Plankton, from the last ice age to the year 3007

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Climate forcing of the environment and biota has been happening since time immemorial, human forcing only for the past 200 years or so. This paper considers, first, climatic changes over the past 30 000 years, as indicated by plankton and their effects on plankton. Only fossilizable plankton can be observed: principally foraminifera, radiolaria, and pteropods in the zooplankton, and their food, principally coccolithophores, diatoms, and dinoflagellate cysts, in the phytoplankton. The soft-bodied zooplankton species—especially copepods—that lived with them can only be inferred. Large, abrupt climate changes took place, aided by positive feedback. Second, this paper attempts to predict how human forcing in the form of anthropogenic climate change is likely to affect marine ecosystems in the future. Past predictions have underestimated the speed at which warming is actually happening: positive feedback has been unexpectedly strong. Thus, the melting of snow and ice, by reducing the earth's albedo, has increased the amount of solar energy absorbed. Also, warming of the surface (water and land) has caused outgassing of methane from buried clathrates (hydrates), and methane is a strong greenhouse gas. Currently, predictions emphasize one or the other of two contrasted alternatives: abrupt cooling caused by a shutdown of the thermohaline circulation (the "ocean conveyor") or abrupt warming caused by copious outgassing of methane. Both arguments (the former from oceanographers and the latter from geophysicists) are equally persuasive, and I have chosen to explore the methane alternative, because I am familiar with an area (the Beaufort Sea and Mackenzie Delta) where outgassing has recently (2007) been detected and is happening now: in the Arctic Ocean and the Canadian Arctic Archipelago, where disappearance of the ice will affect currents, temperature, thermocline, salinity, upwelling, and nutrients, with consequent effects on the zooplankton.

Keywords: Canada, ice age, palaeoecology, plankton, time-series, trends.

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Introduction

Climate forcing has been affecting zooplankton since its first appearance on earth, probably more than a billion years ago, and human forcing for about the past 200 years. Natural climate change has been going on since earth began, and currently, we live in a glacial age that began about 1.8 million years ago, throughout which cold periods (glaciations) have alternated with warmer interglacials in a ~100 000-year cycle. The cycle results from the astronomical setting of the Milankovitch cycle (Pielou, 1991). We are in an interglacial now, probably near the end of it. A history must start somewhere, and 30 000 years ago, the beginning of the last glaciation of the three that together make up the Wisconsinan group of glaciations is an appropriate starting point. The glaciation peaked about 20 ka BP (20 000 years before present) and ended 10 ka BP, and while it lasted, the climate fluctuated abruptly. Cold and warm periods (stadials and interstadials) alternated in cycles, lasting only a few thousand years.

These climatic changes have affected the oceans and ocean life profoundly. Past effects are inferred both from geophysical observations and from fossils, especially microfossils of plankton such as foraminifera, diatoms, radiolaria, shelled pteropods, dinoflagellate cysts, and coccolithophores, that is, all the plankton species with hard parts of carbonate (calcite and aragonite), silica, or cellulose. When cores of seabed sediments are examined, the relative abundances of these fossil species in different layers can be estimated. Radiocarbon dating is the usual method of dating fossils less than 60 000 years old, and the temperature of the water in which the organisms lived is inferred from the fossils' oxygen–isotope ratios ($\delta^{18}O$ ratios).

Corresponding temperatures in the North Atlantic and Arctic Ocean are also obtained from ice cores collected from the Greenland and Antarctic ice sheets. When seawater evaporates, molecules with the light oxygen isotope ^{16}O evaporate more readily than those with heavier ^{18}O. Therefore, the vapour that condenses to become snow contains a smaller proportion of ^{18}O than the seawater from which it came. The snow falls on ice sheets in polar latitudes. Thus, $\delta^{18}O$ is a proxy for the volume of water from the sea that has frozen on land, making it an indirect indicator of ambient temperature and precipitation at the time that the ice froze. The age of the ice is found by counting its annual layers.

Contemporaneously, fossil plankton tests in nearby sediment-core samples were deprived (comparatively) of ^{16}O, so their $\delta^{18}O$ ratios increased. The concentrations of the greenhouse gases (GHG) carbon dioxide and methane, and nutrient-containing wind-borne dust can also be found by measuring the amounts in air bubbles trapped in the ice.

Heinrich events and Dansgaard–Oeschger events

Three large, abrupt drops in temperature are believed to have occurred in the interval 30 ka BP to 20 ka BP (Figure 1). They

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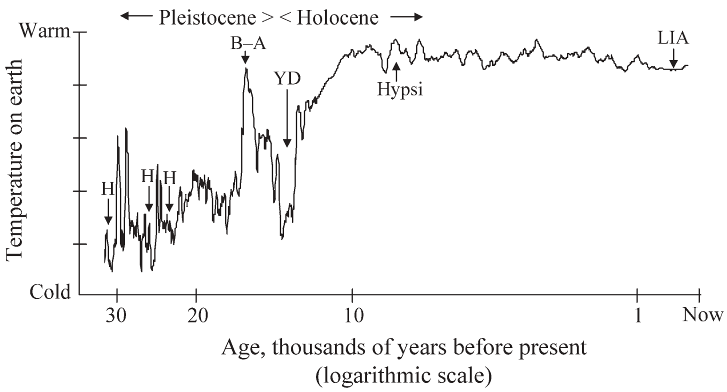

Figure 1. Diagrammatic representation of climate fluctuations over the past 30 000 years, based on Alley (2000b). H, Heinrich events; B–A, Bolling–Allerod warm period; YD, Younger Dryas; Hypsi, Hypsithermal period; LIA, little ice age.

are the most recent in a series of the so-called Heinrich events (named for their discoverer) that recurred cyclically over a period of several tens of thousands of years. They are indicated by Heinrich layers in sediment cores from the North Atlantic, spaced at intervals of 7000 years, on average. Each layer consists of eroded rock fragments and sand much coarser than the fine-grained microfossil sediments above and below it (Hemming, 2004). The fragments are too heavy to have been carried by currents and must have been transported by icebergs broken off from the ice shelves along the margins of the Laurentide ice sheet then covering northeastern North America. Besides the ice-rafted debris that came from eastern Canada, some was from Iceland and Europe (Grousset *et al*., 2001). The ice presumably broke off when the shelves had grown so large that wave action broke them up. The fresh, low-density meltwater from the bergs spread over the Greenland Sea and disrupted the "chimneys" conveying surface water down to the seabed. The chimneys are strong whirlpools near Greenland, where the warm currents of the North Atlantic gyre and the overlying, wind-driven Gulf Stream flow rapidly downwards, and in so doing, initiate the thermohaline current (or THC, also called the ocean conveyor) that links all the oceans (Wadhams, 2004), bringing about heat exchanges across latitudes and depths. When the THC stopped, so did the flow of warm tropical water from the Caribbean to northeastern Europe, and the result was a fall in air temperature of between 5°C and 10°C. Then, as the low-density surface water diffused, the conveyor re-established itself, and the climate warmed up again.

The sudden cooling had pronounced effects on zooplankton. The foram tests in the fine sediments immediately older and younger than the debris layers differed markedly from those within the layers (University of Washington, 2006). Fossil forams of several species were found in the fine sediments, but only the cold-water species *Neogloboquadrina pachyderma* (sinistral) was found in the ice-rafted debris.

A second, superimposed set of climatic fluctuations, of higher frequency and smaller amplitude, was discovered when two ice cores, both more than 3 km long, were obtained in 1992 and 1993, at two sites near the axis of the Greenland ice sheet (Alley, 2000a). Measurements of $\delta^{18}O$ in long sequences of annual layers of ice confirmed what shorter Antarctic cores had previously hinted at: those values periodically rose and fell in 1500-year cycles on average. As in the Heinrich events, fluctuations were found in the concentrations of GHG and wind-borne dust in the air trapped in bubbles in the ice. The peaks of these shorter period oscillations are known as Dansgaard–Oeschger (D–O) events after their discoverers. The sites of the two Greenland cores were 30 km apart. Close agreement between them is convincing evidence that the observations were not merely chance local occurrences. Matching results come from Antarctic ice cores, demonstrating that the events were global. For instance, the Vostok core from Antarctica reveals closely correlated oscillations over the past 150 ka in atmospheric concentrations of carbon dioxide (between 170 and 300 ppm), of methane (between 300 and 700 ppb), and of inferred temperature ranges (Lorius *et al*., 1990). In a single D–O event, air temperature first rose abruptly by ~6°C in a few years or decades, then, somewhat less abruptly, cooled again. The cause of the oscillations is uncertain; not surprisingly, numerous possibilities have been suggested.

The cold intervals in all these oscillations (Heinrich and D–O), during which less incoming solar energy was absorbed, were probably accompanied by lighter winds, slower ocean currents, and weaker upwelling (but see below). At high latitudes, less wind-borne nutrient dust would have reached the sea from the ice-covered land and less river-borne nutrients from frozen rivers. Matching variations in plankton at lower latitudes are exemplified by the observations of Hendy and Kennett (2000) on sediment cores from the Santa Barbara Basin, California. They found that in the cold part of each cycle, the cold-water species *Neogloboquadrina pachyderma* (sinistral) was dominant, whereas in the warm part, the warm-water species *N. pachyderma* (dextral) replaced it. Correlated shifts in $\delta^{18}O$ ratios established that SSTs shifted by about 3°C to 5°C between the warm and the cold phases in D–O events and up to 10°C in Heinrich events. This is a good example (one of many), in which zooplankton evidence from low-latitude sediment cores has proven that climate changes at low latitudes sometimes coincided with corresponding changes, deduced from ice-core evidence, at high latitudes. The reasonable conclusion is that such changes were global.

When evidence from what are believed to be contemporaneous ice-core samples and sediment samples are combined and interpreted, difficulties must arise in distinguishing causes from effects. For example, some cold periods were notable for copious dust, which presumably came from sparsely vegetated land. Is the chain of events: climatic cooling, hence sparse vegetation on land, hence dust? Or alternatively, is it: dust, hence abundant

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nutrients for phytoplankton, hence much sequestering of carbon dioxide by photosynthesis, hence climatic cooling. The latter sequence has been inferred from modern observations in the North Pacific (Bishop *et al.*, 2002). Dust from the Gobi Desert appears to have fertilized the ocean where it was deposited, which led to an increase in the carbon biomass of the plankton.

The Younger Dryas

A pronounced cold interval interrupted the gradual warming that marked the end of the last glaciation: a warm period named Bolling–Allerod (B–A) peaked 14.5 ka BP (Figure 1) and ended abruptly about 13 ka BP, and a very cold period lasting about 10 000 ka then began. This is the famous Younger Dryas (YD). It started with a temperature drop of about 7°C in as little as 10 years. It resembled an extra long and cold Heinrich event and is thought to have been initiated (Broecker, 2003) by a sudden influx of cold, fresh water into the North Atlantic that shut down the THC (for an alternative explanation, see Stocker, 1999). The proximate cause was probably the emptying of the enormous glacial Lake Agassiz, dammed by the Laurentide ice sheet in what is now central Canada, into the Gulf of St Lawrence. The lake was larger than today's Caspian Sea. It drained when the ice front melted back, somewhere along its shores, to the point where it no longer served as a dam, and the water surged suddenly.

This happened first, ca. 11 ka BP, at the lake's southern end, and the water drained away via the Mississippi valley to the Gulf of Mexico, leaving cobbles and boulders up to 30 cm across (Matsch, 1983). The sudden drop in temperature of the water in the Gulf of Mexico is presumably what led to a change in the zooplankton fauna: the warm-water species *Pulleniatina obliquiloculata* was replaced by the cold-water species *Globigerina falconensis*.

Lake Agassiz had not been emptied, however. The ice cliffs of its north shore (see map in Teller and Clayton, 1983) continued to melt back, uncovering several eastwards-trending valleys in succession. These acted as spillways to the Gulf of St Lawrence. Between 10.9 and 9.9 ka BP, three particularly catastrophic floods flowed down them at different times, sometimes directly via Lake Superior, sometimes through Lake Nipigon, then Lake Superior (Clayton, 1983). The prolonged series of floods no doubt accounts for the long duration of the YD when compared with the cold spells associated with Heinrich events. The terrestrial signs of Lake Agassiz's emptying are the spillways it eroded, with deep channels and huge plunge pools, now almost buried. The discharge is believed to have reached 100 000 $m^3 s^{-1}$ at times (Clayton, 1983).

A new theory ascribes the draining of Lake Agassiz to an entirely different cause (Becker *et al.*, 2007; Kennett *et al.*, 2007). Evidence has been found suggesting that what remained of the Laurentide ice sheet at 12.9 ka BP was shattered by the impact of a large meteorite (Becker *et al.*, 2007; Kennett *et al.*, 2007). There are some unexplained discrepancies in the dates of Lake Agassiz's draining as inferred from the three sources of evidence: oceanographic, geomorphic, and now (2007) astronomic. Moreover, three separate hypotheses cannot all be right, so further study remains to be done.

Evidence for the YD comes from all over the world. Ice cores reveal that, during this period, the ice-accumulation rate was low because of low precipitation. Wind-borne dust was abundant, probably from large tracts of unvegetated land. Methane production declined, perhaps by as much as 30%. Broecker (1999) speculates that this was because low-latitude wetlands were cooler, drier, and smaller than they are now.

The YD ended less abruptly than it started (Hughes *et al.*, 1996). The warming is thought to have been caused by an unusually large outgassing of methane hydrate (Kennett *et al.*, 2000). The source may have been at considerable depth below the seabed, but shallow, nearshore sources seem more likely (discussed subsequently). The final warming marked the start of the Holocene epoch during which (at any rate, up to the present) climatic fluctuations have been far less spectacular than in the Pleistocene.

The Holocene until now

With the coming of the Holocene, at 10 ka BP, the climate became much more equable. No big, abrupt changes have disturbed the past 10 ka. Until recently, it has been, climatologically speaking, rather boring. Almost certainly, what has caused the climate to calm down is the absence in the northern hemisphere of large, unstable ice sheets whose margins reached the sea or, in the one case, of an unusually large, ice-dammed lake that drained suddenly.

The only notable increase in temperature since this state was reached has been during the Hypsithermal period, from about 7.5 to about 5.5 ka BP, when temperatures first rose, then fell gradually. An estimate of the highest temperature attained is no more than 2°C or 3°C higher than now. But with climate warming well under way, the meaning of the word "now" has become elusive. We no longer have a static baseline.

The only other notable climatic event in the past 10 ka has been the Little Ice Age, from about 1350 AD to 1870 AD. Average temperatures were between 0.5°C and 1°C lower than they have been since. We have now advanced out of the Little Ice Age unless, possibly, we are still in the process of recovering from it.

The future

The dramatic climate changes happening now appear to terminate the climatologically uninteresting 10 000-year period that just ended, and the changes are undoubtedly being caused by increasing concentrations of GHGs.

My speculations on how matters will unfold start with an assumption as to which of three possible developments (not an exhaustive list) is most likely. These possibilities include: (i) in time, the climate will cool to its long-term Holocene level thus far, with no more big excursions; (ii) accelerated melting of polar ice will reduce salinity of North Atlantic water so much that the THC will shut down with consequent severe cooling of western Europe; or (iii) GHGs will increase suddenly because of copious outgassing of methane, a stronger GHG than carbon dioxide. Positive feedback will set in, and the current global warming will accelerate disastrously. My speculative choice is number (iii), the outgassing of methane, leading rapidly to the complete disappearance of polar ice, on land as well as on the sea. At the time of writing, Arctic sea ice is disappearing rapidly. The reason for this and how it will affect the Arctic Ocean, particularly the Canadian Arctic Archipelago, is what I propose to explore (Figure 2).

Consider, first, the source of the methane. It is known that methane hydrate is locally abundant as frozen hydrate (clathrate) under the seabed and in Arctic permafrost (Dallimore and Collett, 1995). Until recently, it was assumed that methane in the atmosphere came either from active wetlands or from hydrates

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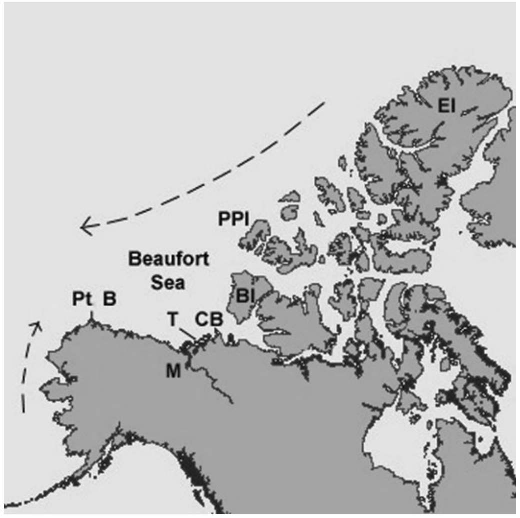

Figure 2. Map of the Canadian Arctic Archipelago showing places mentioned in the text. Pt B, Point Barrow; M, Mackenzie Delta; T, Tuktoyaktuk Peninsula; CB, Cape Bathurst; BI, Banks Island; PPI, Prince Patrick Island; EI, Ellesmere Island. Dashed arrows show surface currents (modified from Pickard and Emery, 1990).

buried at least 200 m under the seabed. Having regard to the pressure and temperature gradients below the seabed, methane hydrate would have been unstable at any lesser depth and would have already been discharged: outgassing would not resume until conditions changed, causing destabilization. In past outgassings, deeply buried hydrates may have been destabilized because of rising temperatures in intermediate-level ocean waters caused by changes in the thermohaline circulation (Kennett *et al.*, 2000). It seems likely now that global warming has started and that much (most?) atmospheric methane comes from the permafrost under the Arctic Ocean's continental shelf and the adjacent coastal plain. These two areas form a continuous expanse of surface that is partly submarine and partly subaerial. For example, some methane is being emitted now, from low (10–35 m) submarine hills on the floor of the Beaufort Sea, at depths of from 20 to 200 m (Blasco *et al.*, 2006). The buried hydrate appears to be unstable only metres below the seabed. It is unknown whether and where methane outgassing is happening elsewhere.

To return to the Beaufort Sea–Mackenzie Delta region, the submarine hills resemble pingos, the small ice-cored conical hills, seldom more than 40 m high, found in thousands on the adjacent coastal plain tundra from Point Barrow, Alaska, to Cape Bathurst, Northwest Territories. The submarine "hillocks" are called pingo-like features, or PLFs. It has been discovered (Paull *et al.*, 2007) that streams of methane bubbles emerge from the summits of some of the PLFs, from their methane hydrate cores. The cores are being forced up by gas pressure from below. How much methane is produced, and how long this has been going on, is not yet known. It could have begun quite recently. The permafrost has been warming, gradually and with some interruptions, ever since the last glaciation ended, and the hydrate it contains may have started to disintegrate at a threshold temperature reached not long ago.

It also seems likely, although this is (again) highly speculative, that terrestrial pingos may be, or may become, methane sources. The manner of their formation (Mackay, 1994) indicates that they originated, and still originate, in shallow lakes on land, and it is natural to suppose that PLFs began as terrestrial pingos that were submerged by the rising sea level as the ice sheets melted. However, an argument against this is that pingos sinking into a rising sea would be expected to be destroyed by wave erosion while they were at shoreline level rather than persisting as hills. Nevertheless, the spatial proximity of three hundred Beaufort Sea PLFs and the densest cluster of pingos on land (on the Mackenzie Delta and Tuktoyaktuk Peninsula) seems more than a coincidence. Altogether, more than 2000 pingos are found on the Arctic coastal plain (Mackay, 1988). Whether they will turn out to be, or to become, methane sources remains to be seen.

Currently, the Arctic Ocean is unimportant from the commercial fisheries point of view, but is a major food source for the indigenous human population, marine mammals, and seabirds. It is the ocean for which warming will certainly bring about the most profound changes. It is the world's smallest and shallowest ocean. Sea surface temperature varies little through the year: the range is between -2°C and 1°C approximately, and there is no permanent thermocline (Pickard and Emery, 1990). Salinity is generally low, between 28 and 34.

As the climate warms and the sea ice disappears, the whole ocean will no doubt be exposed to stronger winds because of the increased energy in the atmosphere. This will impart extra energy to ocean currents. Even hurricanes are likely, which may stir up seabed nutrients and cause phytoplankton blooms, conceivably leading to a reduction in atmospheric carbon dioxide (mentioned earlier).

Looking further into the future, expected geological changes must be taken into account. It is debatable (Keigwin *et al.*, 2006) whether the Bering Strait will eventually become closed. It could happen because of continuing crustal rebound: the earth's crust is still recovering after being depressed by the weight of the Cordilleran ice sheet that lay some distance to the east of it. Whether the strait will disappear depends on whether or not the effects of rebound overtake those of sea-level rise from melting ice and thermal expansion of the water. Closure of the strait would shut off the current that now flows from the North Pacific into the Arctic Ocean. If it does not happen, the winds driving the Beaufort Sea gyre will probably be intensified by the increased atmospheric energy. Intensified upwelling (with nutrients?) may develop all along the adjacent coasts of Alaska and of Ellesmere, Prince Patrick, and Banks Islands and the smaller islands between them.

Before that happens, the stronger winds will carry dust out to sea from the newly ice-free land. The resultant increase in nutrient supplies could then lead to increased quantities of phytoplankton and consequently zooplankton, and a reduction in GHGs followed by some climatic cooling. On the other hand, this sequence of events could be masked by rising methane concentrations.

A most unfortunate result of the melting of all sea ice will be the disappearance of under-ice and ice-edge ecosystems. These are especially well developed around polynyas, tracts of year-round open water forming gaps in the winter ice cover. They support an abundance of life: the ice-edge ecosystems around their margins are famous for their diversity.

The lower surface of sea ice, which nowadays is usually between 2 and 4 m thick, is pitted with pores occupied by living organisms. Green protists are the most abundant (they hang down in long chains). The water below is filled with diatoms and many kinds

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of zooplankton, notably amphipods (e.g. *Gammarus wilkitzkii*) and copepods (e.g. *Calanus glacialis*) which are the principal food of Arctic cod (*Boreogadus saida*) and other fish, and seabirds such as Dovekies (*Alle alle*). Bowhead whales (*Balaena mysticetus*) depend on abundant krill and copepods. Under-ice and ice-edge ecosystems demonstrate considerable regional variation (Gradinger *et al*., 1999). Their loss will cause a serious reduction in Arctic biodiversity, both in the plankton itself and in all the organisms higher up the foodweb. Although advection into still higher latitudes of cold-neritic Arctic Ocean zooplankton, followed by Subarctic and even warm-neritic species (Hooff and Peterson, 2006), may increase local biodiversity, global biodiversity will be diminished by the loss of species especially adapted to near-ice environments.

Perhaps the greatest danger from the increasing concentration of CO_2 in the atmosphere will be the increasing acidity of the ocean (Fabry *et al*., 2008), which threatens to dissolve the calcareous "skeletons" (tests and shells) of three important plankton groups: coccolithophores, foraminifera, and shelled pteropods. Disappearance of these groups will lead to drastic adjustments in the foodweb. Depending on how fast everything happens, some species will starve, whereas new species will evolve and others immigrate from warmer oceans. Future zooplankton assemblages may be wholly unlike those of today.

The melting of Arctic sea ice is now proceeding rapidly. It will probably all be gone early in this century. Land ice may last somewhat longer, but in time, it will disappear too, and a new body of water will probably form in central Greenland. Much of Greenland's land surface is depressed below present sea level by the weight of the ice sheet now overlying it. Jezek (2006) reports that the topography resembles that of eastern North America, with much of the surface scoured and flattened by flowing ice. This low-lying land will be covered by lakes when the ice melts and, if they become united with the ocean, will form coastal bays or perhaps a single, large bay. It (or they) will originate as Hudson Bay did, in a depression in the crust left by the melting of the Laurentide ice sheet (Pielou, 1991).

Because of the rising sea level caused by melting ice and thermal expansion, and the simultaneous rising of the seabed caused by isostatic rebound as the weight of the ice lessens, it is impossible to predict the details of coming coastline changes. The Arctic Islands, particularly the eastern ones, tend to have steep shores and narrow coastal plains; they are believed to be not much smaller now than they were at maximum glaciation, 18 ka BP (see the maps of Dyke and Prest, 1987). Future maps, except those of Greenland and Bering Strait, are unlikely to differ greatly from their present-day versions. As now, much of the ocean will be broken up by numerous islands into a maze of narrow channels. New rivers are unlikely because the islands are individually too small, and too topographically varied, for large drainage basins to develop; the Mackenzie River on the mainland will remain the only large river on the North American side. However, an increase in organic, nutrient-rich detritus will develop on the newly ice-free land and be carried by streams to the sea.

The climate may become so warm that very little ice or snow will be present anywhere on Earth for more than a few days or weeks each winter (perhaps none at all). If this happens, the impending glaciation to be expected in about two thousand years will not happen. The coming cool phase of the Milankovitch cycle will not be cool enough to cause a glaciation, unless it is boosted by positive feedback. In past glaciations, the high albedo of persistent, extensive ice- and snowfields, which prevent absorption of most of the incoming solar radiation, has provided the feedback. This can happen only when Earth's climate is cool enough for winter temperatures to remain below zero until long into summer.

To conclude, marine zooplankton will undergo tremendous changes caused by global warming. If biologists can still afford to conduct research when the climate settles down again (if it ever does), it will be fascinating to observe how the marine biota of the Arctic Ocean fared while, and after, the world was warming and the ice vanishing.

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