How Do Polar Marine Ecosystems Respond to Rapid Climate Change?

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REVIEW

How Do Polar Marine Ecosystems Respond to Rapid Climate Change?

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Climate change will alter marine ecosystems; however, the complexity of the food webs, combined with chronic undersampling, constrains efforts to predict their future and to optimally manage and protect marine resources. Sustained observations at the West Antarctic Peninsula show that in this region, rapid environmental change has coincided with shifts in the food web, from its base up to apex predators. New strategies will be required to gain further insight into how the marine climate system has influenced such changes and how it will do so in the future. Robotic networks, satellites, ships, and instruments mounted on animals and ice will collect data needed to improve numerical models that can then be used to study the future of polar ecosystems as climate change progresses.

How does a changing physical ocean environment affect regional and local marine food webs? Many regions, especially polar seas (*1*, *2*), are experiencing changes in atmospheric/ocean circulation (*3*), ocean properties (*4*, *5*), sea ice cover (*6*, *7*), and ice sheets (*8*, *9*). These rapid climatic changes are triggering pronounced shifts and reorganizations in regional ecosystems and biogeochemical cycles (*10*, *11*). However, it remains difficult to link these ecosystem changes to shifts in the physical system. Overcoming this gap is a critical step in establishing any level of predictive skill.

The West Antarctic Peninsula (WAP), northwestern North America, and the Siberian Plateau are exhibiting rapid regional warming (*1*), but only the WAP has a maritime climate. Thus, the WAP is an ideal location to monitor and understand the impacts of rapid climate change on marine ecosystems. Other regions of Antarctica are exhibiting much smaller rates of warming—and some, such as the Ross Sea (*12*), are even experiencing trends in the opposite direction—but climate models predict strong warming and circumpolar sea ice retreat around Antarctica over the next century (*13*). Understanding the response of the WAP ecosystems to climate change will thus help to predict further changes in the polar ecosystem as a whole and will provide insight into the planetary-scale changes that are likely as greenhouse gas–driven warming continues.

Physical Changes in the WAP

Changes in the WAP are profound (Fig. 1). Midwinter surface atmospheric temperatures have increased by 6°C (more than five times the global average) in the past 50 years (*14*, *15*). Eighty-seven percent of the WAP glaciers are in retreat (*16*), the ice season has shortened by nearly 90 days, and perennial sea ice is no longer a feature of this environment (*17*, *18*). These changes are accelerating (*19*, *20*).

Ocean warming has been implicated as a major driver for this deglaciation (*21*). The ocean has become warmer in the WAP (*17*). Most of this heat comes from the warm, saline Upper Circumpolar Deep Water (UCDW) that penetrates onto the WAP shelf from the Antarctic Circumpolar Current (ACC) in the adjacent deep ocean. The increased supply of heat from the UCDW is believed to be associated with the strengthening of winds over the Southern Ocean (*22*, *23*). Enhanced upwelling of heat to the WAP is complemented by rising summertime surface-ocean heating (*24*), which is associated with the strong retreats in the seasonal sea ice cover (*7*, *18*).

This atmosphere–ocean-ice interplay at the WAP results in a positive feedback that amplifies and sustains atmospheric warming. Understanding these feedbacks will require better knowledge of the processes at the shelf edge and in the adjacent deep ocean to determine where and when the UCDW intrudes from the ACC onto the WAP shelf. Although the ACC is a major current in the

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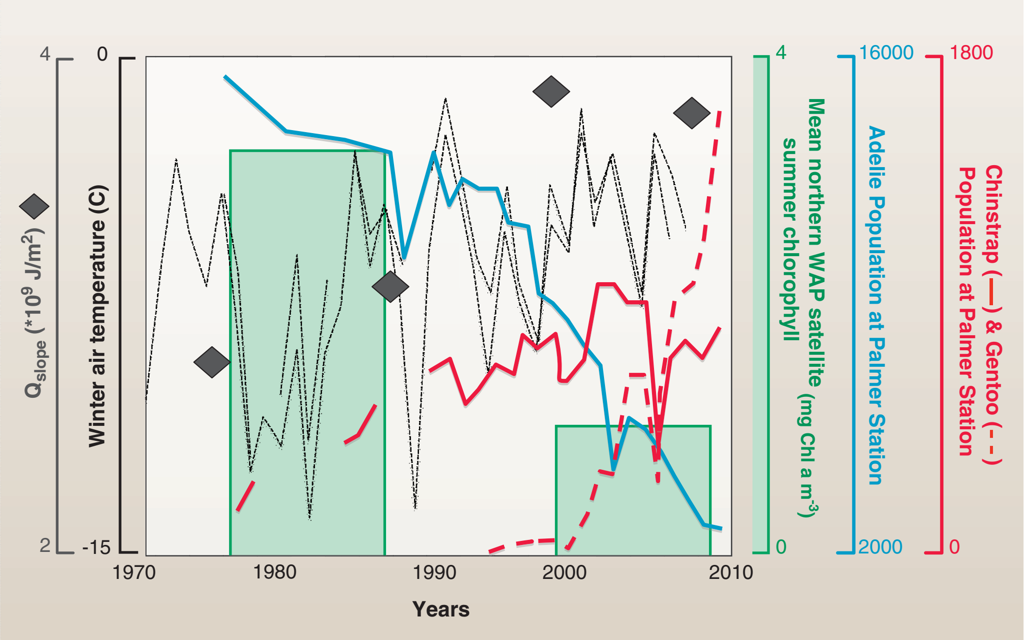

Fig. 1. Changes observed along the WAP over the past 30 years. Annual average air temperatures at Faraday/Vernadsky Station (65°15′S, 64°16′W) and Rothera Station (67°34′S, 68°08′W) have increased. There has been an increase in heat content (relative to freezing) of ACC slope water that had direct access to the WAP continental shelf (black diamonds). Average phytoplankton biomass declined between 1978–1986 and 1998–2006 (between 1987 until 1997, no ocean color satellite imagery was available). There were also large shifts in the penguin populations at Anvers Island from 1975 to 2008.

global ocean circulation system and has undergone substantial warming in recent decades (*25*), coherent sampling of the ACC remains a challenge.

Ecosystem Changes in the WAP

In part because of the heat and nutrients supplied by the UCDW, the WAP hosts an extremely productive marine ecosystem supported by large phytoplankton blooms (*26*). However, over the past 30 years the magnitude of these blooms has decreased by 12% (*27*). The changes have been particularly dramatic in the northern WAP, with declines driven by an increase in cloudy days, deep mixed layers associated with persistently strong winds, and a reduction in the marginal ice zone (*27*). There is evidence that the algal community composition has shifted from large to small cells (*27*, *28*). These changes are not uniform across the Peninsula; areas in the south that were previously mostly covered with ice now have open water, allowing local ocean productivity rates to increase (*27*, *29*). Nevertheless, the net productivity of the WAP appears to have decreased.

The shift in phytoplankton biomass and size has direct consequences for grazer communities, especially Antarctic krill (*Euphausia superba*), which are inefficient at grazing small cells (*30*, *31*). In contrast, tunicates such as the salp (*Salpa thomsoni*) are efficient at grazing the smaller cells. In the WAP, there is evidence that krill are being replaced by salps (*32*, *33*)—a phenomenon that can be magnified over time because salps consume krill eggs and larvae (*34*). The decline in phytoplankton biomass also favors salps, whose filtering apparatus can become clogged when phytoplankton biomass is high (*35*). Lastly, the spawning behavior of Antarctic krill depends on sea ice (*36*). Because krill form a critical trophic link between primary producers and upper-level consumers, the shift in zooplankton community structure suggests that there should be dramatic changes in the higher trophic levels (fish, seals, whales, and penguins and other seabirds) (*37*).

These changes have been documented most dramatically in Antarctic pygoscelid penguins. In the past 30 years in the northern WAP, populations of ice-dependent Adélie penguins (*Pygoscelis adeliae*) have fallen by 90%, whereas those of ice-intolerant Chinstrap (*P. Antarctica*) and Gentoo (*P. papua*) penguins have risen in the northern and mid-Peninsula region (*10*). The latter two species were only recently established at the WAP: The first Chinstraps were observed in 1975, and Gentoos arrived in 1994.

Declines in the polar species have been related to decreasing sea ice cover and its possible effects on prey availability (*10*). Penguins breed in locations with predictably abundant food, allowing them to forage and return to their colonies to feed chicks (*38*). The Adélie penguins breed in locations where deep ocean canyons exist near the land margin; these canyons provide a possible conduit for the warm UCDW to extend to near the land margin (*39*), keeping winter ice low and supporting high primary productivity rates (*26*). The increase in ocean warming has led to lower total ocean productivity and decreased winter sea ice cover, which is a critical habitat for the spawning of krill (*36*) and Antarctic silverfish. Shifts in climate have thus had a cascading effect, with altered sea ice distributions disrupting the evolved life strategies of resident species, leading to changes in community structure and in the abundance of populations, and ultimately altering the nature of local and regional food webs (*40*). These local canyon-associated hot spots provide a singular opportunity to study how global changes that affect the circulation and marine climate in the region of the ACC can ripple through marine food webs. Ecosystem dynamics also reflect top-down effects as many higher trophic levels recover from past whale harvests along the WAP (*41*). The changes along the WAP are just one example of how rapid climate change will affect polar ecosystems, which argues for a polar ocean observational strategy that is capable of studying the interactions and feedbacks between the ocean, the atmosphere, perennial/annual ice, and regional ecosystems.

Toward a New Strategy for Polar Ocean Ecosystem Observation

Cost considerations and the harsh conditions in the polar oceans restrict the coverage that can be provided by research ships. Furthermore, cloud cover is often heavy, hampering remote sensing approaches, whereas sea ice and icebergs make it difficult to deploy surface ocean moorings. To overcome these hurdles, the oceanographic community has been developing technologies that may form the foundation for a coherent observational strategy. The strategy will require a nested multiplatform approach that will enable sustained observations throughout the year in the Southern and Arctic oceans.

Key goals for such a strategy will be to quantify a heat budget for the atmosphere and ocean, understand how the deep ocean is interacting with shelf waters, how this flux changes with time, and how this affects regional marine climate, ice dynamics, and ecology. Achieving these goals will require an expanded number of ocean and atmospheric measurements from automated sensors and long-duration profiling floats (Fig. 2A). Profiling floats are very effective at mapping the properties of the deep ocean. They have, for example, documented the warming of the ACC (*25*). These floats cannot sample in ice or in coastal waters and have a limited capacity to carry chemical/biological sensors. So, the floats need

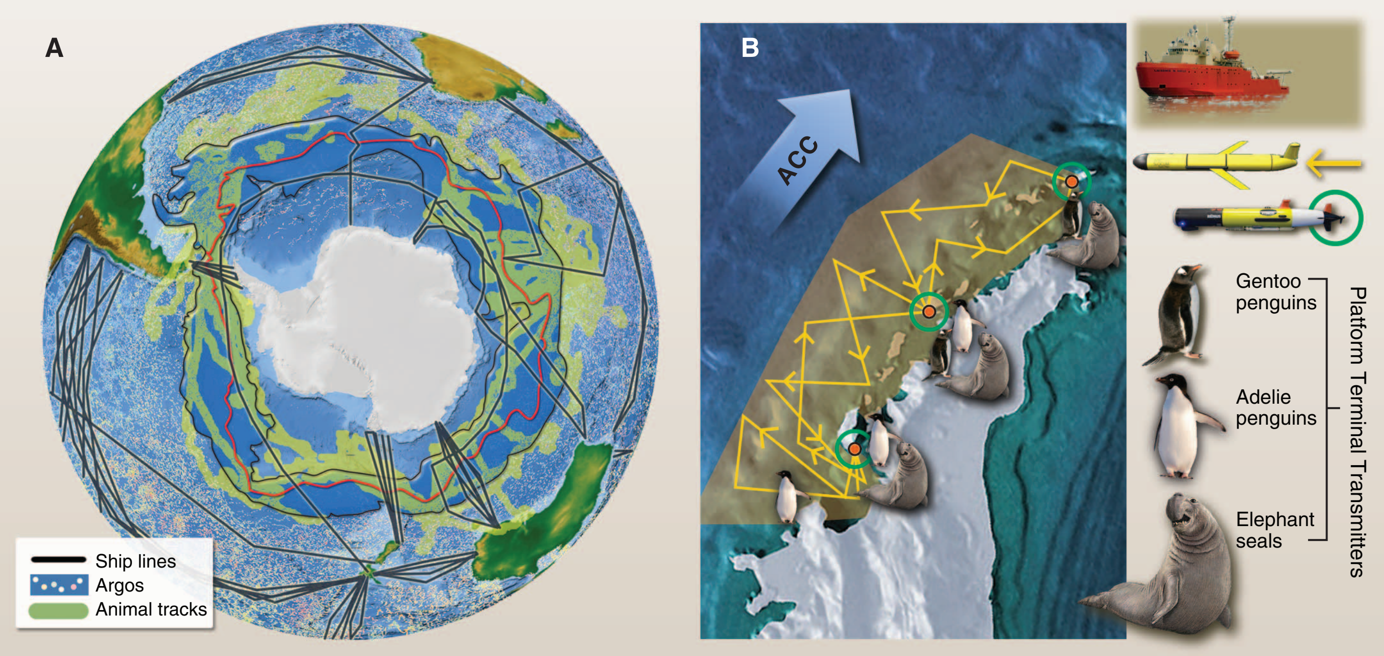

Fig. 2. A potential ocean-observing network for studying the ACC and its role in structuring continental shelf ecosystems. (**A**) The proposed network for studying the ACC (mean current is denoted by a red line, and the bright blue area shows its spatial variability). Hydrography of the ACC will be sampled with profiling floats (colors on the dots indicate individual profiling floats over time) (*25*). Spatial data collected by floats need to be complemented by ships outfitted with automated sensors. Animals (such as whales, seals, and birds) can be outfitted with sensors can also provide spatial data. For example, the bold transparent yellow lines denote the spatial coverage provided by elephant seals [redrawn from data presented in (*43*)]. (**B**) A proposed regional observing network for the West Antarctic Peninsula that could be embedded within the larger ACC-observing network. The system consists of high-resolution sampling conducted by autonomous underwater vehicles and animals outfitted with sensors. These sampling networks will also consist of research vessels and underwater gliders.

to be complemented with data collected by ships through repeat transects or "ships of opportunity" (research vessels, resupply ships, and tourist vessels) that are abundant during the summer months and are increasingly being outfitted with automated sensors that collect atmospheric and ocean data.

Another approach showing promise is the deployment of oceanographic instruments on marine mammals, such as seals, fish, and whales (*42*, *43*). This provides information on animal behavior in relation to oceanographic features and provides vertical profile data to complement the profiling floats. However, instruments deployed on animals can currently only carry a limited set number of sensors; transects by research vessels therefore remain invaluable.

The interaction of the ocean with the cryosphere is a key factor influencing polar marine ecosystems and must be part of any observing system design. Remote sensing techniques can provide regional data on sea ice extent and concentration and have the potential to provide information on sea ice thickness (*44*). In situ measurements are needed to calibrate satellite data and provide detailed local information. For example, ice thickness can be measured with upward-looking sonars, either on fixed moorings to provide time series or on autonomous underwater vehicles for spatial surveys (*45*). Glacial ice also affects the ecosystem response to climate change because glacial ice melt stratify the water column and enhance primary production.

Characterizing how the shifts in the physics alter marine ecosystems is a daunting challenge: Many key species are mobile, requiring sampling networks to span a wide range of spatial and temporal scales. Fortunately, we can prioritize regions to sample by focusing on biological hotspots (*40*, *46*). Many biological hotspots are spatially constrained (~10 to 100 km^2) and distributed throughout polar systems. They are often located near sea mounts, islands, and deep sea canyons that are adjacent to land. The close proximity to land allows a wide range of sampling strategies. Routine shore-based sampling (even during winter) can be augmented with sea-floor cables, which provide high bandwidth and power to sample the benthic communities and the overlying water column (*47*) despite the presence of ice. Time series can then be complemented with spatial data collected by autonomous underwater vehicles and gliders that are capable of providing high-resolution maps of the physics, chemistry, and biology (*48*). Navigation by the mobile platforms would be facilitated by sea floor– and ice-mounted acoustic transponders. Combined, the spatial time series will enable the development of coupled ocean atmosphere–food web numerical models.

Polar Seas in a Changing Climate

The challenges for developing an observing system capable of elucidating the causes and impacts on marine ecosystem changes in polar oceans is not to be underestimated, because these regions are among the harshest in the world. Emerging technology can meet these challenges, because automation will lower the costs associated with ship operations by providing complementary approaches to collecting data. This is fortunate, as there is scientific urgency in deploying such systems given the observed changes in both the Arctic and Southern oceans.

These observational systems will provide insights into potential future ecosystem changes in polar oceans, but their deployment will require international cooperation given the scale of effort required; however, because many of the technologies have been demonstrated to be effective it is not unreasonable to believe that these networks could be deployed in 5 to 10 years. The benefits of better understanding the marine ecosystem, and being better able to predict, protect, and make use of its resources, are strong drivers to make this a reality.

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REVIEW

The Impact of Climate Change on the World's Marine Ecosystems

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Marine ecosystems are centrally important to the biology of the planet, yet a comprehensive understanding of how anthropogenic climate change is affecting them has been poorly developed. Recent studies indicate that rapidly rising greenhouse gas concentrations are driving ocean systems toward conditions not seen for millions of years, with an associated risk of fundamental and irreversible ecological transformation. The impacts of anthropogenic climate change so far include decreased ocean productivity, altered food web dynamics, reduced abundance of habitat-forming species, shifting species distributions, and a greater incidence of disease. Although there is considerable uncertainty about the spatial and temporal details, climate change is clearly and fundamentally altering ocean ecosystems. Further change will continue to create enormous challenges and costs for societies worldwide, particularly those in developing countries.

Earth, with its life-filled ocean, is unusual among planets (*1*). Covering 71% of Earth's surface, the ocean nurtured life on our planet and continues to play a dominating role in regulating its climate. Change has been the norm as Earth has swung through a variety of states in which life has prospered, dwindled, or experienced calamitous declines. In the latter case, intrinsic events (e.g., volcanic activity) or extrinsic events (e.g., large meteorite strikes) have sometimes resulted in hostile conditions that have increased extinction rates and driven ecosystem collapse. There is now overwhelming evidence that human activities are driving rapid changes on a scale similar to these past events (*2*). Many of these changes are already occurring within the world's oceans (Figs. 1 and 2), with serious consequences likely over the coming decades.

Our understanding of how climate change is affecting marine ecosystems has lagged behind that of terrestrial ecosystems. This is partly due to the size and complexity of the ocean, but also to the relative difficulty of taking measurements in marine environments. Long-term studies of climate change in the oceans are rare by comparison to those on land (*3*). Here, we review the impacts of anthropogenic climate change on marine ecosystems, revealing that the majority are changing rapidly with an increased risk of sudden nonlinear transformations. Given the overwhelming importance of the ocean to life on our planet, these changes underscore the urgency with which the international community must act to limit further growth of atmospheric greenhouse gases and thereby reduce the serious risks involved.

Rates of Change

Rising atmospheric greenhouse gas concentrations have increased global average temperatures by ~0.2°C per decade over the past 30 years (*4*), with most of this added energy being absorbed by the world's oceans. As a result, the heat content of the upper 700 m of the global ocean has increased by 14×10^{22} J since 1975 (*5*), with the average temperature of the upper layers of the ocean having increased by 0.6°C over the past 100 years (*2*) (Fig. 1, A and B). These changes are ongoing; global ocean surface temperatures in January 2010 were the second warmest on record for the month of January, and the period June to August 2009 reached 0.58°C above the average global temperature recorded for the 20th century, 16.4°C (*6*).

In addition to acting as the planet's heat sink, the oceans have absorbed approximately one-third of the carbon dioxide produced by human activities. The absorption of anthropogenic CO_2 has acidified the surface layers of the ocean, with a

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