer that was largely independent of chlorophyll changes, resulting in a dramatic rise of POC:chl ratios. Biogenic silica concentrations were low through December but continued to increase throughout summer. We suggest that the spring pigment and particulate matter concentrations resulted from phytoplankton blooms dominated by the haptophyte *Phaeocystis antarctica*, consistent with repeated observations in the region. We further suggest that the late summer POC increase was due to growth of diatoms that exhibited enhanced POC:chl ratios due to iron limitation. POC concentrations in late summer were similar to those in spring, indicating that the summer bloom was substantial. Estimates of productivity from a bio-optical model using variable POC:chl ratios suggest that the summer blooms may be a significant contributor to seasonal productivity, and that estimates of productivity based on satellite pigments underestimate annual production by at least 70%. Satellite productivity estimates have substantial uncertainties in the Ross Sea and need to be constrained using in situ constituent ratios.

Smith, W.O., Jr., D.J. McGillicuddy Jr., E.B. Olson, V. Kosnyrev, E.E. Peacock, and H.M. Sosik. 2017. Mesoscale variability in intact and ghost colonies of *Phaeocystis antarctica* in the Ross Sea: Distribution and abundance. *Journal of Marine Systems* 166: 97-107.

Phaeocystis, a genus with a cosmopolitan distribution and a polymorphic life cycle, was observed during summer in the Ross Sea, Antarctica, where large blooms of this haptophyte regularly occur. The mesoscale vertical and horizontal distributions of colonies of *Phaeocystis antarctica* were assessed using a towed Video Plankton Recorder (VPR). The mean size of colonies was 1.20mm, and mean abundances within the three VPR surveys were 4.86, 1.96, and 11.5 mL−1. In addition to the typical spherical, transparent colonies, the VPR quantified an optically dissimilar form of colony that had a distinctive translucent appearance. It also measured the abundance of collapsed colonies, similar to those observed previously from cultures and mesocosms, which we called “ghost colonies”. The translucent colonial form had a different distribution than the more common colonial form, and at times was more abundant. Relative to intact colonies, the ghost colonies occurred less frequently, with mean abundances in the three surveys being 0.01, 0.08, and 0.0004 mL−1. Ghost colonies generally were found below the euphotic zone, where they often were in greater abundance than intact colonies. However, the relationship of ghost

colonies to intact *P. antarctica* colonies was not direct or consistent, suggesting that the formation of ghost colonies from living colonies and their appearance within the water column were not tightly coupled. Given their relative scarcity and low carbon content, it is unlikely that ghost colonies contribute substantially to vertical flux; however, it is possible that we did not sample periods of major flux events, and as a result minimized the importance of ghost colonies to vertical flux. They do, however, represent a poorly documented feature of polar haptophyte life cycles.

Smith, W.O. Jr., A.R. Shields, J. Dreyer, J.A. Peloquin, and V. Asper. 2011. Inter annual variability in vertical export in the Ross Sea: magnitude, composition, and environmental correlates. *Deep-Sea Research* I 58: 147-159.

The vertical flux of particulate matter from the surface of the Ross Sea, Antarctica, has been suggested as being large, with substantial seasonal and spatial variations. We conducted a study in which vertical flux was quantified using sediment traps deployed at 200 m and compared to estimates calculated from one dimensional budgets of nutrients (nitrogen and silicon). Estimates of flux were collected at two locations in the southern Ross Sea from late December to early February during four years: 2001–2002, 2003–2004, 2004–2005, and 2005–2006. Phytoplankton biomass and vertical flux varied substantially seasonally and spatially between the two sites, and among years. The greatest flux was observed in 2001–2002, with a short-term maximum organic carbon flux of 3.13 mmol m-2 d-1, and the summer mean organic carbon flux equal to 0.93mmol m-2 d-1. In contrast, the mean carbon flux at the same site in 2003–2004 was over an order of magnitude less averaging 0.19 mmol m-2 d-1, despite the fact that productivity in that year was substantially greater. In 2005–2006 the contribution of fecal pellets to flux was smallest among all years, and the pellet contribution ranged from o.1 to more than 50% of organic flux. As the moorings also had surface layer fluorometers, the relationship between surface biomass and sediment trap flux was compared. Temporal lags between surface fluorescence and flux at 200 m maxima in 2003–2004 and 2004–2005 ranged from two to six days; however, in 2005–2006 the temporal offset between biomass and flux was much longer, ranging from 11 to 27 days, suggesting that fecal pellet production appeared to increase the coupling between flux and surface production. Estimates of export from the upper 200 m based on one-dimensional nutrient budgets were greater than those recorded by the sediment traps. Nutrient budgets also indicated that siliceous production averaged ca. 40% of the total annual production. The variations observed in the flux of biogenic matter to depth in the Ross Sea are large, appear to reflect different forcing among years, and at present are not adequately understood. However, such variability needs to be both understood and represented in biogeochemical models to accurately assess and predict the effects of climate change on bio geo chemical cycles

Smith, W.O. Jr., S. Tozzi, P.W. Sedwick, G.R. DiTullio, J.A. Peloquin, M. Long, R. Dunbar, D.A. Hutchins, and Z. Kolber. 2013. Spatial and temporal variations in variable fluorescence in the Ross Sea (Antarctica): environmental and biological correlates. *Deep-Sea Research I* 79: 141-155.

During two cruises to the Ross Sea, Antarctica in austral spring and summer, fast repetition rate fluorometry wasusedtoinvestigatetherelationshipbetweenphytoplanktonphotophysiologyandwater mass characteristics, micronutrient availability, and composition. Particulate organic matter proxies for phytoplankton biomass (chlorophyll a, particulate organic carbon and nitrogen, and biogenic silica) were all elevated in the photic zone during spring and summer. Biogenic silica concentrations were an order of magnitude higher in summer relative to spring, reflecting a shift in composition from *Phaeocystis antarctica* to diatoms. Quantum yields of PSII (Fv/Fm) were generally higher in spring relative to summer, coincident with weaker vertical and horizontal gradients in hydrographic properties. Reduced Fv/Fm values (0.4) were observed in the upper 30 m in both seasons, with maximum values (ca.0.55) observed near the base and below the euphotic zone. No significant relationship between Fv/Fm values

and dissolved Fe could be identified in the merged spring/summer data set. Functional absorption cross sections were significantly higher in spring than summer, presumably reflecting adaptations to lower irradiance in spring; little variation with depth was observed. Phytoplankton composition did not appear to be a major determinant to bulk quantum yield, although diatom-dominated waters exhibited significantly higherfunctionalabsorptioncrosssectionswhencomparedtowatersdominatedby *P. antarctica*. Dominance of *P. antarctica* appears to be related to greater photophysiological resilience and faster photoacclimation to changing light conditions, whereas diatoms were prevalent in shallow summer mixed layers, which likely reflects their enhanced photosynthetic capacity at high irradiance levels.

Smith, W.O., Jr., and R.M. Jones. 2015. Vertical mixing, critical depths, and phytoplankton growth in the Ross Sea. *ICES Journal of Marine Science* 72: 1952-1960.

Phytoplankton growth and biomass accumulation vary spatially and temporally in the Ross Sea, largely as a function of ice concentrations, vertical mixing depths, and iron concentrations. To assess the role of vertical mixing in bloom initiation, we used a high-resolution numerical model to estimate changes in mixed layer depths from October 1 through early December, the period where phytoplankton growth begins and biomass accumulates, and estimate critical depths for this period. Mixed layers in October ranged from the complete water column (.600 m) to ca.200 m; over a 60-day period, the mixed layers decreased on average by 70%. Estimated critical depths were exceeded in October, but would allow growth to proceed in late October due to shoaling of mixed layer depths, consistent with the known onset of the spring bloom in the Ross Sea. We also analysed a series of stations sampled near the Ross Ice Shelf during January 2012. Mean vertical profiles for the stations indicated deep vertical mixing; mixed layer depths averaged 60 m and ranged up to 96 m. Chlorophyll concentrations within the mixed layer averaged 6.60 mg l21, and the pigment contributions were dominated by *Phaeocystis antarctica*. We suggest that this mesoscale region near the ice shelf is elevated in phytoplankton biomass due to frequent mixing events that redistribute biomass to depth and replenish nutrients, which in turn are utilized by an assemblage capable of utilizing low mean irradiance levels. Thus, the deep mixed layers and high biomass concentrations represent growth over long periods under reduced mixing punctuated by short periods of deeper vertical mixing that redistribute biomass. Water column vertical mixing and phytoplankton biomass in the Ross Sea are consistent with the critical depth concept as originally proposed by Sverdrup.

Tagliabue, A., and K.R. Arrigo. 2016. Decadal trends in air-sea CO_2 exchange in the Ross Sea (Antarctica). *Geophysical Research Letters* 43, doi:10.1002/2016GL069071.

Highly productive Antarctic shelf systems, like the Ross Sea, play important roles in regional carbon budgets, but the drivers of local variations are poorly quantified. We assess the variability in the Ross Sea carbon cycle using a regional physical-biogeochemical model. Regionally, total partial pressure of CO_2 (pCO_2) increases are largely controlled by the biological pump and broadly similar to those in the offshore Southern Ocean. However, this masks substantial local variability within the Ross Sea, where inter-annual fluctuations in total pCO_2 are driven by the biological pump and alkalinity, whereas those for anthropogenic pCO_2 are related to physical processes. Overall, the high degree of spatial variability in the Ross Sea carbon cycle causes extremes in aragonite saturation that can be as large as long-term trends. Therefore, Antarctic shelf polynya systems like the Ross Sea will be strongly affected by local processes in addition to larger scale phenomena.

Tison, J.L, T. Maksym, A. D. Fraser, M. Corkill, N Kimura, Y. Nosaka, D. Nomura, M. Vancoppenolle, S. Ackley, S. Stammerjohn, S. Wauthy, F. Van der Linden, G. Carnat, C. Sapart, J.

de Jong, F. Fripiat, B. Delille. 2020. Physical and biological properties of early winter Antarctic sea ice in the Ross Sea. *Annals of Glaciology*, 1–19, https://doi.org/10.1017/aog.2020.43.

This work presents the results of physical and biological investigations at 27 biogeochemical stations of early winter sea ice in the Ross Sea during the 2017 PIPERS cruise. Only two similar cruises occurred in the past, in 1995 and 1998. The year 2017 was a specific year, in that ice growth in the Central Ross Sea was considerably delayed, compared to previous years. These conditions resulted in lower ice thicknesses and Chl-*a* burdens, as compared to those observed during the previous cruises. It also resulted in a different structure of the sympagic algal community, unusually dominated by *Phaeocystis* rather than diatoms. Compared to autumn-winter sea ice in the Weddell Sea (AWECS cruise), the 2017 Ross Sea pack ice displayed similar thickness distribution, but much lower snow cover and therefore nearly no flooding conditions. It is shown that contrasted dynamics of autumnal-winter sea-ice growth between the Weddell Sea and the Ross Sea impacted the development of the sympagic community. Mean/median ice Chl-*a* concentrations were 3–5 times lower at PIPERS, and the community status there appeared to be more mature (decaying?), based on Phaeopigments/Chl-*a* ratios. These contrasts are discussed in the light of temporal and spatial differences between the two cruises.

Tortell, P.D., M.M. Mills, C.D. Payne, M.T. Maldonado, M. Chierici, A. Fransson, A.-C. Alderkamp, and K.R. Arrigo. 2013. Inorganic C utilization and C isotope fractionation by pelagic and sea ice algal assemblages along the Antarctic continental shelf. *Marine Ecology Progress Series* 483: 47-66.

Physiological characteristics of inorganic C uptake were examined in Southern Ocean ice algae and phytoplankton assemblages. Ice algal and phytoplankton assemblages were largely dominated by diatoms and *Phaeocystis antarctica*, and showed a high capacity for HCO_3^- utilization, with direct HCO3− transport accounting for ~60% of total inorganic C uptake. Extracellular carbonic anhydrase (eCA) was detectable in all samples, but with significantly lower activity in sea ice algae. Neither HCO_3^- transport nor eCA activity was related to the *in situ* partial pressure of CO_2 (pCO_2) or taxonomic composition of samples. The half-saturation constant *(K*S) for inorganic C ranged from ~100 to 5000 μM, and showed significantly more variability among sea ice algae than phytoplankton assemblages. For the phytoplankton assemblages, there were significant positive correlations between *in situ* pCO_2 and *K*S (higher C substrate affinity in low pCO_2 waters), and also between *K*S and maximum C uptake rates *(V*max). In contrast, *K*S and *V*max in sea-ice algal assemblages were not correlated to each other, or to any other measured variables. The C isotope composition of particulate organic carbon (δ^{13}C-POC) in the phytoplankton assemblages showed modest variability (range −30 to −24.6‰) and was significantly correlated to the ratio of inferred growth rates (derived from *V*max) and *in situ* CO2 concentrations, but not to any measured C uptake parameters. δ^{13}C-POC in sea ice algal samples (range −25.7 to −12.9‰) was significantly heavier than in the phytoplankton assemblages, and not correlated to any other variables. Our results provide evidence for the widespread occurrence of carbon-concentrating mechanisms in Southern Ocean sea ice algae and phytoplankton assemblages.

Tozzi, S., and W.O. Smith, Jr. 2017. Contrasting photo-physiological responses of the haptophyte *Phaeocystis antarctica* and the diatom *Pseudonitzschia* sp. in the Ross Sea (Antarctica). *AIMS-Geosciences* 3: 142-162, https://doi:10.3934/geosci.2017.2.142

The Antarctic is a unique environment in which substantial variations in irradiance occur over a number of time scales, and as a result phytoplankton need to acclimate and adapt to these changes. We conducted field and laboratory manipulations in the Ross Sea, Antarctica to examine photophysiological differences between *Phaeocystis antarctica* and *Pseudonitzschia* sp. a diatom that commonly occurs in

the Ross Sea, since these are the two functional groups that dominate abundance and productivity. Both exhibited reduced quantum yields due to high irradiances. *P. antarctica*, a haptophyte, displays a distinct photophysiological response to irradiance when compared to diatoms. *P. antarctica* showed a rapid recovery from high light exposure, as indicated by the rapid return to initial, high quantum yields, in contrast to diatoms, which responded more slowly. Absorption cross sections were high in both forms, but those in *P. antarctica* were significantly higher. Both organisms recovered within 24 h to initial quantum yields, suggesting that high irradiance exposure does not have a permanent effect on these organisms. Among all micronutrient additions (iron, cobalt, zinc and vitamin B12), only iron additions resulted in rapid impacts on quantum yields. Iron limitation also can result in reduced photosynthetic efficiency. Understanding these photophysiologial responses and the impact of oceanographic conditions provides constraints on modeling efforts of photosynthesis and primary productivity in the Antarctic.

UPPER TROPHIC LEVELS RESPONDING TO BIO-PHYSICAL VARIABILITY

Ainley, D.G., J. Russell, S. Jenouvrier, E. Woehler, P. O'B. Lyver, W.R. Fraser, and G.L. Kooyman. 2010. Antarctic penguin response to habitat change as earth's troposphere reaches 2°c above pre-industrial levels. *Ecological Monographs* 80: 49-66.

We assess the response of pack ice penguins, Emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*), to habitat variability and, then, by modeling habitat alterations, the qualitative changes to their populations, size and distribution, as Earth's average tropospheric temperature reaches 28C above preindustrial levels (ca. 1860), the benchmark set by the European Union in efforts to reduce greenhouse gases. First, we assessed models used in the Intergovernmental Panel on Climate Change Fourth Assessment Report (AR4) on penguin performance duplicating existing conditions in the Southern Ocean. We chose four models appropriate for gauging changes to penguin habitat: GFDL-CM2.1, GFDL-CM2.0, MIROC3.2 (hi-res), and MRI-CGCM2.3.2a. Second, we analyzed the composited model ENSEMBLE to estimate the point of 28C warming (2025–2052) and the projected changes to sea ice coverage (extent, persistence, and concentration), sea ice thickness, wind speeds, precipitation, and air temperatures. Third, we considered studies of ancient colonies and sediment cores and some recent modeling, which indicate the (space/time) large/centennial scale penguin response to habitat limits of all ice or no ice. Then we considered results of statistical modeling at the temporal interannual-decadal scale in regard to penguin response over a continuum of rather complex, meso- to large-scale habitat conditions, some of which have opposing and others interacting effects. The ENSEMBLE meso/decadal-scale output projects a marked narrowing of penguins' zoogeographic range at the 28C point. Colonies north of 70° S are projected to decrease or disappear: ~50% of Emperor colonies (40% of breeding population) and ~75% of Adélie colonies (70% of breeding population), but limited growth might occur south of 73° S. Net change would result largely from positive responses to increase in polynya persistence at high latitudes, overcome by decreases in pack ice cover at lower latitudes and, particularly for Emperors, ice thickness. Ade´ lie Penguins might colonize new breeding habitat where concentrated pack ice diverges and/or disintegrating ice shelves expose coastline. Limiting increase will be decreased persistence of pack ice north of the Antarctic Circle, as this species requires daylight in its wintering areas. Adélies would be affected negatively by increasing snowfall, predicted to increase in certain areas owing to intrusions of warm, moist marine air due to changes in the Polar Jet Stream.

Ballard, G., A.E. Schmidt, V. Toniolo, S. Veloz, D. Jongsomjit, K.R. Arrigo, and D.G. Ainley. 2019. Fine-scale oceanographic features characterizing successful Adélie penguin foraging in the SW Ross Sea. *Marine Ecology Progress Series* 608: 263–277.

According to central place foraging theory, breeding seabirds should energetically optimize prey acquisition and, therefore, foraging is expected to be located where prey are most available, within limits defined by the energetics of the species. We have shown this previously for Adélie penguins *Pygoscelis adeliae*, using foraging intensity as a proxy for prey patch quality, but we have yet to assess the habitat characteristics where foraging success is highest. Here, we report an effort using biologging instruments that recorded location and an index of foraging success, allowing us to characterize aspects of more or less successful foraging locations on the basis of sea-surface temperature, chlorophyll concentration, sea ice cover, water column stratification, and bathymetry. We retrieved data from 162 breeding Adélie penguins over 5 austral summers, 2005−2008 and 2012, and used a machine-learning algorithm to model the relationship between the number of undulations (>1 m) penguins made (i.e. our index of foraging success) and oceanographic conditions at the fine scale (5 km). We found that most oceanographic features were not predictive of foraging success, although light availability and thermocline strength as measured at the scale of individual penguin foraging dives were both relatively strong predictors. Contrary to previous results obtained at larger scales, we showed that at the fine scale, sea ice concentration is not an important predictor of foraging success, although the associated effect of sea ice cover, i.e. a stratified water column as indicated by thermocline strength, was important. We also confirmed that penguins traveled farther to achieve the same foraging success later in the season despite consistent oceanographic features, indicating that prey become depleted as the breeding season progresses. Our findings suggest that finer spatial and temporal scale data, including from underwater, are necessary to accurately describe the environmental variables that correlate with penguin foraging success, reinforcing the promise of small, animal-borne sensors for evaluating ecosystem processes.

Ballard G., V. Toniolo, D.G. Ainley, C. L. Parkinson, K.R. Arrigo, and P.N. Trathan. 2010. Responding to climate change: Adélie penguins confront astronomical and ocean boundaries. *Ecology* 91: 2056-2069.

Long-distance migration enables many organisms to take advantage of lucrative breeding and feeding opportunities during summer at high latitudes and then to move to lower, more temperate latitudes for the remainder of the year. The latitudinal range of the Adélie Penguin (*Pygoscelis adeliae*) spans 22°. Penguins from northern colonies may not migrate, but due to the high latitude of Ross Island colonies, these penguins almost certainly undertake the longest migrations for the species. Previous work has suggested that Adélies require both pack ice and some ambient light at all times of year. Over a three-year period, which included winters of both extensive and reduced sea ice, we investigated characteristics of migratory routes and wintering locations of Adélie Penguins from two colonies of very different size on Ross Island, Ross Sea, the southernmost colonies for any penguin. We acquired data from 3–16 geolocation sensor tags (GLS) affixed to penguins each year at both Cape Royds and Cape Crozier in 2003–2005. Migrations averaged 12 760 km, with the longest being 17 600 km, and were in part facilitated by pack ice movement. Trip distances varied annually, but not by colony. Penguins rarely traveled north of the main sea-ice pack, and used areas with high sea-ice concentration, ranging from 75% to 85%, about 500 km inward from the ice edge. They also used locations where there was some twilight (2–7 h with sun, < 6° below the horizon). We report the present Ade´ lie Penguin migration pattern and conjecture on how it probably has changed over the past ~12 000 years, as the West Antarctic Ice Sheet withdrew southward across the Ross Sea, a situation that no other Adélie Penguin population has had to confront. As sea ice extent in the Ross Sea sector decreases in the near future, as predicted by climate models, we can expect further changes in the migration patterns of the Ross Sea penguins.

Ballard, G., and D.G. Ainley. 2019. Rapidly diverging population trends of Adélie Penguins reveal limits to a flexible species' adaptability to Anthropocene climate change. Pp. 91-96 in *Biodiversity*

and Climate Change: Transforming the Biosphere **(Editors, T.E. Lovejoy and L. Hannah). Yale University Press, New Haven**.

Adélie penguins (*Pygoscelis adeliae*) thrive in some of the most dramatically variable habitats and weather on Earth. They spend much of their life at sea, more than 40m underwater, often under sea ice, where they find their food. They also spend roughly 3-months per year mostly on land, living in dense colonies for breeding. They regularly contend with the transition between open and frozen ocean, and with terrain alternately blanketed in snow and ice then swept clear by high winds. Adélie penguins are one of only a handful of species to be able to survive extended periods in sub-zero air temperatures, out of the relatively warm water that harbors most of the biodiversity to be found at the highest latitudes of the Southern Ocean. They require both ice free terrain to nest and nearby open water to forage. The combination of these two things is rare in Antarctica, but where they are found, so too are Adélies.

Beltran, R.S., T. Adachi, A. Takahashi, Y. Naito, P.W. Robinson, W.O. Smith, Jr., A.M. Kilpatrick, A.L. Kirkham, G.A. Breed, and J.M. Burns. 2021. Seal dives suggest a vertical ecosystem shift coupled to seasonal phytoplankton blooms. ***Proceedings of the Royal Society B, London*** **288: 20202817, https://doi.org/10.1098/rspb.2020.2817.**

Seasonal resource pulses can have enormous impacts on species interactions. In marine ecosystems, air-breathing predators often drive their prey to deeper waters. However, it is unclear how ephemeral resource pulses such as near-surface phytoplankton blooms alter the vertical trade-off between predation avoidance and resource availability in consumers, and how these changes cascade to the diving behavior of top predators. We integrated data on Weddell seal diving behavior, diet stable isotopes, feeding success and mass gain to examine shifts in vertical foraging throughout ice break-out and the resulting phytoplankton bloom each year. We also tested hypotheses about the likely location of phytoplankton bloom origination (advected in, or produced in situ where seals foraged) based on sea ice break-out phenology and advection rates from several locations within 150 km of the seal colony. In early summer, seals foraged at deeper depths resulting in lower feeding rates and mass gain. As sea ice extent decreased throughout the summer, seals foraged at shallower depths and benefited from more efficient energy intake. Changes in diving depth were not due to seasonal shifts in seal diets or horizontal space use and instead may reflect a change in the vertical distribution of prey. Correspondence between the timing of seal shallowing and the resource pulse was variable from year to year, and could not be readily explained by our existing understanding of ocean and ice dynamics. Phytoplankton advection occurred faster than ice break-out and seal dive shallowing occurred substantially earlier than local break-out. While there remains much to be learned about the marine ecosystem, it appears that an increase in prey abundance and accessibility (via shallower distribution during the resource pulse may could synchronize reproductive phenology across multiple trophic levels synchronize life history phenology across trophic levels in this high-latitude ecosystem.

Emslie, S.D. 2020. Ancient Adélie penguin colony revealed by snowmelt at Cape Irizar, Ross Sea, Antarctica. ***Geology*****, https://doi.org/10.1130/G48230.1**

The Ross Sea (Antarctica) is one of the most productive marine ecosystems in the Southern Ocean and supports nearly one million breeding pairs of Adélie penguins (*Pygoscelis adeliae*) annually. There also is a well-preserved record of abandoned penguin colonies that date from before the Last Glacial Maximum (>45,000 14C yr B.P.) through the Holocene. Cape Irizar is a rocky cape located just south of the Drygalski Ice Tongue on the Scott Coast. In January 2016, several abandoned Adélie penguin sites and abundant surface remains of penguin bones, feathers, and carcasses that appeared to be fresh were being exposed by melting snow and were sampled for radiocarbon analysis. The results indicate the

"fresh" remains are actually ancient and that three periods of occupation by Adélie penguins are represented beginning ca. 5000 calibrated calendar (cal.) yr B.P., with the last occupation ending by ca. 800 cal. yr B.P. The presence of fresh-appearing remains on the surface that are actually ancient in age suggests that only recently has snowmelt exposed previously frozen carcasses and other remains for the first time in ~800 yr, allowing them to decay and appear fresh. Recent warming trends and historical satellite imagery (Landsat) showing decreasing snow cover on the cape since 2013 support this hypothesis. Increased δ13C values of penguin bone collagen further indicate a period of enhanced marine productivity during the penguin "optimum", a warm period at 4000–2000 cal. yr B.P., perhaps related to an expansion of the Terra Nova Bay polynya with calving events of the Drygalski Ice Tongue.

Emslie, S.D., M.J. Polito, R. Brasso, W.P. Patterson, and L. Sun. 2014. Ornithogenic soils and the paleoecology of pygoscelid penguins in Antarctica. *Quaternary International*, http://dx.doi.org/10.1016/j.quaint.2014.07.031.

Ornithogenic or bird-formed soils have accumulated in many coastal regions around Antarctica as a result of breeding activities by pygoscelid penguins, especially the Adélie penguin (*Pygoscelis adeliae*). These soils are often deep, range from hundreds to thousands of years old, and contain a natural archive of penguin tissues and those of their prey. In some regions, these tissues are extremely well preserved by the dry, cold environment and include complete and partial penguin mummies, feathers, bone, and eggshell. Hard parts of prey (fish bones, otoliths, and squid beaks) also commonly occur in these deposits from the penguin guano as it accumulates during soil development. Here, we review how research on these soils and the tissues they contain has progressed since they were first identified and described. These studies have provided not only valuable information on penguin occupation history with climate change since the Pleistocene, but also whole ecosystem responses to perturbations such as the 'krill surplus' that is hypothesized to have occurred following historic depletion of seals and whales in the 18the20th centuries. New findings in the Ross Sea indicate how penguin occupation and abandonment cycles have progressed over millennia in relation to climate change. In addition, stable isotope analysis of $d^{15}N$ and $d^{13}C$ in ancient and modern Adélie penguin tissues (feathers, bone, eggshell and membrane) and guano support the 'krill surplus' hypothesis in showing a dietary shift from fish to krill over the past ~200 years. Other recent studies have focused on stable isotope analyses of penguin prey remains, as well as ancient DNA and mercury analyses of penguin tissues recovered from ornithogenic soils. An analysis of fish otoliths recovered from ancient guano provide a means to investigate values of otolith carbonate $d^{18}O$, which correlates with other paleoclimatic records, and can be used as a proxy for changing ocean temperatures through time. In addition, measurements of total mercury (Hg) in penguin egg membrane from abandoned colonies up to 800 years old indicate significantly higher mercury levels in the past compared to modern penguins, likely due to a greater reliance on higher trophic prey prior to the proposed 'krill surplus'. All of these studies indicate that ornithogenic soils and the natural archive of tissues they contain provide a unique means to integrate both terrestrial and marine records with ecosystem studies and climate change, past and present, in Antarctica.

Garrott, R.A., J.J. Rotella, D.B. Siniff, C.L. Parkinson, and G.E. Stauffer. 2012. Environmental variation and cohort effects in an Antarctic predator [the Weddell seal]. *Oikos* 121: 1027-1040, doi:10.1111/j.1600-0706.2011.19673.x.

Understanding the potential influence of environmental variation experienced by animals during early stages of development on their subsequent demographic performance can contribute to our understanding of population processes and aid in predicting impacts of global climate change on ecosystem functioning. Using data from 4178 tagged female Weddell seal pups born into 20 different cohorts, and 30 years of observations of the tagged seals, we evaluated the hypothesis that environmental

conditions experienced by young seals, either indirectly through maternal effects and/or directly during the initial period of juvenile nutritional independence, have long-term effects on individual demographic performance. We documented an approximately three-fold difference in the proportion of each cohort that returned to the pupping colonies and produced a pup within the first 10 years after birth. We found only weak evidence for a correlation between annual environmental conditions during the juvenile-independence period and cohort recruitment probability. Instead, the data strongly supported an association between cohort recruitment probability and the regional extent of sea ice experienced by the mother during the winter the pup was in utero. We suggest that inter-annual variation in winter sea-ice extent influences the foraging success of pregnant seals by moderating the regional abundance of competing predators that cannot occupy areas of consolidated sea ice, and by directly influencing the abundance of mid-trophic prey species that are sea-ice obligates. We hypothesize that this environmentally-induced variation in maternal nutrition dictates the extent of maternal energetic investment in offspring, resulting in cohort variation in mean size of pups at weaning which, in turn, contributes to an individual's phenotype and its ultimate fitness. These linkages between sea ice and trophic dynamics, combined with demonstrated and predicted changes in the duration and extent of sea ice associated with climate change, suggest significant alterations in Antarctic marine ecosystems in the future.

Lescroël, A., G. Ballard, D. Grémillet, M. Authier, and D.G. Ainley. 2014. Antarctic climate change: extreme events disrupt plastic response in Adélie penguins. *PLoS ONE* 9(1): e85291, doi:10.1371/journal.pone.0085291.

In the context of predicted alteration of sea ice cover and increased frequency of extreme events, it is especially timely to investigate plasticity within Antarctic species responding to a key environmental aspect of their ecology: sea ice variability. Using 13 years of longitudinal data, we investigated the effect of sea ice concentration (SIC) on the foraging efficiency of Adélie penguins (*Pygoscelis adeliae*) breeding in the Ross Sea. A 'natural experiment' brought by the exceptional presence of giant icebergs during 5 consecutive years provided unprecedented habitat variation for testing the effects of extreme events on the relationship between SIC and foraging efficiency in this sea-ice dependent species. Significant levels of phenotypic plasticity were evident in response to changes in SIC in normal environmental conditions. Maximum foraging efficiency occurred at relatively low SIC, peaking at 6.1% and decreasing with higher SIC. The 'natural experiment' uncoupled efficiency levels from SIC variations. Our study suggests that lower summer SIC than currently observed would benefit the foraging performance of Adélie penguins in their southernmost breeding area. Importantly, it also provides evidence that extreme climatic events can disrupt response plasticity in a wild seabird population. This questions the predictive power of relationships built on past observations, when not only the average climatic conditions are changing but the frequency of extreme climatic anomalies is also on the rise.

Paterson, J.T., J.J. Rotella, K.R. Arrigo, and R.A. Garrott. 2015. Tight coupling of primary production and marine mammal reproduction in the Southern Ocean. *Proceedings of the Royal Society* B, London 282(1806), UNSP 20143137, doi: 10.1098/rspb.2014.3137.

Polynyas are areas of open water surrounded by sea ice and are important sources of primary production in high-latitude marine ecosystems. The magnitude of annual primary production in polynyas is controlled by the amount of exposure to solar radiation and sensitivity to changes in sea-ice extent. The degree of coupling between primary production and production by upper trophic-level consumers in these environments is not well understood, which prevents reliable predictions about population trajectories for species at higher trophic levels under potential future climate scenarios. In this study, we find a strong, positive relationship between annual primary production in an Antarctic polynya and pup production by

ice-dependent Weddell seals. The timing of the relationship suggests reproductive effort increases to take advantage of high primary production occurring in the months after the birth pulse. Though the proximate causal mechanism is unknown, our results indicate tight coupling between organisms at disparate trophic levels on a short timescale, deepen our understanding of marine ecosystem processes, and raise interesting questions about why such coupling exists and what implications it has for understanding high-latitude ecosystems.

ROSS SEA MIDDLE TROPHIC LEVELS

Ainley, D.G., G. Ballard, R.M. Jones, D. Jongsomjit, S.D. Pierce, W.O. Smith, Jr., and S. Veloz. 2015. Trophic cascades in the western Ross Sea, Antarctica: revisited. *Marine Ecology Progress Series* 534: 1–16, doi:10.3354/meps11394.

We investigated mesopredator effects on prey availability in the Ross Sea, Antarctica, assessing the reasons why Adélie penguin *Pygoscelis adeliae* foraging trip duration (FTD) increases and diet changes from krill to fish as numbers of foraging penguins and competing cetaceans increase in the penguins' foraging area. To investigate penguins' seasonally changing FTD as a function of foraging-population size—previously investigated indirectly—we used bio-logging to determine the penguins' 3-dimensional foraging volume, while an autonomous glider quantified the depth, abundance, and distribution of potential prey. As numbers of foraging penguins and cetaceans increased, penguins spent more time on foraging trips, traveling farther and deeper, and their diet included more fish, as average maximum depth of krill increased from 45 to 65 m, and that of small fish also deepened, but only from 51 to 57 m. With a need to forage at greater depths for increasingly over lapping prey, the penguins consumed more of the energy dense fish. Krill depth was negatively correlated with chlorophyll (a proxy for krill food), indicating an uncoupling between the two and the overwhelming importance of predation avoidance by the krill relative to food acquisition. Results support the hypotheses that (1) predators remove the grazers from Ross Sea surface waters, controlling their vertical distributions; and (2) the food web has a 'wasp waist' structure, in which middle- and upper-trophic levels are controlled top-down, whereas phytoplankton production and accumulation are regulated bottom-up, largely independent of grazer control. Ross Sea models need revision to reflect this food web structure.

Brooks, C., J. Caccavo, J. Ashford, R. Dunbar, K. Goetz, M. La Mesa, and L. Zane. 2018. Early life history connectivity of Antarctic silverfish (*Pleuragramma antarctica*) in the Ross Sea. *Fisheries Oceanography* 27: 274-287.

A recent population hypothesis for Antarctic silverfish (*Pleuragramma antarctica*), a critical forage species, argued that interactions between life history and circulation associated with glacial trough systems drive circumpolar distributions over the continental shelf. In the Ross Sea, aggregations of eggs and larvae occur under fast ice in Terra Nova Bay, and the hypothesis predicted that dispersing larvae encounter outflow along the western side of Drygalski Trough. The outflow advects larvae towards the shelf-break, and mixing with trough inflow facilitates return toward the inner shelf. To examine the hypothesis, we compared samples of *P. antarctica* collected near Coulman Island in the outflow, along Crary Bank in the inflow, and a third set taken over the rest of the Ross Sea. We ruled out misidentification using an innovative genetic validation. Silverfish larvae comprised 99.5% of the catch, and the highest population densities were found in Drygalski Trough. The results provided no evidence to reject the population hypothesis. Abundance indices, back-calculated hatching dates, length distributions and growth were congruent with a unified early life history in the western Ross Sea, constrained by cryopelagic early stages in Terra Nova Bay. By contrast, a sample in the Bay of Whales revealed much

smaller larvae, suggesting either a geographically separate population in the eastern Ross Sea, or westward connectivity with larvae spawned nearby by fish sourced from troughs upstream in the Amundsen Sea. These results illustrate how hypotheses that integrate population structure with life history can provide precise spatial predictions for subsequent testing.

Davis, L.B., E.E. Hofmann, J.M. Klinck, A. Piñones, and M.S. Dinniman. 2017. Distributions of krill and Antarctic silverfish and correlations with environmental variables in the western Ross Sea, Antarctica. *Marine Ecology Progress Series* 584: 45-65, doi.org/10.3354/meps12347.

Antarctic krill *Euphausia superba*, crystal krill *E. crystallorophias*, and Antarctic silverfish *Pleuragramma antarctica* are key mid-trophic level species in the Ross Sea, connecting primary production to the upper trophic levels. Distributions of these species were constructed from observations made in the western Ross Sea from 1988 to 2004. Distributions of environmental conditions were obtained from a 5-km resolution circulation model (temperature, mixed layer depth, surface speed) and satellite-derived observations (chlorophyll, sea ice cover). A hierarchy of statistical methods determined correlations and relationships between species and environmental conditions. Each species occupies a localized habitat defined by different environmental characteristics. Antarctic krill are concentrated along the northwestern shelf break in a habitat characterized by deep (>1000 m) bottom depth, warm temperature (1 to 1.25°C), decreased sea ice, and proximity to the shelf break. Crystal krill and Antarctic silverfish are concentrated in Terra Nova Bay. Common characteristics of the habitat for these species are southwesterly location, coastal proximity, and cold temperature (-1.75 to -2°C). The habitat characteristics obtained for the 3 species provide a basis for projecting potential distribution changes in response to environmental change and for delineating regions of the Ross Sea for focused management and selection of marine protected areas that support ecosystem-level conservation plans.

Eastman, J.T. 2020. The buoyancy-based biotope axis of the evolutionary radiation of Antarctic cryonotothenioid fishes. *Polar Biology* 43: 1217-1231.

In the absence of any prior comprehensive analysis, I evaluate divergence along the biotope axis in the habitat stage of the evolutionary radiation of Antarctic cryonotothenioids. I utilize the available percentage buoyancy (%B) measurements as habitat proxies for recognition of the pelagic, semipelagic, demersal, and benthic biotopes that include, respectively, 5%, 10%, 73%, and 12% of the 59 species and 1749 specimens in the study. The majority of species retain the ancestral demersal biotope of *Eleginops maclovinus*, and this probably enhances ecological plasticity. Divergence into the pelagic biotope is the most distinctive organismal feature of the radiation and, although only 5% of species are pelagic, this biotope is not depauperate in global comparisons. Pelagic or potentially pelagic species are *Dissostichus mawsoni, D. eleginoides, Pleuragramma antarcticum, Aethotaxis mitopteryx*, and *Gvozdarus svetovidovi*. Small ontogenetic changes in %B with growth are typical; however, this is extensive in D. mawsoni, a species with the potential to transition through benthic to pelagic biotopes over ontogeny. Occupation of the pelagic biotope by large D. mawsoni may be impermanent as it is lipid-dependent, a contingency reliant on the availability of *P. antarcticum* as prey. In unusual conditions, the specialized sacs of *P. antarcticum* can also yield their lipid for metabolism with possible loss of buoyancy. Pelagic species are inordinately important in the food web. In the southwestern Ross Sea a guild of large mammalian and avian predators, which includes D. mawsoni, is reliant on lipid-rich, energy-dense cryonotothenioid prey. This includes asymmetrical intraguild predation on *D. mawsoni*, with *P. antarcticum* as a basal resource for the guild.

La Mesa, M., and J.T. Eastman. 2012. Antarctic silverfish: life strategies of a key species in the high-Antarctic ecosystem. *Fish and Fisheries* 13: 241-266, doi:10.1111/j.1467-2979.2011.00427.x.

Among the endemic notothenioid fish of Antarctica, the Antarctic silverfish (*Pleuragramma antarcticum*) is the only species in which all developmental stages live throughout the water column. It is widely distributed in the shelf waters around the continent, inhabiting both open waters and areas of pack ice at depths from 0 to 900 m. In successfully occupying this habitat, it evolved a suite of specific biological, ecological and physiological adaptations to the environmental conditions in the cold and highly seasonal Antarctic waters. Specialization for the pelagic environment evolved over millions of years enabled life under unusual environmental constraints and colonization of the pelagic realm of the Antarctic continental shelf. A sudden change of environmental conditions driven by the current rapid climate change could negatively affect this weak equilibrium, with a catastrophic cascade effecting higher trophic levels. Indeed, as both adults and early life stages of the Antarctic silverfish appear to be strongly dependent on sea-ice, this species would be especially sensitive to climatic or oceanic changes that reduce the extent of sea-ice cover or the timing of formation of coastal polynyas.

Maas, Amy E., L.E. Elder, H.M. Dierssen, and B.A. Seibel. 2011. Metabolic response of Antarctic pteropods (Mollusca: Gastropoda) to food deprivation and regional productivity. *Marine Ecology Progress Series* 441: 129-139, doi.org/10.3354/meps09358.

Pteropods are an abundant group of pelagic gastropods that, although temporally and spatially patchy in the Southern Ocean, can play an important role in food webs and biochemical cycles. We found that the metabolic rate in *Limacina helicina antarctica* is depressed (similar to 23 %) at lower mean chlorophyll *a* (chl *a*) concentrations in the Ross Sea. To assess the specific impact of food deprivation on these animals, we quantified aerobic respiration and ammonia (NH3) production for 2 dominant Antarctic pteropods, *L. helicina antarctica* and *Clone limacina antarctica*. Pteropods collected from sites west of Ross Island, Antarctica were held in captivity for a period of 1 to 13 d to determine their metabolic response to laboratory-induced food deprivation. *L. helicina antarctica* reduced oxygen consumption by similar to 20% after 4 d in captivity. Ammonia excretion was not significantly affected, suggesting a greater reliance on protein as a substrate for cellular respiration during starvation. The oxygen consumption rate of the gymnosome, *C. limacina antarctica*, was reduced by similar to 35% and NH3 excretion by similar to 55% after 4 d without prey. Our results indicate that there is a link between the large scale chl *a* concentrations of the Ross Sea and the baseline metabolic rate of pteropods which impacts these animals across multiple seasons.

Piñones, A., E.E. Hofmann, M.S. Dinniman, and L.B. Davis, 2016. Modeling the transport and fate of Euphausiids in the Ross Sea. *Polar Biology* 39: 177-187, doi:10.1007/s00300-015-1798-5.

Antarctic krill (*Euphausia superba*) and crystal krill (*Euphausia crystallorophias*), important components of the Ross Sea food web, differ in their population distribution. The objective of this study was to determine whether these differing distributions result primarily from differences in spawning locations, larval development times, and transport by the Ross Sea circulation. To address this objective, Lagrangian particle tracking experiments were used to simulate the transport of larvae of Antarctic krill and crystal krill. The particle simulations showed that regions providing inputs of Antarctic krill to the Ross Sea were along the outer shelf/slope. Crystal krill transport and retention were along the shallow banks on the outer Ross Sea shelf. Particles initialized in the inner shelf off Victoria Land showed high retention in the region south and along the Terra Nova Bay polynya, with timescales consistent with development times of crystal krill. These results suggest that the cyclonic circulation over the shelf contributes significantly to the dispersion and retention of crystal krill in parts of the inner Ross Sea

continental shelf that overlaps with regions with high concentrations of krill-dependent top predators. The westward circulation along the shelf break contributes to the transport and aggregation of Antarctic krill in regions where Circumpolar Deep Water is observed on the outer continental shelf and along the shelf break. The transport pathways and connectivity obtained from this study provide a baseline for assessing the effects of projected changes in the Ross Sea circulation on the distribution of two important krill species.

Saenz, B.T., D.G. Ainley, K.L. Daly, G. Ballard, E. Conlisk, M.L. Elrod, and S.L. Kim. 2020. Drivers of concentrated predation in an Antarctic marginal-ice-zone food web. *Scientific Reports* 10: 7282, https://doi.org/10.1038/s41598-020-63875-y.

Predators impact preyscapes (3-D distribution of forage species) by consuming prey according to their abilities or by altering prey behavior as they avoid being consumed. We elucidate prey (Antarctic silverfish [*Pleuragramma antarctica*] and crystal krill [*Euphausia chrystallorophias*]) responses to predation associated with the marginal ice zone (MIZ) of the McMurdo Sound, Antarctica, polynya. Prey abundance and habitat was sampled across a 30 × 15 km area by remotely-operated vehicle, and included locations that were accessible (ice edge) or inaccessible (solid fast ice) to air-breathing predators. Prey and habitat sampling coincided with bio-logging of Adélie penguins and observations of other air-breathing predators (penguins, seals, and whales), all of which were competing for the same prey. Adélie penguins dived deeper, and more frequently, near the ice edge. Lowered abundance of krill at the ice edge indicated they were depleted or were responding to increased predation and/or higher light levels along the ice edge. Penguin diet shifted increasingly to silverfish from krill during sampling, and was correlated with the arrival of krill-eating whales. Behaviorally-mediated, high trophic transfer characterizes the McMurdo Sound MIZ, and likely other MIZs, warranting more specific consideration in food web models and conservation efforts.

Smith, W.O., Jr., L.M. Delizo, C. Herbolsheimer, and E. Spencer. 2017. Distribution and abundance of mesozooplankton in the Ross Sea, Antarctica. *Polar Biology* 40: 2351-2361, https://doi:10.1007/s00300-017-2149-5.

Zooplankton (meso- and macrozooplankton) distributions and biomass are poorly known in the Ross Sea despite their importance in energy transfer within food webs and biogeochemical cycles. Mesozooplankton abundance and biomass on the continental shelf are spatially variable and span two orders of magnitude during austral summer. Selected sub-regions (near the shelf break or ice shelf) show similar variability, suggesting that other processes, either oceanographic or biological, influence zooplankton on smaller scales. Biomass at one location (76.5_S, 172_ E) was consistently elevated throughout January, although the causes of this ‘‘hotspot’’ were unclear. At a station near the ice shelf, abundance and biomass of the pteropod *Limacina antarctica* was very high. Zooplankton biomass at this location was sevenfold greater than any other station, and while the high biomass was driven by pteropod contributions, copepods were also abundant. Copepods dominated the mesozooplankton composition at all other stations, comprising 90 and 78% on average of the total abundance and biomass. Zooplankton biomass comprised on average 3.96% of the total particulate carbon (0–200 m) and was weakly correlated with chlorophyll and biogenic silica. We suggest that summer zooplankton growth and biomass, while linked to organic matter concentrations, are regulated by other factors (e.g., predation by crystal krill and Antarctic silverfish), as both grazers may be responsible for significant losses. Our data indicate that, contrary to other suggestions, summer zooplankton biomass and abundance in the Ross Sea are similar to those in other Antarctic coastal regions.

Vacchi, M., A.L. DeVries, C.W. Evan, M. Bottaro, L. Ghigliotti, L. Cutroneo, and E. Pisano. 2012. A nursery area for the Antarctic silverfish Pleuragramma antarcticum at Terra Nova Bay (Ross Sea): first estimate of distribution and abundance of eggs and larvae under the seasonal sea ice. *Polar Biology* 35: 1573−1585.

Pleuragramma antarcticum is the dominant pelagic fish in the waters of the continental shelf in high Antarctic regions, where it plays a key role in the food web. A nursery ground for eggs of this species was first identified in 2002 in Terra Nova Bay (Ross Sea), where eggs were found trapped in ice platelets under the sea-ice during the spring. As part of a monitoring program aimed at understanding the geographic and temporal characteristics of this nursery ground, the present study reports on surveys carried out in the austral springs of 2005 and 2006 using a simple and effective method for sampling from the sea-ice. These surveys enabled the evaluation of the spatial range of the nursery area of the Antarctic silverfish in the sea-ice of the coastal area of Victoria Land between the Coulman Island and the Drygalski Glacier Tongue. *P. antarcticum* eggs were concentrated in an area of Terra Nova Bay of about 270 km2, encompassing two adjacent sites, Gerlache Inlet and Silverfish Bay. The present results add information on life cycle and hatching period of the Antarctic silverfish and confirm the importance of the Terra Nova Bay as a nursery area for this important species. Moreover, the survey points to the sea-ice cover and platelet ice as important environmental features of the nursery area.

ROSS SEA UPPER TROPHIC LEVEL INDICATOR SPECIES

POPULATION DECADAL TRENDS AND DEMOGRAPHY

ANTARCTIC TOOTHFISH

Abrams, P.A. 2014. How precautionary is the policy governing the Ross Sea Antarctic toothfish (*Dissostichus mawsoni*) fishery? *Antarctic Science* 26: 3–13, doi:10.1017/S0954102013000801

This article reviews the adequacy of data and models currently being used to estimate the present and future population sizes of the Antarctic toothfish (*Dissostichus mawsoni* Norman) in the Ross Sea regional ecosystem. The current tagging programme is unlikely to provide an accurate picture of total population size, and estimates of both the pre-exploitation spawning stock biomass and the ratio of current to pre-exploitation biomass are unreliable. Many parameters necessary for estimating future population growth or decline have not been measured, and the current objective of a 50% reduction in biomass relative to unexploited biomass may easily fail to prevent a much larger reduction from taking place. The need to guess values of important parameters makes it impossible to set bounds on the potential errors of population forecasts. Current scientific knowledge is far from what is needed to predict the likely effects of food-web responses to harvesting of toothfish in the Ross Sea, or to predict the feedback effects of those food-web changes on toothfish populations.

Abrams, P.A., D.G. Ainley, L.K. Blight, P.K. Dayton, J.T. Eastman, and J.L. Jacquet. 2016. Necessary elements of precautionary management: implications for the Antarctic toothfish. *Fish and Fisheries* 17: 1152–1174, doi: 10.1111/faf.12162

We review the precautionary approach to fisheries management, propose a framework that will allow a systematic assessment of insufficient precaution and provide an illustration using an Antarctic fishery. For a single-species fishery, our framework includes five attributes: (1) limit reference points that recognize gaps in our understanding of the dynamics of the species; (2) accurate measures of population size; (3) ability to detect population changes quickly enough to arrest unwanted declines; (4) adequate

understanding of ecosystem dynamics to avoid adverse indirect effects; and (5) assessment of the first four elements by a sufficiently impartial group of scientists. We argue that one or more of these elements frequently fail to be present in the management of many fisheries. Structural uncertainties, which characterize almost all fisheries models, call for higher limit points than those commonly used. A detailed look into the five elements and associated uncertainties is presented for the fishery on the Antarctic toothfish in the Ross Sea (FAO/CCAMLR Area 88.1, 88.2), for which management was recently described as 'highly precautionary'. In spite of having features that make the Ross Sea fishery ideal for the application of the precautionary approach, gaps in our knowledge and failure to acknowledge these gaps mean that current regulation falls short of being sufficiently precautionary. We propose some possible remedies.

Ainley, D.G., G. Ballard, J.T. Eastman, C.W. Evans, N. Nur, and C.L. Parkinson. 2016. Changed prevalence, not absence, explains toothfish status in McMurdo Sound. ***Antarctic Science*****, doi:10.1017/S0954102016000584.**

We comment on the conjecture by Parker et al. (2016) that Antarctic toothfish recently returned to McMurdo Sound, arguing that this species never departed. Instead, as deduced from a 40-year fishing effort, toothfish water column prevalence became markedly reduced where bottom depths are <500 m, with research continuing to show their presence on the bottom or above the bottom where depths are deeper. We also counter arguments that toothfish departed, and remained absent, during and following a five-year presence of mega-icebergs residing near the opposite coast of Ross Island, the icebergs inhibiting or fomenting conditions that discouraged toothfish presence in the Sound. Available analyses reveal that toothfish movement into the Sound was probably not significantly affected, and additionally that neither changes in hydrography nor in primary productivity in the Sound would have been sufficient to impact toothfish presence through food web alteration. We hypothesize that the local effect of predation by seals and whales and the regional effect of a fishery targeting the largest toothfish (those neutrally buoyant and thus capable of occupying upper levels of the water column) has resulted in the remaining toothfish now being found predominantly closer to the bottom at greater depths.

Ainley, D.G., C.M. Brooks, J.T. Eastman, and M. Massaro. 2012. Unnatural selection of Antarctic Toothfish in the Ross Sea, Antarctica. F. Huettmann (ed.), ***Protection of the Three Poles*****, pp. 53-75, doi: 10.1007/978-4-431-54006-9_3, Springer, Tokyo.**

To ensure that the Ross Sea remains a functioning ecosystem, it is imperative that old, large toothfish are allowed to exist in relatively high abundance. To protect toothfish and this ecosystem for the long term, it is necessary to include major portions of the Ross Sea shelf and slope, as well as some of the seamounts to the north, in a network of marine protected areas (MPAs). Low-level fishing could then be allowed at the edges of these MPSs while keeping the majority of the toothfish population, with a natural age distribution, intact. Many examples of how such MPAs have succeeded in the management of fish stocks are available (Sumaila et al. 2000; Lubchenco et al. 2003), along with examples that failed owing to poor or unenforced management (Longhurst 2010). Currently, longline fishing throughout the entire Antarctic toothfish range extracts the oldest, largest, and likely most fecund fish (see above; Brooks 2008; Brooks and Ashford 2008) (Fig. 3.7). As we argued in this chapter, we believe that these old age classes of Antarctic toothfish need to be restored within this population to avoid irreversible evolutionary and ecological consequences, heightened in an age and area of rapid and profound climate change (Jacobs 2006; Trathan and Agnew 2010).

Ainley, D.G., E.L. Crockett, J.T. Eastman, W.R. Fraser, N. Nur, K. O'Brien, L.A. Salas, and D.B. Siniff. 2017. How overfishing a large piscine mesopredator explains growth in Ross Sea penguin

populations: a framework to better understand impacts of a controversial fishery. *Ecological Modelling* 349: 69-75.

We herein review the modeling approach of Pinkerton et al. (2016, Ecol. Modelling), who tested the hypothesis that fishery depletion of large, neutrally buoyant Antarctic toothfish (*Dissostichus mawsoni*) was implicated in the recent increase in the southern Ross Sea population of Adélie penguins (*Pygoscelis adeliae*). Toothfish are a trophic competitor of penguins for Antarctic silverfish (*Pleuragramma antarctica*) in the southern Ross Sea, hence Ainley et al. (2013) and Lyver et al. (2014) proposed that the effect of the removal of toothfish was through predation release of silverfish. Pinkerton et al. concluded that predation release could not provide sufficient energy to sustain the observed penguin population growth. Critically, however, they failed to consider certain spatial and size-by-depth aspects of diet overlap, and mechanisms associated with population dynamics that could cause the population growth through predation release. In order to effectively test the prey release hypothesis, we suggest a strong inference path that incorporates what we know about population dynamics in penguins and Ross Sea food webs into life history parameterizations of penguins, toothfish and silverfish population dynamics models.

Ainley, D.G., J.T. Eastman, and C.M. Brooks. 2015. Comments on ‘‘The Antarctic toothfish (*Dissostichus mawsoni*): biology, ecology, and life history in the Ross Sea region,’’ by S. Hanchet et al. *Hydrobiologia* 761: 397–414.

We expand the paper by Hanchet et al. (Hydrobiologia 761:397–414, 2015), published in Hydrobiologia, by elaborating upon neutral buoyancy, a critical aspect of Antarctic toothfish life history that was only briefly treated by those authors. Neutral buoyancy, although not common among adult notothenioid fish, is an attribute that expands the water column niche space of this species beyond that available to the bottom-dwelling toothfish that were emphasized in the review. Conversely, also not well covered in the review are the implications involved in the suspected absence of neutral buoyancy in the so-called post-spawning, fat-depleted ‘‘axe-handle’’ fish.

Ainley, D.G., N. Nur, J.T. Eastman, G. Ballard, C.L. Parkinson, C.W. Evans, and A.L. DeVries. 2013. Decadal trends in abundance, size and condition of Antarctic toothfish in McMurdo Sound, Antarctica, 1972-2011. *Fish and Fisheries* 14: 343-363, doi:10.1111/j.1467-2979.2012.00474.x.

We report the analyses of a dataset spanning 39 years of near-annual fishing for *Dissostichus mawsoni* in McMurdo Sound, Antarctica, 1972–2011. Data on total length, condition and catch per unit effort (CPUE) were derived from the > 5500 fish caught, the large majority of which were measured, tagged and released. Contrary to expectation, the length frequency of the McMurdo Sound catch was dominated by fish in the upper two-thirds of the overall distribution exhibited in the industrial catch for the Ross Sea shelf. Fish length and condition increased from the early 1970s to the early 1990s and then decreased. Fish length positively correlated with Ross Sea ice extent in early spring, a relationship possibly caused by more ice encouraging larger fish to move farther south over the shelf and into the study area. Fish condition positively correlated with the amount of open water in the Ross Sea during the previous summer (Feb), perhaps reflecting greater availability of prey with the higher productivity that more open water brings. Decreasing fish size corresponds to the onset of the fishery, which targets the large individuals. CPUE was constant through 2001 and then decreased dramatically. We hypothesize that this decrease is related to the industrial fishery, which began in the 1996–97 austral summer, and concentrates effort over the ice-free Ross Sea continental slope. As a result of limited prey choices and close coupling among mesopredators of the region, Antarctic toothfish included, the fishery appears to be dramatically altering the trophic structure of the Ross Sea.

Ainley, D.G., and D. Pauly. 2014. Fishing down the food web of the Antarctic continental shelf and slope. *Polar Record* 50: 92-107, doi:10.1017/S0032247412000757.

The history of biotic exploitation for the continental margin (shelf and slope) of the Antarctic Large Marine Ecosystem (LME) is reviewed, with emphasis on the period from 1970 to 2010. In the Antarctic Peninsula portion, marine mammals were decimated by the 1970s and groundfish by the early 1980s. Fishing for Antarctic krill *Euphausia superba* began upon the demise of groundfish and now is the only fishing that remains in this region. Surveys show that cetacean and most groundfish stocks remain severely depressed, harvest of which is now prohibited by the International Whaling Commission and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). On the other hand, krill fishing in this region is underway and in recent years has contributed up to 72% of the Southern Ocean catch, depending on fishing conditions and the CCAMLR conservation measures in force. Elsewhere along the Antarctic continental margin, marine mammals were also severely depleted by the 1970s, followed directly by relatively low-level fisheries for krill that continued until the early 1990s. Recently in these areas, where fin-fishing is still allowed, fisheries for Antarctic toothfish *Dissostichus mawsoni* have been initiated, with one of this fish's main prey, grenadiers *Macrourus* spp., being taken significantly as by-catch. Continental margin fishing currently accounts for ~25% of the total toothfish catch of the Southern Ocean. Fishing along the Antarctic continental margin, especially the Antarctic Peninsula region, is a clear case of both the tragedy of the commons and 'fishing down the food web'.

Ashford, J., M. Dinniman, C. Brooks, A.H. Andrews, E. Hofmann, G. Cailliet, C. Jones, and N. Ramanna. 2012. Does large-scale ocean circulation structure life history connectivity in Antarctic toothfish (*Dissostichus mawsoni*)? *Canadian Journal of Fisheries and Aquatic Science* 69: 1–17.

A multidisciplinary approach incorporating otolith chemistry, age data, and numerical Lagrangian particle simulations indicated a single, self-recruiting population of Antarctic toothfish (*Dissostichus mawsoni*) in the Southeast Pacific Basin (SPB) and Ross Sea, with a life history structured by the large-scale circulation. Chemistry deposited prior to capture along otolith edges demonstrated strong environmental heterogeneity, yet the chemistry in otolith nuclei, deposited during early life, showed no differences. Age data showed only adult fish in catches on the Pacific–Antarctic Ridge in the SPB and structuring of life stages consistent with transport pathways from the northern Ross Sea. Lagrangian particle simulations predicted that early life stages following the flow in the SPB would be transported to areas in the Ross Sea where juveniles are caught, whereas the circulation would facilitate adult movement along the shelf slope and back into the SPB where spawning adults are caught. These results suggest that successfully spawning fish spend only a part of their adult life history in the Ross Sea, areas in the eastern Ross Sea contribute disproportionately to the spawning population, and areas in the southwestern Ross Sea may supply fisheries in the southern Indian Ocean.

Ashford, J., M. Dinniman, and C. Brooks. 2017. Physical–biological interactions influencing large toothfish over the Ross Sea shelf. *Antarctic Science*, doi:10.1017/S0954102017000359

We add comments to a recent series of publications in peer-reviewed journals concerning the distribution of large Antarctic toothfish (*Dissostichus mawsoni*) found over the inner shelf of the Ross Sea. We note that earlier fish ecologists advanced innovative hypotheses invoking physical–biological interactions with life history, and that these, far from being disproved, have been relegated by more immediately pressing management concerns. We argue that, despite the considerable advances achieved by research groups working on *D. mawsoni*, an understanding of distribution and abundance is incomplete without reference to the physical structure that supports their life history. We briefly consider hypotheses highlighted by the recent literature in the context of major features of the shelf circulation in

the Ross Sea, in particular intrusions of modified Circumpolar Deep Water along trough systems. We suggest physical–biological interactions that may be involved and call for improvements in the monitoring programme that can help test between the competing hypotheses.

Brooks, C.M., A.H. Andrews, J.R. Ashford, N. Ramanna, C.D. Jones, C.C. Lundstrom, and G.M. Caillet. 2010. Age estimation and lead–radium dating of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea. *Polar Biology*, doi:10.1007/s00300-010-0883-z.

Antarctic toothfish (*Dissostichus mawsoni*) are the target of an important commercial fishery in the Southern Ocean, yet age data used for management have not been comprehensively tested for accuracy. In this study, Antarctic toothfish were aged using counts of otolith growth zones based on criteria established for Patagonian toothfish, *D. eleginoides*, a closely related species. To validate these ages, the radioactive disequilibrium of lead-210 and radium-226 in otolith cores was measured and used as an independent chronometer to accurately determine age across the range of fish caught in large numbers by the fishery. Growth-zone counts indicated Antarctic toothfish live to at least 39 years of age, and were in close agreement with the chronometer, validating the age estimation criteria and the accuracy of age estimates. Von Bertalanffy growth function parameters indicated Antarctic toothfish were relatively slow-growing (k = 0.111), especially in relation to their maximum size (L? = 158.9 cm).

O'Brien, K.M., and E.L. Crockett. 2013. The promise and perils of Antarctic fishes. *European Molecular Biology Organization Reports*,www.nature.com/10.1038/embor.2012.203.

Beneath the surface of the Southern Ocean, in the deep waters of the continental shelf and continental slope of Antarctica, a magnificent fauna consisting of over 320 known species of fish thrives in the cold and dark. These fish are uniquely adapted to the extreme environment in which they live. Over the course of millennia, they have evolved a remarkable range of physiological and biochemical features, the most visually stunning of which is that some lack haemoglobin. Yet, these species are under threat from global climate change and fishing, and the secrets they might unlock for science could be lost in the next decades if action is not taken.

Parker, S.J., S. Mormede, A.L. Devries, S.M. Hanchet, and R. Eisert. 2016. Have Antarctic toothfish returned to McMurdo Sound? *Antarctic Science* 28: 29–34, doi:10.1017/S0954102015000450.

A dramatic reduction in catch rates of Antarctic toothfish in McMurdo Sound, Antarctica, has led to conclusions that the commercial bottom longline fishery for toothfish in the Ross Sea has drastically altered the toothfish population with cascading effects on the McMurdo Sound ecosystem. However, results from a new monitoring programme for Antarctic toothfish and other top predators carried out in McMurdo Sound in 2014 have shown toothfish catch rate, fish size and fish age similar to those observed prior to 2002. These results suggest that either large and old fish have returned to McMurdo Sound following a temporary environmentally driven absence or that they remained locally present but were not detected in the areas sampled. These findings highlight the importance of continued standardized monitoring for detecting the potential effects of fishing on the Ross Sea ecosystem.

Parker, S.J., S. Mormede, S.M. Hanchet, A. Devries, S. Canese, and L. Ghigliotti. 2019. Monitoring Antarctic toothfish in McMurdo Sound to evaluate the Ross Sea region Marine Protected Area. *Antarctic Science* 31: 195–207, doi:10.1017/S0954102019000245.

We developed a random, stratified, vertical longline survey in McMurdo Sound, Antarctica, to compare the local age and size composition, diet and reproductive status of Antarctic toothfish

(*Dissostichus mawsoni*) with those observed from a vessel-based survey of the southern Ross Sea shelf that includes a McMurdo Sound stratum. Results indicated that southern McMurdo Sound toothfish were larger and older than those a short distance away in northern McMurdo Sound. These data, in addition to recoveries of tagged fish, suggest that the large toothfish in McMurdo Sound may have limited mixing with the rest of the population. The potential effects of climate change and fishing in northern areas on toothfish abundance in McMurdo Sound will depend on the mechanism of toothfish recruitment to McMurdo Sound. Understanding the ecological relationships between McMurdo Sound toothfish and the larger population is required to predict these impacts. Furthermore, because toothfish predators (type C killer whales *Orcinus orca*, Weddell seals *Leptonychotes weddelli*i) are abundant in the south-west margins of the Ross Sea, it is important to monitor toothfish in McMurdo Sound as part of the monitoring programme for the Ross Sea region Marine Protected Area.

ADELIE PENGUINS

LaRue, M.A., D.G. Ainley, M. Swanson, K.M. Dugger, P. O'B. Lyver, K. Barton, and G. Ballard. 2013. Climate change winners: receding ice fields facilitate colony expansion and altered dynamics in an Adélie Penguin metapopulation. *PLoS ONE* 8(4): e60568. doi:10.1371/journal.pone.0060568.

There will be winners and losers as climate change alters the habitats of polar organisms. For an Adélie penguin (*Pygoscelis adeliae*) colony on Beaufort Island (Beaufort), part of a cluster of colonies in the southern Ross Sea, we report a recent population increase in response to increased nesting habitat as glaciers have receded. Emigration rates of birds banded as chicks on Beaufort to colonies on nearby Ross Island decreased after 2005 as available habitat on Beaufort increased, leading to altered dynamics of the metapopulation. Using aerial photography beginning in 1958 and modern satellite imagery, we measured change in area of available nesting habitat and population size of the Beaufort colony. Population size varied with available habitat, and both increased rapidly since the 1990s. In accord with glacial retreat, summer temperatures at nearby McMurdo Station increased by, 0.5ºC per decade since the mid-1980s. Although the Ross Sea is likely to be the last ocean with an intact ecosystem, the recent retreat of ice fields at Beaufort that resulted in increased breeding habitat exemplifies a process that has been underway in the Ross Sea during the entire Holocene. Furthermore, our results are in line with predictions that major ice shelves and glaciers will retreat rapidly elsewhere in the Antarctic, potentially leading to increased breeding habitat for Adélie penguins. Results further indicated that satellite imagery may be used to estimate large changes in Adélie penguin populations, facilitating our understanding of metapopulation dynamics and environmental factors that influence regional populations.

LaRue, M., D. Iles, S. Labrousse, L. Salas, G. Ballard, D. Ainley, and B. Saenz. 2019. A possible Adélie penguin sub-colony on fast ice by Cape Crozier, Antarctica. *Antarctic Science*, doi:10.1017/S095410201900018X.

Adélie penguins are renowned for their natal philopatry on land-based colonies, requiring small pebbles to be used for nests. We report on an opportunistic observation via aerial survey, where hundreds of Adélie penguins were documented displaying nesting behaviours on fast ice ~3 km off the coast of Cape Crozier, which is one of the largest colonies in the world. We counted 426 Adélie penguins engaging in behaviours of pair formation, spacing similarly to normal nest distributions and lying in divots in the ice that looked like nests. On our first visit, it was noticed that the guano stain was bright pink, consistent with krill consumption, but had shifted to green over the course of ~2 weeks, indicating that the birds were fasting (a behaviour consistent with egg incubation). However, eggs were not

observed. We posit four hypotheses that may explain the proximate causes of this behaviour and caution against future high-resolution satellite imagery interpretation due to the potential for confusing ice-nesting Adélie penguins with the presence of emperor penguin colonies.

LaRue, M.A., H.J. Lynch, P.O'B Lyver, K. Barton, D.G Ainley, A. Pollard, W.R. Fraser, and G. Ballard. 2014. A method for estimating population colony sizes of Adélie penguins using remote sensing imagery. *Polar Biology*, doi 10.1007/s00300-014-1451-8.

Adélie penguins (*Pygoscelis adeliae*) are important predators of krill (*Euphausia* spp.) and Antarctic silverfish (*Pleuragramma antarctica*) during summer, are a key indicator of the status of the Southern Ocean ecosystem, and are therefore a focal species for the Committee for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program. The ability to monitor the population size of species potentially affected by Southern Ocean fisheries, i.e., the Adélie penguin, is critical for effective management of those resources. However, for several reasons, direct estimates of population size are not possible in many locations around Antarctica. In this study, we combine high-resolution (0.6 m) satellite imagery with spectral analysis in a supervised classification to estimate the sizes of Adélie penguin breeding colonies along Victoria Land in the Ross Sea and on the Antarctic Peninsula. Using satellite images paired with concurrent ground counts, we fit a generalized linear mixed model with Poisson errors to predict the abundance of breeding pairs as a function of the area of current-year guano staining identified in the satellite imagery. Guano-covered area proved to be an effective proxy for the number of penguins residing within. Our model provides a robust, quantitative mechanism for estimating the breeding population size of colonies captured in imagery and identifies terrain slope as a significant component influencing apparent nesting density. While our high-resolution satellite imagery technique was developed for the Adélie penguin, these principles are directly transferrable to other colonially nesting seabirds and other species that aggregate in fixed localities.

Lyver, P.O'B, M. Barron, K.J. Barton, D.G. Ainley, A. Pollard, S. Gordon, S. McNeill, G. Ballard, and P.R. Wilson. 2014. Trends in the breeding population of Adélie Penguins in the Ross Sea, 1981–2012: A Coincidence of Climate and Resource Extraction Effects. *PLoS ONE* 9(3): e91188, doi:10.1371/journal.pone.0091188

Measurements of the size of Adélie penguin (*Pygoscelis adeliae*) colonies of the southern Ross Sea are among the longest biologic time series in the Antarctic. We present an assessment of recent annual variation and trends in abundance and growth rates of these colonies, adding to the published record not updated for more than two decades. High angle oblique aerial photographic surveys of colonies were acquired and penguins counted for the breeding seasons 1981–2012. In the last four years the numbers of Adélie penguins in the Ross and Beaufort Island colonies (southern Ross Sea metapopulation) reached their highest levels since aerial counts began in 1981. Results indicated that 855,625 pairs of Ade´ lie penguins established breeding territories in the western Ross Sea, with just over a quarter (28%) of those in the southern portion, constituting a semi-isolated metapopulation (three colonies on Ross Island, one on nearby Beaufort Island). The southern population had a negative per capita growth rate of 20.019 during 1981–2000, followed by a positive per capita growth rate of 0.067 for 2001–2012. Colony growth rates for this metapopulation showed striking synchrony through time, indicating that large-scale factors influenced their annual growth. In contrast to the increased colony sizes in the southern population, the patterns of change among colonies of the northern Ross Sea were difficult to characterize. Trends were similar to southern colonies until the mid-1990s, after which the signal was lost owing to significantly reduced frequency of surveys. Both climate factors and recovery of whale populations likely played roles in the trends among southern colonies until 2000, after which depletion of another trophic

competitor, the Antarctic toothfish (*Dissostichus mawsoni*), may explain the sharp increasing trend evident since then.

Santora, J.A., M.A. LaRue, and D.G. Ainley. 2020. Geographic structuring of Antarctic penguin populations. *Global Ecology and Biogeography*, doi:10.1111/geb.13144.

We hypothesized that regional spatial organization of Antarctic penguin breeding populations was affected by social factors, that is, proximity and size of adjacent colonies, and by physical factors, that is, availability of breeding habitat and proximity of polynyas and submarine canyons where prey is abundant. The hypothesis of Furness and Birkhead (1984), that forage competition and density-dependence affect geographic structure of seabird populations, was tested previously for Antarctic penguins when biologging to quantify colony foraging areas was less common and when assessments of colony size reflected a compendium of historical counts. These data on foraging areas and colony size are now available following 20 years of frequent biologging and real-time satellite data on colony locations and sizes. We prepared a literature summary on the basis of biologging studies to improve assessment of foraging ranges. We collated colony sizes from recent sources and integrated them with data on submarine canyon systems and polynyas. We used geospatial models to assess the relationships of the latter features to colony size, clustering, and distribution around Antarctica. The equal spacing of emperor penguin colonies was constant, with spacing a function of foraging range. In contrast, colonies of other penguin species were clustered, with small colonies adjacent to one another and within the outer edge of the foraging area of large colonies. Colonies and especially clusters occurred near polynyas and canyons around Antarctica. Density-dependent processes and geography explained penguin colony distribution. We conclude that inter- and intraspecific trophic competition affects the geographic structuring of colony distribution and size, although not necessarily in the same way among species. Results are relevant to assessing effects of climate, ecosystem dynamics, fisheries and other factors on penguin population trends at regional scales. We suggest that considering penguin colony distribution and abundance at the regional or cluster level is necessary to understand changes in these attributes.

Youngflesh , C., S. Jenouvrier, Y. Li, R. Ji, D.G. Ainley, G. Ballard, C. Barbraud, K. Delord, K.M. Dugger, L.M. Emmerson, W.R. Fraser, J.T. Hinke, P. O'B. Lyver, S. Olmastroni, C.J. Southwell, S.G. Trivelpiece, W.Z. Trivelpiece, and H. J. Lynch. 2017. Circumpolar analysis of the Adélie Penguin reveals the importance of environmental variability in phenological mismatch. *Ecology* 98: 940–951.

Evidence of climate-change-driven shifts in plant and animal phenology have raised concerns that certain trophic interactions may be increasingly mismatched in time, resulting in declines in reproductive success. Given the constraints imposed by extreme seasonality at high latitudes and the rapid shifts in phenology seen in the Arctic, we would also expect Antarctic species to be highly vulnerable to climate-change-driven phenological mismatches with their environment. However, few studies have assessed the impacts of phenological change in Antarctica. Using the largest database of phytoplankton phenology, sea-ice phenology, and Adélie Penguin breeding phenology and breeding success assembled to date, we find that, while a temporal match between Penguin breeding phenology and optimal environmental conditions sets an upper limit on breeding success, only a weak relationship to the mean exists. Despite previous work suggesting that divergent trends in Adélie Penguin breeding phenology are apparent across the Antarctic continent, we find no such trends. Furthermore, we find no trend in the magnitude of phenological mismatch, suggesting that mismatch is driven by interannual variability in environmental conditions rather than climate-change-driven trends, as observed in other systems. We propose several criteria necessary for a species to experience a strong climate-change-driven phenological mismatch, of which several may be violated by this system.

EMPEROR PENGUINS

Fretwell, P., M. LaRue, P. Morin, G. Kooyman, B. Wienecke, N. Ratcliffe, A. Fox, A. Fleming, C. Porter, and P. Trathan. 2012. An Emperor Penguin population estimate: the first global, synoptic survey of a species from space. *PLoS ONE* 7: e33751-e33751.

Our aim was to estimate the population of emperor penguins (*Aptenodytes fosteri*) using a single synoptic survey. We examined the whole continental coastline of Antarctica using a combination of medium resolution and Very High Resolution (VHR) satellite imagery to identify emperor penguin colony locations. Where colonies were identified, VHR imagery was obtained in the 2009 breeding season. The remotely-sensed images were then analysed using a supervised classification method to separate penguins from snow, shadow and guano. Actual counts of penguins from eleven ground truthing sites were used to convert these classified areas into numbers of penguins using a robust regression algorithm. We found four new colonies and confirmed the location of three previously suspected sites giving a total number of emperor penguin breeding colonies of 46. We estimated the breeding population of emperor penguins at each colony during 2009 and provide a population estimate of ~238,000 breeding pairs (compared with the last previously published count of 135,000–175,000 pairs). Based on published values of the relationship between breeders and non-breeders, this translates to a total population of ~595,000 adult birds. There is a growing consensus in the literature that global and regional emperor penguin populations will be affected by changing climate, a driver thought to be critical to their future survival. However, a complete understanding is severely limited by the lack of detailed knowledge about much of their ecology, and importantly a poor understanding of their total breeding population. To address the second of these issues, our work now provides a comprehensive estimate of the total breeding population that can be used in future population models and will provide a baseline for long-term research.

Fretwell, P.T., P.N. Trathan, B. Wienecke, and G.L. Kooyman. 2014. Emperor penguins breeding on iceshelves. *PLoS ONE 9(1): e85285.*

We describe a new breeding behaviour discovered in emperor penguins; utilizing satellite and aerial-survey observations four emperor penguin breeding colonies have been recorded as existing on ice-shelves. Emperors have previously been considered as a sea-ice obligate species, with 44 of the 46 colonies located on sea-ice (the other two small colonies are on land). Of the colonies found on ice-shelves, two are newly discovered, and these have been recorded on shelves every season that they have been observed, the other two have been recorded both on ice-shelves and sea-ice in different breeding seasons. We conduct two analyses; the first using synthetic aperture radar data to assess why the largest of the four colonies, for which we have most data, locates sometimes on the shelf and sometimes on the sea-ice, and find that in years where the sea-ice forms late, the colony relocates onto the ice-shelf. The second analysis uses a number of environmental variables to test the habitat marginality of all emperor penguin breeding sites. We find that three of the four colonies reported in this study are in the most northerly, warmest conditions where sea-ice is often sub-optimal. The emperor penguin's reliance on sea-ice as a breeding platform coupled with recent concerns over changed sea-ice patterns consequent on regional warming, has led to their designation as "near threatened" in the IUCN red list. Current climate models predict that future loss of sea-ice around the Antarctic coastline will negatively impact emperor numbers; recent estimates suggest a halving of the population by 2052. The discovery of this new breeding behaviour at marginal sites could mitigate some of the consequences of sea-ice loss; potential benefits and

whether these are permanent or temporary need to be considered and understood before further attempts are made to predict the population trajectory of this iconic species.

Kooyman, G. L., and P.J. Ponganis. 2013. Chick production at the largest emperor penguin colony decreases by 50% from 2008–10. *Antarctic Science* 26: 33-37, doi:10.1017/S0954102013000515.

The emperor penguin colony at Coulman Island is reputedly the largest known. This reputation is based on intermittent ground and aerial surveys performed since 1958. From an aerial survey obtained on 28 October 2010 we discovered that the total number of chicks was 56% of the lowest previous estimate of 2006 and only 41% of the most recent estimate in 2008. All of the counts tallied since 1983 were determined either by ground counts or from aerial film or digital photographs, or estimates from adult counts. We also determined the sea ice conditions in autumn, which is close to the time the adults arrive to breed. We present three hypotheses of what might have happened from 2008–10 to cause the step change in chick production, the small recovery of chick numbers in 2011, and the complete recovery of number of adults from 2010–11. We conclude that local circumstances may have strongly influenced the breeding behaviour of the emperor penguins in 2010 and to a lesser degree in 2011 when many adults elected not to breed.

Kooyman, G. L. and P.J. Ponganis. 2017. Rise and fall of Ross Sea emperor penguin colony populations: 2000 to 2012. *Antarctic Science* 29: 201-208, doi:10.1017/S0954102016000559.

There are seven emperor penguin (*Aptenodytes forsteri*) colonies distributed throughout the traditional boundaries of the Ross Sea from Cape Roget to Cape Colbeck. This coastline is *c.* 10% of the entire coast of Antarctica. From 2000 to 2012, there has been a nearly continuous record of population size of most, and sometimes all, of these colonies. Data were obtained by analysing aerial photographs. We found large annual variations in populations of individual colonies, and conclude that a trend from a single emperor penguin colony may not be a good environmental sentinel. There are at least four possibilities for census count fluctuations: i) this species is not bound to a nesting site like other penguins, and birds move within the colony and possibly to other colonies, ii) harsh environmental conditions cause a die-off of chicks in the colony or of adults elsewhere, iii) the adults skip a year of breeding if pre-breeding foraging is inadequate and iv) if sea ice conditions are unsatisfactory at autumn arrival of the adults, they skip breeding or go elsewhere. Such variability indicates that birds at all Ross Sea colonies should be counted annually if there is to be any possibility of understanding the causes of population changes.

Schmidt, A.E., and G. Ballard. 2020. Significant chick loss after early fast ice breakup at a high-latitude emperor penguin colony. *Antarctic Science*, doi:10.1017/S0954102020000048

Emperor penguins require stable fast ice, sea ice anchored to land or ice shelves, on which to lay eggs and raise chicks. As the climate warms, changes in sea ice are expected to lead to substantial declines at many emperor penguin colonies. The most southerly colonies have been predicted to remain buffered from the direct impacts of warming for much longer. Here, we report on the unusually early breakup of fast ice at one of the two southernmost emperor penguin colonies, Cape Crozier (77.5°S), in 2018, an event that may have resulted in a substantial loss of chicks from the colony. Fast ice dynamics can be highly variable and dependent on local conditions, but earlier fast ice breakup, influenced by increasing wind speed, as well as higher surface air temperatures, is a likely outcome of climate change. What we observed at Cape Crozier in 2018 highlights the vulnerability of this species to untimely storm events and could be an early sign that even this high-latitude colony is not immune to the effects of warming. Long-term monitoring will be key to understanding this species' response to climate change and altered sea ice dynamics.

Trathan, P.N., B. Wienecke, C. Barbraud, S. Jenouvrier, G. Kooyman, C. Le Bohec, D.G. Ainley, A. Ancel, D.P. Zitterbart, S.L. Chown, M. LaRuen, R. Cristofari, J. Younger, G. Clucas, C.-A. Bost, J.A. Brown, H.J. Gillett, and P.T. Fretwell. 2019. The emperor penguin - vulnerable to projected rates of warming and sea ice loss. *Biological Conservation*, https://doi.org/10.1016/j.biocon.2019.108216.

We argue the need to improve climate change forecasting for ecology, and importantly, how to relate long-term projections to conservation. As an example, we discuss the need for effective management of one species, the emperor penguin, *Aptenodyptes forsteri*. This species is unique amongst birds in that its breeding habit is critically dependent upon seasonal fast ice. Here, we review its vulnerability to ongoing and projected climate change, given that sea ice is susceptible to changes in winds and temperatures. We consider published projections of future emperor penguin population status in response to changing environments. Furthermore, we evaluate the current IUCN Red List status for the species, and recommend that its status be changed to Vulnerable, based on different modelling projections of population decrease of ≥50% over the current century, and the specific traits of the species. We conclude that current conservation measures are inadequate to protect the species under future projected scenarios. Only a reduction in anthropogenic greenhouse gas emissions will reduce threats to the emperor penguin from altered wind regimes, rising temperatures and melting sea ice; until such time, other conservation actions are necessary, including increased spatial protection at breeding sites and foraging locations. The designation of large-scale marine spatial protection across its range would benefit the species, particularly in areas that have a high probability of becoming future climate change refugia. We also recommend that the emperor penguin is listed by the Antarctic Treaty as an Antarctic Specially Protected Species, with development of a species Action Plan.

Younger, J. L., G.V. Clucas, G.L. Kooyman, B. Wienecke, A.R. Rogers, P.N. Trathan, T. Hart, and K.J. Miller. 2015. Too much of a good thing: sea ice extent may have forced emperor penguins into refugia during the last glacial maximum. *Global Change Biology* 21 (6): doi: 10.1111/gcb.12882

The relationship between population structure and demographic history is critical to understanding microevolution and for predicting the resilience of species to environmental change. Using mitochondrial DNA from extant colonies and radiocarbon-dated subfossils, we present the first microevolutionary analysis of emperor penguins (*Aptenodytes forsteri*) and show their population trends throughout the last glacial maximum (LGM, 19.5–16 kya) and during the subsequent period of warming and sea ice retreat. We found evidence for three mitochondrial clades within emperor penguins, suggesting that they were isolated within three glacial refugia during the LGM. One of these clades has remained largely isolated within the Ross Sea, while the two other clades have intermixed around the coast of Antarctica from Adélie Land to the Weddell Sea. The differentiation of the Ross Sea population has been preserved despite rapid population growth and opportunities for migration. Low effective population sizes during the LGM, followed by a rapid expansion around the beginning of the Holocene, suggest that an optimum set of sea ice conditions exist for emperor penguins, corresponding to available foraging area.

WEDDELL SEALS

Ainley, D. G., M.A. LaRue, I. Stirling, S. Stammerjohn, and D.B. Siniff. 2015. An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast. *Marine Mammal Science,* doi:10.1111/mms.12220.

Ground counts during 1959–1968 compared with counts using high resolution (0.6 m2) satellite imagery during 2008–2012 indicated many fewer Weddell seals (*Leptonychotes weddellii*) at two major molting areas in the western Ross Sea: Edisto Inlet-Moubray Bay, northern Victoria Land, and McMurdo Sound, southern Victoria Land. Breeding seals have largely disappeared from Edisto-Moubray, though the breeding population in McMurdo Sound appears to have recovered from harvest in the 1960s. The timing of decline, or perhaps spreading (lower numbers of seals in more places), is unknown but appears unrelated to changes in sea ice conditions. We analyzed both historic and satellite-derived ice data confirming a large expansion of pack ice mostly offshore of the Ross Sea, and not over the continental shelf (main Weddell seal habitat), and a thinning of fast ice along Victoria Land (conceivably beneficial to seals). Timing of fast ice presence and extent in coves and bays along Victoria Land, remains the same. The reduction in numbers is consistent with an altered food web, the reasons for which are complex. In the context of a recent industrial fishery targeting a seal prey species, a large-scale seal monitoring program is required to increase understanding of seal population changes.

LaRue, M.A., D.G. Ainley, J. Pennycook, K. Stamatiou, L. Salas, N. Nur, S. Stammerjohn, and L. Barrington. 2019. Engaging 'the crowd' in remote sensing to learn about habitat affinity of the Weddell seal in Antarctica. *Remote Sensing in Ecology and Conservation* 6 (1):70–78.

Satellites Over Seals (SOS), a project initiated in late 2016, is a crowdsourced method to determine factors behind the presence/absence patterns and to ultimately determine the global population of the Weddell seal (*Leptonychotes weddellii*). An iconic species, the Weddell seal is proposed to be part of the Antarctic Research and Monitoring Program required in the newly designated Ross Sea Region Marine Protected Area. This species is easy to detect via satellite imagery, due to its large size (3–4 m long, 1 m wide) and its dark color contrasting with the Antarctic coastal fast ice, where it aggregates on during breeding season. Using very high-resolution satellite imagery (VHR; 0.31–

0.60 m resolution) and the online platform Tomnod, we used VHR images from November 2010 and 2011 to cover the entirety of available fast ice around Antarctica. Before correcting for time of day or date, we searched for the presence/absence to identify a subset of where abundance estimates should be concentrated. More than 325 000 citizen scientists searched 790 VHR images, covering 268 611 km2 of fast ice, to determine the locations of seals. Algorithms ranked searchers to the degree their votes corresponded with others, a measure of searcher relative quality that we used to filter out unreliable searchers. Seal presence was detected on only 0.55% of available maps (total n = 1 116 058) within fast ice, revealing a sparse, irregular distribution. The rate of false-negative detections was 1.7%, though false positives were high (67%), highlighting the importance of training for image interpretation to ensure differentiation between seals and landscape features (such as large rocks, ice chunks or depressions/holes in the ice). This approach not only allowed us to assess image resolution and quality, but also training, outreach and the effectiveness of this platform for introducing citizen scientists to the ecology of the Southern Ocean.

LaRue, M.A., J.J. Rotella, R.A. Garrott, D.B. Siniff, D.G. Ainley, G.E. Stauffer, C.C. Porter, and P.J. Morin. 2011. Satellite imagery can be used to detect variation in abundance of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica. *Polar Biology* 34: 1727-1737.

The Weddell seal population in Erebus Bay, Antarctica, represents one of the best-studied marine mammal populations in the world, providing an ideal test for the efficacy of satellite imagery to inform about seal abundance and population trends. Using high-resolution (0.6 m) satellite imagery, we compared counts from imagery to ground counts of adult Weddell seals and determined temporal trends in Erebus Bay during November 2004–2006 and 2009, and December 2007. Seals were counted from

Quick-Bird-2 and WorldView-1 images, and these counts were compared with ground counts at overlapping locations within Erebus Bay during the same time. Counts were compared across years and within individual haul-out locations. We counted a total of 1,000 adult Weddell seals from five images across all years (for a total of 21 satellite-to-ground count comparisons), approximately 72% of the total counted on the ground at overlapping locations. We accurately detected an increase in abundance during 2004–2009. There was a strong, positive correlation ($r = 0.98$, $df = 3$, $P < 0.003$) between ground counts and counts derived from the imagery. The correlation between counts at individual haul-out locations was also strong ($r = 0.80$, $df = 19$, $P < 0.001$). Detection rates ranged from 30 to 88%. Overall, our results showed the utility of high-resolution imagery to provide an accurate way to detect the presence and variation in abundance of Weddell seals. Our methods may be applied to other species in polar regions, such as walruses or polar bears, particularly in areas where little is known about population status.

LaRue, M.A., L. Salas, N. Nur, D.G. Ainley, S. Stammerjohn, L. Barrington, K. Stamatiou, J. Pennycook, M. Dozier, J. Saints, and H. Nakamura. 2019. Physical and ecological factors explain the distribution of Ross Sea Weddell seals during the breeding season. *Marine Ecology Progress Series* 612: 193–208.

Weddell seal *Leptonychotes weddellii* populations can potentially serve as indicators of change in Southern Ocean food web structure, but tracking populations at regional to continental scales has so far been impossible. Here, we combined citizen science with remote sensing to learn about environmental and biological factors that explain fine-scale distribution of Weddell seal haul-outs in the Ross Sea, Antarctica. We employed the crowd-sourcing platform Tomnod (DigitalGlobe) to host high-resolution (~0.5−0.6 m) satellite imagery of the Antarctic fast ice during November in 2010 and 2011 and asked volunteers to identify seals on images. We created a 5 km × 5 km grid of seal presence per year, and modeled habitat suitability for seals using a generalized linear model. The top Ross Sea-wide model that best explained seal presence included proximity to fast-ice cracks, deep water, and emperor penguin *Aptenodytes forsteri* colonies. This model also revealed that seal presence decreased with proximity to Adélie penguin *Pygoscelis adeliae* colonies and size of the nearest emperor penguin colony, suggesting the potential for trophic competitive exclusion by large penguin colonies. With respect to 3 sub-regions within the Ross Sea (North and South Victoria Land in the western Ross Sea, and Marie Byrd Land in the east), we found that 3 habitat variables differed in their effects among sub-regions: proximity to emperor penguin colonies, proximity to deep water, and relative ice width. Our results represent a step toward effectively monitoring Weddell seal population trends, and disentangling biological and environmental factors influencing locations of Weddell seal haul-outs around Antarctica.

CETACEANS

Ainley, D.G., and G. Ballard. 2012. Trophic Interactions and the decrease in Killer Whale (*Orcinus orca*) prevalence with reduced availability of large fish in the southern Ross Sea. *Aquatic Mammals* 38: 153-160.

Foraging events and related trends in numbers of Type-B and -C killer whales (*Orcinus orca*) are reported for the vicinity of Ross Island, Ross Sea, Antarctica between 2002 and 2010. Updating an earlier report, the frequency of sightings and the number of individuals per sighting of Ross Sea killer whales (Type-C; RSKWs), a fishing-eating ecotype, has continued to decrease in a pattern coincident with a decrease in the number and size of an important prey: Antarctic toothfish (*Dissostichus mawsoni*). Increasingly rare, large fish are much more energetically dense and may also be socially important to the whales, a relationship with potential parallels to that known between well-studied fish-eating killer whales

and large Chinook salmon (*Oncorhynchus tshaw-ytscha)* in the northeast Pacific. In contrast, the prevalence of the larger, mammal-eating Type-B killer whales has not changed in the southern Ross Sea study area. Predation events by Type-B killer whales involving Weddell seals (*Leptonychotes weddellii*), interest in large penguins, such as emperors (*Aptenodytes forsteri*), and lack of interest in small penguins, such as Adélies (*Pygoscelis adeliae*), are presented. In the case of both killer whale forms, the progressive seasonal breakup of fast ice in large bays bordering the Ross Sea likely provides reliable, enhanced foraging opportunities as prey are exposed one area at a time during summer. Given the apparent relationship between RSKW prevalence and the availability of large toothfish, we speculate that the current management strategy of Antarctic toothfish in the Ross Sea region threatens current population levels of RSKWs.

Ainley, D.G., G. Ballard, L.K. Blight, S. Ackley, S.D. Emslie, A. Lescroël, S. Olmastroni, S.E. Townsend, C.T. Tynan, P. Wilson, and E. Woehler. 2010. Impacts of cetaceans on the structure of Southern Ocean food webs. *Marine Mammal Science* 26: 482-489.

In three sections we present a suite of hypotheses on the direct role of top-down pressures involving cetaceans in structuring Southern Ocean food webs. Recent population fluctuations of cetaceans, as top predators, appear to play an important role in past and present changes seen in the Antarctic marine ecosystem (see also Mori and Butterworth 2006). Incorporating ecological processes of trophic cascades, competition, predation, and facilitation into models attempting to address climate effects on populations should result in a more realistic understanding of these systems. Indeed, owing to simplification via the loss of top-most predators and the ongoing removal of other predators (large fish), much of the Southern Ocean ecosystem is currently in a potentially fragile state, further compromising its ability to withstand rapid climate change (see Osterblom et al. 2007, Cury *et al.* 2008, Watermeyer et al. 2008*a*, *b*).

Ainley, D.G., D. Jongsomjit, G. Ballard, D. Thiele, W.R. Fraser, and C.T. Tynan. 2012. Modeling the relationship of Antarctic minke whales to major ocean boundaries. *Polar Biology* 35: 281-290.

The population size of Antarctic minke whales *Balaenoptera bonaerensis* has been changing simultaneously with profound changes in the physics, i.e., mesopredator habitat features, of the Southern Ocean. Although the two trends may not be related, distinguishing among the factors responsible requires a better understanding of minke whale habitat preferences. For the Wrst time at a large geographic scale, i.e., between 140° E and 35° W, we use data not constrained by vessels needing to avoid sea ice to model the habitat affinities of this pagophilic mesopredator. Using Maxent, we modeled minke whale proximity to the Antarctic Shelf Break Front (ASBF) and the southern boundary of Antarctic Circumpolar Current (sbACC), as well as association with sea ice, given that global climate change is altering the positions or intensity of these features. We also included water depth and chlorophyll (proxy for productivity) as variables. Minke whale presence data were gathered using strip and line census on 55 cruises on board icebreakers during late spring and summer, 1976–2005. The most important variable was distance to ASBF, followed by water depth and sea-ice concentration. That is, found principally in waters south of the sbACC during summer, minke whales were most abundant near the outer edge of the continental shelf (shallow depth), including areas heavily covered by sea ice. We propose that as the sbACC moves south and sea ice disappears, as projected by global climate models, minke whale habitat will shrink, and likely intra- and inter-specific competition will increase.

Ainley, D.G., K. Lindke, G. Ballard, P.O'B. Lyver, S. Jennings, V. Toniolo, J. Pennycook, A. Lescroël, M. Massaro, and J.A. Santora. 2017. Spatio-temporal occurrence patterns of cetaceans

near Ross Island, Antarctica, 2002-2015: implications for foodweb dynamics. *Polar Biology* 40: 1761-1775, doi:10.1007/s00300-017-2100-9.

The Ross Sea pelagic food web is closely coupled, with the foraging among abundant upper level species affecting the foraging of one another. To investigate the roles cetaceans may have in such interspecific interactions in this system, we studied within-season and interannual occurrence patterns of Antarctic minke whales (*Balaenoptera bonaerensis*) and type-B and type-C killer whales (*Orcinus orca*) within the southwestern Ross Sea, 2002–2015. Time series analysis summarized daily observations made from 3 shore localities: Capes Crozier, Bird, and Royds distributed around the ~120 km periphery of Ross Island. In early mid-November, both species arrived at Crozier, the easternmost point and westward edge of the Ross Sea Polynya marginal ice zone. Subsequently, coinciding with decreased sea ice cover and numbers off Crozier, both species appeared off Bird, then Royds, 80 and 117 km to the west/southwest, respectively. Arrival in either area coincided with SIC decreasing to <80%, consistent with observations elsewhere. Within-season off Crozier, both species occurred in cycles of multi-day presence followed by absence, perhaps reflecting the spatio-temporal patchiness of prey indicated also by penguin foraging patterns. Within-season off Royds, especially for killer whales, occurrence was even more episodic; type-Bs arrived before type-Cs, and results support previously described resident and transient portions of the type-C population. Combined with results showing that whale arrival leads to food stress among penguins, we suggest that relatively few cetaceans can alter food availability to alter the foraging behavior of other mesopredators, despite primary productivity being the richest in the Southern Ocean.

Branch, T.A. 2011. Humpback whale abundance south of 60°S from three complete circumpolar sets of surveys. *J. Cetacean Res. Management (Special Issue*) 3: 53–69

Austral summer estimates of abundance are obtained for humpback whales (*Megaptera novaeangliae*) in the Southern Ocean from the IWC's IDCR and SOWER circumpolar programmes. These surveys have encircled the Antarctic three times: 1978/79–1983/84 (CPI), 1985/86–1990/91 (CPII) and 1991/92–2003/04 (CPIII), criss-crossing strata totalling respectively 64.3%, 79.5% and 99.7% of the open-ocean area south of 60°S. Humpback whales were absent from the Ross Sea, but were sighted in all other regions, and in particularly high densities around the Antarctic Peninsula, in Management Area IV and north of the Ross Sea. Abundance estimates are presented for each CP, for Management Areas, and for assumed summer feeding regions of each Breeding Stock. Abundance estimates are negatively biased because some whales on the trackline are missed and because some humpback whales are outside the survey region. Circumpolar estimates with approximate midpoints of 1980/81, 1987/88 and 1997/98 are 7,100 (CV = 0.36), 10,200 (CV = 0.30) and 41,500 (CV = 0.11). When these are adjusted simply for unsurveyed northern areas, the estimated annual rate of increase is 9.6% (95% CI 5.8–13.4%). All Breeding Stocks are estimated to be increasing but increase rates are significantly greater than zero only for those on the eastern and western coasts of Australia. Given the observed rates of increase, the current total Southern Hemisphere abundance is greater than 55,000, which is similar to the summed northern breeding ground estimates (~60,000 from 1999–2008). Some breeding ground abundance estimates are far greater, and others far lower, than the corresponding IDCR/SOWER estimates, in a pattern apparently related to the latitudinal position of the Antarctic Polar Front.

Pitman, R.L., H. Fearnbach, and J.W. Durban. 2018. Abundance and population status of Ross Sea killer whales (*Orcinus orca*, type C) in McMurdo Sound, Antarctica: evidence for impact by commercial fishing? *Polar Biology* 41: 781-792, https://doi.org/10.1007/s00300-017-2239-4.

For over a century, the Ross Sea killer whale (RSKW; *Orcinus orca*, Antarctic type C), a fish-eating ecotype, has been commonly reported in McMurdo Sound (McM), Ross Sea, Antarctica. However, a significant population decline reported at Ross Island after 2006 has been linked to a commercial fishery

that began in the Ross Sea in 1996–1997 and targets large Antarctic toothfish (*Dissostichus mawsoni*)—the presumed primary prey of RSKW. We assessed RSKW population abundance and trends using photo-identification data collected in McM during seven summers from 2001–2002 to 2014–2015. We identified 352 individual RSKWs and estimated an average annual population of 470 distinctly marked whales. Using a Bayesian mark–recapture model, we identified two population clusters: 'regulars' showed strong inter- and intra-annual site fidelity and an average annual abundance of 73 distinctive individuals (95% probability: 57–88); 'irregulars' were less frequently encountered but comprised a larger population with an annual estimate of 397 distinctive individuals (287–609). The number of seasonally resident regulars appeared to be stable over the period of purported RSKW decline, with the estimated annual number of deaths (6; 95% probability: 1–22) offset by the number of recruits (6; 2–19). As an alternative to the decline-due-to-fishery hypothesis, we suggest that the presence of mega-iceberg B-15 at Ross Island during the "iceberg years" (2000–2001 to 2005–2006) could have temporarily disrupted normal RSKW movement patterns, resulting in an apparent decline. Continued population monitoring of toothfish and their predators will be important for assessing ecosystem impacts of commercial fishing in the Ross Sea.

Thomas, P.O., R.R. Reeves, and R.L. Brownell, Jr. 2016. Status of the world's baleen whales. *Marine Mammal Science* 32: 682–734.

No global synthesis of the status of baleen whales has been published since the 2008 IUCN Red List assessments. Many populations remain at low numbers from historical commercial whaling, which had ceased for all but a few by 1989. Fishing gear entanglement and ship strikes are the most severe current threats. The acute and long-term effects of anthropogenic noise and the cumulative effects of multiple stressors are of concern but poorly understood. The looming consequences of climate change and ocean acidification remain difficult to characterize. North Atlantic and North Pacific right whales are among the species listed as Endangered. Southern right, bowhead, and gray whales have been assessed as Least Concern but some subpopulations of these species - western North Pacific gray whales, Chile-Peru right whales, and Svalbard/Barents Sea and Sea of Okhotsk bowhead whales - remain at low levels and are either Endangered or Critically Endangered. Eastern North Pacific blue whales have reportedly recovered, but Antarctic blue whales remain at about 1% of pre-exploitation levels. Small isolated subspecies or subpopulations, such as northern Indian Ocean blue whales, Arabian Sea humpback whales, and Mediterranean Sea fin whales are threatened while most subpopulations of sei, Bryde's, and Omura's whales are inadequately monitored and difficult to assess.

OTHER IMPORTANT SPECIES

Schwaller, M.R., H.J. Lynch, A. Tarroux, and B. Prehn. 2018. A continent-wide search for Antarctic petrel breeding sites with satellite remote sensing. *Remote Sensing of Environment* 210: 444-451, https://doi.org/10.1016/j.rse.2018.02.071.

The Antarctic petrel (*Thalassoica antarctica*) has been identified as a key species for monitoring the status and health of the Southern Ocean and Antarctic ecosystems. Breeding colonies of the Antarctic petrel are often found on isolated nunataks far from inhabited stations, some up to hundreds of kilometers from the shoreline. It is difficult therefore to monitor and census known colonies, and it is believed that undiscovered breeding locations remain to be found. We developed an algorithm that can detect Antarctic petrel colonies and used it to complete a continent-wide survey using Landsat-8 Operational Line Imager (OLI) imagery in Antarctica up to the southernmost extent of Landsat's orbital view at 82.68°S. Our survey successfully identified 8 known Antarctic petrel colonies containing 86% of the known population

of Antarctic petrels. The survey also identified what appears to be a significant population of breeding birds in areas not known to host breeding Antarctic petrel colonies. Our survey suggests that the breeding population at Mt. Biscoe (66°13'S 51°21'E), currently reported to be in the 1000s, may actually be on the order of 400,000 breeding pairs, which would make it the largest known Antarctic petrel breeding colony in the world. The algorithm represents a first-ever attempt to apply satellite remote sensing to assess the distribution and abundance of the Antarctic petrel on a continent-wide basis. As such, we note several algorithm shortcomings and identify research topics for algorithm improvement. Even with these caveats, our algorithm for identifying Antarctic petrel colonies with Landsat imagery demonstrates the feasibility of monitoring their populations using satellite remote sensing and identifies breeding locations, including Mt. Biscoe, that should be considered high priorities for validation with directed field surveys.

DEMOGRAPHIC PROCESSES

ADELIE PENGUINS

Dugger, K.M., D.G. Ainley, P. O'B. Lyver, K.M. Barton, and G. Ballard. 2010. Survival differences and the effect of environmental instability on breeding dispersal in an Adélie penguin meta-population. *Proceedings of the National Academy of Sciences*, doi:10.1073 pnas 1000623107.

High survival and breeding philopatry was previously confirmed for the Adélie penguin (*Pygoscelis adeliae*) during a period of stable environmental conditions. However, movements of breeding adults as a result of an unplanned natural experiment within a four colony meta-population provided interesting insights into this species' population dynamics.We used multistate mark-recapture models to investigate apparent survival and dispersal of breeding birds in the southwestern Ross Sea during 12 breeding seasons (1996–2007). The natural experiment was facilitated by the temporary grounding of two immense icebergs that (i) erected a veritable fence separating colonies and altering migration routes and (ii) added additional stress by trapping extensive sea ice intheregionduring5 of12y. Colony size varied by orders of magnitude, allowing investigation of apparent survival and dispersal rates in relation to both environmental conditions and colony size within this meta-population. Apparent survival was lowest for the smallest colony (4,000 pairs) and similar for the medium (45,000 pairs) and large colonies (155,000 pairs), despite increased foraging effort expended by breeders at the largest colony. Dispersal of breeding birds was low (<1%), except during years of difficult environmental conditions when movements increased, especially away from the smallest colony (3.5%). Decreased apparent survival at the smallest colony could reflect differences in migration chronology and winter habitat use compared with the other colonies, or it may reflect increased permanent emigration to colonies outside this meta-population. Contrary to current thought, breeding penguins are not always philopatric. Rather, stressful conditions can significantly increase dispersal rates.

Dugger, K.M., G. Ballard, D.G. Ainley, P. O'B. Lyver, and C. Schine. 2014. Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. *Frontiers in Ecology and Evolution* 2:68, doi: 10.3389/fevo.2014.00068.

We investigated life history responses to extreme variation in physical environmental conditions during a long-term demographic study of Adélie penguins at 3 colonies representing 9% of the world population and the full range of breeding colony sizes. Five years into the 14-year study (1997–2010) two very large icebergs (spanning 1.5 latitude degrees in length) grounded in waters adjacent to breeding colonies, dramatically altering environmental conditions during 2001–2005. This natural experiment allowed us to evaluate the relative impacts of expected long-term, but also extreme, short-term climate

perturbations on important natural history parameters that can regulate populations. The icebergs presented physical barriers, not just to the penguins but to polynya formation, which profoundly increased foraging effort and movement rates, while reducing breeding propensity and productivity, especially at the smallest colony. We evaluated the effect of a variety of environmental parameters during breeding, molt, migration and wintering periods during years with and without icebergs on penguin breeding productivity, chick mass, and nesting chronology. The icebergs had far more influence on the natural history parameters of penguins than any of the other environmental variables measured, resulting in population level changes to metrics of reproductive performance, including delays in nesting chronology, depressed breeding productivity, and lower chick mass. These effects were strongest at the smallest, southern-most colony, which was most affected by alteration of the Ross Sea Polynya during years the iceberg was present. Additionally, chick mass was negatively correlated with colony size, supporting previous findings indicating density-dependent energetic constraints at the largest colony. Understanding the negative effects of the icebergs on the short-term natural history of Adélie penguins, as well as their response to long-term environmental variation, are important to our overall understanding of climate change effects in this and other species facing both rapid and persistent environmental change.

EMPEROR PENGUINS

Larue, M.A., G. Kooyman, H.J Lynch, and P. Fretwell, P. (2015). Emigration in emperor penguins: implications for interpretation of long-term studies. *Ecography* 38: 114-120. doi:10.1111/ecog.00990.

Site fidelity is an important evolutionary trait to understand, as misinterpretation of philopatric behavior could lead to confusion over the key drivers of population dynamics and the environmental or anthropogenic factors influencing populations. Our objective was to explore the hypothesis that emperor penguins are strictly philopatric using satellite imagery, counts from aerial photography, and literature reports on emperor penguin distributions. We found six instances over three years in which emperor penguins did not return to the same location to breed. We also report on one newly-discovered colony on the Antarctic Peninsula that may represent the relocation of penguins from the Dion Islands, recently confirmed as having been abandoned. Using evidence from aerial surveys and the historical literature, we suggest that emigration may have been partly responsible for the population decline at Pointe Géologie during the 1970s. Our study is the first to use remote sensing imagery to suggest that emperor penguins can and do move between, and establish new, colonies. Metapopulation dynamics of emperor penguins have not been previously considered and represent an exciting, and important, avenue for future research. Life history plasticity is increasingly being recognized as an important aspect of climate change adaptation, and in this regard our study offers new insight for the long-term future of emperor penguins.

WEDDELL SEALS

Brusa, J.L., J.J. Rotella, R.A. Garrott, J.T. Paterson, and W.A. Link. 2019. Variation of annual apparent survival and detection rates with age, year and individual identity in male Weddell seals (*Leptonychotes weddellii*) from long-term mark-recapture data. *Population Ecology* 62:134–150, https://doi.org/10.1002/1438-390X.12036.

Exploring age- and sex-specific survival rates provides insight regarding population behavior and life-history trait evolution. However, our understanding of how age-specific patterns of survival, including actuarial senescence, compare between the sexes remains inadequate. Using 36 years of mark-

recapture data for 7,516 male Weddell seals (*Leptonychotes weddellii*) born in Erebus Bay, Antarctica, we estimated age-specific annual survival rates using a hierarchical model for mark-recapture data in a Bayesian framework. Our male survival estimates were moderate for pups and yearlings, highest for 2-year-olds, and gradually declined with age thereafter such that the oldest animals observed had the lowest rates of any age. Reports of senescence in other wildlife populations of species with similar longevity occurred at older ages than those presented here. When compared to recently published estimates for reproductive Weddell seal females, we found that peak survival rates were similar (males: 0.94, 95% CI = 0.92–0.96; females: 0.92, 95% CI = 0.93–0.95), but survival rates at older ages were lower in males. Age-specific male Weddell seal survival rates varied across years and individuals, with greater variation occurring across years. Similar studies on a broad range of species are needed to contextualize these results for a better understanding of the variation in senescence patterns between the sexes of the same species, but our study adds information for a marine mammal species to a research topic dominated by avian and ungulate species.

Chambert, T.C., J.J. Rotella, and R.A. Garrott. 2012. Environmental extremes versus ecological extremes: Impact of a massive iceberg on the population dynamics of a high-level Antarctic marine predator. *Proceedings of the Royal Society B: Biological Sciences* 279: 4532-4541, https://doi.org/10.1098/rspb.2012.1733.

Extreme events have been suggested to play a disproportionate role in shaping ecological processes, but our understanding of the types of environmental conditions that elicit extreme consequences in natural ecosystems is limited. Here, we investigated the impact of a massive iceberg on the dynamics of a population of Weddell seals. Reproductive rates of females were reduced, but survival appeared unaffected. We also found suggestive evidence for a prolonged shift towards higher variability in reproductive rates. The annual number of females attending colonies showed unusual swings during the iceberg period, a pattern that was apparently the consequence of changes in sea-ice conditions. In contrast to the dramatic effects that were recorded in nearby populations of emperor penguins, our results suggest that this unusual environmental event did not have an extreme impact on the population of seals in the short-term, as they managed to avoid survival costs and were able to rapidly re-achieve high levels of reproduction by the end of the perturbation. Nevertheless, population projections suggest that even this modest impact on reproductive rates could negatively affect the population in the long run if such events were to occur more frequently, as is predicted by models of climate change.

Chambert, T.C., J.J. Rotella, and R.A. Garrott. 2014. An evolutionary perspective on reproductive individual heterogeneity in a marine vertebrate. *Journal of Animal Ecology* 84: 1158-1168, https://doi.org/10.1111/1365-2656.12211.

Although the quantification of individual heterogeneity in wild populations' vital rates has recently attracted growing interest among ecologists, the investigation of its evolutionary consequences remains limited, mainly because of the difficulties in assessing fitness and heritability from field studies on free-ranging animals. In the presence of individual variability, evaluation of fitness consequences can notably be complicated by the existence of trade-offs among different vital rates. In this study, to further assess the evolutionary significance of previously quantified levels of individual heterogeneity in female Weddell seal (*Leptonychotes weddellii* Lesson) reproductive rates (Chambert *et al*. 2013), we investigated how several life-history characteristics of female offspring were related to their mother's reproductive rate, as well as to other maternal traits (age and experience) and environmental conditions at birth. The probability and age of first reproduction (recruitment) of female offspring was not related to their mother's reproductive rate, suggesting the absence of a maternal trade-off between the number and quality of offspring a female produces. Evidence of a positive, but relatively weak, relationship between the

reproductive rates of a mother and her female offspring was found, suggesting some degree of heritability in this trait. Using a simulation approach based on these statistical findings, we showed that substantial differences in the number of grandchildren, produced through female progeny, can be expected among females with different reproductive rates. Despite the presence of substantial stochastic variability, due to environmental fluctuations and other unidentified mechanisms, and in the light of the fact that the metrics obtained do not provide a full measure of real fitness, our results do suggest that the individual reproductive variability found in female Weddell seals could potentially have important fitness consequences.

Chambert, T., J.J. Rotella, and M.D. Higgs. 2014. Use of posterior predictive checks as an inferential tool for investigating individual heterogeneity in animal population vital rates. *Ecology and Evolution* 4: 1389-1397, https://doi.org/10.1002/ece3.993.

The investigation of individual heterogeneity in vital rates has recently received growing attention among population ecologists. Individual heterogeneity in wild animal populations has been accounted for and quantified by including individually varying effects in models for mark–recapture data, but the real need for underlying individual effects to account for observed levels of individual variation has recently been questioned by the work of Tuljapurkar et al. (Ecology Letters, 12, 93, 2009) on dynamic heterogeneity. Model-selection approaches based on information criteria or Bayes factors have been used to address this question. Here, we suggest that, in addition to model-selection, model-checking methods can provide additional important insights to tackle this issue, as they allow one to evaluate a model's misfit in terms of ecologically meaningful measures. Specifically, we propose the use of posterior predictive checks to explicitly assess discrepancies between a model and the data, and we explain how to incorporate model checking into the inferential process used to assess the practical implications of ignoring individual heterogeneity. Posterior predictive checking is a straightforward and flexible approach for performing model checks in a Bayesian framework that is based on comparisons of observed data to model-generated replications of the data, where parameter uncertainty is incorporated through use of the posterior distribution. If discrepancy measures are chosen carefully and are relevant to the scientific context, posterior predictive checks can provide important information allowing for more efficient model refinement. We illustrate this approach using analyses of vital rates with long-term mark–recapture data for Weddell seals and emphasize its utility for identifying shortfalls or successes of a model at representing a biological process or pattern of interest.

Chambert, T., J.J. Rotella, M.D. Higgs, and R.A. Garrott. 2013. Individual heterogeneity in reproductive rates and cost of reproduction in a long-lived vertebrate. *Ecology and Evolution* 3:2047-2060, https://doi.org/10.1002/ece3.615.

Individual variation in reproductive success is a key feature of evolution, but also has important implications for predicting population responses to variable environments. Although such individual variation in reproductive outcomes has been reported in numerous studies, most analyses to date have not considered whether these realized differences were due to latent individual heterogeneity in reproduction or merely random chance causing different outcomes among like individuals. Furthermore, latent heterogeneity in fitness components might be expressed differently in contrasted environmental conditions, an issue that has only rarely been investigated. Here, we assessed (i) the potential existence of latent individual heterogeneity and (ii) the nature of its expression (fixed vs. variable) in a population of female Weddell seals (*Leptonychotes weddellii*), using a hierarchical modeling approach on a 30-year mark–recapture data set consisting of 954 individual encounter histories. We found strong support for the existence of latent individual heterogeneity in the population, with “robust” individuals expected to produce twice as many pups as “frail” individuals. Moreover, the expression of individual heterogeneity

appeared consistent, with only mild evidence that it might be amplified when environmental conditions are severe. Finally, the explicit modeling of individual heterogeneity allowed us to detect a substantial cost of reproduction that was not evidenced when the heterogeneity was ignored.

Paterson, J.T., J.J. Rotella, W.A. Link, and R.A. Garrott. 2018. Variation in the vital rates of an Antarctic marine predator: the role of individual heterogeneity. *Ecology* 99: 2385-2396, https://doi.org/10.1002/ecy.2481.

Variation in life-history traits such as lifespan and lifetime reproductive output is thought to arise, in part, due to among-individual differences in the underlying probabilities of survival and reproduction. However, the stochastic nature of demographic processes can also generate considerable variation in fitness-related traits among otherwise-identical individuals. An improved understanding of life-history evolution and population dynamics therefore depends on evaluating the relative role of each of these processes. Here, we used a 33-yr data set with reproductive histories for 1,274 female Weddell seals from Erebus Bay, Antarctica, to assess the strength of evidence for among-individual heterogeneity in the probabilities of survival and reproduction, while accounting for multiple other sources of variation in vital rates. Our analysis used recent advances in Bayesian model selection techniques and diagnostics to directly compare model fit and predictive power between models that included individual effects on survival and reproduction to those that did not. We found strong evidence for costs of reproduction to both survival and future reproduction, with breeders having rates of survival and subsequent reproduction that were 3% and 6% lower than rates for non-breeders. We detected age-related changes in the rates of survival and reproduction, but the patterns differed for the two rates. Survival rates steadily declined from 0.92 at age 7 to 0.56 at the maximal age of 31 yr. In contrast, reproductive rates increased from 0.68 at age 7 to 0.79 at age 16 and then steadily declined to 0.37 for the oldest females. Models that included individual effects explained more variation in observed life histories and had better estimated predictive power than those that did not, indicating their importance in understanding sources of variation among individuals in life-history traits. We found that among-individual heterogeneity in survival was small relative to that for reproduction. Our study, which found patterns of variation in vital rates that are consistent with a series of predictions from life-history theory, is the first to provide a thorough assessment of variation in important vital rates for a long-lived, high-latitude marine mammal while taking full advantage of recent developments in model evaluation.

Rotella, J.J., W.A. Link, T. Chambert, G.E. Stauffer, and R.A. Garrott. 2012. Evaluating the demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years of mark-recapture data. *Journal of Animal Ecology* 81: 162-173, https://doi.org/10.1111/j.1365-2656.2011.01902.x

Life-history theory predicts that those vital rates that make larger contributions to population growth rate ought to be more strongly buffered against environmental variability than are those that are less important. Despite the importance of the theory for predicting demographic responses to changes in the environment, it is not yet known how pervasive demographic buffering is in animal populations because the validity of most existing studies has been called into question because of methodological deficiencies. We tested for demographic buffering in the southern-most breeding mammal population in the world using data collected from 5558 known-age female Weddell seals over 30 years. We first estimated all vital rates simultaneously with mark–recapture analysis and then estimated process variance and covariance in those rates using a hierarchical Bayesian approach. We next calculated the population growth rate's sensitivity to changes in each of the vital rates and tested for evidence of demographic buffering by comparing properly scaled values of sensitivity and process variance in vital rates. We found evidence of positive process covariance between vital rates, which indicates that all vital rates are affected

in the same direction by changes in annual environment. Despite the positive correlations, we found strong evidence that demographic buffering occurred through reductions in variation in the vital rates to which population growth rate was most sensitive. Process variation in vital rates was inversely related to sensitivity measures such that variation was greatest in breeding probabilities, intermediate for survival rates of young animals and lowest for survival rates of older animals. Our work contributes to a small but growing set of studies that have used rigorous methods on long-term, detailed data to investigate demographic responses to environmental variation. The information from these studies improves our understanding of life-history evolution in stochastic environments and provides useful information for predicting population responses to future environmental change. Our results for an Antarctic apex predator also provide useful baselines from a marine ecosystem when its top- and middle-trophic levels were not substantially impacted by human activity.

Proffitt, K.M., J.J. Rotella, and R.A. Garrott. 2010. Effects of pup age, maternal age, and birth date on pre-weaning survival of Weddell seals in Erebus Bay, Antarctica. *Oikos* 119: 1255-1264, https://doi.org/10.1111/j.1600-0706.2009.18098.x.

Identifying factors affecting juvenile survival is important to understanding the dynamics of populations and may also provide insights into life history theory and the selective forces shaping evolution. Quantifying the relative influence of the various potential selective forces for the post-birth, maternal dependency, and independent periods is difficult and often limits investigators to estimating a single juvenile survival rate for the first year of life, or from birth to recruitment. We examined survival of individually marked Weddell seal *Leptonychotes weddellii* pups during the maternal dependency period in Erebus Bay, Antarctica from 2005–2007. We used mark-recapture models to evaluate competing a priori hypotheses regarding variation in daily pre-weaning survival rates (φ) during the first 42 days of age. The a priori model receiving the most support from the data supported several of our predictions: $\hat{\varphi}$ increased with pup age and was higher for pups born later in the season and to older mothers. Increases in $\hat{\varphi}$ with increasing pup age may have been due to improved resilience to the environment, phenotypic selection against the frailest pups, or both. Maternal age was more important to $\hat{\varphi}$ than was maternal experience or age of primiparity, potentially indicating that age-related increases in body mass allow greater offspring provisioning, or age-related improvements in competitive abilities benefit offspring during the period of maternal care. Depending on the timing of birth and the age of the mother, $\hat{\varphi}^{42\text{ days}}$ ranged from 0.79 (SE = 0.05) to 0.98 (SE = 0.01). These exceptionally high pre-weaning survival rates contrast with estimates from other large terrestrial and marine mammal species where neonate survival is considerably lower and suggest that in species with similar life histories, pre-weaning survival probability may be buffered from both predators and environmental fluctuations during the period of maternal nutritional dependency. Climatic changes affecting stability of ice used for pupping substrate or extent of fast-ice buffering pupping colonies from predators have the potential to reduce pre-weaning survival and may have important implications for population growth rates.

Stauffer, G.E., J.J. Rotella, R.A. Garrott, and W.L. Kendall. 2014. Environmental correlates of temporary emigration for female Weddell seals and consequences for recruitment. *Ecology* 95: 2526-2536.

In colonial-breeding species, prebreeders often emigrate temporarily from natal reproductive colonies then subsequently return for one or more years before producing young. Variation in attendance–nonattendance patterns can have implications for subsequent recruitment. We used open robust-design multistate models and 28 years of encounter data for prebreeding female Weddell seals (*Leptonychotes*

weddellii [Lesson]) to evaluate hypotheses about (1) the relationships of temporary emigration (TE) probabilities to environmental and population size covariates and (2) motivations for attendance and consequences of nonattendance for subsequent probability of recruitment to the breeding population. TE probabilities were density dependent (ˆ bBPOP¼0.66, SEc ¼0.17; estimated effects [b] and standard errors of population size in the previous year) and increased when the fast-ice edge was distant from the breeding colonies (ˆ bDIST ¼ 0.75, SEc ¼ 0.04; estimated effects and standard errors of distance to the sea-ice edge in the current year on TE probability in the current year) and were strongly age and state dependent. These results suggest that trade-offs between potential benefits and costs of colony attendance vary annually and might influence motivation to attend colonies. Recruitment probabilities were greatest for seals that consistently attended colonies in two or more years (e.g., wˆ age10 ¼ 0.56, SD ¼ 0.17) and lowest for seals that never or inconsistently attended prior to recruitment (e.g., wˆ age10 ¼ 0.32, SD ¼ 0.15), where wˆ age10 denotes the mean recruitment probability (over all years) for 10-year-old seals for the specified prebreeder state. In colonial-breeding seabirds, repeated colony attendance increases subsequent probability of recruitment to the adult breeding population; our results suggest similar implications for a marine mammal and are consistent with the hypothesis that prebreeders were motivated to attend reproductive colonies to gain reproductive skills or perhaps to optimally synchronize estrus through close association with mature breeding females.

Stauffer, G.E., J.J. Rotella, and R.A. Garrott. 2013. Birth-year and current-year influences on survival and recruitment rates of female Weddell seals. *Population Ecology* 55: 405-415.

In long-lived species, juvenile survival typically is lower and more variable than adult survival, and modeling such variation is important for understanding population dynamics. Variability in juvenile survival can be related to birth- or current-year influences, and the birth-year influences can be transient, persistent, or intermediate in duration. We used multi-state models and data collected from 5,459 known-aged prebreeder female Weddell seals (*Leptonychotes weddellii* Lesson) tagged in Erebus Bay, Antarctica from 1980–2007 to evaluate the duration of potential birth-year influences on survival rates and the importance of birth- and current-year influences on survival and recruitment rates. Survival rates differed for each birth cohort and were positively related to current-year winter sea-ice conditions. The estimated duration of birth-cohort effects on survival was intermediate (6 years) rather than transient (2 years) or permanent. Estimated survivorship from birth to 6 years of age varied among cohorts from 0.13 (SE = 0.04) to 0.42 (SE = 0.06), and averaged 0.25 (SE = 0.02). Recruitment rates (probability of transitioning from prebreeder to breeder state) varied annually but apparently were not related to birth-year conditions. Our results provide evidence that birth- and current-year conditions act in combination to influence survival. Although for many long-lived species the influences of either birth- or current-year conditions on survival are well-studied, we suggest that modeling survival rates as a function of birth- and current-year influences simultaneously could lead to better understanding of survival and improved stochastic models to project population dynamics.

Stauffer, G.E., J.J. Rotella, and R.A. Garrott. 2013. Variability in temporary emigration rates of individually marked female Weddell seals prior to first reproduction. *Oecologia* 172: 129-140.

In many species, temporary emigration (TE) is a phenomenon, often indicative of life-history characteristics such as dormancy, skipped reproduction, or partial migration, whereby certain individuals in a population are temporarily unobservable at a particular site. TE may be a flexible condition-dependent strategy that allows individuals to mitigate effects of adverse conditions. Consequently, TE rates ought to be highly variable, but sources of variations are poorly understood for most species. We used data from known-aged female Weddell seals (*Leptonychotes weddellii*) tagged in Erebus Bay, Antarctica, to investigate sources of variation in TE rates prior to reproduction and to evaluate possible

implications for age-specific probability of first reproduction. TE rates were near 1 the year after birth, decreased to an average of 0.15 (SEˆSE^ = 0.01) by age 8, and were similar thereafter. TE rates varied substantially from year-to-year and were lower for seals that attended reproductive colonies the previous year than for seals that did not attend (e.g., $\overline{\hat{\psi}^{\mathrm{UU}}_{i,\mathrm{age\,8}} - \hat{\psi}^{\mathrm{PU}}_{i,\mathrm{age\,8}}} = 0.22$). Recruitment rates were marginally greater for seals that did attend than for seals that did not attend colonies the previous year. For Weddell seals specifically, our results suggest that (1) motivation to attend colonies varied temporally, (2) as seals grew older they had increased motivation to attend even before reproductive maturity, and (3) seals appear to follow various attendance strategies. More broadly, our results support the idea of TE as a variable, condition-dependent strategy, and highlight the utility of TE models for providing population and life-history insights for diverse taxa.

FORAGING BEHAVIOR AND ECOLOGY

ADELIE PENGUINS

Ainley, D.G., and G. Ballard. 2011. Non-consumptive factors affecting foraging patterns in Antarctic penguins: a review and synthesis. *Polar Biology* 35: 1–13.

Recent research has clearly shown that the fear of predation, i.e. aversion to taking risks, among mesopredators or grazers, and not merely flight from an apex predator to avoid predation, is an important aspect of ecosystem structuring. In only a few, though well-documented cases, however, has this been considered in the marine environment. Herein, we review studies that have quantified behavioral responses of Adélie penguins *Pygoscelis adeliae* and emperor penguins *Aptenodytes forsteri* to the direct presence of predators, and question why the penguins avoid entering or exiting the water at night. We also show, through literature review and new analyses of Adélie penguin diving data, that Antarctic penguins are capable of successful prey capture in the dark (defined here as\3.4 lux). Finally, we summarize extensive data on seasonal migration relative to darkness and prey availability. On the basis of our findings, we propose that penguins' avoidance of foraging at night is due to fear of predation, and not to an inability to operate effectively in darkness. We further propose that, at polar latitudes where darkness is more a seasonal than a year-round, daily feature, this ''risk aversion'' affects migratory movements in both species, consistent with the ''trade-off'' hypothesis seen in other marine vertebrates weighing foraging success against predation risk in their choice of foraging habitat. Such non-consumptive, behavioral aspects of species interactions have yet to be considered as important in Southern Ocean food webs, but may help to explain enigmatic movement patterns and choice of foraging grounds in these penguin species.

Ainley, D.G., K.M. Dugger, M. La Mesa, G. Ballard, K.J. Barton, S. Jennings, B.J. Karl, A. Lescroël, P.O'B. Lyver, A. Schmidt, and P. Wilson. 2018. Post-fledging survival of Adélie penguins at multiple colonies: chicks raised on fish do well. *Marine Ecology Progress Series* 601: 239-251.

We assessed whether the mass of Adélie penguin *Pygoscelis adeliae* fledglings at 3 colonies of markedly disparate size on Ross Island, Ross Sea, correlated with their eventual return as subadults. We compared our results with those from Anvers Island, Bellingshausen Sea. Colony sizes at Ross Island have been increasing, contrary to decreasing size at Anvers Island. At Ross Island, during the month prior to fledging, chick diet consisted equally of energy-dense Antarctic silverfish *Pleuragramma antarctica* and less-caloric crystal krill *Euphausia crystallorophias*, while at Anvers Island the diet was principally Antarctic krill *E. superba*. At Ross Island, the mass of fledglings who subsequently returned (mean ± SE:

3.4 ± 0.0411 kg) exceeded that of those not seen again (3.2 ± 0.0251 kg), compared to Anvers Island (3.2 vs. 3.0 kg, respectively). At Ross Island, fledging mass was inversely related to colony size and, at the largest colony, fledging mass decreased as the colony grew. Average mass of returnees at the largest colony was less than the mass at Anvers Island for those fledglings that did not return. The mean proportion of fish in the chicks' diet decreased at the largest Ross Island colony over time, as did fledging mass. We hypothesize that intraspecific competition increased along with colony size, decreasing the availability of fish. We further hypothesize that at the large Ross Island colony, post-fledging penguins must be finding adequate prey, and more energy-dense fish, just outside the colony's foraging area to explain opposing trends in colony trajectories.

Ballard, G., K.M. Dugger, N. Nur, and D.G. Ainley. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series* 405: 287–302.

Animals modulate breeding effort by balancing investment in self-maintenance against investment in their young, potentially impacting reproductive success when faced with difficult conditions. This life history trade-off model has been evaluated for flying birds, especially those that forage over large pelagic regions of relatively sparse prey availability. We evaluated its applicability to penguins which, lacking flight, depend on reliably available prey relatively close to colonies. We used transponders and an automated weighing system to monitor 40 to 75 breeding Adélie penguins *Pygoscelis adeliae* per season for 10 seasons, while environmental conditions varied dramatically, measuring foraging trip duration, parental mass change, and total food load delivered to chicks. Parents that lost the most mass during breeding provided more food to chicks while maintaining their own condition. In contrast, in years when adult mass was lower to begin with, parents recovered their own condition and delivered less food to chicks. Food loads were also related to environmental variables, with parents making longer trips and delivering less food when access to prey was more difficult, but delivering more food to 2-chick broods than to 1-chick broods. Penguins did not alternate between short (chick provisioning) and long (self-maintenance) trips, as has been observed in far ranging seabirds. Nevertheless, our results indicate they regulated their condition depending on environmental and physiological factors, with impacts on the amount of food delivered to young and pre-fledging mass. Parental choice of multiple foraging habitats and depletion of prey in the nearest habitat due to intraspecific competition have important implications in explaining contrasting patterns observed among studies investigating the life history trade-off model in birds.

Ford, R.G., D.G. Ainley, A. Lescroël, P.O'B. Lyver, V. Toniolo, and G. Ballard. 2015. Testing assumptions of central place foraging theory: a study of Adélie penguins *Pygoscelis adeliae* in the Ross Sea. *Journal of Avian Biology* 46: 193-205, doi:10.1111/jav.00491.

We investigated central place foraging (CPF) in the context of optimal foraging theory in Ad é lie penguins *Pygoscelis adeliae* of the southern Ross Sea by using satellite tracking and time-depth recorders to explore foraging at two spatio-temporal scales: within the day-to-day (sub-mesoscale: single foraging trip, 10s of km^2) and the entire breeding season (mesoscale: trips by multiple individuals across the collective foraging area, 100s of km^2). Specifically, we examine whether three basic assumptions of the Orians – Pearson CPF model, shown to occur in other CPF species, are met: 1) within a patch, the rate of prey acquisition declines with time spent in that patch; 2) food is distributed in discrete patches and is not available between those patches; and 3) CPF species have knowledge of the potential (or average, at least) feeding rate within their universe of patches, and use this knowledge to determine their foraging strategy when planning or engaging in a foraging trip. We found that prey consumption rates did not decline with time spent in patches, and penguins foraged to some degree most of the time when at sea. Food

availability, as measured by foraging dive rate, appeared to be predictable within the same day at the same location, but predictability broke down after 2 d at distances _ 10 km away. We conclude that the assumptions of the Orians – Pearson CPF model are not a good fi t to the circumstances of Ross Sea penguins, which clearly are central place foragers.

Grémillet, D., A. Lescroël, G. Ballard, K.M. Dugger, M. Massaro, E.L. Porzig, and D.G. Ainley. 2018. Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. *Functional Ecology* 2018: 1–11, doi:10.1111/1365-2435.13074.

Evaluating the fitness of organisms is an essential step towards understanding their responses to environmental change. Connections between energy expenditure and fitness have been postulated for nearly a century. However, testing this premise among wild animals is constrained by difficulties in measuring energy expenditure while simultaneously monitoring conventional fitness metrics such as survival and reproductive output. We addressed this issue by exploring the functional links between field metabolic rate (FMR), body condition, sex, age and reproductive performance in a wild population. We deployed 3D accelerometers on 115 Adélie penguins *Pygoscelis adeliae* during four breeding seasons at one of the largest colonies of this species, Cape Crozier, on Ross Island, Antarctica. The demography of this population has been studied for the past 18 years. From accelerometry recordings, collected for birds of known age and breeding history, we determined the vector of the dynamic body acceleration (VeDBA) and used it as a proxy for FMR. This allowed us to demonstrate relationships among FMR, a breeding quality index (BQI) and body condition. Notably, we found a significant quadratic relationship between mean VeDBA during foraging and BQI for experienced breeders, and individuals in better body condition showed lower rates of energy expenditure. We conclude that using FMR as a fitness component complementary to more conventional fitness metrics will yield greater understanding of evolutionary and conservation physiology.

Jennings, S., A. Varsani, K.M. Dugger, G. Ballard, and D.G. Ainley. 2016. Sex-based differences in Adélie Penguin (*Pygoscelis adeliae*) chick growth rates and diet. *PLoS ONE* 11(3): e0149090, doi:10.1371/journal.pone.0149090.

Sexually size-dimorphic species must show some difference between the sexes in growth rate and/or length of growing period. Such differences in growth parameters can cause the sexes to be impacted by environmental variability in different ways, and understanding these differences allows a better understanding of patterns in productivity between individuals and populations. We investigated differences in growth rate and diet between male and female Adélie Penguin (*Pygoscelis adeliae*) chicks during two breeding seasons at Cape Crozier, Ross Island, Antarctica. Adélie Penguins are a slightly dimorphic species, with adult males averaging larger than adult females in mass (~11%) as well as bill (~8%) and flipper length (~3%). We measured mass and length of flipper, bill, tibiotarsus, and foot at 5-day intervals for 45 male and 40 female individually-marked chicks. Chick sex was molecularly determined from feathers. We used linear mixed effects models to estimate daily growth rate as a function of chick sex, while controlling for hatching order, brood size, year, and potential variation in breeding quality between pairs of parents. Accounting for season and hatching order, male chicks gained mass an average of 15.6 g d-1 faster than females. Similarly, growth in bill length was faster for males, and the calculated bill size difference at fledging was similar to that observed in adults. There was no evidence for sex-based differences in growth of other morphological features. Adélie diet at Ross Island is composed almost entirely of two species—one krill (*Euphausia crystallorophias*) and one fish (*Pleuragramma antarctica*), with fish having a higher caloric value. Using isotopic analyses of feather samples, we also determined that male chicks were fed a higher proportion of fish than female chicks. The related

differences in provisioning and growth rates of male and female offspring provides a greater understanding of the ways in which ecological factors may impact the two sexes differently.

Jennings, S., K.M. Dugger, G. Ballard, and D.G. Ainley. 2021. Effects of diet and provisioning behavior on chick growth in Adélie Penguins (*Pygoscelis adeliae*). *Waterbirds*, in press.

When provisioning chicks, parents trade-off their time, energy, and other resources to maximize reproductive success. As parents adjust investment to maximize their fitness, impacts on offspring growth can occur. We investigated provisioning and chick growth of Adélie Penguins (*Pygoscelis adeliae*) at one of the largest colonies (~175,000 pairs), during one year of normal chick growth and survival and in a year which, by chance, was characterized by low chick growth and survival ("difficult" year). We measured daily average amount and quality of food delivered, as well as foraging-trip duration, and compared them to chick mass and skeletal growth during two years of contrasting conditions. We used mixed-effects models to test the prediction that increased parental investment would lead to increased growth rates, while accounting for various confounding effects. There was no evidence of an effect of parent age. All provisioning measures predicted growth of at least one morphological character but, especially during the year of normal reproductive success, no provisioning measure strongly predicted growth across most morphological characters. However, during the difficult year parental investment positively affected growth rates, especially for males that were fed relatively more fish. The observed variation in growth rates between males and females, and between years of contrasting apparent resource availability, was large enough to lead to size differences that may subsequently affect post-fledging survival and ultimately population processes.

Kappes, P.J., K.M. Dugger, A. Lescroël, D.G. Ainley, G. Ballard, K.J. Barton, P.O'B. Lyver, and P.R. Wilson. 2021. Age-related reproductive performance of the Adélie penguin, a long-lived seabird exhibiting similar outcomes regardless of individual life-history strategy. *Journal of Animal Ecology*, doi:10.1111/1365-2656.13422.

Age-related variation in reproductive performance in long-lived iteroparous vertebrate species is common, with performance being influenced by within-individual processes, such as improvement and senescence, in combination with among-individual processes, such as selective appearance and disappearance. Few studies of age-related reproductive performance have compared the role of these drivers within a metapopulation, subject to varying degrees of resource competition. We accounted for within-and among-individual changes among known-aged Adélie penguins *Pygoscelis adeliae* during 17 years (1997–2013), at three clustered colonies of disparate size, to understand patterns in age-related reproductive success during early and late adulthood. Age at first reproduction (AFR) was lowest, and number of breeding attempts highest, at the largest colony. Regardless of AFR, success improved with early post-recruitment experience. For both oldest and youngest recruitment groups, peak performance occurred at the end of their reproductive life span indicating a possible cost of reproduction. Intermediate recruitment groups reached peak performance in their mid-reproductive life span and with intermediate breeding experience, before decreasing. Breeding success was lowest for the initial breeding attempt regardless of AFR, but we observed subsequent variation relative to recruitment age. Gaining experience by delaying recruitment positively influenced reproductive performance early in the reproductive life span and was most evident for the youngest breeders. Oldest recruits had the highest initial and peak breeding success. Differences in AFR resulted in trade-offs in reproductive life span or timing of senescence but not in the overall number of breeding attempts. Patterns differed as a function of colony size, and thus competition for resources. Early life improvement in performance at the larger colonies was primarily due to within-individual factors and at the largest colony, AFR, Regardless of colony size.

Lescroël, A., G. Ballard, V. Toniolo, K.J. Barton, P.R. Wilson, P. O'B. Lyver, and D.G. Ainley. 2010. Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology* 91: 2044–2055.

In animal populations, a minority of individuals consistently achieves the highest breeding success and therefore contributes the most recruits to future generations. On average, foraging performance is important in determining breeding success at the population level, but evidence is scarce to show that more successful breeders (better breeders) forage differently than less successful ones (poorer breeders). To test this hypothesis, we used a 10-year, three-colony, individual-based longitudinal data set on breeding success and foraging parameters of a long-lived bird, the Adélie Penguin, *Pygoscelis adeliae*. Better breeders foraged more efficiently than poorer breeders under harsh environmental conditions and when offspring needs were higher, therefore gaining higher net energy profit to be allocated to reproduction and survival. These results imply that adverse ''extrinsic'' conditions might select breeding individuals on the basis of their foraging ability. Adélie Penguins show sufficient phenotypic plasticity that at least a portion of the population is capable of surviving and successfully reproducing despite extreme variability in their physical and biological environment, variability that is likely to be associated with climate change and, ultimately, with the species' evolution. This study is the first to demonstrate the importance of ''extrinsic'' conditions (in terms of environmental conditions and offspring needs) on the relationship between foraging behavior and individual quality.

Lescroël, A., G. Ballard, M. Massaro, K. Dugger, S. Jennings, A. Pollard, E. Porzig, A. Schmidt, A. Varsani, D. Grémillet, and D. Ainley. 2019. Evidence of age-related improvement in the foraging efficiency of Adélie penguins. *Scientific Reports* 9:3375, https://doi.org/10.1038/s41598-019-39814-x.

Age variation in reproductive performance is well-documented but the mechanisms underlying this variation remain unclear. Foraging efficiency is likely to be a key source of demographic variation as it determines the amount of energy that can be invested in fitness-related activities. Evidence of age related changes in the foraging efficiency of adult seabirds is scarce and inconsistent. We investigated the effects of age on the foraging efficiency of breeding Adélie penguins, a relatively short-lived seabird species, in order to gain a broader perspective on the processes driving variation in ageing rates. We found support for a positive effect of age, either linear or levelling off at old ages, on both our proxies for daily catch rate and catch per unit effort. Across all age classes, males were more performant foragers than females. We found no strong evidence for differing ageing patterns between sexes or individual quality levels, and no evidence for senescence. We infer that continuous individual improvement could be responsible for a larger amount of the variation in foraging efficiency with age at our study site, compared with selective disappearance of underperforming phenotypes. The different results reported by other studies highlight the need to conduct longitudinal studies across a range of species in different environments.

Lescroël, A., P.O'B. Lyver, D. Jongsomjit, S. Veloz1, K.M. Dugger, P. Kappes, B.J. Karl, A.L. Whitehead, R. Pech, T.L. Cole, and G. Ballard. 2020. Inter-individual differences in the foraging behavior of breeding Adélie penguins are driven by individual quality and sex. *Marine Ecology Progress Series* 636: 189–205.

Inter-individual differences in demographic traits of iteroparous species can arise through learning and maturation, as well as from permanent differences in individual 'quality' and sex-specific constraints. As the ability to acquire energy determines the resources an individual can allocate to reproduction and self-maintenance, foraging behavior is a key trait to study to better understand the mechanisms underlying these differences. So far, most seabird studies have focused on the effect of

maturation and learning processes on foraging performance, while only a few have included measures of individual quality. Here, we investigated the effects of age, breeding experience, sex, and individual breeding quality on the foraging behavior and location of 83 known-age Adélie penguins at Cape Bird, Ross Sea, Antarctica. Over a 2 yr period, we showed that (1) high-quality birds dived deeper than lower quality ones, apparently catching a higher number of prey per dive and targeting different foraging locations; (2) females performed longer foraging trips and a higher number of dives compared to males; (3) there were no significant age related differences in foraging behavior; and (4) breeding experience had a weak influence on foraging behavior. We suggest that high-quality individuals have higher physiological ability, enabling them to dive deeper and forage more effectively. Further inquiry should focus on determining the physiological differences among penguins of different quality.

Lyver, P.O'B., C.J. MacLeod, G. Ballard, B.J. Karl, K.J. Barton, J. Adams, D.G. Ainley, and P.R. Wilson. 2011. Intra-seasonal variation in foraging behavior among Adélie penguins (*Pygocelis adeliae*) breeding at Cape Hallett, Ross Sea, Antarctica. *Polar Biology* 34:49–67.

We investigated intra-seasonal variation in foraging behavior of chick-rearing Adélie penguins, *Pygoscelis adeliae*, during two consecutive summers at Cape Hallett, northwestern Ross Sea. Although foraging behavior of this species has been extensively studied throughout the broad continental shelf region of the Ross Sea, this is the first study to report foraging behaviors and habitat affiliations among birds occupying continental slope waters. Continental slope habitat supports the greatest abundances of this species throughout its range, but we lack information about how intra-specific competition for prey might affect foraging and at-sea distribution and how these attributes compare with previous Ross Sea studies. Foraging trips increased in both distance and duration as breeding advanced from guard to crèche stage, but foraging dive depth, dive rates, and vertical dive distances travelled per hour decreased. Consistent with previous studies within slope habitats elsewhere in Antarctic waters, Antarctic krill (*Euphausia superba*) dominated chick meal composition, but fish increased four-fold from guard to crèche stages. Foraging-, focal-, and core areas all doubled during the crèche stage as individuals shifted distribution in a southeasterly direction away from the coast while simultaneously becoming more widely dispersed (i.e., less spatial overlap among individuals). Intra-specific competition for prey among Adélie penguins appears to influence foraging behavior of this species, even in food webs dominated by Antarctic krill.

Massaro, M., D.G. Ainley, J.A. Santora, P. Quillfeldt, A. Lescroël, A. Whitehead, A. Varsani, G. Ballard, and P.O'B. Lyver. 2020. Diet segregation in Adélie penguins: some individuals attempt to overcome colony-induced and annual foraging challenges. *Marine Ecology Progress Series* 645: 205–218.

Intraspecific competition for food can be especially high in colonial breeding seabirds. To minimize colony-induced or annual foraging challenges, diet may vary among individuals, but few studies have simultaneously investigated the effects of both extrinsic conditions (e.g. colony or year effects) and parameters of an individual (e.g. sex, age or individual quality) on diet in seabirds. Using stable isotope analyses, we studied the diet of 214 Adélie penguins *Pygoscelis adeliae* of known sex, age and breeding quality, nesting in 2 colonies on Ross Island, Antarctica, over 3 breeding seasons. During the study, δ15N and δ13C isotope values were lower in penguins breeding at Cape Crozier compared to those at Cape Bird, revealing a difference in prey proportions. Cape Bird penguins were estimated to consistently consume more energy-rich silverfish *Pleuragramma antarctica*, while birds at Cape Crozier ate more crystal krill *Euphausia crystallorophias*. We also found inter-annual differences in diet, with a higher dietary fish proportion in both colonies during 2011. Males had significantly higher δ15N values, indicating a higher fish consumption than females. This sexual segregation in diet was particularly

pronounced at Cape Bird, where the overall isotopic niche was wider than at Cape Crozier. Differences in diet among adults of varying ages only existed at Cape Bird, where middle-aged penguins consumed more fish than old and young penguins. This study provides evidence that Adélie penguin diet is largely driven by annual, seasonal and local abundances of prey, with only some individuals selectively foraging for more nutritional prey if prey choices are present.

Whitehead, A.L., P.O'B. Lyver, G. Ballard, K. Barton, B.J. Karl, K.M. Dugger, S. Jennings, A. Lescroël, P.R. Wilson, and D.G. Ainley. 2015. Factors driving Adélie penguin chick size, mass and condition at colonies of differing size in the southern Ross Sea. ***Marine Ecology Progress Series*** **523: 199–213.**

Body size, mass and condition can affect an organism's ability to cope with variation in resource availability or metabolic demand, particularly as juveniles reach independence. It follows that changes to parental provisioning efficiency (size and frequency of meals) through intraspecific competition or environmental conditions that affect prey availability may affect chick size, mass and condition and ultimately post-fledging survival. We examined how Adélie penguin chick size, mass and condition varied among colonies of different sizes on Ross Island during a 15 yr period of high environmental variability and varying intraspecific competition. Aiding the study was a natural experiment in which the presence of 2 giant icebergs midway through the study abnormally increased sea ice concentration (SIC), altering adults' access to food. Concurrently, the colonies were rapidly increasing in size; based on previous work, this indicated increased trophic competition near colonies, a trend likely indicating a changing food web in the greater region. Results showed that increased amounts of sea ice, which reduced the ability of adults to access food, had a negative effect on the size and mass of chicks. However, a greater proportion of fish (vs. krill) in the diet had a positive effect on chick size. Moreover, in some cases, increased intraspecific competition may be a more important driver of provisioning rate and chick size than abiotic factors, with chicks showing the effects of reduced food delivery at larger colonies. Understanding these patterns will allow better understanding of how factors such as climate change and altered food webs may affect Adélie penguin populations.

EMPEROR PENGUINS

Kooyman, G. 2015. Marine Mammals and emperor penguins: a few applications of the Krogh principle. ***AJP Regulatory Integrative and Comparative Physiology*****, https://doi.org/10.1152/ajpregu.00264.2014**

The diving physiology of aquatic animals at sea began 50 years ago with studies of the Weddell seal. Even today with the advancements in marine recording and tracking technology, only a few species are suitable for investigation. The first experiments were in McMurdo Sound, Antarctica. In this paper are examples of what was learned in Antarctica and elsewhere. Some methods employed relied on willingness of Weddell seals and emperor penguins to dive under sea ice. Diving depth and duration were obtained with a time depth recorder. Some dives were longer than an hour and as deep as 600 m. From arterial blood samples, lactate and nitrogen concentrations were obtained. These results showed how Weddell seals manage their oxygen stores, that they become reliant on a positive contribution of anaerobic metabolism during a dive duration of more than 20 min, and that nitrogen blood gases remain so low that lung collapse must occur at about 25 to 50 m. This nitrogen level was similar to that determined in elephant seals during forcible submersion with compression to depths greater than 100 m. These results led to further questions about diving mammal's terminal airway structure in the lungs. Much of the strengthening of the airways is not for avoiding the "bends," by enhancing lung collapse at depth,

but for reducing the resistance to high flow rates during expiration. The most exceptional examples are the small whales that maintain high expiratory flow rates throughout the entire vital capacity, which represents about 90% of their total lung capacity.

Kooyman, G.L., K. Goetz, C.L. Williams, P.J. Ponganis, K. Sato, S. Eckert, M. Horning, P.T. Thorson, and R.P. Van Dam. 2020. Crary bank: a deep foraging habitat for emperor penguins in the western Ross Sea. *Polar Biol* 43: 801–811, https://doi.org/10.1007/s00300-020-02686-3.

Although most dives of emperor penguins (*Aptenodytes forsteri*) are less than 100 m, penguins from the Cape Washington colony regularly perform deep dives > 400 m. To evaluate the significance and location of these deep dives of birds on foraging trips from Cape Washington, we report the satellite tracks of three birds. We also review the frequency of deep dives in the 35 of 42 birds that performed deep dives during seven research seasons over 22 years. Records included 83,314 dives, of which 1418 were > 400 m deep (deepest 552 m). Durations of these deep dives ranged from 7 to 13 min, up to more than twice the aerobic dive limit. Inter-deep-dive-intervals (IDDIs) between most deep dives were 10–20 min. The travel routes of satellite-tagged birds showed that all three spent time over Crary Bank, about 100 km from Cape Washington. Dives > 400 m only occurred over Crary Bank in the two satellite-tracked birds that were also equipped with dive recorders. The depths of the dives were consistent with the distribution of the most common, and energy-dense prey item found in their diet, *Pleuragramma antarctica*. We conclude that significant food resources are located over Crary Bank, accounting for the deep dives and success of birds from Cape Washington, the second largest, stable colony of emperor penguins known.

Kooyman, G., B. McDonald, and K. Goetz. 2015. Why do satellite transmitters on emperor penguins stop transmitting? *Animal Biotelemetry* 3(1): 1-7.

Investigation of early transmission failure from animal-borne, satellite transmitters should reveal vital information about the reliability of the technology, and the risk of application to the animal. Current technology available to the investigator does not provide firm evidence for causes of transmitter blackout. We address the five most likely causes of satellite transmitter failure on 20 adult (10 male and 10 female) emperor penguins tagged near Cape Colbeck, Antarctica, and one near the Drygalski Ice Tongue, Western Ross Sea, during late summer, 2013. They are: 1. Technical failure of the transmitter, 2. Instrument breakage, 3. Instrument loss because of attachment failure, 4. Predation, and 5. Icing of the salt water detection switch. The longest record of 323 days suggests that prior losses were not due to power failure. Various possibilities of transmission blackout are discussed, and we speculate about the most likely causes of termination of transmissions. A loss of transmission from six tags at similar locations early in the deployments suggests predation. Later losses at random times and locations may be because of antenna breakage or attachment failure. Definite conclusions cannot be made because of the indirect assessment of transmission loss. We suggest some changes in deployment procedures to improve our ability to determine cause of satellite transmission termination in the future. Understanding causes of blackout is important both scientifically and ethically in terms of accurate data interpretation and balancing the benefits of scientific gain with the costs of animal disturbance.

Kooyman, G. L., B.I. McDonald, C.L. Williams, J.U. Meir, and P.J. Ponganis. 2020. The aerobic dive limit: After 40 years, still rarely measured but commonly used. *Comparative Biochemistry and Physiology, Part A* 252, 110841.

The aerobic dive limit (ADL) and the hypothesis that most dives are aerobic in nature have become fundamental to the understanding of diving physiology and to the interpretation of diving behavior and foraging ecology of marine mammals and seabirds. An ADL, the dive duration associated

with the onset of post-dive blood lactate accumulation, has only been documented with blood lactate analyses in five species. Applications to other species have involved behavioral estimates or use of an oxygen store / metabolic rate formula. Both approaches have limitations, but have proved useful to the evaluation of the dive behavior and ecology of many species.

Kooyman, G.L., R.P. van Dam, and L.A. Hückstädt. 2018. Night diving by some emperor penguins during the winter breeding period at Cape Washington. *Journal of Experimental Biology* 221: jeb170795, doi:10.1242/jeb.170795.

All through the bird literature and feature films, there is much ado about dedicated emperor penguin males fasting for 115 days while they do all the incubation of the single egg. Sometimes, they may not fast for so long. Based on a winter visit to Cape Washington, we obtained evidence that some birds may feed before the egg is laid, and if they do, and some are males, then their fast is much less than 115 days. The consequence of a shorter fast for the male is a better chance of completing the 65 day incubation fast and success in fledging the chick. For those in northern colonies that may migrate south, there will be closer access to open water, but there will be the need to dive in the dark.

Gearheart, G., G. Kooyman, K. Goetz, and B. McDonald. 2014. Migration front of post-moult emperor penguins. Polar Biology 34: 435-439, doi:10.1007/s00300-014-1449-2.

The moult is arguably the most critical period in the life of emperor penguins (Aptenodytes forsteri). Birds from western Ross Sea colonies travel yearly to and from the pack ice of the eastern Ross Sea to moult. Despite the suspected large numbers of penguins involved, this migration had never been directly observed. Here, we provide the first description of a migratory front of penguins travelling east to west between their moulting habitat and to the breeding colonies. Early autumn ship-bound visual surveys showed density of birds increased significantly as we approached the eastern Ross Sea and was not related to ice type, per cent ice cover or primary productivity. This supports the hypothesis of a dense "source" of post-moult birds in the eastern Ross Sea migrating in near-synchrony and gradually dispersing towards breeding colonies in the southwest and northwest Ross Sea. Emperor penguins travelled alone or in small groups of up to 8 individuals, concentrating around narrow leads or isolated water holes, and were occasionally seen far from open water, suggesting they move primarily by swimming, complemented by tobogganing. Their new coats indicated they had completed the moult. Aggregations of birds and guano stains suggested they were feeding while migrating.

Goetz, K., G.L Kooyman, and B.I. McDonald. 2018. Post-molt movement and dive behavior of non-breeding emperor penguins in the eastern Ross Sea, Antarctica. *Marine Ecology Progress Series* 593: 155-171.

Emperor penguins *Aptenodytes forsteri* are important predators in the Ross Sea ecosystem, yet little is known about their movement and foraging behavior outside the breeding season or within different demographic groups. In early March 2013, we instrumented 20 non-breeding emperor penguins in the eastern Ross Sea with satellite-linked recorders and analyzed their habitat preference and dive behavior. Track length ranged from 273 km to nearly 9000 km and dive data were obtained for over 96000 dives (mean maximum depth: 90.2 ± 77.8 (SD) m, mean dive duration: 4.6 ± 2.3 min), 17 of which exceeded the previous duration record of 27.6 min. Overall, emperor penguins preferred areas north of Cape Colbeck that were beyond the shelf break and received more sunlight. In these areas, penguins performed dives that were deeper, longer, faster, and more pelagic than dives located near the colony. Birds exhibited various movement and foraging strategies ('shelf' and 'gyre'; benthic and pelagic). The occurrence of deeper and longer dives during the day (n = 28318) and at twilight (n = 60171) than at night (n = 7582), especially at high latitudes, is consistent with emperor penguins being visual predators.

Observed differences in both movement and dive behavior as a function of light may indicate a change in prey preference across space and time. Our study offers novel insight into the habitat preferences and dive behavior for a previously unstudied demographic group, at a time when emperor penguins experience the most severe environmental conditions of their annual life cycle.

Sato, K., K. Shiomi, G. Marshall, G.L. Kooyman, and P.J. Ponganis. 2011. Stroke rates and diving air volumes of emperor penguins: implications for dive performance. *Journal of Experimental Biology 214*(17): 2854-2863, doi:10.1242/jeb.055723.

Emperor penguins (*Aptenodytes forsteri*), both at sea and at an experimental dive hole, often have minimal surface periods even after performance of dives far beyond their measured 5.6 min aerobic dive limit (ADL: dive duration associated with the onset of post-dive blood lactate accumulation). Accelerometer-based data loggers were attached to emperor penguins diving in these two different situations to further evaluate the capacity of these birds to perform such dives without any apparent prolonged recovery periods. Minimum surface intervals for dives as long as 10 min were less than 1 min at both sites. Stroke rates for dives at sea were significantly greater than those for dives at the isolated dive hole. Calculated diving air volumes at sea were variable, increased with maximum depth of dive to a depth of 250 m, and decreased for deeper dives. It is hypothesized that lower air volumes for the deepest dives are the result of exhalation of air underwater. Mean maximal air volumes for deep dives at sea were approximately 83% greater than those during shallow (<50 m) dives. We conclude that (a) dives beyond the 5.6 min ADL do not always require prolongation of surface intervals in emperor penguins, (b) stroke rate at sea is greater than at the isolated dive hole and, therefore, a reduction in muscle stroke rate does not extend the duration of aerobic metabolism during dives at sea, and (c) a larger diving air volume facilitates performance of deep dives by increasing the total body O_2 store to 68 ml O_2 kg^{-1}. Although increased O_2 storage and cardiovascular adjustments presumably optimize aerobic metabolism during dives, enhanced anaerobic capacity and hypoxemic tolerance are also essential for longer dives. This was exemplified by a 27.6 min dive, after which the bird required 6 min before it stood up from a prone position, another 20 min before it began to walk, and 8.4 h before it dived again.

Williams, C.L., J.C. Hagelin, and G. Kooyman. 2015. Hidden keys to survival: the type, density, pattern and functional role of emperor penguin body feathers. *Proceedings of the Royal Society B,* doi:10.1098/rspb.2015.2033.

Antarctic penguins survive some of the harshest conditions on the planet. Emperor penguins breed on the sea ice where temperatures drop below −40°C and forage in −1.8°C waters. Their ability to maintain 38°C body temperature in these conditions is due in large part to their feathered coat. Penguins have been reported to have the highest contour feather density of any bird, and both filoplumes and plumules (downy feathers) are reported absent in penguins. In studies modelling the heat transfer properties and the potential biomimetic applications of penguin plumage design, the insulative properties of penguin plumage have been attributed to the single afterfeather attached to contour feathers. This attribution of the afterfeather as the sole insulation component has been repeated in subsequent studies. Our results demonstrate the presence of both plumules and filoplumes in the penguin body plumage. The downy plumules are four times denser than afterfeathers and play a key, previously overlooked role in penguin survival. Our study also does not support the report that emperor penguins have the highest contour feather density.

WEDDELL SEALS

Ainley, D.G., P.A. Cziko, N. Nur, J.J. Rotella, J.T. Eastman, M. LaRue, I. Stirling, and P.A. Abrams. 2020. Further evidence that Antarctic toothfish are important in Weddell seal diet. *Antarctic Science*, doi:10.1017/S0954102020000437.

Antarctic toothfish *Dissostichus mawsoni* and Weddell seals *Leptonychotes weddellii* are important mesopredators in the waters of the Antarctic continental shelf. They compete with each other for prey, yet the seals also prey upon toothfish. Such intraguild predation means that prevalence and respective demographic rates may be negatively correlated, but quantification is lacking. Following a review of their natural histories, we initiate an approach to address this deficiency by analysing scientific fishing catch per unit effort (CPUE; 1975–2011 plus sporadic effort to 2018) in conjunction with an annual index of seal abundance in McMurdo Sound, Ross Sea. We correlated annual variation in scientific CPUE to seal numbers over a 43 year period (1975–2018), complementing an earlier study in the same locality showing CPUE to be negatively correlated with spatial proximity to abundant seals. The observed relationship (more seals with lower CPUE, while controlling for annual trends in each) indicates the importance of toothfish as a dietary item to Weddell seals and highlights the probable importance of intra- and inter-specific competition as well as intraguild predation in seal-toothfish dynamics. Ultimately, it may be necessary to supplement fishery management with targeted ecosystem monitoring to prevent the fishery from having adverse effects on dependent species.

Beltran, R.S., A.L. Kirkham, G.A. Breed, J.W. Testa, and J.M. Burns. 2019. Reproductive success delays moult phenology in a polar mammal. *Scientific Reports* 9: 5221, doi:10.1038/s41598-019-41635-x.

Animals can respond to dynamic environments through phenological plasticity of life history events; however, changes in one part of the annual cycle can diminish the success of subsequent life history events. Our aims were to determine the associations between reproduction and moult phenology across years and to quantify phenological plasticity across varying environmental conditions. We conducted demographic surveys of 4,252 flipper-tagged Weddell seals (Leptonychotes weddellii) in the Ross Sea, Antarctica during four austral summers. At each sighting, seals were assigned a moult code based on the visible presence of new fur and the start date of each animal's moult was back-calculated. Reproductive success and parturition dates were obtained for the breeding season prior to and following the moult. We found that successful reproduction delayed moult by 16 days relative to non-parturient females. Phenology of the intervening moult was indicative of previous reproductive dynamics but not predictive of subsequent reproductive outcomes. Across years, moult phenology varied by about two weeks and covaried strongly with sea ice break-out timing for all reproductive categories. Our findings suggest these polar mammals have some flexibility within the annual cycle that allows adjustment of moult phenology to fluctuating environmental conditions without compromising future reproductive success.

Beltran, R.S., J.W. Testa, and J.M. Burns. 2017. An agent-based bioenergetics model for predicting impacts of environmental change on top predators. *Ecological Modelling* 351 (10): 36–50, https://doi.org/10.1016/j.ecolmodel.2017.02.002.

Understanding why animals move as they do when searching for resources is a central question in ecology, and a prerequisite for the development of predictive process-based models for conservation and management. Many species are central-place foragers (CPF). While several models for CPFs have been proposed, they often assume well-defined return rules to the focal point (like breeding). For some CPFs,

however, the decisions to return to central sites are governed by multiple interactions between environmental and physiological factors. We present AgentSeal, a behaviour- and physiology-based, spatially explicit, agent-based model. We use harbour seals, a marine CPF, as a case study and focus on individuals outside their breeding and moulting seasons to capture general fine- and large-scale movements and drivers behind CPF. We model movement decisions based on optimal foraging strategy, cognitive and physiological processes in a realistic landscape, coupled with realistic prey distribution and tuned to a range of behavioural and physiological patterns observed at different scales and levels of organisation (pattern-orientated modelling, POM). The model can reproduce energetic, movement and other behavioural patterns such as net energy balance, at-sea and on land site fidelity, daily activity budgets and trip extents. The model reveals the crucial elements needed to model return-trips of CPFs including movement characteristics that vary as a function of local environmental conditions, cognitive mapping of foraging areas as points of attraction in subsequent foraging trips, and physiological requirements defining switches between resting and foraging. We discuss potential applications and extensions of the model, including investigations of fundamental questions in foraging ecology: how spatial distribution and aggregation of resources affect movement of marine CPFs; what are the main drivers behind their at-sea site-fidelity to foraging patches? We also discuss applied objectives such as improving our understanding of population-level consequences of anthropogenic disturbances and ultimately evolving AgentSeal into a practical management tool.

Beltran, R.S., J.M. Burns, and G. Breed. 2018. Convergence of biannual moulting strategies across birds and mammals. *Proceedings of Biological Science* 285(1878): 20180318, doi: 10.1098/rspb.2018.0318

Birds and mammals have developed numerous strategies for replacing worn feathers and hair. Moulting usually occurs on an annual basis; however, moults that take place twice per year (biannual moults) also occur. Here, we review the forces driving the evolution of various moult strategies, focusing on the special case of the complete biannual moult as a convergence of selection pressures across birds and mammals. Current evidence suggests that harsh environmental conditions or seasonality (e.g. larger variation in temperatures) drive evolution of a biannual moult. In turn, the biannual moult can respond to secondary selection that results in phenotypic alteration such as colour changes for mate choice dynamics (sexual selection) or camouflage requirements (natural selection). We discuss the contributions of natural and sexual selection to the evolution of biannual moulting strategies in the contexts of energetics, niche selection, functionality and physiological mechanisms. Finally, we suggest that moult strategies are directly related to species niche because environmental attributes drive the utility (e.g. thermoregulation, camouflage, social dynamics) of the hair or feathers. Functional efficiency of moult may be undermined if the pace of evolution fails to match that of the changing climate. Thus, future research should seek to understand the plasticity of moult duration and phenology, especially in the context of annual cycles.

Brault, E., P. Koch, D. Costa, M. McCarthy, L. Hückstädt, K. Goetz, K. Mcmahon, M. Goebel, O. Karlsson, J. Teilmann, T. Harkonen, and K. Harding. 2018. Trophic position and foraging ecology of Ross, Weddell, and Crabeater Seals revealed by compound-specific isotope analysis. *Marine Ecology Progress Series* 611: 1-18.

Ross seals (*Ommatophoca rossii*) are one of the least studied marine mammals, with little known about their foraging ecology. Research to date using bulk stable isotope analysis suggests that Ross seals have a trophic position intermediate between that of the Weddell (*Leptonychotes weddellii*) and crabeater (*Lobodon carcinophaga*) seals. However, consumer bulk isotope values not only reflect trophic dynamics, but also variations in baseline isotope values, which can be substantial. Here, we use a compound specific isotope analysis of amino acids (CSI-AA) to separate isotopic effects of a shifting baseline versus trophic

structure on the foraging ecology of these ecologically important, but poorly understood Antarctic pinnipeds. We find that all three seals use different foraging habitats; Ross seals forage in a pelagic food web distinct from that of crabeater and Weddell seals. Crabeater and Weddell seals are foraging within similar food webs closer to shore. However, isotopic evidence suggests that crabeater seals are likely following sea ice, while Weddell seals target productive areas of the continental shelf of Western Antarctica. In addition, our CSI-AA data indicate that Ross seals have a high trophic position equivalent to that of Weddell seals, contrary to prior conclusions from nitrogen isotope results on bulk tissues. CSI-AA indicates that crabeater seals are at a trophic position lower than that of Ross and Weddell seals, consistent with a krill-dominated diet. Our results redefine the view of the Ross seal trophic dynamics and foraging ecology, while also highlighting the importance of 46 quantifying baseline isotope variations in foraging studies.

Chambert, T.C., J.J. Rotella, and R.A. Garrott. 2015. Female Weddell seals show flexible strategies of colony attendance related to varying environmental conditions. *Ecology* 96: 479-88, doi:10.1890/14-0911.1.

Many animal life cycles involve movements among different habitats to fulfill varying resource demands. There are inherent costs associated with such movements, and the decision to leave or stay at a given location ought to be motivated by the benefits associated with potential target habitats. Because movement patterns, especially those associated with reproduction, can have important implications for the success (survival, reproduction) of individual animals, and therefore a population's dynamics, it is important to identify and understand their sources of variation (environmental and individual). Here, using a mark-recapture, multistate modeling approach, we investigated a set of a priori hypotheses regarding sources and patterns of variation in breeding-colony attendance for Weddell seal (*Leptonychotes weddellii*) females on sabbatical from pup production. For such females, colony attendance might be motivated by predation avoidance and positive social interactions related to reproduction, but some costs, such as reduced foraging opportunities or aggressive interactions with conspecifics, might also exist. We expected these benefits and costs to vary with a female's condition and the environment. Results revealed that the probability of being absent from colonies was higher (1) in years when the extent of local sea ice was larger, (2) for the youngest and oldest individuals, and (3) for females with less reproductive experience. We also found substantial levels of residual individual heterogeneity in these rates. Based on our a priori predictions, we postulate that the decision to attend breeding colonies or not is directly influenced by an individual's physiological condition, as well as by the ice-covered distance to good foraging areas, availability of predator-free haul-out sites, and the level of negative interactions with conspecifics inside colonies. Our results support the idea that in iteroparous species, and colonial animals in particular, seasonal and temporary movements from/to reproductive sites represent flexible behavioral strategies that can play an important role in coping with environmental variability.

Cziko, P.A., L.M. Munger, N.R. Santos, and J.M. Terhune. 2020. Weddell seals produce ultrasonic vocalizations. *Journal of the Acoustical Society of America* 148: 3784–3796, https://doi.org/10.1121/10.0002867

Seals (phocids) are generally not thought to produce vocalizations having ultrasonic fundamental frequencies (≥20 kHz), although previous studies could have been biased by sampling limitations. This study characterizes common, yet, previously undescribed, ultrasonic Weddell seal (*Leptonychotes weddellii*) vocalizations. The vocalizations were identified in more than one year (2017–2018) of broadband acoustic data obtained by a continuously recording underwater observatory in McMurdo Sound, Antarctica. Nine recurrent call types were identified that were composed of single or multiple

vocal elements whose fundamental frequencies spanned the ultrasonic range to nearly 50 kHz. Eleven vocal elements had ultrasonic center frequencies (≥20 kHz), including chirps, whistles, and trills, with two elements at >30 kHz. Six elements had fundamental frequencies always >21 kHz. The fundamental frequency of one repetitive U-shaped whistle element reached 44.2 kHz and descending chirps (≥3.6 ms duration) commenced at ≤49.8 kHz. The source amplitude of one fully ultrasonic chirp element (29.5 kHz center frequency) was 137 dB re 1 lPa-m. Harmonics of some vocalizations exceeded 200 kHz. Ultrasonic vocalizations occurred throughout the year with the usage of repetitive ultrasonic chirp-based calls appearing to dominate in winter darkness. The functional significance of these high-frequency vocalizations is unknown.

Davis, R.W. 2014. A review of the multi-level adaptations for maximizing aerobic dive duration in marine mammals: from biochemistry to behavior. *Journal of Comparative Physiology B* 184:23–53, DOI 10.1007/s00360-013-0782-z

Marine mammals exhibit multi-level adaptations, from cellular biochemistry to behavior, that maximize aerobic dive duration. A dive response during aerobic dives enables the efficient use of blood and muscle oxygen stores, but it is exercise modulated to maximize the aerobic dive limit at different levels of exertion. Blood volume and concentrations of blood hemoglobin and muscle myoglobin are elevated and serve as a significant oxygen store that increases aerobic dive duration. However, myoglobin is not homogeneously distributed in the locomotory muscles and is highest in areas that produce greater force and consume more oxygen during aerobic swimming. Muscle fibers are primarily fast and slow twitch oxidative with elevated mitochondrial volume densities and enhanced oxidative enzyme activities that are highest in areas that produce more force generation. Most of the muscle mitochondria are interfibriller and homogeneously distributed. This reduces the diffusion distance between mitochondria and helps maintain aerobic metabolism under hypoxic conditions. Mitochondrial volume densities and oxidative enzyme activities are also elevated in certain organs such as liver, kidneys, and stomach. Hepatic and renal function along with digestion and assimilation continue during aerobic dives to maintain physiological homeostasis. Most ATP production comes from aerobic fat metabolism in carnivorous marine mammals. Glucose is derived mostly from gluconeogenesis and is conserved for tissues such as red blood cells and the central nervous system. Marine mammals minimize the energetic cost of swimming and diving through body streamlining, efficient, lift-based propulsive appendages, and cost-efficient modes of locomotion that reduce drag and take advantage of changes in buoyancy with depth. Most dives are within the animal's aerobic dive limit, which maximizes time underwater and minimizes recovery time at the surface. The result of these adaptations is increased breath-hold duration and enhanced foraging ability that maximizes energy intake and minimizes energy output while making aerobic dives to depth. These adaptations are the long, evolutionary legacy of an aquatic lifestyle that directly affects the fitness of marine mammal species for different diving abilities and environments.

Davis, R.W., L.A. Fuiman, K.M. Madden, and T.M. Williams. 2013. Classification and behavior of free-ranging Weddell seal dives based on three-dimensional movements and video-recorded observations. *Deep-Sea Research II* 88-89: 65-77. dx.doi.org/10.1016/j.dsr2.2012.07.006

The goal of this study was to classify free-ranging (FR) dives of Weddell seals (*Leptonychotes weddellii*) and to compare them to isolated hole (IH) dives. Classification and comparisons were based on 58 descriptors for three-dimensional dive paths computed from data obtained by attaching video and data recorders to the backs of 12 adult Weddell seals that were free-ranging in eastern McMurdo Sound, Antarctica. We then inferred behavioral functions for the dive classes based on video-recorded observations. Three of the four dive types previously identified from seals diving at an IH occurred in FR seals. Although there were differences associated with location, Types 1, 2 and 3 dives clustered in a

similar pattern in the discriminant analysis for FR and IH dives. Most prey (79%) captures occurred during Type 1 dives, and the primary (99%) prey was Antarctic silverfish (*Pleuragramma antarcticum*). Type 1 dives were the deepest (mean maximum depth 324–378 m), longest in duration (15.0– 27.0 min), covered the greatest total distance (1470–2197 m), and had the steepest dive angles (descents: _301; ascents: þ271). Types 2 and 3 dives formed a continuum from short duration (3.6– 7.5 min), shallow (mean maximum depth 30–66 m) dives that were close to the ice hole (farpoint distance 75–130 m) and often involved aggressive interactions with other seals for breathing opportunities (Type 2) to progressively longer (7.9–17.2 min), deeper (mean maximum depth 81– 143 m) dives that covered greater total distances (878–1194 m) and were associated with transiting between holes, exploring and occasionally foraging (Type 3). Very long distance Type 4 exploratory dives that were identified in the IH study were completely absent in FR seals.

Davis, R.W., and T.M. Williams. 2012. The marine mammal dive response is exercise modulated to maximize aerobic dive duration. *Journal of Comparative Physiology A* 198: 583–591 DOI 10.1007/s00359-012-0731-4.

When aquatically adapted mammals and birds swim submerged, they exhibit a dive response in which breathing ceases, heart rate slows, and blood flow to peripheral tissues and organs is reduced. The most intense dive response occurs during forced submersion which conserves blood oxygen for the brain and heart, thereby preventing asphyxiation. In free-diving animals, the dive response is less profound, and energy metabolism remains aerobic. However, even this relatively moderate bradycardia seems diametrically opposed to the normal cardiovascular response (i.e., tachycardia and peripheral vasodilation) during physical exertion. As a result, there has been a longstanding paradox regarding how aquatic mammals and birds exercise while submerged. We hypothesized based on cardiovascular modeling that heart rate must increase to ensure adequate oxygen delivery to active muscles. Here, we show that heart rate (HR) does indeed increase with flipper or fluke stroke frequency (SF) during voluntary, aerobic dives in Weddell seals (HR = 1.48SF - 8.87) and bottlenose dolphins (HR = 0.99SF + 2.46), respectively, two marine mammal species with different evolutionary lineages. These results support our hypothesis that marine mammals maintain aerobic muscle metabolism while swimming submerged by combining elements of both dive and exercise responses, with one or the other predominating depending on the level of exertion.

Goetz, K.T. 2015. Seasonal habitat preference and foraging behavior of Weddell seals in the western Ross Sea, Antarctica. In *Movement, Habitat, and Foraging Behavior of Weddell Seals (Leptonychotes Weddellii) in the Western Ross Sea, Antarctica*. Unpubl. PhD dissertation, University of California, Santa Cruz.

Weddell seals (*Leptonychotes weddellii)* are top predators in the Southern Ocean and have the southernmost distribution of any mammal on Earth. While the McMurdo Sound population of seals has been extensively studied in the summer, over 20 years have passed since attempts were made to understand their overwinter behavior. Between January and February 2010-2012, we tagged 60 Weddell seals in McMurdo Sound and north along the Victoria Land coast using bio-logging technology. We used general additive models to explain and predict the probability of Weddell seal presence and foraging behavior from eight environmental variables: ice concentration, distance from the 10% ice concentration contour, bathymetry, bathymetric slope, mixed layer depth, modified circumpolar deep water index, distance from the coast, and distance from the continental shelf break. Furthermore, we examined the relationship between foraging behavior and three dive metrics: dive duration, descent rate, and dive depth relative to bathymetric depth. The environmental variables that were significant in explaining Weddell seal presence showed different relationships from those explaining foraging behavior and changed

seasonally. Overall, we found that Weddell seal foraging behavior was relatively low in the summer compared to the rest of the year, which may be attributed to the limited foraging that occurs during reproduction and molting. Habitat and foraging models showed the importance of the seasonal sea-ice extent, open water polynyas, and the diverse topography in explaining the habitat preference and foraging behavior of Weddell seals in the western Ross Sea. In addition, using dive parameters to predict foraging behavior, we found that foraging was higher when seals were either less than 30% to the bottom (pelagic) or were near or at the bottom (bentho-pelagic). Across seasons, Weddell seals preferentially exploited the diverse topography of the Ross Sea, which is composed of a series of shallow banks (< 400 m) and deeper troughs (>500 m) that provides pathways for productive circumpolar deep water (CDW) to flow onto the shelf. This study highlights the importance of overwinter foraging, specifically in recouping body mass lost during the previous summer due to the energetic demands associated with breeding and molting. Knowing how seals respond to seasonal shifts in their natural environment may provide clues as to how Weddell seals will modify their habitat preferences and foraging behavior in response to climate change.

Goetz, K., L. Hückstädt, M. Shero, J. Burns, and D. Costa. 2017. Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. *Deep Sea Research II. Topical Studies in Oceanography* 140: 36-44, https://doi.org/10.1016/j.dsr2.2016.05.017.

Weddell seals (*Leptonychotes weddellii*) are important predators in the Antarctic marine ecosystem, yet little is known about their diet. Previous studies have used scat and stomach content analyses to examine Weddell seal diet, however, these methods are biased towards prey with indigestible hard parts. To provide a more complete picture of their diet, we analyzed the stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$ values) of red blood cells (RBC, n=96, representing a time scale of weeks to months) and vibrissae (n=45, representing months to a year) collected over a three year period (2010–2012). Our objectives were to (1) examine isotopic variation in relation to Weddell seal mass, sex, season, location, percent lipid, and age, and (2) quantify the contribution of prey items to overall diet. Body mass was a significant predictor of $\delta^{13}C$ and $\delta^{15}N$ values for both tissues, though the strength and direction of the relationship varied by year. The prey group consisting of *Pleurogramma antarcticum* and *Trematomus newnesi* was found to be an important dietary component, but its proportional contribution to Weddell seal diet varied with the timeframe represented by each tissue type [median RBC (range): 59.2% (40.2–8 1.1%); median mean vibrissae (range): 69.3% (43.9–89.6%)]. Results from mixing models ran for each seal indicate individual variation in diet. Overall, this study presents novel information on the isotopic variation and diet of Weddell seals over two time scales and provides insight into the feeding ecology of an important Antarctic predator.

Hindell, M.A., R.R. Reisinger, Y. Ropert-Coudert, L.A. Hückstädt, P.N. Trathan, H. Bornemann, K. Goetz ... and Lea, M. A. 2020. Tracking of marine predators to protect Southern Ocean ecosystems. *Nature*, 580(7801):87-92, doi:10.1038/s41586-020-2126-y.

Southern Ocean ecosystems are under pressure from resource exploitation and climate change. Mitigation requires the identification and protection of Areas of Ecological Significance (AESs), which have so far not been determined at the ocean-basin scale. Here, using assemblage-level tracking of marine predators, we identify AESs for this globally important region and assess current threats and protection levels. Integration of more than 4,000 tracks from 17 bird and mammal species reveals AESs around sub-Antarctic islands in the Atlantic and Indian Oceans and over the Antarctic continental shelf. Fishing pressure is disproportionately concentrated inside AESs, and climate change over the next century is predicted to impose pressure on these areas, particularly around the Antarctic continent. At present, 7.1% of the ocean south of 40°S is under formal protection, including 29% of the total AESs. The establishment

and regular revision of networks of protection that encompass AESs are needed to provide long-term mitigation of growing pressures on Southern Ocean ecosystems.

Kim, S.Z., D.G. Ainley, J. Pennycook, and J.T. Eastman. 2011. Antarctic toothfish heads found along tide cracks of the McMurdo Ice Shelf. *Antarctic Science* 23: 469-470.

On 15 November 2009, we found 45 Antarctic toothfish (*Dissostichus mawsoni* Norman) heads along a 3 km stretch of the 10–15 km long tide crack that ran east–west in the McMurdo Ice Shelf just north of Bratina Island (Fig. 1). From 77°59.1'S, 165°36.2'E, we walked along the crack to a seal breathing hole at 78°00.1', 165°31.3'. We walked the same stretch on 7 December, finding also two pieces of fish skin, each 15–20 cm long; and again in November 2010, when we found no new heads. It is possible that the presence of large toothfish is what attracts seals and entices them to remain at under-ice-shelf localities despite the challenge of maintaining breathing holes and foraging continuously from the same fixed point. If toothfish are important to the isolated White Island seals' existence, the recent severe reduction of toothfish in McMurdo Sound (DeVries *et al*. 2008) could have grave negative repercussions for this interesting, scientifically unique population of seals.

Macdonald, K.R., J.J. Rotella, R.A. Garrott, and W.A. Link. 2020. Sources of variation in maternal allocation in a long-lived mammal. *Journal of Animal Ecology* 89:1927–1940, https://doi.org/10.1111/1365-2656.13243.

Life history theory predicts allocation of energy to reproduction varies with maternal age, but additional maternal features may be important to the allocation of energy to reproduction. We aimed to characterize age-specific variation in maternal allocation and assess the relationship between maternal allocation and other static and dynamic maternal features. Mass measurements of 531 mothers and pups were used with Bayesian hierarchical models to explain the relationship between diverse maternal attributes and both the proportion of mass allocated by Weddell seal mothers, and the efficiency of mass transfer from mother to pup during lactation as well as the weaning mass of pups. Our results demonstrated that maternal mass was strongly and positively associated with the relative reserves allocated by a mother and a pup's weaning mass but that the efficiency of mass transfer declines with maternal parturition mass. Birthdate was positively associated with proportion mass allocation and pup weaning mass, but mass transfer efficiency was predicted to be highest at the mean birthdate. The relative allocation of maternal reserves declined with maternal age but the efficiency of mass transfer to pups increases, suggestive of selective disappearance of poor-quality mothers. These findings highlight the importance of considering multiple maternal features when assessing variation in maternal allocation.

Madden, K.M., L.A. Fuiman, T.M. Williams, and R.W. Davis. 2014. Weddell seal foraging dives: comparison of free-ranging and isolated-hole paradigms. *Antarctic Science*, doi:10.1017/S0954102014000297.

Weddell seals are polar predators that must partition their time between many behaviours, including hunting prey at depth and breathing at the surface. Although they have been well studied, little is known about how foraging behaviour changes when access to breathing holes is restricted, such as in the isolated-hole paradigm. The current study took advantage of previously gathered data for seals diving at an isolated hole to compare with foraging behaviour of free-ranging seals that had access to multiple holes. We examined dive structure, hunting tactics, and allocation of time, locomotor activity and energy based on three-dimensional dive profiles and video imagery of prey encounters for two free-ranging and six isolated-hole seals. Midsummer foraging dives of free-ranging seals were remarkably similar to those of seals diving at an isolated hole, but there were differences in two behavioural states and the frequency of several behavioural transitions. Results indicate that seals employ an energetically more conservative

foraging strategy when access to breathing holes is limited and prey are less abundant. These results highlight the importance of understanding the complex interactions between breathing hole access, prey abundance and other factors that may result in different Weddell seal foraging strategies under changing future conditions.

Paterson, J.T., J.J Rotella, J.M. Mannas, and R.A. Garrott. 2016. Patterns of age-related change in reproductive effort differ in the prenatal and postnatal periods in a long-lived mammal. *Journal of Animal Ecology* 85: 1540-1551, https://doi.org/10.1111/1365-2656.12577.

Age-related changes in maternal reproductive allocation for long-lived species are a key prediction from life-history theory. Theoretical and empirical work suggests that allocation may increase with age due to constraint (increases with experience) or restraint (increases with age in the face of declining residual reproductive value), and may decrease among the oldest aged animals due to senescence in reproductive function. Here, we use a hierarchical modelling approach to investigate the age-related patterns of change in maternal reproductive effort in the Weddell seal, a long-lived marine mammal with a protracted period of maternal care during which mothers allocate a large proportion of body mass while feeding little. We find that maternal allocation increases with age for young mothers during both the pre-natal and post-natal periods. In contrast, older mothers demonstrate a senescent decline in pre-natal allocation but allocate more of their declining resources to their offspring during the post-natal period. We also find strong evidence for the importance of individual effects in reproductive allocation among mothers: some mothers consistently produce heavier (or lighter) pups than expected. Our results indicate that maternal allocation changes over a mother's reproductive life span and that age-specific differences differ in notable ways in pre-natal and post-natal periods.

Pearson, L.E., H.E.M. Liwanag, M.O. Hammill, and J.M. Burns. 2014. Thermoregulatory strategy varies among neonatal polar phocids. *Comparative Biochemistry and Physiology, Part A* 178: 59-67, doi:10.1016/j.cbpa.2014.08.006.

Cold environmental conditions and small body size promote heat loss and may create thermoregulatory challenges for marine mammals born in polar regions. However, among polar-born phocid seal species there are variations in physical attributes and environmental conditions at birth, allowing for an interesting contrast in thermoregulatory strategy. We compared thermoregulatory strategies through morphometrics, sculp attributes (conductivity and resistance), nonshivering thermogenesis (NST via uncoupling protein 1; UCP1), and muscle thermogenesis (via enzyme activity) in neonatal harp (*Pagophilus groenlandicus*), hooded (*Cystophora cristata*), and Weddell seals (*Leptonychotes weddellii*). Harp seals are the smallest at birth (9.8±0.7 kg), rely on lanugo (82.49±3.70% of thermal resistance), and are capable of NST through expression of UCP1 in brown adipose tissue (BAT). In contrast, hooded seal neonates (26.8±1.3 kg) have 2.06±0.23 cm of blubber, accounting for 38.19±6.07% of their thermal resistance. They are not capable of NST, as UCP1 is not expressed. The large Weddell seal neonates (31.5±4.9 kg) rely on lanugo (89.85±1.25% of thermal resistance) like harp seals, but no evidence of BAT was found. Muscle enzyme activity was highest in Weddell seal neonates, suggesting that they rely primarily on muscle thermogenesis. Similar total thermal resistance, combined with marked differences in thermogenic capacity of NST and ST among species, strongly supports that thermoregulatory strategy in neonatal phocids is more closely tied to pups' surface area to volume ratio (SA:V) and potential for early water immersion rather than mass and ambient environmental conditions.

Rotella, J.J., J.T. Paterson, and R.A. Garrott. 2016. Birth dates vary with fixed and dynamic maternal features, offspring sex, and extreme climatic events in a high-latitude marine mammal. *Ecology and Evolution* 6: 1930-1941, doi: 10.1002/ece3.1985.

Reproductive synchrony tends to be widespread in diverse species of plants and animals, especially at higher latitudes. However, for long-lived mammals, birth dates for different individuals can vary by weeks within a population. A mother's birth timing can reveal useful information about her reproductive abilities and have important implications for the characteristics and survival of her offspring. Despite this, our current knowledge of factors associated with variation in birth dates is modest. We used long-term data for known-age Weddell seals in Antarctica and a Bayesian hierarchical modeling approach to study how birth dates varied with fixed and temporally varying features of mothers, whether sex allocation varied with birth timing, and annual variation in birth dates. Based on birth dates for 4465 pups born to 1117 mothers aged 4-31, we found that diverse features of mothers were associated with variation in birth dates. Maternal identity was the most important among these. Unlike most studies, which have reported that birth dates occur earlier as mothers age, we found that birth dates progressively occurred earlier in the year in the early part of a mother's reproductive life, reached a minimum at age 16, and then occurred later at later ages. Birth dates were positively related to a mother's age at primiparity and recent reproductive effort. The earliest birth dates were for pups born to prime-age mothers who did not reproduce in the previous year but began reproduction early in life, suggesting that females in the best condition gave birth earlier than others. If so, our finding that male pups tended to be born earlier than females provides support for the Trivers-Willard sex-allocation model. Average birth dates were quite consistent across years, except for 2 years that had notable delays and occurred during the period when massive icebergs were present and disrupted the ecosystem.

Salas, L., N. Nur, D. Ainley, J. Burns, J. Rotella, and G. Ballard. 2017. Coping with loss of large, energy-dense prey: A potential bottleneck for Weddell Seals in the Ross Sea. *Ecological Applications* 27: 10-25.

Extraction of Antarctic toothfish (*Dissostichus mawsoni*) in the Ross Sea began in 1997, following a management plan that targets the largest fish with a goal of reducing the spawning biomass by 50% over 35 yr. We investigate the potential long-term consequences of the reduced availability of this prey for Weddell seals (*Leptonychotes weddellii*). Energy demands in seals are acute, especially immediately following lactation, when females must recover substantial mass and cope with molting costs. We tested the hypothesis that toothfish are critically important for adult female seals during this period. Toothfish body mass is three orders of magnitude greater, and its energy density nearly double that of the most common seal prey, Antarctic silverfish (*Pleuragramma antarcticum*). Reduction or elimination of toothfish consumption could impair a female's ability to sufficiently recover and successfully produce a pup in the following pupping season. Our goals are to (1) illustrate mechanisms and conditions whereby toothfish depletion might plausibly affect seal population trends; (2) identify measurable parameters of the seals' ecology that may help better understand the potential negative impact of toothfish depletion on seal populations; and (3) promote a precautionary management approach for the fishery that includes monitoring of seal populations We constructed a set of inter-linked models of seal diving behavior, physiological condition, and demography based on existing information. We evaluate the effect of the following factors on seal mass recovery and intrinsic population growth rates: fishery depletion rate, daily diving limits, probability of a successful dive, and body mass recovery target. We show that loss of toothfish has the greatest potential impact on seal populations' growth rate. Under some scenarios, populations may decrease at >10% per year. Critical parameters to better understand fishery impacts include prevalence and size of toothfish in the seals' diet; the relationship between diet and the rate of mass recovery; and female breeding propensity in relation to body condition at the end of the molting period. Our results lend support to concerns about the potential negative impact of toothfish extraction in the Ross Sea; and to advocate for a precautionary management approach by the fishery.

Shero, MR, K.T. Goetz, D.P. Costa, and J.M. Burns. 2018. Temporal changes in Weddell seal dive behavior over winter: are females increasing foraging efforts to support gestation? *Ecology and Evolution*, doi:10.1002/ece3.4643.

In capital-breeding marine mammals, prey acquisition during the foraging trip coinciding with gestation must provide energy to meet the immediate needs of the growing fetus and also a store to meet the subsequent demands of lactation. Weddell seals (*Leptonychotes weddellii*) that give birth following the gestational (winter) foraging period gain similar proportions of mass and lipid as compared to females that fail to give birth. Therefore, any changes in foraging behavior can be attributed to gestational costs. To investigate differences in foraging effort associated with successful reproduction, twenty-three satellite tags were deployed on post-molt female Weddell seals in the Ross Sea. Of the 20 females that returned to the area the following year, 12 females gave birth and eight did not. Females that gave birth the following year began the winter foraging period with significantly longer and deeper dives, as compared to non-reproductive seals. Mid- to late winter, reproductive females spent a significantly greater proportion of the day diving, and either depressed their diving metabolic rates (DMR), or exceeded their calculated aerobic dive limit (cADL) more frequently than females that returned without a pup. Moreover, non-reproductive females organized their dives into 2–3 short bouts per day on average ($BOUT_{short}$; 7.06 ± 1.29 hr; mean ± 95% CI), whereas reproductive females made 1–2 $BOUT_{short}$ per day (10.9 ± 2.84 hr), comprising one long daily foraging bout without rest. The magnitude of the increase in dive activity budgets and depression in calculated DMR closely matched the estimated energetic requirements of supporting a fetus. This study is one of the first to identify increases in foraging effort that are associated with successful reproduction in a top predator and indicates that reproductive females must operate closer to their physiological limits to support gestational costs.

Shero, M.R., D.P. Costa, and J. M. Burns. 2015. Scaling matters: incorporating body composition into Weddell seal seasonal oxygen store comparisons reveals maintenance of aerobic capacities. Journal of Comparative Physiology B. 185: 811-24. doi: 10.1007/s00360-015-0922-8.

Adult Weddell seals (*Leptonychotes weddellii*) haul-out on the ice in October/November (austral spring) for the breeding season and reduce foraging activities for ~4 months until their molt in the austral fall (January/February). After these periods, animals are at their leanest and resume actively foraging for the austral winter. In mammals, decreased exercise and hypoxia exposure typically lead to decreased production of O2-carrying proteins and muscle wasting, while endurance training increases aerobic potential. To test whether similar effects were present in marine mammals, this study compared the physiology of 53 post-molt female Weddell seals in the austral fall to 47 pre-breeding females during the spring in McMurdo Sound, Antarctica. Once body mass and condition (lipid) were controlled for, there were no seasonal changes in total body oxygen (TBO2) stores. Within each season, hematocrit and hemoglobin values were negatively correlated with animal size, and larger animals had lower mass-specific TBO2 stores. But because larger seals had lower mass-specific metabolic rates, their calculated aerobic dive limit was similar to smaller seals. Indicators of muscular efficiency, myosin heavy chain composition, myoglobin concentrations, and aerobic enzyme activities (citrate synthase and β-hydroxyacyl CoA dehydrogenase) were likewise maintained across the year. The preservation of aerobic capacity is likely critical to foraging capabilities, so that following the molt Weddell seals can rapidly regain body mass at the start of winter foraging. In contrast, muscle lactate dehydrogenase activity, a marker of anaerobic metabolism, exhibited seasonal plasticity in this diving top predator and was lowest after the summer period of reduced activity.

Shero, M.R, Krotz, R.T, Costa, D.P, Avery, J.P, and J.M. Burns. 2015. How do overwinter changes in body condition and hormone profiles influence Weddell seal reproductive success? *Functional Ecology* 29: 1278-1291, doi:10.1111/1365-2435.12434.

Reproductive success can be influenced by maternal physiological condition at the time of embryo implantation and by foraging success during gestation. Polar marine mammals experience drastic fluctuations in body composition (lipid stores) as a result of life-history events and large-scale changes in seasonal productivity and environmental conditions. These species provide the opportunity to explore physiological parameters important to reproductive success. There are conflicting physiological demands on Weddell seal (*Leptonychotes weddellii*) females during the moult period, when animals are at their leanest but still must generate an energetically costly new pelage and begin active gestation. To investigate the impact of post-moult condition and hormonal mediators on the reproductive success of the southernmost breeding mammal, body composition was determined for post-moult (fall; 53 non-reproductive) and pre-breeding (spring; 31 non-reproductive, 17 reproductive) adult female Weddell seals. Animals were significantly larger and had greater lipid stores in spring, after the winter foraging period. There were no differences in the proportion of mass or condition gained overwinter between females that gave birth (n = 12) and those that did not (n = 8) the following year. Changes in body condition were correlated with endocrine factors that influence energy allocation, such as cortisol, growth hormone (GH), insulin-like growth factor (IGF)-1 and thyroid hormones (T_3 and T_4). Of these, GH and T_4 were significantly higher during the post-moult period, likely to promote protein sparing and hair regeneration. In addition, females that had higher T_4 concentrations in fall were significantly more likely to have a pup the following year, possibly due to the role of thyroid hormones in embryo attachment. This suggests that hormones influencing fuel use during the moult may also impact subsequent reproductive success. Unlike some other large pinnipeds, Weddell seals are not capital breeders. This work indicates that gestating Weddell seals do not gain as much mass or energy overwinter in preparation for lactation the following year as lower-latitude phocid species, which might explain why female Weddell seals rely on foraging to meet energetic demands during lactation.

Walcott, S., M. Horning, A. Kirkham, and J.M. Burns. 2020. Thermoregulatory costs in molting Antarctic Weddell seals: impacts of physiological and environmental conditions. *Conservation Physiology* 8(1): coaa022, doi: 10.1093/conphys/coaa022.

For polar marine mammals, the energetic cost of thermoregulation depends on ambient conditions in the highly variable surrounding environment. Heat conservation strategies used by pinnipeds to reduce total heat loss include small surface area to volume ratios, the ability to limit perfusion and thick subcutaneous blubber layers. There are limits to how cool the skin surface may remain without compromising function, especially during the annual pelage molt, when hair and skin are replaced. To determine if actively molting seals incur higher thermoregulatory costs, surface temperature (ST) and heat flux (HF) were measured in 93 adult female Weddell seals (Leptonychotes weddellii) both prior to and during the active molting period using direct sensors and infrared imaging. Linear mixed-effect models revealed that ST increased significantly with increased ambient temperature and decreased wind speed (contributing 44.6 and 41.7% of the attributed variance, respectively). Seal STs were not impacted by molt status, but were maintained at 11.2 ± 0.3°C warmer than the ambient temperature. Infrared imaging results averaged 15.1 ± 1.4°C warmer than direct ST measurements. In contrast, HF was significantly higher in seals in early molting stages compared to the pre-molt season ($P < 0.001$) and molt status accounted for 66.5% of the variance in HF. Thermoregulatory costs calculated from estimated basal metabolic rate and measured HF were more than double for molting seals as compared to those in pre-molt. This suggests that perfusion is increased during molt to support follicle development, despite the increased energetic costs associated with higher HF rates. Because ST, HF and thermoregulatory costs are

strongly influenced by ambient conditions, molt timing is likely under selective pressure to occur during the warmest period of the year. Shifts in environmental conditions that delay molt phenology or increase HF rates could negatively impact seal populations by further increasing thermoregulatory costs.

CETACEANS

Ainley, D., T. Joyce, B. Saenz, R. Pitman, J. Durban, G. Ballard, K. Daly, and S. Kim. 2020. Foraging patterns of Antarctic minke whales in McMurdo Sound, Ross Sea. ***Antarctic Science*** **32(6):454-465, doi:10.1017/S0954102020000310.**

Evidence indicates that Antarctic minke whales (AMWs) in the Ross Sea affect the foraging behaviour, especially diet, of sympatric Adélie penguins (ADPEs) by, we hypothesize, influencing the availability of prey they have in common, mainly crystal krill. To further investigate this interaction, we undertook a study in McMurdo Sound during 2012–2013 and 2014–2015 using telemetry and biologging of whales and penguins, shore-based observations and quantification of the preyscape. The 3D distribution and density of prey were assessed using a remotely operated vehicle deployed along and to the interior of the fast-ice edge where AMWs and ADPEs focused their foraging. Acoustic surveys of prey and foraging behaviour of predators indicate that prey remained abundant under the fast ice, becoming successively available to air-breathing predators only as the fast ice retreated. Over both seasons, the ADPE diet included less krill and more Antarctic silverfish once AMWs became abundant, but the penguins' foraging behaviour (i.e. time spent foraging, dive depth, distance from colony) did not change. In addition, over time, krill abundance decreased in the upper water column near the ice edge, consistent with the hypothesis (and previously gathered information) that AMW and ADPE foraging contributed to an alteration of prey availability.

Lauriano, G., E. Pirotta, T. Joyce, R. L. Pitman, A. Borrell, and S. Panigada. 2020. Movements, diving behaviour and diet of type-C killer whales (*Orcinus orca*) in the Ross Sea, Antarctica. ***Aquatic Conservation*****, doi: 10.1002/aqc.3371.**

The fish-eating, type-C ecotype, killer whale is a top predator in the Ross Sea, Antarctica. Increasing knowledge of this animal's foraging habitats, diet and movement patterns is listed amongst the research priorities adopted under the framework of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). To contribute to this goal, satellite transmitters were deployed on 10 type-C killer whales and skin biopsies were obtained from seven individuals in Terra Nova Bay (Ross Sea) during austral summer (January–February) 2015. Hierarchical switching state–space models (hSSSM) were applied to Argos satellite tracking data to describe the movements of tagged whales, which were then paired with available diving data. Stable isotopes analyses were performed on the biopsy samples to describe the diet. A total of 8,803 Argos locations were available to fit the hSSSM. All whales engaged in potential foraging activity in localized areas along the Ross Sea coastline, followed by uninterrupted travel (i.e. migration) outside Antarctic waters, with no evidence of foraging activity. The pattern of deeper dives matched the occurrence of encamped behaviour indicated by the hSSSM results. The stable isotopes analysis indicated that Antarctic toothfish comprised the largest component (35%) of the prey biomass, raising concerns since this species is targeted by commercial fishery in the Ross Sea Region. These results provide new insights into the ecology of type-C killer whales in the Ross Sea Region, underlining a potential threat from commercial fishing in the area. Considering the recent establishment of the Ross Sea Region Marine Protected Area, these findings will contribute to the required Research and Monitoring Programme of the Marine Protected Area and provide new empirical evidence to inform conservation measures in the existing Terra Nova Bay Antarctic Special Protected Area.

Pitman, R.L., J.W. Durban, T. Joyce, H. Fearnbach, S. Panigada, and G. Lauriano. 2019. Skin in the game: epidermal molt as a driver of long-distance migration in whales. *Marine Mammal Science*, doi:10.1111/mms.12661.

Long-distance migration in whales has historically been described as an annual, round-trip movement between high latitude, summer feeding grounds, and low-latitude, winter breeding areas, but there is no consensus about why whales travel to the tropics to breed. Between January 2009 and February 2016, we satellite-tagged 62 Antarctic killer whales (*Orcinus orca*) of four different ecotypes, of which at least three made short-term (6–8 weeks), long-distance (maximum 11,000 km, round trip), essentially nonstop, migrations to warm waters (SST 20C–24C), and back. We previously suggested that Antarctic killer whales could conserve body heat in subfreezing (to −1.9C) waters by reducing blood flow to their skin, but that this might preclude normal (i.e., continuous) epidermal molt, and necessitate periodic trips to warm waters for routine skin maintenance ("skin molt migration," SMM). In contrast to the century-old "feeding/breeding" migration paradigm, but consistent with a "feeding/molting" hypothesis, the current study provides additional evidence that deferred skin molt could be the main driver of long-distance migration for antarctic killer whales. Furthermore, we argue that for all whales that forage in polar latitudes and migrate to tropical waters, SMM might also allow them to exploit rich prey resources in a physiologically challenging environment and maintain healthy skin.

Wellard, R., R. Pitman, J. Durban, and C. Erbe. 2020. Cold call: the acoustic repertoire of Ross Sea Killer Whales (*Orcinus orca*, Type C) in McMurdo Sound, Antarctica. *Royal Society Open Science* 7: 191228, doi:10.1098/rsos.191228.

Killer whales (*Orcinus orca*) are top marine predators occurring globally. In Antarctic waters, five ecotypes have been described, with Type C being the smallest form of killer whale known. Acoustic recordings of nine encounters of Type C killer whales were collected in 2012 and 2013 in McMurdo Sound, Ross Sea. In a combined 3.5 h of recordings, 6386 killer whale vocalizations were detected and graded based on their signal-to-noise ratio. Spectrograms of the highest-quality calls were examined for characteristic patterns yielding a catalogue of 28 call types (comprising 1250 calls). Acoustic parameters of each call were measured and summarized by call type. Type C killer whales produced complex calls, consisting of multiple frequency-modulated, amplitude-modulated and pulsed components. Often, two components occurred simultaneously, forming a biphonation; although the biphonic components did not necessarily start and end together, with one component lasting over several others. The addition and deletion of components yielded call subtypes. Call complexity appears stable over time and may be related to feeding ecology. Characterization of the Type C acoustic repertoire is an important step for the development of passive acoustic monitoring of the diverse assemblage of killer whale ecotypes in Antarctica's rapidly changing marine ecosystems.

ROSS SEA BENTHIC COMMUNITIES AND PROCESSES

Bjordal, C. G., and P.K. Dayton. 2020. First evidence of microbial wood degradation in the coastal waters of the Antarctic. *Scientific Reports* 10(1), doi:10.1038/s41598-020-68613-y.

Wood submerged in saline and oxygenated marine waters worldwide is efciently degraded by crustaceans and molluscs. Nevertheless, in the cold coastal waters of the Antarctic, these degraders seem to be absent and no evidence of other wood-degrading organisms has been reported so far. Here we examine long-term exposed anthropogenic wood material (Douglas Fir) collected at the seafloor close to McMurdo station, Antarctica. We used light and scanning electron microscopy and demonstrate that two

types of specialized lignocellulolytic microbes—soft rot fungi and tunnelling bacteria—are active and degrade wood in this extreme environment. Fungal decay dominates and hyphae penetrate the outer 2–4 mm of the wood surface. Decay rates observed are about two orders of magnitude lower than normal. The fungi and bacteria, as well as their respective cavities and tunnels, are slightly smaller than normal, which might represent an adaptation to the extreme cold environment. Our results establish that there is ongoing wood degradation also in the Antarctic, albeit at a vastly reduced rate compared to warmer environments. Historical shipwrecks resting on the seafloor are most likely still in good condition, although surface details such as wood carvings, tool marks, and paint slowly disintegrate due to microbial decay.

Buckley, B.A. 2013. Rapid change in shallow water fish species composition in an historically stable Antarctic environment. *Antarctic Science* 25: 676–680, doi:10.1017/S0954102013000114.

McMurdo Sound, Antarctica, is home to a unique marine biota with an ecology that has evolved in this frigid environment over millions of years. The region is one of the least disturbed, and possibly the last pristine, marine ecosystem on Earth. Here, the results of three seasons of fishing in the shallow nearshore waters of McMurdo Sound are reported. A shift in the composition of small fish species at one site, Inaccessible Island, has been observed in just five years. The shift in shallow water species composition occurred during a period that followed the maturation of a commercial fishery for the Antarctic toothfish, *Dissostichus mawsoni* Norman, a predator of smaller fish, and the presence of a large iceberg, termed B-15, at the mouth of McMurdo Sound during the early 2000s that trapped the annual sea ice in the area leading to the unusual accrual of multi-year sea ice. The data presented here provide a current record of species composition and physiological condition of small, shallow water fishes at three sites in McMurdo Sound, providing a current baseline for the assessment of future changes wrought by environmental changes and unprecedented fishery pressures in the Ross Sea.

Bowser, S.S., S.E. Walker, and P. Cziko. 2019. Population dynamics in the Antarctic benthos: Inter-annual fluctuation of foraminiferal, tunicate, and scallop abundances in Explorers Cove, western McMurdo Sound. *PaleoBios*, *36*.

To understand whether or how climate change will drive changes in Antarctic marine benthic ecosystems, one must first understand baseline population dynamics of the system. Species abundances may change seasonally, annually, or on decadal scales, for example, or due to rare cataclysmic events unrelated to a changing climate. We used SCUBA to collect foraminiferan protists in Explorers Cove, McMurdo Sound in austral spring in 1986 to 2016. Our research involved the cell biology and molecular evolution of large (>1mm), early evolving, agglutinated members of this assemblage, but during the course of this work we also charted changes in their populations from bulk surface sediment collection and semi-quantitative 0.25-m^2 to 1-m^2 quadrat sampling. We focused on two species of *Astrammina,* two species of *Crithionina*, *Notodendrodes hyalinosphaira*, larger calcareous species (*Pyrgo peruviana*, *Cornuspira* sp., *Glandulina* sp.), as well as *Gromia* cf. *oviformis*. During the 1990s, we noted that relative species abundances fluctuated substantially on an inter-annual basis. For example, *Astrammina rara* was very abundant in 1990 (75.9% of the total assemblage), dipped in 1993 and 1994 (54.9% and 58.7%, respectively), and rebounded in 1998 and 1999 (65% and 67%). By contrast, *Astrammina triangularis* abundances were low in 1990 (0.3%), peaked in 1993 (18.3%) and declined to 6.5% of the total assemblage in 1998. During the 2000s, we began tracking numerical densities quantitatively by taking 7.4cm-diameter cores and wet-picking specimens recovered from the top cm of sediment. Similar fluctuations were observed in target species. Most notable was the rapid increase in a “silver saccamminid” species, first recognized at low abundance in 1998. In 2005 there were 412/m2 and since that time their numbers have increased to become the dominant species in the area (186,732/m2 in 2016). Over our study period, we also noted changes in meio- and macrofauna. In particular, we noted a dramatic

increase in the numerical density of small epifaunal and infaunal tunicates (360/m2 in 2005 to 11,379 in 2016). We also observed a dramatic, qualitative reduction in the population of the Antarctic scallop *Adamussium colbecki* along the Explorers Cove ice wall, prompting us to examine the extent of their decrease by re-sampling the six stations reported by Stockton in 1982 using his methods. The results were surprising: The average scallop population had decreased 74%. Similar results were obtained in 2015 and 2016. Although the cause of the reduction remains unknown, we noted new recruits on the seafloor in 2016, indicating initial recovery from this event. Clearly, the Antarctic benthos is anything but static. Standardized, long-term environmental monitoring is necessary to uncover changes attributable to climate change. Explorer's cove, with its proximity to McMurdo Station and the Taylor Dry Valley LTER site, is a prime candidate for such an endeavor.

Cronin, K.E., S.E. Walker, and S.S. Bowser. 2021. Striae in the Antarctic scallop *Adamussium colbecki* provide environmental insights but not reliable age increments. *Polar Biology* 44: 729–738.

Subannual growth increments in bivalves provide insight into past seasonal seawater conditions at high temporal resolution. The Antarctic scallop *Adamussium colbecki* (Smith 1902) accretes putatively fortnightly surficial growth lines (striae) and interstrial growth increments have the potential to archive sea ice variations. Cycles of paired groups of wide and narrow striae are sometimes used to determine ontogenetic age in these scallops, but previous quantitative work describing strial grouping and formation is limited to a few months of juvenile growth. Here, we analyze striae patterns in *A. colbecki* collected from two sites on western McMurdo Sound, Antarctica that differ by sea ice duration: Explorers Cove with multi-annual sea ice and Bay of Sails with annual sea ice. At both sites, visual analysis of striae groups and cycles (using the methods of previous authors) and wavelet analysis of interstrial increments suggest that striae groups are too variable to age *A. colbecki*. Only ~ 40% of striae groups and cycles conformed to expectations from annual cycles of fortnightly growth increments (~ 26 striae per cycle). Moreover, only one scallop from each study site displayed consistent periodicity at ~ 26 striae throughout juvenile growth in wavelet analysis. Though striae grouping was inconsistent, analysis of concurrent growth of juvenile scallops from Explorers Cove suggested strong environmental control on interstrial increment size and thus that strial increments are suitable for further analysis as sea ice proxies. Finally, the multi-annual sea ice site had smaller interstrial growth increments and less valve wear than the annual sea ice site, indicating overall slower growth and possibly lower metabolic activity.

Cziko, P., A. Devries, and C.H. Cheng. 2014. High-resolution benthic seawater temperature record 1999–2012 (25–40 m depth) from near intake jetty at McMurdo Station, Antarctica. *Integrated Earth Data Applications*. [dataset]

Cziko, P., and C.H. Cheng. 2006. A New Species of Notothenиid (Perciformes: Notothenioidei) Fish from McMurdo Sound, Antarctica. *Copeia* 2006(4): 752-759.

A new species of notothenиid fish, *Cryothenia amphitreta*, is described from a single gravid female collected in mid-November 2004 by divers in McMurdo Sound in the Ross Sea region of Antarctica. The new species closely resembles the only known congener, *C. peninsulae*, collected off the west coast of the Antarctic Peninsula, but differs substantially in pelvic-fin length (13.4 vs. 19.3-24.4% SL), total vertebrae (57 vs. 50-53), body size at maturity (261 vs. 100-144 mm), and interorbital-pit morphology. The neutrally-buoyant *C. amphitreta* is characterized by a wide, well-defined interorbital pit divided by a raised medial ridge, scales anterior to this depression in the interorbital region, and a dark pigmentation of the mouth, gill, and body cavity linings. This species is protected against freezing by high levels of antifreeze proteins in its body fluids. Phylogenetic reconstruction using the mitochondrial NADH dehydrogenase subunit 2 (mtND2) suggests that *C. amphitreta* falls within the current designation

of the nototheniid subfamily Trematominae. Spawning behaviour and early development in the naked dragonfish *Gymnodraco acuticeps*.

Dayton, P.K., G.A. Robilliard, J.S. Oliver, S. Kim, K. Hammerstrom, K. O'Connor, J. Fisher, J. Barber, and S. Jarrell. 2018. Long-term persistence of wood on the sea floor at McMurdo Sound, Antarctica. *Antarctic Science* 30: 355-356.

Most wood in the ocean is quickly colonized and consumed by many types of animals and microbes. Wood falls in the deep sea have been well studied and include a diverse macrofaunal assemblage, including over 40 species of Xylophagainae bivalves and many species of crustaceans, polychaetes and even anemones (Turner 2002, Bernardino et al. 2010). Two pieces of wood were recovered from the sea floor at McMurdo Station, Antarctica in November 2010, having lain there for c. 50 years with no obvious deterioration. Archaeologists usually study ancient wood from anaerobic conditions, but these samples are from highly oxygenated waters. There are many parallels between the benthos of McMurdo Sound and that of the deep sea (Dayton & Oliver 1977), and therefore a comparison with the deep sea is of interest.

Dayton, P.K., and K. Hammerstrom. 2018. A hagfish at Salmon Bay, McMurdo Sound, Antarctica? *Antarctic Science* 30: 243–244.

While installing some experiments in the extremely dark conditions at Salmon Bay in the extreme south-western part of McMurdo Sound in December 1988, a white patch was observed and photographed, and in the dark, it was assumed to be another example of the nermertean *Parborlasia corrugatus* (McIntosh, 1876) responding to the release of sperm from *Laternula elliptica* (King & Broderip, 1831) and foraging on the clam (Dayton et al. unpublished data). Lacking underwater lights on that dive, the animal was not observed, and only recently the photograph was retrieved and it was realized that the animal was not a nemertean, but looked like a hagfish. The idea was discounted, as hagfish have never been observed in the high Antarctic despite over a century of extensive use of seal and fish baited traps that surely would have attracted hagfish.

Dayton, P.K., K. Hammerstrom, S.C. Jarrell, S. Kim, W. Nordhausen, D.J. Osborne, and S.F. Thrush. 2016. Unusual coastal flood impacts in Salmon Valley, McMurdo Sound, Antarctica. *Antarctic Science* 28: 1-7, doi:10.1017/S0954102016000171.

Large floods bringing significant sediments into the coastal oceans have not been observed in Antarctica. We report evidence of a large flood event depositing over 50 cm of sediment onto the nearshore benthic habitat at Salmon Bay, Antarctica, between 1990 and 2010. Besides direct observations of the sedimentation, the evidence involves a debris flow covering old tyre tracks from the early 1960s, as well as evidence of a considerable amount of sediment transported onto the Salmon Creek delta. We believe that the flood was sourced from the Salmon Glacier and possibly the smaller Blackwelder Glacier. Such floods will be more common in the future and it is important to better understand their ecological impacts with good monitoring programmes.

Dayton, P., S. Jarrell, S. Kim, S. Thrush, K. Hammerstrom, M. Slattery, and E. Parnell. 2016. Surprising episodic recruitment and growth of Antarctic sponges: Implications for ecological resilience. *Journal of Experimental Marine Biology and Ecology* 482:38-55, http://dx.doi.org/10.1016/j.jembe.2016.05.001.

Sponges are the most conspicuous component of the Antarctic benthic ecosystem, a system under stress both from climate change and fishing activities. Observations over four decades are compiled and

reveal extremely episodic sponge recruitment and growth. Recruitment occurred under different oceanographic conditions on both sides of McMurdo Sound. Most of the sponges appear to have recruited in the late 1990s–2000. Observations from 2000 to 2010 follow thirty years of relative stasis with very little sponge recruitment or growth followed by a general pattern of recruitment by some forty species of sponges. That there was almost no recruitment observed on natural substrata emphasizes the contrast between potential and realized recruitment. This unique data set was derived from a region noted for physical stasis, but the episodic ecological phenomena highlight the importance of rare events. Against a background of intermittent food resources and the low metabolic costs of stasis, understanding the causes of irregular larval supply, dispersal processes, recruitment success and survivorship becomes critical to predicting ecosystem dynamics and resilience in response to increasing environmental change. Our time-series emphasizes that long-term data collection is essential for meaningful forecasts about environmental change in the unique benthic ecosystems of the Antarctic shelf.

Dayton, P.K., S.C. Jarrell, S. Kim, E. Parnell, S.F. Thrush, K. Hammerstrom, and J.J. Leichter. 2019. Benthic responses to an Antarctic regime shift: food particle size and recruitment biology. *Ecological Applications 29*(1), p.e01823.

Polar ecosystems are bellwether indicators of climate change and offer insights into ecological resilience. In this study, we describe contrasting responses to an apparent regime shift of two very different benthic communities in McMurdo Sound, Antarctica. We compared species-specific patterns of benthic invertebrate abundance and size between the west (low productivity) and east (higher productivity) sides of McMurdo Sound across multiple decades (1960s–2010) to depths of 60 m. We present possible factors associated with the observed changes. A massive and unprecedented shift in sponge recruitment and growth on artificial substrata observed between the 1980s and 2010 contrasts with lack of dramatic sponge settlement and growth on natural substrata, emphasizing poorly understood sponge recruitment biology. We present observations of changes in populations of sponges, bryozoans, bivalves, and deposit-feeding invertebrates in the natural communities on both sides of the sound. Scientific data for Antarctic benthic ecosystems are scant, but we gather multiple lines of evidence to examine possible processes in regional-scale oceanography during the eight years in which the sea ice did not clear out of the southern portion of McMurdo Sound. We suggest that large icebergs blocked currents and advected plankton, allowed thicker multi-year ice, and reduced light to the benthos. This, in addition to a possible increase in iron released from rapidly melting glaciers, fundamentally shifted the quantity and quality of primary production in McMurdo Sound. A hypothesized shift from large to small food particles is consistent with increased recruitment and growth of sponges on artificial substrata, filter-feeding polychaetes, and some bryozoans, as well as reduced populations of bivalves and crinoids that favor large particles, and echinoderms *Sterechinus neumayeri* and *Odontaster validus* that predominantly feed on benthic diatoms and large phytoplankton mats that drape the seafloor after spring blooms. This response of different guilds of filter feeders to a hypothesized shift from large to small phytoplankton points to the enormous need for and potential value of holistic monitoring programs, particularly in pristine ecosystems, that could yield both fundamental ecological insights and knowledge that can be applied to critical conservation concerns as climate change continues.

Dayton P.K., S. Kim, S.C. Jarrell, J.S. Oliver, K. Hammerstrom, J.L. Fisher, K. O'Connor, J.S. Barber, G. Robilliard, J. Barry, A.R. Thurber, and K. Conlan. 2013. Recruitment, growth and mortality of an Antarctic hexactinellid sponge, *Anoxycalyx joubini*. *PLoS ONE* 8(2): e56939, doi:10.1371/journal.pone.0056939.

Polar ecosystems are sensitive to climate forcing, and we often lack baselines to evaluate changes. Here we report a nearly 50-year study in which a sudden shift in the population dynamics of an

ecologically important, structure-forming hexactinellid sponge, *Anoxycalyx joubini* was observed. This is the largest Antarctic sponge, with individuals growing over two meters tall. In order to investigate life history characteristics of Antarctic marine invertebrates, artificial substrata were deployed at a number of sites in the southern portion of the Ross Sea between 1967 and 1975. Over a 22-year period, no growth or settlement was recorded for *A. joubini* on these substrata; however, in 2004 and 2010, *A. joubini* was observed to have settled and grown to large sizes on some but not all artificial substrata. This single settlement and growth event correlates with a region-wide shift in phytoplankton productivity driven by the calving of a massive iceberg. We also report almost complete mortality of large sponges followed over 40 years. Given our warming global climate, similar system-wide changes are expected in the future.

Dayton, P.K., J.S. Oliver, S.F. Thrush, and K. Hammerstrom. 2019. Bacteria defend carrion from scavengers. *Antarctic Science* 31: 13-15, doi:10.1017/s0954102018000457.

Carrion in the form of dead seal pups and algal mats placed on soft bottom habitats at Explorers Cove and Salmon Bay, McMurdo Sound, attract scavenging invertebrates that are driven away by hydrogen sulphide produced by sulphate-reducing bacteria sequestered below a layer of Beggiatoa/Thioploca-like filamentous bacteria. This system is usually found for lipid-rich marine mammal carrion, but also occurred with natural algal mats.

Kim, S., and C. Collins. 2021. Iceberg disturbance to benthic communities in McMurdo Sound, Antarctica. *Polar Record, i*n press.

On the continental shelf of the Antarctic the major disturbance to benthic ecosystems is from iceberg scouring, however, this is based on observations from the Peninsula region. We combine observation and experimentation in the McMurdo Sound region of the Ross Sea to determine if community recovery patterns there are similar to those in better-studied Antarctic regions, and if local immigration is an important factor in recovery dynamics. We found that regardless of habitat differences in depth, substrate, and oceanographic setting, iceberg disturbance strongly impacted benthic communities in McMurdo Sound. Notably, in shallow water (<30 m) where anchor ice is an annual disturbance, both the benthic communities and recovery processes were more variable than at deeper locations. A manipulative experiment performed in a shallow area indicated that recruitment might be more important than immigration to infaunal community recovery. We conclude that whilst disturbance frequency influences dominant epifauna, recovery from iceberg disturbance is a slow ecological progression that is dependent on the extremely inconsistent recruitment processes of the high Antarctic benthic ecosystem.

Kim, S. 2019. Complex life under the McMurdo Ice Shelf, and some speculations on food webs. *Antarctic Science* 31: 80-88, doi:10.1017/S0954102018000561.

Habitats under ice shelves are minimally explored, primarily because of technological limitations. These areas are separated from photosynthetic primary productivity by thick ice and distance to open water. Nevertheless, a diverse macrofaunal benthic community was discovered at 188 m depth, 80 km back from the edge of the McMurdo Ice Shelf. The general habitat was fine sediment with occasional dropstones, and dominant taxa were polychaetes and brittle stars, with alcyonacean soft corals and anemones on hard substrates. Gelatinous animals were abundant near the seafloor, and possibly part of a food web that supports the benthic community.

Kim, S., K. Hammerstrom, K.W. Conlan, and A.R. Thurber. 2010. Polar ecosystem dynamics: recovery of communities from organic enrichment in McMurdo Sound, Antarctica. *Integrative and Comparative Biology* 50: 1031–1040, doi:10.1093/icb/icq058.

Community structure and diversity are influenced by patterns of disturbance and input of food. In Antarctica, the marine ecosystem undergoes highly seasonal changes in availability of light and in primary production. Near research stations, organic input from human activities can disturb the regular productivity regime with a consistent input of sewage. McMurdo Sound has both high-productivity and low-productivity habitats, thereby providing an ideal test bed for community recovery dynamics under polar conditions. We used experimental manipulations of the subtidal communities to test the hypotheses that (1) benthic communities respond differently to disturbance from organic enrichment versus burial and (2) community response also varies in areas with different natural patterns of food supply. Both in low and high-food habitats, the strongest community response was to organic enrichment and resulted in dominance of typical organic-enrichment specialists. In habitats with highly seasonal productivity, community response was predictable and recovery was rapid. In habitats with low productivity, community variability was high and caging treatments suggested that inconsistencies were due to patchy impacts by scavengers. In areas normally subject to regular organic enrichment, either from primary production or from further up the food web (defecation by marine mammals), recovery of benthic communities takes only years even in a polar system. However, a low-productivity regime is as common in near shore habitats around the continent; under these conditions, recovery of benthic communities from disturbance is likely to be much slower and follow a variable ecological trajectory.

Kim, S., K. Hammerstrom, and P. Dayton. 2019. Epifaunal community response to iceberg-mediated environmental change in McMurdo Sound, Antarctica. ***Marine Ecology Progress Series*** **613, doi:10.3354/meps12899.**

High-latitude marine communities are dependent on sea ice patterns. Sea ice cover limits light, and hence primary production and food supply. Plankton, carried by currents from open water to areas under the sea ice, provides a transitory food resource that is spatially and temporally variable. We recorded epifaunal abundances at 17 sites in McMurdo Sound, Antarctica, over 12 yr, and found differences in communities based on location and time. The differences in location support patterns observed in long-term infaunal studies, which are primarily driven by currents, food availability, and larval supply. The temporal differences, highlighting 2004 and 2009 as years of change, match the altered persistence of sea ice in the region, caused by the appearance and disappearance of mega-icebergs. The temporal changes were driven by changes in abundance of species that filter feed on large particulates. The shift in current patterns that occurred due to mega-icebergs decreased the normal food supply in the region. In addition to the decrease in food availability, we suggest that the reduced light resulting from thicker-than-normal sea ice resulted in a shift to smaller phytoplankton. A change in food quality as well as quantity may have influenced the temporal change in epifaunal communities.

Lawrence, J.D., B.E. Schmidt, L. Winslow, P. Doran, J.J. Buffo, S. Kim, C.C. Walker, M. Skidmore, K.M. Soderlund, J.S. Greenbaum, D.D. Blankenship, N. Bramall, A. Johnson, F. Rack, W.B. Stone, and the SIMPLE Field Team. 2017. McMurdo ice shelf as an ocean world analog: Supercooled water and ice mass balance. 2017. ***Astrobiology Science Conference***

Lawrence, J.D., B.E. Schmidt, L. Winslow, P. Doran, S. Kim, C.C. Walker, J.J. Buffo, M. Skidmore, K.M. Soderulund, D.D. Blankenship, N. Bramall, A. Johnson, F. Rack, W.B. Stone, and the SIMPLE Field Team. Insights into ice-ocean interactions on Earth and Europa. 2016. ***47th Lunar and Planetary Science Conference*****.**

Lesser, M.P., and M. Slattery. 2015. Picoplankton consumption supports the ascidian ***Cnemidocarpa verrucosa*** **in McMurdo Sound, Antarctica.** ***Marine Ecology Progress Series*** **525: 117-126.**

Polar marine ecosystems commonly have a seasonal pulse of primary productivity with large diatoms or prymnesiophytes dominating. Along with benthic production (i.e. micro - phyto benthos), the annual phytoplankton bloom provides an essential source of food for several trophic levels, including many invertebrate communities. The oceanographic and productivity patterns in McMurdo Sound, Antarctica, result in benthic communities that include high-density assemblages of active and passive suspension feeders. For many years, it has been assumed that these benthic suspension-feeding communities went into a period of quiescence during the austral winter and spring in response to the low food and chronically low temperatures as a strategy to conserve energy. There is increasing evidence, however, that suspension feeders can feed throughout most of the year, with many using picoplankton (0.2 to 2.0 μm) as a food source. It is now recognized that picoplankton, especially heterotrophic prokaryotes, are a diverse and important component of the Southern Ocean bacterio plankton community and a dominant component of the plankton during austral winter and early austral spring in McMurdo Sound. Here, we show that the common ascidian *Cnemidocarpa verrucosa* consumes picoplankton prior to the annual spring bloom. Differences in food availability at different sites (Cape Armitage versus Cape Evans) and differences in filtration efficiencies on different fractions of the plankton community result in this ascidian acquiring significantly more carbon and energy at Cape Evans, where higher densities of *C. verrucosa* reside. This study emphasizes the importance of picoplankton as a food resource for the Antarctic benthic suspension-feeding community.

Marsh, A.G., and A.A. Pasqualone. 2014. DNA methylation and temperature stress in an Antarctic polychaete, *Spiophanes tcherniai*. *Frontiers in Physiology* 5*:* 173, doi:10.3389/fphys.2014.00173.

Epigenetic modifications of DNA and histones are a primary mechanism by which gene expression activities may be modified in response to environmental stimuli. Here we characterize patterns of methyl-cytosine composition in the marine polychaete *Spiophanes tcherniai* from McMurdo Sound, Antarctica. We cultured adult worms at two temperatures, −1.5°C (ambient control) and +4°C (warm treatment), for 4 weeks. We observed a rapid capacity for *S. tcherniai* organismal respiration rates and underlying catalytic rates of citrate synthase at +4°C to return to control levels in less than 4 weeks. We profiled changes in the methylation states of CpG sites in these treatments using an NGS strategy to computationally reconstruct and quantify methylation status across the genome. In our analysis we recovered 120,000 CpG sites in assembled contigs from both treatments. Of those, we were able to align 28,000 CpG sites in common between the two sample groups. In comparing these aligned sites between treatments, only 3000 (11%) evidenced a change in methylation state, but over 85% of changes involved a gain of a 5-methyl group on a CpG site (net increase in methyation). The ability to score CpG sites as partially methylated among gDNA copies in a sample opens up a new avenue for assessing DNA methylation responses to changing environments. By quantitatively distinguishing a “mixed” population of copies of one CpG site, we can begin to identify dynamic, non-binary, continuous-response reactions in DNA methylation intensity or density that previously may have been overlooked as noise.

McClintock, J.B., M.O. Amsler, R.A. Angus, R.C. Challener, J.B. Schram, C.D. Amsler, C.L. Mah, J. Cuce, and B.J. Baker. 2011. The Mg-calcite composition of Antarctic echinoderms: important implications for predicting the impacts of ocean acidification. *The Journal of Geology* 119: 457-466.

The Southern Ocean is considered to be the canary in the coal mine with respect to the first effects of ocean acidification (OA). This vulnerability is due to naturally low carbonate ion concentrations that result from the effect of low temperature on acid-base dissociation coefficients, from the high solubility of CO2 at low temperature, and from ocean mixing. Consequently, the two calcium carbonate polymorphs, aragonite and calcite, are expected to become undersaturated in the Southern Ocean within 50 and 100 years, respectively. Marine invertebrates such as echinoderms, whose skeletons are classified

as high-magnesium carbonate (>4% mol MgCO3), are even more vulnerable to OA than organisms whose skeletons consist primarily of aragonite or calcite, with respect to both increased susceptibility to skeletal dissolution and further challenge to their production of skeletal elements. Currently, despite their critical importance to predicting the effects of OA, there is almost no information on the Mg-calcite composition of Antarctic echinoderms, a group known to be a major contributor to the global marine carbon cycle. Here we report the Mg-calcite compositions of 26 species of Antarctic echinoderms, representing four classes. As seen in tropical and temperate echinoderms, Mg-calcite levels varied with taxonomic class, with sea stars generally having the highest levels. When combined with published data for echinoderms from primarily temperate and tropical latitudes, our findings support the hypothesis that Mg-calcite level varies inversely with latitude. Sea stars and brittle stars, key players in Antarctic benthic communities, are likely to be the first echinoderms to be challenged by near-term OA.

Moran, A.L., H.A. Woods, C.M. Shishido, S.J. Lane, and B.W. Tobalske. 2018. Predatory behavior of giant Antarctic sea spiders (*Colossendeis*) in nearshore environments. *Invertebrate Biology* 137*:* 116-123.

Pycnogonids in the genus *Colossendeis* are found in the deep sea and Southern Ocean. Although the genus contains the largest and most conspicuous species of sea spiders, little is known about their ecology or behavior. We documented two species feeding on a variety of benthic and pelagic invertebrates during three diving field seasons at McMurdo Station, Antarctica. Individuals of one species, *Colossendeis megalonyx*, fed on a variety of pelagic organisms, particularly the pteropod *Clione antarctica*. We used video to document rapid capture of individuals of *C. antarctica* by captive specimens of *C. megalonyx* in the laboratory, and we suggest that, at least in the nearshore environment, pelagic invertebrates are an important food source for this and potentially other pycnogonid species.

Moran, A.L., and H.A. Woods. 2012. Why might they be giants? Towards an understanding of polar gigantism. *Journal of Experimental Biology* 215*:* 1995-2002, doi:10.1242/jeb.067066.

Beginning with the earliest expeditions to the poles, over 100 years ago, scientists have compiled an impressive list of polar taxa whose body sizes are unusually large. This phenomenon has become known as ‘polar gigantism’. In the intervening years, biologists have proposed a multitude of hypotheses to explain polar gigantism. These hypotheses run the gamut from invoking release from physical and physiological constraints, to systematic changes in developmental trajectories, to community-level outcomes of broader ecological and evolutionary processes. Here we review polar gigantism and emphasize two main problems. The first is to determine the true strength and generality of this pattern: how prevalent is polar gigantism across taxonomic units? Despite many published descriptions of polar giants, we still have a poor grasp of whether these species are unusual outliers or represent more systematic shifts in distributions of body size. Indeed, current data indicate that some groups show gigantism at the poles whereas others show nanism. The second problem is to identify underlying mechanisms or processes that could drive taxa, or even just allow them, to evolve especially large body size. The contenders are diverse and no clear winner has yet emerged. Distinguishing among the contenders will require better sampling of taxa in both temperate and polar waters and sustained efforts by comparative physiologists and evolutionary ecologists in a strongly comparative framework.

O’Loughlin, P.M., G. Paulay, N. Davey, and F. Michonneau. 2011. The Antarctic region as a marine biodiversity hotspot for echinoderms: Diversity and diversification of sea cucumbers. *Deep-Sea Research II* 58: 264-275, dx.doi.org/10.1016/j.dsr2.2010.10.011.

The Antarctic region is renowned for its isolated, unusual, diverse, and disharmonic marine fauna. Holothuroids are especially diverse, with 187 species (including 51 that are undescribed) recorded

south of the Antarctic Convergence. This represents ~4% of the documented Antarctic marine biota, and ~10% of the world's holothuroid diversity. We present evidence that both inter-regional speciation with southern cold-temperate regions and intra-regional diversification has contributed to species richness. The Antarctic fauna is isolated, with few shallow-water Antarctic species known from north of the Convergence, yet several species show recent transgression of this boundary followed by genetic divergence. Interchange at longer time scales is evidenced by the scarcity of endemic genera (10of55) and occurrence of all six holothuroid orders within the region. While most Antarctic holothuroid morphospecies have circum-polar distributions, mtDNA sequence data demonstrate substantial geographic differentiation in many of these. Thus, most of the 37 holothuroid species recorded from shelf/slope depths in the Weddell Sea have also been found in collections from Prydz Bay and the RossSea. Yet 17of28 morphospecies and complexes studied show allopatric differentiation around the continent, on average into three divergent lineages each, suggesting that morphological data fails to reflect the level of differentiation. Interchange and local radiation of colonizers appear to have rapidly built diversity in the Antarctic, despite the potential of cold temperatures (and associated long generation times) to slow the rate of evolution.

Rhodes, A.C., N.F. Carvalho, T.A. Palmer, L.J. Hyde, and P.A. Montagna. 2015. Distribution of two species of the genus *Nototanais* spp.(Tanaidacea) in Winter Quarters Bay and waters adjoining McMurdo Station, McMurdo Sound, Antarctica. *Polar Biology* 38: 1623-1629.

Nototanais is the most commonly found peracarid crustacean genus in Antarctic waters. The only two species in the genus, *Nototanais dimorphus* and *Nototanais antarcticus*, have been found to have overlapping circumpolar distributions in depths from 7 m to 585 m around Antarctica. However, only one species, *N. dimorphus*, has been recorded during yearly sampling from 2000 to 2010 at nine shallow (12–36 m) benthic pollution monitoring sites in Winter Quarters Bay and waters adjoining McMurdo Station, McMurdo Sound, Antarctica. These stations varied by depth, anchor ice formation and anthropogenic contamination. In 2011 and 2012, 1071 specimens of *Nototanais* spp. were collected and separated by species, gender and life stage. *N. antarcticus* was confirmed to co-occur with *N. dimorphus* at four of nine long-term monitoring sites. One station had no occurrences of either species. *N. antarcticus* was found in very low abundances in relation to *N. dimorphus*, indicating that individual species distributions may be modified by pollution and anchor ice, among other biological factors.

Szuta, D. 2017. *Community structure and zonation of Antarctic benthic invertebrates: using a remotely operated vehicle under ice to define biological patterns*. MSc Thesis, Moss Landing Marine Lab, CA, doi: https://doi.org/10.31979/etd.nvk8-486g.

The Ross Sea, Antarctica is a deep bay of the Southern Ocean that exhibits seasonal sea ice and is adjacent to a permanent ice shelf overlying seawater. In 2008 and 2009, imagery of the seafloor under the McMurdo Ice Shelf and under the seasonal ice in the Ross Sea was collected via remotely operated vehicle (ROV) at depths to 300 m. Distinct differences in Antarctic benthic communities were observed over multiple environmental gradients. Species abundance typically exhibited a unimodal distribution with depth with mid-depth peaks, reflecting a food limitation at the deep end and potentially ice disturbance on the shallow end. Diversity and depth had a unimodal relationship at two of three sites encompassing a depth gradient. In terms of functional groups, the proportion of suspension feeders decreased with depth at one site, and no pattern was found at other sites. The group of sessile predators, comprised of several species of anemones, increased with depth proportionally, suggesting that they use a range of feeding strategies to adapt to life at depth. Benthic communities under seasonal ice were different than those under permanent ice shelves, with higher overall species diversity, a greater proportion of suspension feeders, and a degree of magnitude higher abundance.

Thurber, A.R., S. Seabrook, and R.M. Welsh 2020. Riddles in the cold: Antarctic endemism and microbial succession impact methane cycling in the Southern Ocean. ***Proceedings of the Royal Society B*** **287: 20201134, http://dx.doi.org/10.1098/rspb.2020.1134.**

Antarctica is estimated to contain as much as a quarter of earth's marine methane, however we have not discovered an active Antarctic methane seep limiting our understanding of the methane cycle. In 2011, an expansive (70 m × 1 m) microbial mat formed at 10 m water depth in the Ross Sea, Antarctica which we identify here to be a high latitude hydrogen sulfide and methane seep. Through 16S rRNA gene analysis on samples collected 1 year and 5 years after the methane seep formed, we identify the taxa involved in the Antarctic methane cycle and quantify the response rate of the microbial community to a novel input of methane. One year after the seep formed, ANaerobic MEthane oxidizing archaea (ANME), the dominant sink of methane globally, were absent. Five years later, ANME were found to make up to 4% of the microbial community, however the dominant member of this group observed (ANME-1) were unexpected considering the cold temperature (−1.8°C) and high sulfate concentrations (greater than 24 mM) present at this site. Additionally, the microbial community had not yet formed a sufficient filter to mitigate the release of methane from the sediment; methane flux from the sediment was still significant at 3.1 mmol CH_4 m^{-2} d^{-1}. We hypothesize that this 5 year time point represents an early successional stage of the microbiota in response to methane input. This study provides the first report of the evolution of a seep system from a non-seep environment, and reveals that the rate of microbial succession may have an unrealized impact on greenhouse gas emission from marine methane reservoirs.

Wing, S.R., J.J. Leichter, L.C. Wing, D. Stokes, S.J.Genovese, R.M. McMullin, and O.A. Shatova. 2018. Contribution of sea ice microbial production to Antarctic benthic communities is driven by sea ice dynamics and composition of functional guilds. ***Global Change Biology*** **24: 3642-3653, doi:10.1111/gcb.14291**.

Organic matter produced by the sea ice microbial community (SIMCo) is an important link between sea ice dynamics and secondary production in near-shore food webs of Antarctica. Sea ice conditions in McMurdo Sound were quantified from time series of MODIS satellite images for Sept. 1 through Feb. 28 of 2007-2015. A predictable sea ice persistence gradient along the length of the Sound and evidence for a distinct change in sea ice dynamics in 2011 were observed. We used stable isotope analysis (δ13 C and δ15 N) of SIMCo, suspended particulate organic matter (SPOM) and shallow water (10-20 m) macroinvertebrates to reveal patterns in trophic structure of, and incorporation of organic matter from SIMCo into, benthic communities at eight sites distributed along the sea ice persistence gradient. Mass-balance analysis revealed distinct trophic architecture among communities and large fluxes of SIMCo into the near-shore food web, with the estimates ranging from 2 to 84% of organic matter derived from SIMCo for individual species. Analysis of patterns in density, and biomass of macroinvertebrate communities among sites allowed us to model net incorporation of organic matter from SIMCo, in terms of biomass per unit area (g/m^2), into benthic communities. Here, organic matter derived from SIMCo supported 39 to 71 per cent of total biomass. Furthermore, for six species, we observed declines in contribution of SIMCo between years with persistent sea ice (2008-2009) and years with extensive sea ice breakout (2012-2015). Our data demonstrate the vital role of SIMCo in ecosystem function in Antarctica and strong linkages between sea ice dynamics and near-shore secondary productivity. These results have important implications for our understanding of how benthic communities will respond to changes in sea ice dynamics associated with climate change and highlight the important role of shallow water macroinvertebrate communities as sentinels of change for the Antarctic marine ecosystem.

ROSS SEA POLLUTION AND WILDLIFE HEALTH

Buck, C.B.., Van Doorslaer, K., Peretti, A,. Geoghegan, E.M., Tisza, M.J., An, P., Katz, J.P., Pipas, J.M., McBride, A.A., Camus, A.C., McDermott, A.J., Dill, J.A., Delwart, E., Ng, T.F., Farkas, K., Austin, C., Kraberger, S., Davison, W., Pastrana, D.V., Varsani, A. 2016. The Ancient Evolutionary History of Polyomaviruses. PLoS Pathog 12:e1005574.

Polyomaviruses are a family of DNA tumor viruses that are known to infect mammals and birds. To investigate the deeper evolutionary history of the family, we used a combination of viral metagenomics, bioinformatics, and structural modeling approaches to identify and characterize polyomavirus sequences associated with fish and arthropods. Analyses drawing upon the divergent new sequences indicate that polyomaviruses have been gradually co-evolving with their animal hosts for at least half a billion years. Phylogenetic analyses of individual polyomavirus genes suggest that some modern polyomavirus species arose after ancient recombination events involving distantly related polyomavirus lineages. The improved evolutionary model provides a useful platform for developing a more accurate taxonomic classification system for the viral family *Polyomaviridae*.

Chen, D., R.C. Hale, M.J. La Guardia, D. Luellen, S. Kim, and H.N. Geisz. 2015. Hexabromocyclododecane flame retardant in Antarctica: Research stations as sources. *Environmental Pollution* 206: 611-618.

Historical persistent organic pollutants (POPs) are banned from Antarctica under international treaty; but contemporary-use POPs can enter as additives within polymer and textile products. Over their useful lives these products may release additives in-situ. Indeed, we observed 226 and 109 ng/g dry weight (dw) of the total concentrations of α-, β- and γ-hexabromocyclododecane (HBCD) in indoor dust from McMurdo Station (U.S.) and Scott Station (New Zealand), respectively. Sewage sludge collected from wastewater treatment facilities at these stations exhibited ∑HBCD of 45 and 69 ng/g dw, respectively. Contaminants originally within the bases may exit to the local outdoor environment via wastewaters. Near McMurdo, maximum ∑HBCD levels in surficial marine sediments and aquatic biota (invertebrates and fish) were 2350 ng/g (total organic carbon basis) and 554 ng/g lipid weight, respectively. Levels declined with distance from McMurdo. Our results illustrate that Antarctic research stations serve as local HBCD sources to the pristine Antarctic environment.

Collins, C.A. 2015. *Natural and anthropogenic disturbance in McMurdo Sound, Antarctica: Iceberg scours, human-derived pollutants, and their effects on benthic communities*. Unpubl. MSc thesis, Moss Landing Marine Lab, CA, doi: https://doi.org/10.31979/etd.bu3s-5bp7

The purpose of this study was to explore the impact of icebergs on infaunal communities in McMurdo Sound, using cores taken from naturally occurring scours, experimental plots simulating iceberg disturbance, and undisturbed reference areas spanning a 24 year time period. Iceberg scours and experimental plots altered infaunal abundances, reduced diversity, and changed species compositions. Abundances were lower at inside scour locations, dominated by a suite of mobile crustaceans. Common sessile space-dominating species were higher at scour edges, suggesting that recolonization of scours occur inward from the edges. When compared to other samples from the McMurdo Sound exposed to varying degrees of anthropogenic disturbance and environmental conditions, iceberg scour samples had high levels of abundance and species richness, with reduced levels of diversity. These results suggest Antarctic benthic communities are resilient to episodic iceberg disturbance, yet lack the ability to cope with high levels of human-derived pollutants.

Conlan, K.E., S.L. Kim, A.R. Thurber, and E. Hendrycks. 2010. Benthic changes at McMurdo Station, Antarctica following local sewage treatment and regional iceberg-mediated productivity decline. *Marine Pollution Bulletin* 60: 419–432.

McMurdo Station, the largest research station in Antarctica, ceased on-site garbage dumping in 1988 and initiated sewage treatment in 2003. In 2003–2004 its sea-ice regime was altered by the massive B-15A and C-19 iceberg groundings in the Ross Sea, approximately 100 km distant. Here we follow macrofaunal response to these changes relative to a baseline sampled since 1988. In the submarine garbage dump, surface contaminants levels have declined but associated macrofaunal recolonization is not yet evident. Although sewage-associated macrofauna were still abundant around the outfall nearly 2 yr after initiation of treatment, small changes downcurrent as far as 434 m from the outfall suggest some community recovery. Widespread community changes in 2003–2004, not seen in the decade previously, suggests that the benthos collectively responded to major changes in sea-ice regime and phytoplankton production caused by the iceberg groundings.

Fahsbender, E., J.M. Burns, S. Kim, S. Kraberger, G. Frankfurter, A. Eilers, M. Shero, R. Beltran, A. Kirkham, R. McCorkell, R. Berngartt, M.F. Male, G. Ballard, D.G. Ainley, M. Breitbart, and A. Varsani. 2017. Diverse and highly recombinant anelloviruses associated with Weddell seals in Antarctica. *Virus Evolution* 3(1): vex017, doi:10.1093/ve/vex017.

The viruses circulating among Antarctic wildlife remain largely unknown. In an effort to identify viruses associated with Weddell seals (*Leptonychotes weddellii*) inhabiting the Ross Sea, vaginal and nasal swabs, and faecal samples were collected between November 2014 and February 2015. In addition, a Weddell seal kidney and South Polar skua (*Stercorarius maccormicki*) faeces were opportunistically sampled. Using high throughput sequencing, we identified and recovered 152 anellovirus genomes that share 63-70% genome-wide identities with other pinniped anelloviruses. Genome-wide pairwise comparisons coupled with phylogenetic analysis revealed two novel anellovirus species, tentatively named torque teno *Leptonychotes weddellii* virus (TTLwV) -1 and -2. TTLwV-1 (n = 133, genomes encompassing 40 genotypes) is highly recombinant, whereas TTLwV-2 (n = 19, genomes encompassing three genotypes) is relatively less recombinant. This study documents ubiquitous TTLwVs among Weddell seals in Antarctica with frequent co-infection by multiple genotypes, however, the role these anelloviruses play in seal health remains unknown.

Grimaldi, W., D.G. Ainley, and M. Massaro. 2018. Multi-year serological evaluation of three viral agents in the Adélie Penguin (*Pygoscelis adeliae*) on Ross Island, Antarctica. *Polar Biology* 41: 2023–2031, https://doi.org/10.1007/s00300-018-2342-1.

Serological assays are commonly used in wildlife health studies to screen for exposure of an individual or a population to infectious agents. Such assays can therefore provide useful information regarding the health status of an individual or for determining the prevalence of a pathogen within a population. In this study, serological assays of three viral agents have been conducted on the Adélie Penguin (*Pygoscelis adeliae*) on Ross Island, Ross Sea, Antarctica. We sampled adult Adélie Penguins during three consecutive summer breeding seasons (2010–2011, 2011–2012 and 2012–2013), and tested those samples for antibodies to avian influenza A virus, Newcastle disease virus, and infectious bursal disease virus. No antibodies were detected for avian influenza A virus in any season. Two samples in 2012–2013 were positive for Newcastle disease virus antibodies and a total of 10 samples were positive for infectious bursal disease virus antibodies during this study. This information establishes baseline data for these three viruses in Adélie Penguins at this location and can be used for future comparisons of disease prevalence in this population.

Grimaldi, W., J. Jabour, and E.J. Woehler. 2010. Considerations for minimising the spread of infectious disease in Antarctic seabirds and seals. *Polar Record,* doi:10.1017/S0032247410000100.

Before 1998, concern was raised over the potential for human activities in Antarctica to introduce infectious disease organisms to native wildlife. A workshop was held that year to address this issue. In the last decade, there has been a dramatic increase in human traffic to the Antarctic and the number of commercial tourists visiting the Antarctic has steadily risen. Personnel of national science programmes, though relatively few in numbers, have the most intimate contact with wildlife and thus the greater potential to introduce organisms through their research activities. Many visitors are now able to arrive in the Antarctic from temperate regions within hours by aircraft, and from northern polar regions within 24 to 36 hours. Tourists, by their high numbers, also have the potential to transfer infectious disease agents among commonly visited sites. As of 2009, no outbreaks of infectious diseases in the Antarctic reported in the literature have been directly attributed to human activity, but the ameliorating climate may break down the barriers that have kept Antarctic wildlife relatively free of infectious diseases. Several agents of infectious diseases reported in Antarctic seabirds and seals are assessed for their likelihood to occur more frequently in terms of the characteristics of the agent, the behaviour of Antarctic wildlife, and the effects of an ameliorating climate (regional warming) in conjunction with continued increasing human activities.

Grimaldi, W.W., P.J. Seddon, P.O'B. Lyver, S. Nakagawa, and D.M. Tompkins. 2015. Infectious diseases of Antarctic penguins: current status and future threats. *Polar Biology*, doi 10.1007/s00300-014-1632-5.

Until roughly 200 years ago, the Antarctic was untouched by humankind. With ratification of the Antarctic Treaty in 1961, this region was set aside forever for peaceful purposes and as a science preserve. However, Antarctic national programs and tourism activities are growing, increasing the risks of introduction of infectious diseases into wildlife within the Antarctic Treaty area. The immunological naiveté of Antarctic species makes them vulnerable to pathogen's commonplace in other parts of the world. We review past disease investigations of Antarctic penguins, and outline potential drivers of future disease emergence. Efforts to establish the nature of disease agents in Antarctic penguins, although ongoing since the late 1950s, remain not only patchy and limited in scope but are a lower priority issue for the majority of Antarctic Treaty parties. Pollution, increased connectivity, and global environmental change affecting pathogens and vectors at high latitudes are likely to drive future disease emergence in this region. However, a coordinated plan for disease emergence monitoring is lacking with no formally established programs in place, and surveillance is currently left up to individual interested research groups. We propose possible steps toward the goal of establishing baseline data and tracking infectious diseases in Antarctic penguin species, with the anticipated further increase in human activity and environmental changes in the Antarctic in mind.

Grimaldi, W.W., R.J. Hall, D.D. White, J. Wang, M. Massaro, and D.M. Tompkins. 2015. First report of a feather loss condition in Adélie penguins (*Pygoscelis adeliae*) on Ross Island, Antarctica, and a preliminary investigation of its cause. *Emu* 115: 185–189, http://dx.doi.org/10.1071/MU14068.

Since the mid-1980s, observations of marine animals with alopecia have been reported worldwide, although in most cases specific causes and consequences have not been elucidated. Adding to that list, an unprecedented feather loss condition affecting ~1 in 1000 adult Adélie penguins was observed at the beginning of December 2011 at each of three colonies on Ross Island, Antarctica. Feather loss was again observed in 2012–13 and 2013–14. The condition was characterised by irregular patches of bare skin on various parts of the body well before the usual period of moult. Blood samples, plucked feathers

and cloacal swabs were obtained to investigate the cause or causes of this abnormal loss of feathers. No ectoparasites were detected on physical inspection of any birds or by scanning electron microscopy of feathers removed from birds experiencing feather loss. Blood smears were negative for hemoparasites. There was statistical support for mild lymphocytosis and moderate basophilia from the results of white blood-cell differentials in penguins with feather loss compared with those with no feather loss. Blood samples were negative to aPCR diagnostic specific for beak and feather disease virus. Three new putative RNA viruses were detected by high-throughput sequencing of cloacal samples, showing similarity to rotaviruses, astroviruses and picornaviruses. Although the significance of these viruses is not known, extended investigation into this feather loss condition is needed.

Kennicutt, M.C. II, A. Klein, P. Montagna, S. Sweet, T. Wade, T. Palmer, J. Sericano, and G. Denoux. 2010. Temporal and spatial patterns of anthropogenic disturbance at McMurdo Station, Antarctica. *Environmental Research Letters* 5: 1-10.

Human visitations to Antarctica have increased in recent decades, raising concerns about preserving the continent's environmental quality. To understand the spatial and temporal patterns of anthropogenic disturbances at the largest scientific station in Antarctica, McMurdo Station, a long-term monitoring program has been implemented. Results from the first nine years (1999–2007) of monitoring are reported. Most physical disturbance of land surfaces occurred prior to 1970 during initial establishment of the station. Hydrocarbons from fuel and anthropogenic metals occur in patches of tens to hundreds of square meters in areas of fuel usage and storage. Most soil contaminant concentrations are not expected to elicit biological responses. Past disposal practices have contaminated marine sediments with polychlorinated biphenyls (PCBs), petroleum hydrocarbons, and metals in close proximity to the station that often exceed concentrations expected to elicit biological responses. Chemical contamination and organic enrichment reduced marine benthic ecological integrity within a few hundred meters offshore of the station. Contaminants were detected in marine benthic organisms confirming bioavailability and uptake. PCBs in sediments are similar to suspected source materials, indicating minimal microbial degradation decades after release. Anthropogenic disturbance of the marine environment is likely to persist for decades. A number of monitoring design elements, indicators and methodologies used in temperate climates were effective and provide guidance for monitoring programs elsewhere in Antarctica.

Klein, A.G., Sweet, S.T., Kennicutt II, M.C., Wade, T.L., Palmer, T.A. and Montagna, P., 2014. Long-Term Monitoring of Human Impacts to the Terrestrial Environment at McMurdo Station. In *Antarctic Futures* (pp. 213-227). Springer, Dordrecht.

Klein, A.G., S.T. Sweet, T.L. Wade, J.L. Sericano, and M.C. Kennicutt, II. 2012. Spatial patterns of total petroleum hydrocarbons in the terrestrial environment at McMurdo Station, Antarctica. *Antarctic Science* 24: 450-466, doi:10.1017/S0954102012000429.

Fossil fuels are used throughout the United States Antarctic Program. Accidental releases of petroleum hydrocarbons are the leading source of environmental contamination. Since 1999 McMurdo Station has been the site of the most extensive environmental monitoring programme in Antarctica. Nearly 2500 surface soil samples were collected from 1999–2007 to determine the spatial ‘‘footprint’’ of petroleum hydrocarbons. Total petroleum hydrocarbons (TPH) concentrations were measured using a high-resolution capillary gas chromatographic method with flame ionization detection. Three distinct TPH patterns were detected: low molecular weight gasoline/JP5/AN8, residual weathered petroleum and an unresolved complex mixture of high molecular weight material. Overall TPH concentrations were low with 38% of the samples having TPH concentrations below 30 ppm and 58% below 100 ppm. Total petroleum hydrocarbon concentrations above 30 ppm are largely confined to the central portions of the

station, along roads and in other areas where elevated TPH would be expected. Peripheral areas typically have TPH concentrations below 15 ppm. Areas of elevated TPH concentrations are patchy and of limited spatial extent, seldom extending over distances of 100 m. This environmental monitoring programme is ongoing and can serve as an example to other Antarctic programmes concerned with monitoring environmental impacts.

Lenihan, H.S., C.H. Peterson, R.J. Miller, M. Kayal, and M. Potoski. 2018. Biotic disturbance mitigates effects of multiple stressors in a marine benthic community. *Ecosphere 9*(6), p.e02314, doi:10.1002/ecs2.2314.

Predicting how communities respond to multiple stressors is challenging because community dynamics, stressors, and animal–stressor interactions can vary with environmental conditions, including the intensity of natural disturbance. Nevertheless, environmental laws stipulate that we predict, measure, and mitigate the ecological effects of some human-induced stressors in the environment, including chemical contaminants in aquatic ecosystems. We conducted an experiment in Antarctica to test how a marine soft-sediment benthic community responded to multiple chemical contaminants and biotic disturbance by manipulating organic carbon enrichment, copper metal contamination, access by large epibenthic animals, and their interaction. Biotic disturbance caused mainly by large echinoderms was manipulated with exclusion cages and cage-control treatments. Colonization patterns in sediment trays revealed that total infaunal abundance and arthropods decreased with toxic Cu (0, 100, and 500 ppm) and total organic carbon (TOC; 0%, 1%, and 2% by wt), as enrichment produced increasing levels of sediment hypoxia/anoxia. Annelids and echinoderms decreased with Cu but increased with TOC because many colonizing polychaete worms, seastars, and epifaunal sea urchins were deposit feeders. Bioturbation by echinoderms disturbed sediments, leading to a substantial decline in total infaunal abundance in uncontaminated sediments, but also an increase in the relative abundance in contaminated sediments, as bioturbation mitigated the effect of both chemical stressors. Biotic disturbance also caused substantial shifts in the species composition of the invertebrate assemblages and an overall increase in species diversity. Prior predictions about the response of benthic marine phyla to the separate and combined effects of Cu and carbon enrichment appear robust to variation in natural biotic disturbance

Morandini, V., K.M. Dugger, G. Ballard, M. Elrod , A. Schmidt, V. Ruoppolo , A. Lescroël, D. Jongsomjit, M. Massaro, J. Pennycook, G.L. Kooyman, K. Schmidlin, S. Kraberger, D.G. Ainley, and A. Varsani. 2019. Identification of a novel Adélie Penguin circovirus at Cape Crozier (Ross Island, Antarctica). *Viruses* 11, 1088, http://dx.doi.org/10.3390/v11121088.

Understanding the causes of disease in Antarctic wildlife is crucial, as many of these species are already threatened by environmental changes brought about by climate change. In recent years, Antarctic penguins have been showing signs of an unknown pathology: a feather disorder characterised by missing feathers, resulting in exposed skin. During the 2018–2019 austral summer breeding season at Cape Crozier colony on Ross Island, Antarctica, we observed for the first time an Adélie penguin chick missing down over most of its body. A guano sample was collected from the nest of the featherless chick, and using high-throughput sequencing, we identified a novel circovirus. Using abutting primers, we amplified the full genome, which we cloned and Sanger-sequenced to determine the complete genome of the circovirus. The Adélie penguin guano-associated circovirus genome shares <67% genome-wide nucleotide identity with other circoviruses, representing a new species of circovirus; therefore, we named it penguin circovirus (PenCV). Using the same primer pair, we screened 25 previously collected cloacal swabs taken at Cape Crozier from known-age adult Adélie penguins during the 2014–2015 season, displaying no clinical signs of feather-loss disorder. Three of the 25 samples (12%) were positive for a PenCV, whose genome shared >99% pairwise identity with the one identified in 2018–2019. This is the

first report of a circovirus associated with a penguin species. This circovirus could be an etiological agent of the feather-loss disorder in Antarctic penguins.

Palmer, T.A., A.G. Klein, S.T. Sweet, P.A. Montagna, L.J. Hyde, J. Sericano, T.L. Wade, M.C. Kennicutt II, and J.B. Pollack. 2021. Long-term changes in contamination and macrobenthic communities adjacent to McMurdo Station, Antarctica. *Science of the Total Environment* 764: 142798, https://doi.org/10.1016/j.scitotenv.2020.142798.

Improved waste management at McMurdo Station, Antarctica beginning in the 1980s has been followed by decreases in polycyclic aromatic hydrocarbon (PAH) and metal contamination in the adjacent marine sediments. However, determining the effect of the decreased contamination on marine ecological indicators (macrobenthic fauna) is confounded by concurrent changes in climate cycles and other physical forces. Between 2000 and 2013, there was a decrease in concentrations of some contaminants including mercury, copper, organochlorines, and PAHs in marine sediments adjacent to McMurdo Station. PAH concentrations in Winter Quarters Bay decreased an order of magnitude from 2000/2003 to 2012/2013 and were within an order of magnitude of reference area concentrations by 2013. Macrobenthic communities did not indicate any sign of recovery and have not become more similar to reference communities over this same period of time. Temporal changes in macrobenthic community composition during the study period had higher correlations with climatic and sea ice dynamics than with changes in contaminant concentrations. The Interdecadal Pacific Oscillation climatic index had the highest correlation with macrobenthic community composition. The Antarctic Oscillation climatic index, maximum ice extent and other natural environmental factors also appear to influence macrobenthic community composition. Despite large improvements in environmental management at McMurdo Station, continuing environmental vigilance is necessary before any noticeable improvement in ecological systems is likely to occur. The effects of climate must be considered when determining temporal changes in anthropogenic effects in Antarctica. Maintaining long-term monitoring of both contaminants and ecological indicators is important for determining the localized and global influences of humans on Antarctica, which will have implications for the whole planet.

Smeele, Z.E., D.G. Ainley, and A. Varsani. 2017. Viruses associated with Antarctic wildlife: From serology based detection to identification of genomes using high throughput sequencing. *Virus Research* 243: 91-105.

The Antarctic, sub-Antarctic islands and surrounding sea-ice provide a unique environment for the existence of organisms. Nonetheless, birds and seals of a variety of species inhabit them, particularly during their breeding seasons. Early research on Antarctic wildlife health, using serology-based assays, showed exposure to viruses in the families Birnaviridae, Flaviviridae, Herpesviridae, Orthomyxoviridae and Paramyxoviridae circulating in seals (Phocidae), penguins (Spheniscidae), petrels (Procellariidae) and skuas (Stercorariidae). It is only during the last decade or so that polymerase chain reaction-based assays have been used to characterize viruses associated with Antarctic animals. Furthermore, it is only during the last five years that full/whole genomes of viruses (adenoviruses, anelloviruses, orthomyxoviruses, a papillomavirus, paramyoviruses, polyomaviruses and a togavirus) have been sequenced using Sanger sequencing or high throughput sequencing (HTS) approaches. This review summaries the knowledge of animal Antarctic virology and discusses potential future directions with the advent of HTS in virus discovery and ecology.

Smeele, Z.E., Burns, J.M., Van Doorsaler, K., Fontenele, R.S., Waits, K., Stainton, D., Shero, M.R., Beltran, R.S., Kirkham, A.L., Berngartt, R., Kraberger, S., Varsani, A. 2018. Diverse papillomaviruses identified in Weddell seals. J Gen Virol 99:549-557.

Papillomaviridae is a diverse family of circular, double-stranded DNA (dsDNA) viruses that infect a broad range of mammalian, avian and fish hosts. While papillomaviruses have been characterized most extensively in humans, the study of non-human papillomaviruses has contributed greatly to our understanding of their pathogenicity and evolution. Using high-throughput sequencing approaches, we identified 7 novel papillomaviruses from vaginal swabs collected from 81 adult female Weddell seals (*Leptonychotes weddellii*) in the Ross Sea of Antarctica between 2014–2017. These seven papillomavirus genomes were amplified from seven individual seals, and six of the seven genomes represented novel species with distinct evolutionary lineages. This highlights the diversity of papillomaviruses among the relatively small number of Weddell seal samples tested. Viruses associated with large vertebrates are poorly studied in Antarctica, and this study adds information about papillomaviruses associated with Weddell seals and contributes to our understanding of the evolutionary history of papillomaviruses.

Smith, S.M. 2014. *Long term effects of human activity on benthic macrofauna adjacent to McMurdo Station, Antarctica*. MSc thesis, Texas A&M University–Corpus Christi, TX, http://hdl.handle.net/1969.6/570.

Sediments in McMurdo Sound, Antarctica have been altered through contamination derived from McMurdo Station. Long-term monitoring of benthic communities provides a basis for assessment of impacts located near known sources of historic pollution. The objectives of the present study are to determine if any changes in benthic community abundance, biomass, and diversity occurred over time and if the change was due to contamination effects by comparing benthic communities between polluted and reference stations. Benthic cores were collected from either three or four transects at depths of 12, 24, and 36 meters during the austral summers of 2000 and 2003 to 2012. Transects included: Winter Quarters Bay and the Sewage Outfall, located near known sources of historic pollution; and Intake Jetty and Cape Armitage that are non-polluted, reference transects. Macrofauna metrics and a Benthic Index of Biological Integrity (BIBI) were used to test for spatial and temporal changes in macrofaunal communities. Disturbance-related spatial differences were detected using BIBI-ranks at Winter Quarters Bay indicating pollution effects in benthic communities at that location. Benthic community composition changed among all stations, disturbed and reference, over time. Therefore, the observed shifts in macrofaunal communities can primarily be attributed to natural processes rather than changes from contamination effects.

Stark, J.S., K.E. Conlan, K.A. Hughes, S. Kim, and C.C. Martins. 2016. Sources, dispersal and impacts of sewage and wastewater in Antarctica. *Antarctic Environments Portal*, doi:10.18124/zpkd-y002.

The discharge of sewage and wastewater into the Antarctic environment represents a serious and significant risk of environmental impacts that includes the introduction of non-native micro-organisms and pathogens, genetic pollution and accumulation of, and exposure to, contaminants. Wastewater discharges could lead to long term impacts on wildlife health, biodiversity and community structure in the vicinity of Antarctic stations. Treatment and disposal practices vary widely, as each Party to the Antarctic Treaty determines their own standards with varying interpretation of requirements under the Protocol on Environmental Protection. Further research and monitoring of the impacts of wastewater on Antarctic ecosystems will assist in quantifying the potential risks and impacts. Currently, no guidelines exist that describe permissible levels of bacteria, chemical and other contaminants being discharged from outfalls within the Treaty area, but their development would be beneficial in setting a baseline for monitoring. One of the highest priorities of the Committee for Environmental Protection (CEP) is addressing the introduction of non-native species. Wastewater discharge is a significant source of potential introductions, but advanced wastewater treatment could substantially reduce this and other associated risks.

Stark, J. S., S.L. Kim, and J.S. Oliver. 2014. Anthropogenic disturbance and biodiversity of marine benthic communities in Antarctica: A regional comparison. *PloS One 9*(6), e98802.

The impacts of two Antarctic stations in different regions, on marine sediment macrofaunal communities were compared: McMurdo, a very large station in the Ross Sea; and Casey, a more typical small station in East Antarctica. Community structure and diversity were compared along a gradient of anthropogenic disturbance from heavily contaminated to uncontaminated locations. We examined some of the inherent problems in comparing data from unrelated studies, such as different sampling methods, spatial and temporal scales of sampling and taxonomic uncertainty. These issues generated specific biases which were taken into account when interpreting patterns. Control sites in the two regions had very different communities but both were dominated by crustaceans. Community responses to anthropogenic disturbance (sediment contamination by metals, oils and sewage) were also different. At McMurdo the proportion of crustaceans decreased in disturbed areas and polychaetes became dominant, whereas at Casey, crustaceans increased in response to disturbance, largely through an increase in amphipods. Despite differing overall community responses there were some common elements. Ostracods, cumaceans and echinoderms were sensitive to disturbance in both regions. Capitellid, dorvelleid and orbiniid polychaetes were indicative of disturbed sites. Amphipods, isopods and tanaids had different responses at each station. Biodiversity and taxonomic distinctness were significantly lower at disturbed locations in both regions. The size of the impact, however, was not related to the level of contamination, with a larger reduction in biodiversity at Casey, the smaller, less polluted station. The impacts of small stations, with low to moderate levels of contamination, can thus be as great as those of large or heavily contaminated stations. Regional broad scale environmental influences may be important in determining the composition of communities and thus their response to disturbance, but there are some generalizations regarding responses which will aid future management of stations.

Van Doorslaer, K., V. Ruoppolo, A. Schmidt, A. Lescroel, D. Jongsomjit, M. Elrod, S. Kraberger, D. Stainton, K.M. Dugger, G. Ballard, D.G. Ainley, and A. Varsani. 2017. Unique genome organization of non-mammalian papillomaviruses provides insights into the evolution of viral early proteins. *Virus Evolution* 3(2): vex027, doi:10.1093/ve/vex027.

The family Papillomaviridae contains more than 320 papillomavirus types, with most having been identified as infecting skin and mucosal epithelium in mammalian hosts. To date, only nine non-mammalian papillomaviruses have been described from birds (n¼5), a fish (n¼1), a snake (n¼1), and turtles (n¼2). The identification of papillomaviruses in sauropsids and a sparid fish suggests that early ancestors of papillomaviruses were already infecting the earliest Euteleostomi. The Euteleostomi clade includes more than 90 per cent of the living vertebrate species, and progeny virus could have been passed on to all members of this clade, inhabiting virtually every habitat on the planet. As part of this study, we isolated a novel papillomavirus from a 16-year-old female Adélie penguin (*Pygoscelis adeliae*) from Cape Crozier, Ross Island (Antarctica). The new papillomavirus shares _64 per cent genome-wide identity to a previously described Adélie penguin papillomavirus. Phylogenetic analyses show that the non-mammalian viruses (expect the python, *Morelia spilota*, associated papillomavirus) cluster near the base of the papillomavirus evolutionary tree. A papillomavirus isolated from an avian host (Northern fulmar; *Fulmarus glacialis*), like the two turtle papillomaviruses, lacks a putative E9 protein that is found in all other avian papillomaviruses. Furthermore, the Northern fulmar papillomavirus has an E7 more similar to the mammalian viruses than the other avian papillomaviruses. Typical E6 proteins of mammalian papillomaviruses have two Zinc finger motifs, whereas the sauropsid papillomaviruses only have one such motif. Furthermore, this motif is absent in the fish papillomavirus. Thus, it is highly likely

that the most recent common ancestor of the mammalian and sauropsid papillomaviruses had a single motif E6. It appears that a motif duplication resulted in mammalian papillomaviruses having a double

Zinc finger motif in E6. We estimated the divergence time between Northern fulmar-associated papillomavirus and the other Sauropsid papillomaviruses be to around 250 million years ago, during the Paleozoic-Mesozoic transition and our analysis dates the root of the papillomavirus tree between 400 and 600 million years ago. Our analysis shows evidence for niche adaptation and that these non-mammalian viruses have highly divergent E6 and E7 proteins, providing insights into the evolution of the early viral (onco-)proteins.

Van Doorslaer, K., Kraberger, S., Austin, C., Farkas, K., Bergeman, M., Paunil, E., Davison, W., Varsani, A. 2018. Fish polyomaviruses belong to two distinct evolutionary lineages. J Gen Virol 99:567-573.

The P*olyomaviridae* is a diverse family of circular double-stranded DNA viruses. Polyomaviruses have been isolated from a wide array of animal hosts. An understanding of the evolutionary and ecological dynamics of these viruses is essential to understanding the pathogenicity of polyomaviruses. Using a high throughput sequencing approach, we identified a novel polyomavirus in an emerald notothen (*Trematomus bernacchii*) sampled in the Ross sea (Antarctica), expanding the known number of fish-associated polyomaviruses. Our analysis suggests that polyomaviruses belong to three main evolutionary clades; the first clade is made up of all recognized terrestrial polyomaviruses. The fish-associated polyomaviruses are not monophyletic, and belong to two divergent evolutionary lineages. The fish viruses provide evidence that the evolution of the key viral large T protein involves gain and loss of distinct domains.

Varsani, A., S. Kraberger, S. Jennings, E.L. Porzig, L. Julian, M. Massaro, A. Pollard, G. Ballard, and D.G. Ainley. 2014. A novel papillomavirus in Adélie penguin (*Pygoscelis adeliae*) faeces sampled at the Cape Crozier colony, Antarctica. *Journal of General Virology* 95: 1352–1365.

Papillomaviruses are epitheliotropic viruses that have circular dsDNA genomes encapsidated in non-enveloped virions. They have been found to infect a variety of mammals, reptiles and birds, but so far they have not been found in amphibians. Using a next-generation sequencing de novo assembly contig-informed recovery, we cloned and Sanger sequenced the complete genome of a novel papillomavirus from the faecal matter of Ade´ lie penguins (Pygoscelis adeliae) nesting on Ross Island, Antarctica. The genome had all the usual features of a papillomavirus and an E9 ORF encoding a protein of unknown function that is found in all avian papillomaviruses to date. This novel papillomavirus genome shared ~60% pairwise identity with the genomes of the other three known avian papillomaviruses: *Fringilla coelebs* papillomavirus 1 (FcPV1), *Francolinus leucoscepus* papillomavirus 1 (FlPV1) and Psittacus erithacus papillomavirus 1. Pairwise identity analysis and phylogenetic analysis of the major capsid protein gene clearly indicated that it represents a novel species, which we named Pygoscelis adeliae papillomavirus 1 (PaCV1). No evidence of recombination was detected in the genome of PaCV1, but we did detect a recombinant region (119 nt) in the E6 gene of FlPV1 with the recombinant region being derived from ancestral FcPV1-like sequences. Previously only paramyxoviruses, orthomyxoviruses and avian pox viruses have been genetically identified in penguins; however, the majority of penguin viral identifications have been based on serology or histology. This is the first report, to our knowledge, of a papillomavirus associated with a penguin species.

Varsani, A., E.L. Porzig, S. Jennings, S. Kraberger, K. Farkas, L. Julian, M. Massaro, G. Ballard, and D.G. Ainley. 2015. Identification of an avian polyomavirus associated with Adélie penguins (*Pygoscelis adeliae*). *Journal of General Virology* 96: 851–857.

Little is known about viruses associated with Antarctic animals, although they are probably widespread. We recovered a novel polyomavirus from Adélie penguin (*Pygoscelis adeliae*) faecal matter sampled in a subcolony at Cape Royds, Ross Island, Antarctica. The 4988 nt Adélie penguin polyomavirus (AdPyV) has a typical polyomavirus genome organization with three ORFs that encoded capsid proteins on the one strand and two non-structural protein-coding ORFs on the complementary strand. The genome of AdPyV shared ~60% pairwise identity with all avipolyomaviruses. Maximum-likelihood phylogenetic analysis of the large T-antigen (T-Ag) amino acid sequences showed that the T-Ag of AdPyV clustered with those of avipolyomaviruses, sharing between 48 and 52% identities. Only three viruses associated with Adélie penguins have been identified at a genomic level, avian influenza virus subtype H11N2 from the Antarctic Peninsula and, respectively, *Pygoscelis adeliae* papillomavirus and AdPyV from capes Crozier and Royds on Ross Island.

Varsani, A., Frankfurter, G., Stainton, D., Male, M.F., Kraberger, S., Burns, J.M. 2017. Identification of a polyomavirus in Weddell seal (*Leptonychotes weddellii*) from the Ross Sea (Antarctica). Arch Virol 162:1403-1407.

Viruses are ubiquitous in nature, however, very few have been identified that are associated with Antarctic animals. Here we report the identification of a polyomavirus in the kidney tissue of a deceased Weddell seal from the Ross Sea, Antarctica. The circular genome (5186 nt) has typical features of polyomaviruses with a small and larger T-antigen open reading frames (ORFs) and three ORFs encoding VP1, VP2 and VP3 capsid proteins. The genome of the Weddell seal polyomavirus (WsPyV) shares 85.4% genome-wide pairwise identity with a polyomavirus identified in a California sea lion. To our knowledge WsPyV is the first viral genome identified in Antarctic pinnipeds and the third polyomavirus to be identified from an Antarctic animal, the other two being from Adelie penguin (*Pygoscelis adeliae*) and a sharp-spined notothen (*Trematomus pennellii*), both sampled in the Ross sea.

Zawar-Reza, P., Arguello-Astorga, G.R., Kraberger, S., Julian, L., Stainton, D., Broady, P.A., Varsani, A. 2014. Diverse small circular single-stranded DNA viruses identified in a freshwater pond on the McMurdo Ice Shelf (Antarctica). Infect Genet Evol 26:132-8.

Antarctica has some of the harshest environmental conditions for existence of life on Earth. In this pilot study we recovered eight diverse circular single-stranded DNA (ssDNA) viral genome sequences (1904–3120 nts) from benthic mats dominated by filamentous cyanobacteria in a freshwater pond on the McMurdo Ice Shelf sampled in 1988. All genomes contain two to three major open reading frames (ORFs) that are uni- or bi-directionally transcribed and all have an ORF encoding a replication-associated protein (Rep). In one genome, the second ORF has similarity to a capsid protein (CP) of Nepavirus which is most closely related to geminiviruses. Additionally, all genomes have two intergenic regions that contain putative stem loop structures, six genomes have NANTATTAC as the nonanucleotide motif, while one has CCTTATTAC, and another has a non-canonical stem loop. In the large intergenic region, we identified iterative sequences flanking the putative stem-loop elements which are a hallmark of most circular ssDNA viruses encoding rolling circle replication (RCR) initiators of the HUH endonuclease superfamily. The Reps encoded by ssDNA viral genomes recovered in this study shared <38% pairwise identity to all other Reps of known ssDNA viruses. A previous study on Lake Limnopolar (Livingston Island, South Shetland Islands), using next-generation sequencing identified circular ssDNA viruses and their putative Reps share <35% pairwise identity to those from the viral genomes removed in

this study. It is evident from our pilot study that the global diversity of ssDNA viruses is grossly underestimated and there is limited knowledge on ssDNA viruses in Antarctica.

SYNTHESES AND SUMMARYS

Ainley, D.G. 2010. A history of the exploitation of the Ross Sea, Antarctica. *Polar Record* 46 (238): 233–243.

Recent analyses of anthropogenic impacts on marine systems have shown that the Ross Sea is the least affected stretch of ocean on Earth, although historical effects were not included in those studies. Herein the literature is reviewed in order to quantify the extent of extraction of biological resources from the Ross Sea continental shelf and slope from the start of the 20th century. There was none before that time. An intense extraction of Weddell seals *Leptonychotes weddellii* by the expeditions of the 'heroic' period and then by New Zealand to feed sled dogs in the 1950–1980s caused the McMurdo Sound population to decrease permanently. Otherwise no other sealing occurred.

Blue whales *Balaenoptera musculus intermedia* were extirpated from waters of the shelf break front during the 1920s, and have not reappeared. Minke whales *B. bonaerensis* probably expanded into the blue whale vacated habitat, but were then hunted during the 1970–1980s; their population has since recovered. Some minke whales are now taken in 'scientific whaling', twice more from the slope compared to the shelf. Other hunted cetaceans never occurred over the shelf and very few ever occurred in slope waters, and therefore their demise from whaling does not apply to the Ross Sea. No industrial fishing occurred in the Ross Sea until the 1996–1997 summer, when a fishery for Antarctic toothfish *Dissostichus mawsoni* was initiated, especially along the slope. This fishery has grown since then with effects on the ecosystem recently becoming evident. There is probably no other ocean area where the details of biological exploitation can be so elucidated. It appears that the Ross Sea continental shelf remains the least affected of any on the globe. However the same cannot be said of the slope.

Ainley, D.G, G. Ballard, and J. Weller. 2010. Ross Sea Bioregionalization. Part I: Validation of the 2007 CCAMLR Bioregionalization Workshop Results Towards Including the Ross Sea in a Representative Network of Marine Protected Areas in the Southern Ocean *CCAMLR WG-EMM-10/11*, Hobart.

This report provides the scientific basis, validating the results of the CCAMLR Bioregionalization Workshop (2007) as well as the report of ASOC (2010), for identifying the Ross Sea as one of 11 areas deserving close scrutiny for inclusion in a network of marine protected areas. CCAMLR (2007) identified the Ross Sea as an area of high biodiversity on the basis of its high physical heterogeneity; ASOC (2010) compared characteristics of the Ross Sea to areas designated under various international agreements instituted to preserve biodiversity. The CCAMLR (2007) subsequently was endorsed in the joint meeting of CCAMLR's Scientific Committee and the Environmental Protocol's Committee on Environmental Protection (ATCM XXXII-CEP XII, Final Report, 2009). Considered herein is the Ross Sea shelf and slope, which is a smaller portion of the area identified in CCAMLR (2007) as "Ross Sea shelf".

Ballard, G., D. Jongsomjit, S.D. Veloz, and D.G. Ainley 2012. Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. *Biological Conservation* 156: 72-82.

Designation of an effective marine protected area (MPA) requires substantial knowledge of the spatial use of the region by key species, particularly those of high mobility. Within the Ross Sea, Antarctica, the least altered marine ecosystem on Earth, unusually large and closely interacting populations of several marine bird and mammal species co-exist. Understanding how that is possible is important to maintaining the ecological integrity of the system, the major goal in designating the Ross Sea as an MPA. We report analyses of niche occupation, two-dimensional habitat use, and overlap for the majority (9) of mesopredator species in the Ross Sea considering three components: (1) diet, (2) vertical distribution and (3) horizontal distribution. For (1) and (2) we used information in the literature; for (3) we used maximum entropy modeling to project species' distributions from occurrence data from several ocean cruises and satellite telemetry, correlated with six environmental variables. Results identified and ranked areas of importance in a conservation prioritization framework. While diet overlapped intensively, some spatial partitioning existed in the vertical dimension (diving depth). Horizontal partitioning, however, was the key structuring factor, defined by three general patterns of environmental suitability: (1) continental shelf break, (2) shelf and slope, and (3) marginal ice zone of the pack ice surrounding the Ross Sea post-polynya. In aggregate, the nine mesopredators used the entire continental shelf and slope, allowing the large populations of these species to co-exist. Conservation prioritization analyses identified the outer shelf and slope and the deeper troughs in the Ross Sea shelf to be most important. Our results substantially improve understanding of these species' niche occupation and imply that a piecemeal approach to MPA designation in this system is not likely to be successful.

Fripiat, F., K.M. Meiners, M. Vancoppenolle, S.F. Ackley, K.R. Arrigo, G. Carnat, S. Cozzi, B. Delille, G.S. Dieckmann, R.B. Dunbar, H. Eicken, A. Fransson, G. Kattner, H. Kennedy, D. Lannuzel1, D.R. Munro, D. Nomura, S. Papadimitriou, J.-M. Rintala, V. Schoemann, J. Stefels, N. Steiner, D.N. Thomas, and J.-L. Tison, 2017, Macro-nutrient concentrations in Antarctic pack ice: Overall patterns and overlooked processes. ***Elementa: Science of the Anthropocene*****, 5-13, doi.org/10.1525/elementa.217**.

Antarctic pack ice is inhabited by a diverse and active microbial community reliant on nutrients for growth. Seeking patterns and overlooked processes, we performed a large-scale compilation of macro-nutrient data (hereafter termed nutrients) in Antarctic pack ice (306 ice-cores collected from 19 research cruises). Dissolved inorganic nitrogen and silicic acid concentrations change with time, as expected from a seasonally productive ecosystem. In winter, salinity-normalized nitrate and silicic acid concentrations (C*) in sea ice are close to seawater concentrations (Cw), indicating little or no biological activity. In spring, nitrate and silicic acid concentrations become partially depleted with respect to seawater (C* < Cw), commensurate with the seasonal build-up of ice microalgae promoted by increased insolation. Stronger and earlier nitrate than silicic acid consumption suggests that a significant fraction of the primary productivity in sea ice is sustained by flagellates. By both consuming and producing ammonium and nitrite, the microbial community maintains these nutrients at relatively low concentrations in spring. With the decrease in insolation beginning in late summer, dissolved inorganic nitrogen and silicic acid concentrations increase, indicating imbalance between their production (increasing or unchanged) and consumption (decreasing) in sea ice. Unlike the depleted concentrations of both nitrate and silicic acid from spring to summer, phosphate accumulates in sea ice (C* > Cw). The phosphate excess could be explained by a greater allocation to phosphorus-rich biomolecules during ice algal blooms coupled with convective loss of excess dissolved nitrogen, preferential remineralization of phosphorus, and/or phosphate adsorption onto metal-organic complexes. Ammonium also appears to be efficiently adsorbed onto organic matter, with likely consequences to nitrogen mobility and availability. This dataset supports the view that the sea ice microbial community is highly efficient at processing nutrients but with a dynamic quite different from that in oceanic surface waters calling for focused future investigations.

Massom, R.A., and S.E. Stammerjohn. 2010. Antarctic sea ice change and variability – physical and ecological implications. *Polar Science* 4: 149-186, doi:10.1016/j.polar.2010.05.001.

Although Antarctic sea ice is undergoing a slight increase in overall extent, major regional changes are occurring in its spatio-temporal characteristics (most notably in sea ice seasonality). Biologically significant aspects of Antarctic sea ice are evaluated, emphasising the importance of scale and thermodynamics versus dynamics. Changing sea ice coverage is having major direct and indirect though regionally-dependent effects on ecosystem structure and function, with the most dramatic known effects to date occurring in the West Antarctic Peninsula region. There is mounting evidence that loss of sea ice has affected multiple levels of the marine food web in a complex fashion and has triggered cascading effects. Impacts on primary production, Antarctic krill, fish, marine mammals and birds are assessed, and are both negative and positive. The review includes recent analysis of change/variability in polynyas and fast ice, and also highlights the significance of extreme events (which have paradoxical impacts). Possible future scenarios are investigated in the light of the predicted decline in sea ice by 2100 e.g. increased storminess/waviness, numbers of icebergs and snowfall. Our current lack of knowledge on many aspects of sea ice-related change and biological response is emphasised.

Morley S. A., D. Abele, D.K.A. Barnes, C.A/ Cárdenas, C. Cotté, J. Gutt, S.F. Henley, J. Höfer., K..A. Hughes, S.M. Martin, C. Moffat, M. Raphae, S.E. Stammerjohn, C.C. Suckling, V.J.D. Tulloch, C.L. Waller, and A.J. Constable. 2020. Global Drivers on Southern Ocean Ecosystems: Changing Physical Environments and Anthropogenic Pressures in an Earth System. *Frontiers in Marine Science* 7:547188, doi: 10.3389/fmars.2020.547188.

The manuscript assesses the current and expected future global drivers of Southern Ocean (SO) ecosystems. Atmospheric ozone depletion over the Antarctic since the 1970s, has been a key driver, resulting in springtime cooling of the stratosphere and intensification of the polar vortex, increasing the frequency of positive phases of the Southern Annular Mode (SAM). This increases warm air-flow over the East Pacific sector (Western Antarctic Peninsula) and cold air flow over the West Pacific sector. SAM as well as El Niño Southern Oscillation events also affect the Amundsen Sea Low leading to either positive or negative sea ice anomalies in the west and east Pacific sectors, respectively. The strengthening of westerly winds is also linked to shoaling of deep warmer water onto the continental shelves, particularly in the East Pacific and Atlantic sectors. Air and ocean warming has led to changes in the cryosphere, with glacial and ice sheet melting in both sectors, opening up new ice free areas to biological productivity, but increasing seafloor disturbance by icebergs. The increased melting is correlated with a salinity decrease particularly in the surface 100 m. Such processes could increase the availability of iron, which is currently limiting primary production over much of the SO. Increasing CO_2 is one of the most important SO anthropogenic drivers and is likely to affect marine ecosystems in the coming decades. While levels of many pollutants are lower than elsewhere, persistent organic pollutants (POPs) and plastics have been detected in the SO, with concentrations likely enhanced by migratory species. With increased marine traffic and weakening of ocean barriers the risk of the establishment of non-indigenous species is increased. The continued recovery of the ozone hole creates uncertainty over the reversal in sea ice trends, especially in the light of the abrupt transition from record high to record low Antarctic sea ice extent since spring 2016. The current rate of change in physical and anthropogenic drivers is certain to impact the Marine Ecosystem Assessment of the Southern Ocean (MEASO) region in the near future and will have a wide range of impacts across the marine ecosystem.

Ribic, C.A. D.G. Ainley, R.G. Ford, W.R. Fraser, C.T. Tynan, and E.J. Woehler. 2011. Water masses, ocean fronts, and the structure of Antarctic seabird communities: Putting the eastern Bellingshausen Sea in perspective. *Deep-Sea Research II* 58: 1695–1709.

Waters off the western Antarctic Peninsula (i.e., the eastern Bellingshausen Sea) are unusually complex owing to the convergence of several major fronts. Determining the relative influence of fronts on occurrence patterns of top-trophic species in that area, therefore, has been challenging. In one of the few ocean-wide seabird data syntheses, in this case for the Southern Ocean, we analyzed ample, previously collected cruise data, Antarctic-wide, to determine seabird species assemblages and quantitative relationships to fronts as a way to provide context to the long-term Palmer LTER and the winter Southern Ocean GLOBEC studies in the eastern Bellingshausen Sea. Fronts investigated during both winter (April–September) and summer (October–March) were the southern boundary of the Antarctic Circumpolar Current (ACC), which separates the High Antarctic from the Low Antarctic water mass, and within which are embedded the marginal ice zone and Antarctic Shelf Break Front; and the Antarctic Polar Front, which separates the Low Antarctic and the Subantarctic water masses. We used clustering to determine species' groupings with water masses, and generalized additive models to relate species' densities, biomass and diversity to distance to respective fronts. Antarctic-wide, in both periods, highest seabird densities and lowest species diversity were found in the High Antarctic water mass. In the eastern Bellingshausen, seabird density in the High Antarctic water mass was lower (as low as half that of winter) than found in other Antarctic regions. During winter, Antarctic-wide, two significant species groups were evident: one dominated by Adélie penguins (*Pygoscelis adeliae*) (High Antarctic water mass) and the other by petrels and prions (no differentiation among water masses); in eastern Bellingshausen waters during winter, the one significant species group was composed of species from both Antarctic-wide groups. In summer, Antarctic-wide, a High Antarctic group dominated by Ade´ lie penguins, a Low Antarctic group dominated by petrels, and a Subantarctic group dominated by albatross were evident. In eastern Bellingshausen waters during summer, groups were inconsistent. With regard to frontal features, Antarctic-wide in winter, distance to the ice edge was an important explanatory factor for nine of 14 species, distance to the Antarctic Polar Front for six species and distance to the Shelf Break Front for six species; however, these Antarctic-wide models could not successfully predict spatial relationships of winter seabird density (individual species or total) and biomass in the eastern Bellingshausen. Antarctic-wide in summer, distance to land/Antarctic continent was important for 10 of 18 species, not a surprising result for these summer-time Antarctic breeders, as colonies are associated with ice-free areas of coastal land. Distance to the Shelf Break Front was important for 8 and distance to the southern boundary of the ACC was important for 7 species. These summer models were more successful in predicting eastern Bellingshausen species density and species diversity but failed to predict total seabird density or biomass. Antarctic seabirds appear to respond to fronts in a way similar to that observed along the well-studied upwelling front of the California Current. To understand fully the seabird patterns found in this synthesis, multi-disciplinary at-sea investigations, including a quantified prey field, are needed.

Sequeira, A.M.M., J. P. Rodríguez, V. M. Eguíluz, R. Harcourt, M. Hindell, D. W. Sims, C. M. Duarte, D. P. Costa, …. M. Thums. 2018. Convergence of marine megafauna movement patterns in coastal and open oceans. *Proceedings of the National Academy of Sciences*, doi.org/10.1073/pnas.1716137115.

The extent of increasing anthropogenic impacts on large marine vertebrates partly depends on the animals' movement patterns. Effective conservation requires identification of the key drivers of movement including intrinsic properties and extrinsic constraints associated with the dynamic nature of the environments the animals inhabit. However, the relative importance of intrinsic versus extrinsic factors remains elusive. We analyze a global dataset of ~2.8 million locations from >2,600 tracked individuals across 50 marine vertebrates evolutionarily separated by millions of years and using different locomotion modes (fly, swim, walk/paddle). Strikingly, movement patterns show a remarkable convergence, being strongly conserved across species and independent of body length and mass, despite

these traits ranging over 10 orders of magnitude among the species studied. This represents a fundamental difference between marine and terrestrial vertebrates not previously identified, likely linked to the reduced costs of locomotion in water. Movement patterns were primarily explained by the interaction between species-specific traits and the habitat(s) they move through, resulting in complex movement patterns when moving close to coasts compared with more predictable patterns when moving in open oceans. This distinct difference may be associated with greater complexity within coastal microhabitats, highlighting a critical role of preferred habitat in shaping marine vertebrate global movements. Efforts to develop understanding of the characteristics of vertebrate movement should consider the habitat(s) through which they move to identify how movement patterns will alter with forecasted severe ocean changes, such as reduced Arctic sea ice cover, sea level rise, and declining oxygen content.

Smith, W.O. Jr., D.G. Ainley, R. Cattaneo-Vietti, and E.E. Hofmann. 2012. The Ross Sea continental shelf: Regional biogeochemical cycles, trophic interactions, and potential future changes. In: *Antarctic Ecosystems: An Extreme Environment in a Changing World* (A.D. Rogers, N.M. Johnston, E.J. Murphy and A. Clarke, Eds.). Chapter 7, Blackwell Publishing, London, pp. 213-242.

The Ross Sea continental shelf, lying between Cape Adare, Victoria Land (71° 17'S, 170° 14'E) and Cape Colbeck, Marie Byrd Land (77 ° 07'S, 157 ° 54'W) and stretching from the continent north to the 800m isobaths, is a unique region of the Antarctic, both with regard to its physics and its ecology. It is now clear that the various regions among Antarctic continental shelf systems have unifying characteristics, but also marked regional differences. Among cold water continental shelves, the Ross Sea is the least impacted by anthropogenic factors of any on Earth. Its broad extent (the widest in the Antarctic, and covering ca. 433,000 km2), extreme seasonality of its trophic linkages (its high-latitude Antarctic location induces complete darkness during winter), numerous polynyas (regions of open water surrounded by sea ice), a massive ice shelf – the Ross Ice Shelf (RIS, the largest in the world, covering nearly half of the continental shelf) and substantial vertical and horizontal exchanges, both with waters of the continental slope (between 800–3000 m) and with those under the RIS, provide a dynamic environment. It is because of these characteristics that the Ross Sea food web differs from those in many other areas of the Southern Ocean.

Smith, W.O. Jr., D.G. Ainley, K.R. Arrigo, and M.S. Dinniman. 2014. The oceanography and ecology of the Ross Sea. *Annual Review of Marine Science* 6: 469–487.

The continental shelf of the Ross Sea exhibits substantial variations in physical forcing, ice cover, and biological processes on a variety of time and space scales. Its circulation is characterized by advective inputs from the east and exchanges with off-shelf regions via the troughs along the northern portions. Phytoplankton biomass is greater there than anywhere else in the Antarctic, although nitrate is rarely reduced to levels below 10 μmol L−1. Overall growth is regulated by irradiance (via ice at the surface and by the depths of the mixed layers) and iron concentrations. Apex predators reach exceptional abundances, and the world's largest colonies of Adélie and emperor penguins are found there. Krill are represented by two species (*Euphausia superba* near the shelf break and *Euphausia crystallorophias* throughout the continental shelf region). Equally important and poorly known is the Antarctic silverfish (*Pleuragramma antarcticum*), which is also consumed by most upper-trophic-level predators. Future changes in the Ross Sea environment will have profound and unpredictable effects on the food web.

Smith, W.O. Jr., P.N. Sedwick, K.R. Arrigo, D.G. Ainley, and A.H. Orsi. 2012. The Ross Sea in a sea of change. *Oceanography* 25: 44-57.

The continental shelf of the Ross Sea, Antarctica, is characterized by extreme seasonal and interannual changes in atmospheric and oceanographic processes, which result in distinct temporal patterns in phytoplankton biomass and assemblage composition. However, the environmental forcing of these variations remains uncertain, especially when a series of correlated variables are considered. Hydrological profiles, dissolved nutrients, particulate matter, and phytoplankton pigments were measured in the southern Ross Sea in austral spring and summer during four years (1996–97, 2003–04, 2004–05, and 2005–06), and a series of multivariate analyses were conducted to assess the causative mechanisms in the control of phytoplankton distributions in the Ross Sea. Our results demonstrate that the significant interannual, seasonal and spatial variability that occurs in the southern Ross Sea in hydrographic and chemical properties is highly correlated with the variability in phytoplankton distributions. Although multiple controlling mechanisms were suggested, mixed layer depths did not appear to be a dominant factor regulating phytoplankton biomass or composition; conversely, we found a significant role of water column temperature in structuring phytoplankton assemblage composition in the southern Ross Sea, in that cooler water strongly selects for *Phaeocystis antarctica*, which is a dominant control of carbon flux to depth, and thus of substantial biogeochemical importance.

Walsh, J.E., D.H. Bromwich, J. E. Overland, M.C. Serreze, and K.R. Wood. 2018. 100 years of progress in polar meteorology. *Meteorological Monographs* 59, pages 21.1-21.36, doi: 10.1175/AMSMONOGRAPHS-D-18-0003.1

The polar regions present several unique challenges to meteorology, including remoteness and a harsh environment. We summarize the evolution of polar meteorology in both hemispheres, beginning with measurements made during early expeditions and concluding with the recent decades in which polar meteorology has been central to global challenges such as the ozone hole, weather prediction, and climate change. Whereas the 1800s and early 1900s provided data from expeditions and only a few subarctic stations, the past 100 years have seen great advances in the observational network and corresponding understanding of the meteorology of the polar regions. For example, a persistent view in the early twentieth century was of an Arctic Ocean dominated by a permanent high pressure cell, a glacial anticyclone. With increased observations, by the 1950s it became apparent that, while anticyclones are a common feature of the Arctic circulation, cyclones are frequent and may be found anywhere in the Arctic. Technology has benefited polar meteorology through advances in instrumentation, especially autonomously operated instruments. Moreover, satellite remote sensing and computer models revolutionized polar meteorology. We highlight the four International Polar Years and several high-latitude field programs of recent decades. We also note outstanding challenges, which include understanding of the role of the Arctic in variations of midlatitude weather and climate, the ability to model surface energy exchanges over a changing Arctic Ocean, assessments of ongoing and future trends in extreme events in polar regions, and the role of internal variability in multiyear-to-decadal variations of polar climate.

METHODS AND TECHNOLOGY DEVELOPMENT

Barker, L.D., S.L. Kim, B.T. Saenz, D.J. Osborne, and K.L. Daly. 2016. Towable instrumentation for use with a hand-deployed Remotely Operated Vehicle. *OCEANS 2016 MTS/IEEE Monterey* (pp. 1-6). IEEE.

A new class of small, hand-deployable underwater vehicles is playing an increasingly important role in oceanographic science. Due to the small nature of these vehicles, traditional incorporation of

oceanographic instrumentation into a vehicle's body can result in a device too massive or cumbersome to deployed by hand. In this paper, we present a towed instrument package, FATTI, as an alternative means of sensor integration for small underwater vehicles, specifically for the Remotely Operated Vehicle (ROV) SCINI. The flexibly attached instrument package is comprised of a 120 kHz scientific echosounder and fluorometer, and was deployed in the McMurdo Sound, Antarctica to map the spatial and temporal dynamics of krill, fishes, and phytoplankton. The tow package proved modular and fieldable, and performed over 100 dives during the 2012/13 and 2014/15 Antarctic field seasons.

Frankfurter, G., R.S. Beltran, H. Hoard, and J.M. Burns. 2019. Rapid Prototyping and 3D Printing of Antarctic Seal Flipper Tags. *WSB-18-127*, doi.org/10.1002/wsb.964

Recent miniaturization of biologging devices has enabled widespread efforts to document the vertical and horizontal movements of pinnipeds; however, the attachment methods have been slower to evolve. We used rapid prototyping to develop a novel, adaptable flipper tag that could be used to deploy a biologging tag on seals that would remain attached through the annual molt cycle. The prototype flipper tag was designed using three-dimensional (3D) modeling software and produced using 3D printing. Two tags were deployed on adult, female Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica, during the Austral Summer 2015. One animal did not return to the study area. The other tag was successfully recovered after 341 days. Upon tag removal, the flipper holes were well-healed with no evidence of pressure necrosis or irritation. This tag will provide opportunities to gain insight about animal behaviors during the annual molt, when annual hair loss precludes instrument attachment by glue. The rapid expansion of 3D printing design, material, and manufacturing tools has enabled the development of new tools for wildlife studies. © 2019 The Wildlife Society. Existing attachment methods for biologging and telemetry devices on marine mammals are often constrained by available off-the-shelf tags and resources. Using rapid prototyping and 3D printing we developed a custom flipper tag for deployment of transmitters on Weddell seals.

Beltran, R.S., B. Ruscher-Hill, A.L. Kirkham, and J.M. Burns. 2018. An evaluation of three-dimensional photogrammetric and morphometric techniques for estimating volume and mass in Weddell Seals, *Leptonychotes weddellii*. *PLOS One*, doi: 10.1371/journal.pone. 0189865.

Body mass dynamics of animals can indicate critical associations between extrinsic factors and population vital rates. Photogrammetry can be used to estimate mass of individuals in species whose life histories make it logistically difficult to obtain direct body mass measurements. Such studies typically use equations to relate volume estimates from photogrammetry to mass; however, most fail to identify the sources of error between the estimated and actual mass. Our objective was to identify the sources of error that prevent photogrammetric mass estimation from directly predicting actual mass, and develop a methodology to correct this issue. To do this, we obtained mass, body measurements, and scaled photos for 56 sedated Weddell seals (*Leptonychotes weddellii*). After creating a three-dimensional silhouette in the image processing program PhotoModeler Pro, we used horizontal scale bars to define the ground plane, then removed the below-ground portion of the animal's estimated silhouette. We then re-calculated body volume and applied an expected density to estimate animal mass. We compared the body mass estimates derived from this silhouette slice method with estimates derived from two other published methodologies: body mass calculated using photogrammetry coupled with a species-specific correction factor, and estimates using elliptical cones and measured tissue densities. The estimated mass values (mean ± standard deviation 345±71 kg for correction equation, 346±75 kg for silhouette slice, 343±76 kg for cones) were not statistically distinguishable from each other or from actual mass (346±73 kg) (ANOVA with Tukey HSD post-hoc, $p>0.05$ for all pairwise comparisons). We conclude that volume

overestimates from photogrammetry are likely due to the inability of photo modeling software to properly render the ventral surface of the animal where it contacts the ground. Due to logistical differences between the “correction equation”, “silhouette slicing”, and “cones” approaches, researchers may find one technique more useful for certain study programs. In combination or exclusively, these three-dimensional mass estimation techniques have great utility in field studies with repeated measures sampling designs or where logistic constraints preclude weighing animals.

Cazenave, F., R. Zook, D. Carroll, M. Flagg, and S. Kim. 2011. Development of the ROV SCINI and deployments in McMurdo Sound, Antarctica. *The Journal of Ocean Technology* 6(3): 39-58.

Remotely Operated Vehicles (ROVs) are powerful tools whose use has become common in many aquatic systems, for many purposes, from commercial to research applications. Polar regions, because of ice cover and harsh conditions, remain difficult locations for ROV work. This paper outlines the development of an ROV designed to facilitate exploration and scientific research under sea ice, giving easier access to largely unexplored regions of the seafloor. The ROV SCINI (Submersible Capable of under Ice Navigation and Imaging) was developed at Moss Landing Marine Laboratories and deployed in Antarctica for four field seasons, from 2007 to 2011. Ice provides a convenient deployment platform but commercially available ROVs require a large hole in the ice and much logistic support, which restricts their use in polar regions. Unlike other ROVs, SCINI has a slender torpedo shape (length: 1.4 m, diameter: 15 cm), which allows it to be deployed through a 20 cm hole in the ice. This small hole can be drilled by two people, using a handheld drill. The entire SCINI system and personnel (three or more persons) can fit in one helicopter, thus giving easy and quick access to remote sites. SCINI is a modular vehicle that can easily be modified or serviced in the field. It is also rugged and designed for harsh polar conditions. SCINI is equipped with two video cameras, scaling lasers, and lights. Its maximum depth capability is 300 m. A long baseline acoustic positioning system is used for navigation. SCINI is a highly manoeuvrable vehicle, better suited for flying transects over the seafloor than most ROVs. Engineering tests and scientific surveys were based out of McMurdo Station, Antarctica, and carried out at various sites within a 100 km radius. Knowledge gained from these deployments led to numerous modifications and improvements to the vehicle. This paper provides details on the vehicle's most recent configuration, including mechanical design, electrical design, software, and navigation system. Deployment methods, vehicle behaviour, and results of field testing are described. Four scientific surveys are also briefly described as examples.

Frazer, E., P. Langhorne, M. Williams, K. Goetz, and D. Costa. 2018. A method for correcting seal-borne oceanographic data and application to the estimation of regional sea ice thickness. *Journal of Marine Systems* 187: 250-259, https://doi.org/10.1016/j.jmarsys.2018.08.002.

The high-latitude oceans surrounding Antarctica are substantially undersampled compared to lower latitudes. Mammal based instruments such as Conductivity-Temperature-Depth Satellite Relay Data Loggers (CTD-SRDLs) present one possible solution. Unfortunately, these are subject to instrument-dependent offsets in absolute salinity. This study investigates a set of satellite-transmitted data collected by CTD-SRDLs mounted on Weddell seals (*Leptonychotes weddellii*) in the South-western Ross Sea in 2011. The uncorrected salinity offset between devices was found to be up to 1.4 g kg−1 , making the data unsuitable for some oceanographic studies without correction. Here, a correction method was developed that uses profiles from pairs of CTD-SRDLs that are considered to be co-located and to sample the same body of water if they occur within defined time and space windows. Using least squares, a best-fit solution to the matrix of offsets in co-located pairs was found that reduces salinity offsets between the CTD-SRDLs. These offsets are smaller than the original offsets by a factor of 10. A calibrated reference instrument, that was co-located with some of the devices, provided further improvement in the absolute

accuracy of all the CTD-SRDLs. Using the corrected CTD-SRDL data we estimate the rejection of salt into the water column by sea ice formation, and derived the time evolution of sea ice thickness in the South-western Ross Sea. Our estimates of regional sea ice thickness are in agreement with direct sea ice thickness measurements taken over a limited area in November 2011, providing further affirmation of our method.

Harcourt, R., A. Sequeira, X. Zhang ,F. Roquet, K. Komatsu, M. Heupel, C. McMahon, F. Whoriskey, M. Meekan, G. Carroll, S. Brodie, C. Simpfendorfer, M. Hindell, I. Jonsen, D. Costa, B. Block, M. Muelbert, B. Woodward, M. Weises, K. Aarestrup, M. Biuw, L. Boehme, S. Bograd, D. Cazau, J. Charrassin, S.Cooke, P. Cowley, P.J. Bruyn, T. Du Dot, C. Duarte , V.Eguíluz , L. Ferreira, J. Fernández-Gracia, K. Goetz, et al. 2019. Animal-Borne Telemetry: an integral component of the ocean observing System. *Frontiers in Marine Science*, https://doi.org/10.3389/fmars.2019.00326.

Animal telemetry is a powerful tool for observing marine animals and the physical environments that they inhabit, from coastal and continental shelf ecosystems to polar seas and open oceans. Satellite-linked biologgers and networks of acoustic receivers allow animals to be reliably monitored over scales of tens of meters to thousands of kilometers, giving insight into their habitat use, home range size, the phenology of migratory patterns and the biotic and abiotic factors that drive their distributions. Furthermore, physical environmental variables can be collected using animals as autonomous sampling platforms, increasing spatial and temporal coverage of global oceanographic observation systems. The use of animal telemetry, therefore, has the capacity to provide measures from a suite of essential ocean variables (EOVs) for improved monitoring of Earth's oceans. Here we outline the design features of animal telemetry systems, describe current applications and their benefits and challenges, and discuss future directions. We describe new analytical techniques that improve our ability to not only quantify animal movements but to also provide a powerful framework for comparative studies across taxa. We discuss the application of animal telemetry and its capacity to collect biotic and abiotic data, how the data collected can be incorporated into ocean observing systems, and the role these data can play in improved ocean management.

Hays, G., H. Bailey, S.J. Bograd, W.D. Bowen, C. Campagna, R.H. Carmichael, P. Halpin, K. Goetz, et al. 2019. Translating marine animal tracking data into conservation policy and management. *Trends in Ecology and Evolution* 34(5): 459-473, doi:10.1016/j.tree.2019.01.009.

There have been efforts around the globe to track individuals of many marine species and assess their movements and distribution, with the putative goal of supporting their conservation and management. Determining whether, and how, tracking data have been successfully applied to address real-world conservation issues is, however, difficult. Here, we compile a broad range of case studies from diverse marine taxa to show how tracking data have helped inform conservation policy and management, including reductions in fisheries bycatch and vessel strikes, and the design and administration of marine protected areas and important habitats. Using these examples, we highlight pathways through which the past and future investment in collecting animal tracking data might be better used to achieve tangible conservation benefits

Kimball, P., E. Clark, M. Scully, K. Richmond, C. Flesher, L. Lindzey, J. Harman, K. Huffstutler, J. Lawrence, S. Lelievre, J. Moor, B. Pease, V. Siegel, L. Winslow, S. Kim, D. Blankenship, P. Doran, B. Schmidt, and B. Stone. 2017. The ARTEMIS Under-Ice AUV Docking System. *Journal of Field Robotics*, doi: 10.1002/rob.21740.

The ARTEMIS docking system demonstrates autonomous docking capability applicable to robotic exploration of sub-ice oceans and sub-glacial lakes on planetary bodies, as well as here on Earth. In these applications, melted or drilled vertical access shafts restrict vehicle geometry as well as the in-water infrastructure that may be deployed. The ability of the vehicle to return reliably and precisely to the access point is critical for data return, battery charging, and/or vehicle recovery. This paper presents the mechanical, sensor, and software components that make up the ARTEMIS docking system, as well as results from field deployment of the system to McMurdo Sound, Antarctica in the austral spring of 2015. The mechanical design of the system allows the vehicle to approach the dock from any direction and to pitch up after docking for recovery through a vertical access shaft. It uses only a small volume of in-water equipment and may be deployed through a narrow vertical access shaft. The software of the system reduces position estimation error with a hierarchical combination of dead reckoning, acoustic aiding, and machine vision. The system provides critical operational robustness, enabling the vehicle to return autonomously and precisely to the access shaft and latch to the dock with no operator input.

Knuth, S.L. and J.J. Cassano. 2014: Estimating sensible and latent heat fluxes using the integral method from in situ aircraft measurements. ***Journal of Atmosphere and Ocean Technology*** **31: 1964-1981, doi:10.1175/JTECH-D-14-00008.1.**

In September 2009, several Aerosonde unmanned aerial vehicles (UAVs) were flown from McMurdo Station to Terra Nova Bay, Antarctica, with the purpose of collecting three-dimensional measurements of the atmospheric boundary layer (ABL) overlying a polynya. Temperature, pressure, wind speed, and relative humidity measurements collected by the UAVs were used to calculate sensible and latent heat fluxes (SHF and LHF, respectively) during three flights. Fluxes were calculated over the depth of the ABL using the integral method, in which only measurements of the mean atmospheric state (no transfer coefficients) were used. The initial flux estimates assumed that the observations were Lagrangian. Subsequent fluxes were estimated using a robust and innovative methodology that included modifications to incorporate adiabatic and non-Lagrangian processes as well as the heat content below flight level. The SHF ranged from 12 to 485 W m^{-2}, while the LHF ranged from 56 to 152 W m^{-2}. The importance of properly measuring the variables used to calculate the adiabatic and non-Lagrangian processes is discussed. Uncertainty in the flux estimates is assessed both by varying the calculation methodology and by accounting for observational errors. The SHF proved to be most sensitive to the temperature measurements, while the LHF was most sensitive to relative humidity. All of the flux estimates are sensitive to the depth of the boundary layer over which the values are calculated. This manuscript highlights these sensitivities for future field campaigns to demonstrate the measurements most important for accurate flux estimates.

Knuth, S.L., Cassano, J.J., Maslanik, J.A., Herrmann, P.D., Kernebone, P.A., Crocker, R.I., and Logan, N.J., 2013: Unmanned aircraft system measurements of the atmospheric boundary layer over Terra Nova Bay, Antarctica. ***Earth System Science Data*** **5: 57-69, doi:10.5194/essd-5-57-2013.**

In September 2009, a series of long-range unmanned aircraft system (UAS) flights collected basic atmospheric data over the Terra Nova Bay polynya in Antarctica. Air temperature, wind, pressure, relative humidity, radiation, skin temperature, GPS, and operational aircraft data were collected and quality controlled for scientific use. The data have been submitted to the United States Antarctic Program Data Coordination Center (USAP-DCC) for free access (doi:10.1594/USAP/0739464).

Lawrence, J., B.E. Schmidt, M.R. Meister, D. Dichek, C. Ramey, C., B. Hurwitz, A. Spears, A. Mullen, F.E. Bryson, J.J. Lutz, and J.P. Lawrence. 2018, December. Life under ice: Antarctic

Ocean world analogs with HROV icefin and RISE UP. *AGU Fall Meeting Abstracts* (Vol. 2018, pp. P21E-3402).

Icefin is a 3.5 m long, 24 cm diameter, 1500 m rated hybrid remote or autonomous underwater vehicle (HROV) developed for sub-ice observations in Dr. Britney Schmidt's Planetary Habitability and Technology Lab at Georgia Tech (US). First deployed beneath McMurdo Ice Shelf (MIS) in 2014, Icefin conducts basal ice, water column, and benthic surveys through ≥ 35 cm boreholes with a modular oceanographic sensor payload including CTD, DO, fDOM, turbidity, pH/ORP, ADCP, 2D forward sonar, altimetry, sidescan, and HD or 4K imaging. With live data streams via fiber-optic tether, remote or autonomous survey ability, and 5 km range Icefin provides a novel platform for better understanding ocean circulation, ice mass balance, and ecosystem diversity in sub-ice environments. Currently, the Icefin team is conducting Antarctic fieldwork under the NASA PSTAR-funded RISE UP program (Ross Ice Shelf and Europa Underwater Probe). RISE UP aims to autonomously characterize habitability and under-ice environments on broad spatial scales via robotic platforms toward future exploration of ocean worlds. In addition to Icefin work, complementary water column profiling to constrain sub-ice habitability includes CTD profiling, nutrient concentrations, cell counts, and 16S/18S rRNA gene surveys. Here, we present updates from an ongoing 2018 Antarctic field season (October - December 2018) with observations from beneath McMurdo Ice Shelf, McMurdo Sound sea ice, and nearby Erebus Glacier Tongue of water column structure, benthic geology, and fauna from the basal ice interface to the seafloor 900 meters below. Continued work includes collaborations with the Antarctica New Zealand Ross Ice Shelf Programme (2019/20, PI Christina Hulbe) at Ross Ice Shelf Grounding Zone, and the International Thwaites Glacier Collaboration with MELT (2019/20, PIs Keith Nicholls, David Holland). Icefin also serves as a novel oceanographic sensor development and test platform. Microfluidic cell counting, holographic microscopy, and onboard ice/sediment/water sampling modules are also currently in design and assembly phases.

Roquet, F., C. Wunsch, G. Forget, P. Heimback, C. Guinet, G. Reverdin, J. Charrassin, B. Frederic, D. Costa, L. Hückstädt, K. Goetz, K. Kovacs, C. Lydersen, M. Biuw, O. Nost, H. Bornemass, J. Ploetz, M. Bester, T. McIntyre, M. Muelbert, M. Hindell, C. McMahon, G. Williams, R. Harcourt, I. Field, L. Chafik, K. Nicholls, L. Boehme, and M. Fedak. 2013. Estimates of the Southern Ocean general circulation improved by animal-borne instruments. *Geophysical Research Letters* 40: 1-5, https://doi.org/10.1002/2013GL058304

Over the last decade, several hundred seals have been equipped with conductivity-temperature-depth sensors in the Southern Ocean for both biological and physical oceanographic studies. A calibrated collection of seal-derived hydrographic data is now available, consisting of more than 165,000 profiles. The value of these hydrographic data within the existing Southern Ocean observing system is demonstrated herein by conducting two state estimation experiments, differing only in the use or not of seal data to constrain the system. Including seal-derived data substantially modifies the estimated surface mixed-layer properties and circulation patterns within and south of the Antarctic Circumpolar Current. Agreement with independent satellite observations of sea ice concentration is improved, especially along the East Antarctic shelf. Instrumented animals efficiently reduce a critical observational gap, and their contribution to monitoring polar climate variability will continue to grow as data accuracy and spatial coverage increase.

Shah, K., G. Ballard, A. Schmidt, and M. Schwager. 2020. Multidrone aerial surveys of penguin colonies in Antarctica. *Science Robotics* 5, eabc3000.

Speed is essential in wildlife surveys due to the dynamic movement of animals throughout their environment and potentially extreme changes in weather. In this work, we present a multirobot path-planning method for conducting aerial surveys over large areas designed to make the best use of limited flight time. Unlike current survey path-planning solutions based on geometric patterns or integer programs, we solve a series of satisfiability modulo theory instances of increasing complexity. Each instance yields a set of feasible paths at each iteration and recovers the set of shortest paths after sufficient time. We implemented our planning algorithm with a team of drones to conduct multiple photographic aerial wildlife surveys of Cape Crozier, one of the largest Adélie penguin colonies in the world containing more than 300,000 nesting pairs. Over 2 square kilometers was surveyed in about 3 hours. In contrast, previous human-piloted single-drone surveys of the same colony required over 2 days to complete. Our method reduces survey time by limiting redundant travel while also allowing for safe recall of the drones at any time during the survey. Our approach can be applied to other domains, such as wildfire surveys in high-risk weather conditions or disaster response.

Shero, M.R., G. Adams, and J.M. Burns. 2015. Field use of ultrasonography to characterize the reproductive tract and early pregnancy in a phocid, the Weddell seal (*Leptonychotes weddellii*). *The Anatomical Record* 298: 1970-1977, doi: 10.1002/ar.23264.

The utility of transrectal ultrasonography was tested in a field setting to characterize the reproductive tract and detect early pregnancy (embryonic vesicles < 3 mm in diameter) in 17 multiparous female Weddell seals (*Leptonychotes weddellii*). Female Weddell seals give birth in October/November each year, followed by the breeding season (December) and embryonic diapause. Transrectal ultrasonography was attempted in January/February 2014 to examine the entire reproductive tract (uterine horns and body, ovaries with follicles and corpora lutea) using a 5–10 MHz linear-array probe with a 70 cm-long extension. A single pregnancy was detected in 14 of 17 seals (82.4%) as a circular or guitar-pick shaped nonechogenic (black) vesicle with a clearly visible echogenic border within the lumen of the uterus. The stage of embryonic development (ostensibly the gestational age) varied markedly among individuals, ranging from a vesicle with no embryo proper to a large fetus with an ocular orbit, nose/mouth, limb buds, spinal column, umbilical cord, and prominent vasculature. Two of the pregnant seals were re-examined 3-6 days after the initial examination to obtain longitudinal growth rates. Images of one or both ovaries were obtained in nine and seven of the 19 examinations, respectively. Numerous ovarian follicles (3 to 12 mm diameter) were detected and animals typically had a single well-perfused corpus luteum (determined by Doppler color-flow) ipsilateral to the uterine horn containing the pregnancy. We conclude that real-time transrectal ultrasonography is an effective tool for characterizing reproductive events in phocids including ovarian dynamics, and for elucidating the nature of embryonic diapause.

Shero, M.R., L.E. Pearson, D.P. Costa, and J.M. Burns 2014. Improving the precision of our ecosystem calipers: Evaluation of a modified morphometric technique for estimating marine mammal body composition. *PLOS One*, doi: 10.1371/journal.pone.0091233.

Mass and body composition are indices of overall animal health and energetic balance and are often used as indicators of resource availability in the environment. This study used morphometric models and isotopic dilution techniques, two commonly used methods in the marine mammal field, to assess body composition of Weddell seals (*Leptonychotes weddellii*, N=111). Findings indicated that traditional morphometric models that use a series of circular, truncated cones to calculate marine mammal blubber volume and mass overestimated the animal's measured body mass by 26.9±1.5% SE. However, we developed a new morphometric model that uses elliptical truncated cones, and estimates mass with only −2.8±1.7% error (N=10). Because this elliptical truncated cone model can estimate body mass without the need for additional correction factors, it has the potential to be a broadly applicable method in marine

mammal species. While using elliptical truncated cones yielded significantly smaller blubber mass estimates than circular cones (10.2±0.8% difference; or 3.5±0.3% total body mass), both truncated cone models significantly underestimated total body lipid content as compared to isotopic dilution results, suggesting that animals have substantial internal lipid stores (N=76). Multiple linear regressions were used to determine the minimum number of morphometric measurements needed to reliably estimate animal mass and body composition so that future animal handling times could be reduced. Reduced models estimated body mass and lipid mass with reasonable accuracy using fewer than five morphometric measurements (root-mean-square-error: 4.91% for body mass, 10.90% for lipid mass, and 10.43% for % lipid). This indicates that when test datasets are available to create calibration coefficients, regression models also offer a way to improve body mass and condition estimates in situations where animal handling times must be short and efficient.

Smith, W.O., Jr., K.T. Goetz, D.E. Kaufman, B.Y. Queste, V. Asper, D.P. Costa, M.S. Dinniman, M.A.M. Friedrichs, E.E. Hofmann, K.J. Heywood, J.M. Klinck, J.T. Kohut, and C.M. Lee. 2014. Multi-platform, multi-disciplinary investigations of the Ross Sea, Antarctica. *Oceanography* 27: 180-185.

In 2010–2011, three projects combined to characterize the temporal and spatial distributions of Modified Circumpolar Deep Water (MCDW) in the Ross Sea using icebreaker-based sampling, gliders, instrumented seals, and hindcasts from a numerical circulation model. The fieldwork clearly identified MCDW throughout the Ross Sea, and the data were used to determine its influence on potential heat and nutrient inputs and biotic distributions. Furthermore, the numerical simulations confirm its apparent trajectory and location. Substantial small-scale variability in oceanographic and biological distributions suggests that such variability may play an important role in biogeochemical cycles. Data from the three projects provide a view of hydrographic variability in the Ross Sea that is impossible to obtain using traditional sampling. Multiplatform investigations are promising approaches to future polar experiments where logistical considerations are of paramount importance.

APPENDIX D

UNITED STATES RESEARCHERS' RECENTLY COMPLETED (2020) AND CURRENT ROSS SEA PROJECTS RELEVANT TO THE ROSS SEA MARINE ECOSYSTEM (as of April 2021)

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PHYSICAL OCEANOGRAPHY/METEOROLOGY

"Assessment of Sea Ice from Satellite Imagery." NASA Earth Science Division at NASA Goddard Space Flight Center, Greenbelt MD, and Jet Propulsion Lab, California Institute of Technology, Pasadena, CA.

Extend and analyze the satellite-derived records of sea ice in the Ross Sea and elsewhere in the Southern Ocean, placing sea ice changes in the Ross Sea in the larger context of the Southern Ocean and Antarctic climate change.

"Collaborative: Antarctic Automatic Weather Station Program 2019-2022." NSF-OPP (Antarctic Ocean and Atmospheric Sciences); Co-PIs: M Lazzara, L Welhouse

Oversee and manage the US network of Automatic Weather Stations across the Antarctic, including around the Ross Sea.

"Collaborative: Antarctic Meteorological Research and Data Center." NSF-OPP (Polar Cyberinfrastructure); **co-PIs: M. Lazzara, L Welhouse, J Philips, J Robaidek, J Havens**

Develop a formal data repository for US Antarctic meteorological datasets, along with associated data stewardship, data tasking, etc.

"West Antarctic Ice Shelf-Ocean Interactions." NSF-OPP, co-PIs: S Jacobs, W Smethie Jr., F Nitsche

This project extends and combines historical and recent ocean data sets to investigate ice-ocean-interactions along the Pacific continental margin of the West Antarctic Ice Sheet. The synthesis focuses on the strikingly different environments on and near the cold Ross Sea and warm Amundsen Sea continental shelves, where available measurements reach back to ~1958 and 1994, respectively. On the more extensively covered Ross Sea continental shelf, multiple reoccupations of ocean stations and transects are used to extend our knowledge of long-term ocean freshening and the mass balance of the world's largest ice shelf.

"Surface Energy Balance on West Antarctica and the Ross Ice Shelf." NSF-OPP, PI: D Lubin

UCSD scientists will deploy a suite instruments to measure downwelling and net shortwave and longwave fluxes, sensible and latent heat fluxes, and near-surface meteorology. These measurements will be analyzed and interpreted to determine mesoscale conditions that govern surface melt in West Antarctica, in the context of improving coupled climate model parameterizations.

"Unpinning of the Ross Ice Shelf from Ross Bank." NSF-OPP, PI: P Bart

The research investigates the how, why and when the Ross Ice Shelf (RIS) unpinned from Ross Bank to assess ice sheet and ice shelf behavior during a recent unpinning event. Changes in West Antarctic Ice Sheet flow patterns as suggested by flow stripes and rift tracks preserved on the RIS suggest recent evolution (i.e. last millennial) of the ice shelf. Existing ice core data along with the collection of data from two cruises to the Ross Sea will be used to reconstruct past ice shelf dynamics around Ross Bank to determine RIS future susceptibility and response of unpinning.

"The Influence of Sea Ice Motion on Antarctic Sea Ice Expansion." NSF-OPP, co-PIs: I Eisenman, T Wagner

Sea ice motion has recently emerged as one of the candidates to explain the Antarctic sea ice expansion but a systematic investigation of how sea ice motion influences sea ice concentration has not been presented to date. Researchers will conduct a process-oriented study of the relationship between sea ice motion and Antarctic sea ice extent using a hierarchy of models.

"Circulation of the Ross Gyre." NSF-OCE, PI: K Speer

The large-scale gyre circulation, eddy fluxes, and advection in the Ross Gyre act to produce net exchange between the Antarctic Circumpolar Current (ACC) and the Antarctic margin. The main objectives are to determine the structure and transport of the Ross Gyre and associated sub-gyres, to quantify the interactions between the ACC and Ross Gyre, including the role of topography in localizing meridional exchange and to determine the connection between the Antarctic Slope Current and the Ross Gyre.

"RAPID: An Improved Understanding of Mesoscale Wind and Precipitation Variability in the Ross Island Region Based on Radar Observations." NSF-OPP, co-PIs: J Cassano, D Kingsmill, M Seefeldt

The Ross Island region of Antarctica is a topographically complex region that results in large variations in the mesoscale high wind and precipitation features across the region. The goals of this project are to increase the understanding of the three-dimensional structure of these mesoscale meteorology features. This project will leverage observations from the scanning X-band radar installed during the AWARE field campaign in 2016 and the installation of an EWR Radar Systems X-band scanning radar (E700XD) to be deployed during the 2019-20 field season, at McMurdo.

"Collaborative: Assessing Drivers of Climate Model Biases on the Pacific Continental Shelf of Antarctica." NSF-OPP, PI: L Padman

Current-generation GCMs exhibit substantial biases in their projections of present-day hydrography and sea ice state. Previous projections of the coastal cryosphere have applied simple bias corrections. However, this approach does not remedy the underlying physical and numerical errors responsible for these biases. This project seeks the relevance of biases to the interpretation of GCM projections by identifying their local and/or remote origins and their variation across regions and with different climate models. It will leverage the wealth of new simulations becoming available through the Coupled Model Intercomparison Project, phase 6 (CMIP6), and will focus on the rapidly-changing Pacific sector of the coastal Antarctic.

BIO-PHYSICAL

"Collaborative: Elucidating Environmental Controls of Productivity Hot-Spots around Antarctica." NSF-OPP; co-PIs: K Arrigo, E Hofmann, M Dinniman

The goals of this project are to determine 1) What environmental factors exert the greatest control of primary production in polynyas around Antarctica? and 2) What are the controlling physics that lead to the heterogeneity of dissolved iron (dFe) supply to the euphotic zone in polynyas around the Antarctic continental shelf and what effect does this have on local rates of primary production and carbon export?

"Collaborative: P2P, Predators to Plankton: Biophysical Controls in Antarctic Polynyas." NSF-GEO-NERC; co-PIs: D Ainley, W Smith, K Heywood, G Ballard, A Varsani

Using three buoyancy gliders, quantify the preyscape, and bio-physical factors affecting it, within and outside the large foraging area of Cape Crozier penguins, while biologging both penguin species to determine distribution and foraging behaviour as the summer progresses. Satellite imagery will quantify abundance/distribution of competing whales and seals.

"Collaborative: Cobalamin and Iron Co-Limitation of Phytoplankton Species in Terra Nova Bay." NSF-OPP; PI: R Dunbar

Phytoplankton blooms in the coastal waters of the Ross Sea, Antarctica are typically dominated by either diatoms or Phaeocystis Antarctica (a flagellated algae that often can form large colonies in a gelatinous matrix). The project seeks to determine if an association of bacterial populations with *Phaeocystis antarctica* colonies can directly supply Phaeocystis with Vitamin B12, which can be an important co-limiting micronutrient in the Ross Sea. The study will test whether a mutualistic symbioses between attached bacteria and Phaeocystis provides colonial cells a mechanism for alleviating chronic Vitamin B12 co-limitation effects thereby conferring them with a competitive advantage over diatom communities.

"Fe Behavior and Bioavailability in Sub-aerial Runoff into the Ross Sea." NSF-OPP, co-PIs: WB Lyons, C Gardner

This project will investigate in-stream processes and characteristics controlling dissolved iron draining into the Ross Sea including photoreduction, temperature, and complexation with organic matter.

"Hot spots in the ice: revealing the importance of polynyas for sustaining present and future Antarctic marine ecosystems." NASA-Ecological Forecasting. Co-PIs: A DuVivier, C Brooks, S Jenouvrier.

This project proposes a holistic synthesis of the ecosystem within Antarctic polynyas to: 1. Quantify the role polynyas play in mediating access to food resources for key Antarctic marine ecosystem species around the Antarctic continent. 2. Assess how the spatiotemporal distribution of polynyas and their role in mediating ecological interactions may change over the next several decades due to natural climate variability and human-driven climate change. 3. Develop an ecosystem productivity index that incorporates multiple trophic levels and provides guidance for forecasting which polynyas are most critical to protect biodiversity.

"Collaborative: Polynyas in Coastal Antarctica (PICA): Linking Physical Dynamics to Biological Variability." NSF-OPP, co-PIs: W Zhang, R. Ji, S. Jenouvrier, T. Maksym

The main objectives are to form a comprehensive understanding of the temporal and spatial variability of Antarctic coastal polynyas and the physical controls of polynya ecosystems. The project takes an interdisciplinary approach and seeks to establish a modeling system centered on the Regional Ocean Modeling System. This system links the ice and ocean conditions to the plankton ecology and penguin population. In particular, this study will test a set of hypothesized effects of winds, offshore water intrusion, ice-shelf melting, sea-ice formation, glacier tongues, and ocean stratification on the timing of polynya phytoplankton bloom and the overall polynya biological productivity.

"Collaborative: Have Transantarctic Dispersal Corridors Impacted Antarctic Marine Biodiversity?" NSF-OPP, PI: A Mahon

The overarching goal is to understand environmental factors that have shaped patterns of present-day diversity in Antarctic benthic marine invertebrates. Evidence from sediment cores and modeling suggests ice shelf collapses have occurred multiple times in the last few million years. During these periods, transantarctic seaways connected the Ross and Weddell Seas. This research will assess whether the presence of transantarctic waterways helps explain observed similarities between the Ross and Weddell seas benthic marine invertebrate fauna better than other current hypotheses (e.g., dispersal by the Antarctic Circumpolar Current, or expansion from common glacial refugia).

"Collaborative: The Antarctic Scallop as Key to Paleoenvironments and Sea Ice Conditions: Understanding the Modern to Predict the Past." NSF-OPP, co-PIs: S Walker, D Gillikin, A Perez-Huerta, CF Andrus

The primary goal of this project is to assess the differences in growth, lifespan, and chemistry (stable isotopes, trace elements) archived in the shell of the Antarctic scallop that may be indicative of two ice states: persistent (multiannual) sea ice at Explorers Cove (EC) and annual sea ice (that melts out every year) at Bay of Sails (BOS), western McMurdo Sound, Antarctica. This project will investigate growth and lifespan proxies (physical and geochemical) and will use high-resolution records of stable oxygen isotopes to determine if a melt-water signal is archived in A. colbecki shells and whether that signal captures the differing ice behavior at two sites (EC versus BOS).

ECOLOGICAL/BEHAVIORAL

"Opening the Black Box - Integrating Winter Ecology into the Management of the Ross Sea Region Marine Protected Area." NASA-ROSES; co-PIs: G Ballard, A Schmidt, D Ainley

Assess dependence of Ross Sea Adélie penguin migration on sea ice movements and the strength of ocean currents (Ross Gyre); (2) Identify high-use foraging areas and habitat characteristics for penguins during the austral winter; and (3) Assess whether the RSRMPA general protection zone (unfished) includes important penguin winter foraging habitat boundaries and zones.

"A Full Lifecycle Approach to Understanding Adélie Penguin Response to Changing Ice Conditions in the Ross Sea." NSF-OPP; co-PIs: D Ainley, G Ballard, K Dugger

Using 19 years of colony-based data, as well as collecting additional information on individually marked, known-age and known-history penguins, from new recruits to possibly senescent individuals, determine 1) how changing winter sea ice conditions in the Ross Sea region affect penguin migration, behavior and survival and alter the carry-over effects (COEs) to subsequent reproduction; 2) the interplay between extrinsic and intrinsic factors influencing COEs over multiple years of an individual's lifetime; and 3) how local environmental change may affect population change via impacts to nesting habitat, interacting with individual quality and COEs.

"Collaborative: Population Growth at the Southern Extreme: Effects of Early Life Conditions on Adélie penguin Individuals and Colonies." NSF-OPP; co-PIs: G Ballard, K Dugger, A Schmidt, J Santora, A Varsani

Deploy newly invented tags on penguins over 4 field seasons, leveraging biologging and demographic data collected by our team since 1996; simultaneously investigate diet. Evaluate hypotheses related to early-life conditions and behavior to reveal mechanisms behind population growth and resilience to address our overarching question: How is it possible for some penguin populations to continue growing, well beyond hypothesized energetic and competitive constraints, while other populations remain small?

"Collaborative: A Multi-scale Approach to Understanding Spatial and Population Variability in Emperor Penguins." NSF-OPP, co-PIs: M LaRue, E Ito, S Jenouvrier

Quantify emperor penguin presence/absence, and colony size and trajectory, across the entire Antarctic continent using high-resolution satellite imagery. For a subset of the colonies, population estimates derived from high-resolution satellite images will be compared with those

determined by aerial surveys. This validated information will be used to determine population estimates for all emperor penguin colonies through iterations of supervised classification and maximum likelihood calculations on the high-resolution imagery.

"CAREER: Foraging Ecology and Physiology of Emperor Penguins in the Ross Sea." NSF-OPP, PI: B McDonald

This study combines a suite of technological and analytical tools to gain essential knowledge on Ross Sea emperor penguin foraging energetics, ecology, and habitat use during critical periods in their life history, especially during late chick-rearing periods. Energy management is particularly crucial during this time as parents need to feed both themselves and their rapidly growing offspring, while being constrained to regions near the colony.

"The Consequences of Maternal Effects and Environmental Conditions on Offspring Success in an Antarctic Predator." NSF-OPP; co-PIs: J Rotella, D Siniff, R Garrott

Evaluate the survival and reproductive consequences of early-life environmental conditions and variation in offspring traits that are related to maternal attributes (e.g. birth date, birth mass, weaning mass, and swimming behavior) in a population of Weddell seals in Erebus Bay, Ross Sea. Also, allow the documentation of the population status that will contribute to the unique long-term database for the local population that dates back to 1978. We are also analyzing population trends, temporal variation in production of pups and potential covariates of variation, changes in population composition through time. Our research team also tags all Weddell seals encountered during two annual visits to White Island, south of McMurdo Station, to monitor that population and to provide tissue samples for genetic analyses of that small, isolated population.

"RUI: Growing Up on Ice: Physiological Adaptations and Developmental Plasticity in Weddell Seal Pups across Two Extreme Physical Environments." NSF-OPP, co-PIs: H Liwanag, L Tomanek, L Pearson, S Johnson

The project seeks to better understand how Weddell seal pups rapidly develop (within weeks) the capacity to transition between these two extreme environments (that differ greatly in their abilities to conduct heat) and how they budget their energy during the transition. Though the biology and physiology of adult Weddell seals is well studied, the energetic and physiological strategies of pups during development is still unclear.

"Collaborative: Physiological and Genetic Correlates of Reproductive Success in High-versus Low-Quality Weddell Seals." NSF-IOS, PI: A Hindle

This study aims to distinguish which physiological mechanisms (energy dynamics, aerobic capacity, and fertility) and underlying genetic factors make some Weddell seal females particularly successful at producing pups year after year, while others produce far fewer pups than the population average. In this project, an Organismal Energetics approach will identify key differences between high- and low-quality females in how they balance current and future reproductive success by tracking lactation costs, midsummer foraging success and pregnancy rates, and overwinter foraging patterns and live births the next year.