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Supplementary Materials

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Materials and Methods
Fig. S1
Table S1
References (132–135)
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REVIEW

Marine Ecosystem Responses to Cenozoic Global Change

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The future impacts of anthropogenic global change on marine ecosystems are highly uncertain, but insights can be gained from past intervals of high atmospheric carbon dioxide partial pressure. The long-term geological record reveals an early Cenozoic warm climate that supported smaller polar ecosystems, few coral-algal reefs, expanded shallow-water platforms, longer food chains with less energy for top predators, and a less oxygenated ocean than today. The closest analogs for our likely future are climate transients, 10,000 to 200,000 years in duration, that occurred during the long early Cenozoic interval of elevated warmth. Although the future ocean will begin to resemble the past greenhouse world, it will retain elements of the present “icehouse” world long into the future. Changing temperatures and ocean acidification, together with rising sea level and shifts in ocean productivity, will keep marine ecosystems in a state of continuous change for 100,000 years.

Marine ecosystems are already changing in response to the multifarious impacts of humanity on the living Earth system (1, 2), but these impacts are merely a prelude to what may occur over the next few millennia (3–9). If we are to have confidence in projecting how marine ecosystems will respond in the future, we need a mechanistic understanding of Earth system interactions over the full 100,000-year time scale of the removal of excess CO₂ from the atmosphere (10). It is for this reason that the marine fossil record holds the key to understanding our future oceans (Fig. 1). Here, we review the marine Cenozoic record [0 to 66 million years ago (Ma)], contrast it with scenarios for future oceanic environmental change, and assess the implications for the response of ecosystems.

In discussions of the geologic record of global change, it is important to distinguish between

mean and transient states. Mean climate states consist of the web of abiotic and biotic interactions that develop over tens of thousands to millions of years and incorporate slowly evolving parts of Earth's climate, ocean circulation, and tectonics. Transient states, in comparison, are relatively short intervals of abrupt (century- to millennium-scale) climate change, whose dynamics are contingent on the leads and lags in interactions among life, biogeochemical cycles, ice growth and decay, and other aspects of Earth system dynamics. Ecosystems exhibit a range in response rates: Animal migration pathways and ocean productivity may respond rapidly to climate forcing, whereas a change in sea level may reset growth of a marsh (11) or sandy bottoms on a continental shelf (12) for thousands of years before these ecosystems reach a new dynamic equilibrium. Thus, both mean and transient dynamics are important for understanding past and future marine ecosystems (13).

Past Mean States: The Cenozoic

The evolution of marine ecosystems through the Cenozoic can be loosely divided into those of the “greenhouse” world (~34 to 66 Ma) and those

of the modern “icehouse” world (0 to 34 Ma) (Fig. 1). We explore what these alternative mean states were like in terms of physical conditions and ecosystem structure and function.

Greenhouse World Physical Conditions

Multiple lines of proxy evidence suggest that atmospheric partial pressure of CO₂ (*p*CO₂) reached concentrations above 800 parts per million by volume (ppmv) between 34 and 50 Ma (14) (Fig. 2). Tropical sea surface temperatures (SSTs) reached as high as 30° to 34°C between 45 and 55 Ma (Fig. 2). The poles were unusually warm, with above-freezing winter polar temperatures and no large polar ice sheets (15, 16). Because most deep water is formed by the sinking of polar surface water, the deep ocean was considerably warmer than now, with temperatures of 8° to 12°C during the Early Eocene (~50 Ma) versus 1° to 3°C in the modern ocean (15). The lack of water storage in large polar ice sheets caused sea level to be ~50 m higher than the modern ocean, creating extensive shallow-water platforms (15, 17).

In the warm Early Eocene (~50 Ma), tectonic connections between Antarctica and both Australia and South America allowed warm subtropical waters to extend much closer to the Antarctic coastline, helping to prevent the formation of an extensive Antarctic ice cap (16) and limiting the extent of ocean mixing and nutrient delivery to plankton communities in the Southern Ocean (18). Tectonic barriers and a strong poleward storm track maintained the Arctic Ocean as a marine anoxic “lake” with a brackish surface-water lens over a poorly ventilated marine water column (19). Indeed, the Arctic surface ocean was occasionally dominated by the freshwater fern *Azolla*, indicating substantial freshwater runoff (20).

Greenhouse World Ecosystems

The warm oceans of the early Paleogene likely supported unusual pelagic ecosystems from a modern perspective. The warm Eocene saw oligotrophic open-ocean ecosystems that extended to the mid- and high latitudes and productive equatorial zones that extended into what is now the

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warm subtropics (17). In the modern ocean, most primary productivity in warm, low-latitude gyres is generated by small phytoplankton with highly

efficient recycling of organic matter and nutrients (21). Such picophytoplankton-dominated ecosystems typically support long food chains

where the loss of energy between trophic levels limits the overall size of top predator populations (5, 22). Although the radiations of many

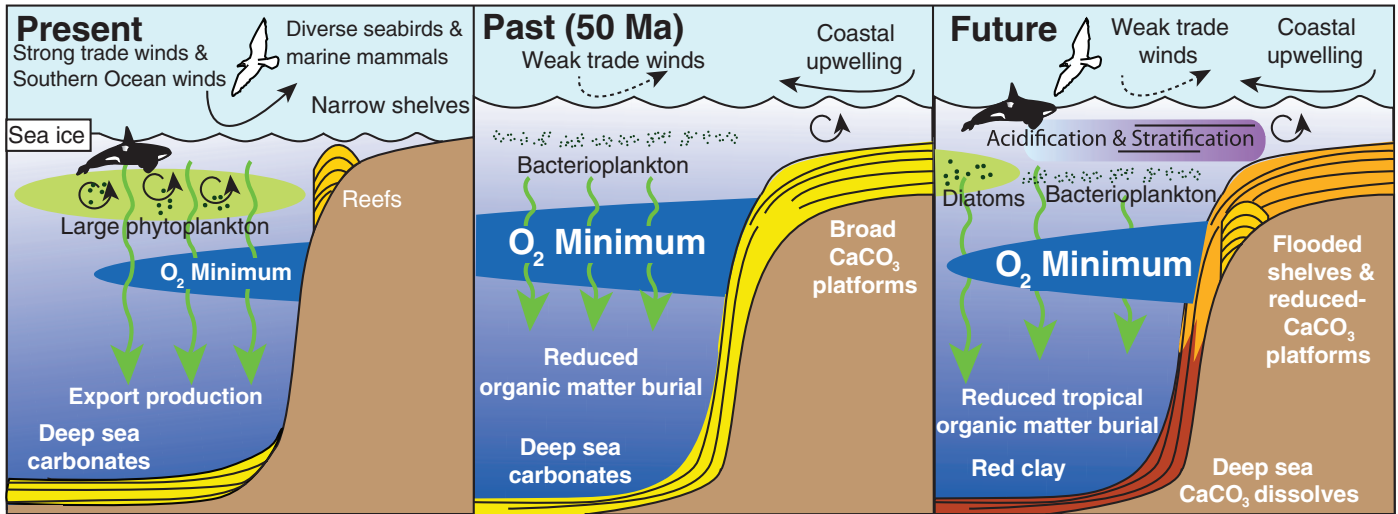


Fig. 1. Comparison of present, past, and future ocean ecosystem states. In the geologic past (middle panel), a warmer, less oxygenated ocean supported longer food chains based in phytoplankton smaller than present-day phytoplankton (left panel). The relatively low energy transfer between trophic levels in the past made it hard to support diverse and abundant top predators dominated by marine mammals and seabirds, and also reduced deep-sea organic matter burial. Equilibration of weathering with high atmospheric $p\text{CO}_2$ allowed carbonates to accumulate in parts of the deep sea. Reef construction was limited by high temperatures and coastal runoff even as high

sea level created wide, shallow coastal oceans. In the future (right panel), warming will eventually reproduce many features of the past warm world but will also add transient impacts such as acidification and stratification of the surface ocean. Acidification will eventually be buffered by dissolving carbonates in the deep ocean, which create carbonate-poor “red clay.” Stratification and the disappearance of multiyear sea ice will gradually eliminate parts of the polar ecosystems that have evolved in the past 34 million years and will restrict the abundance of short-food chain food webs that support marine vertebrates in the polar seas.

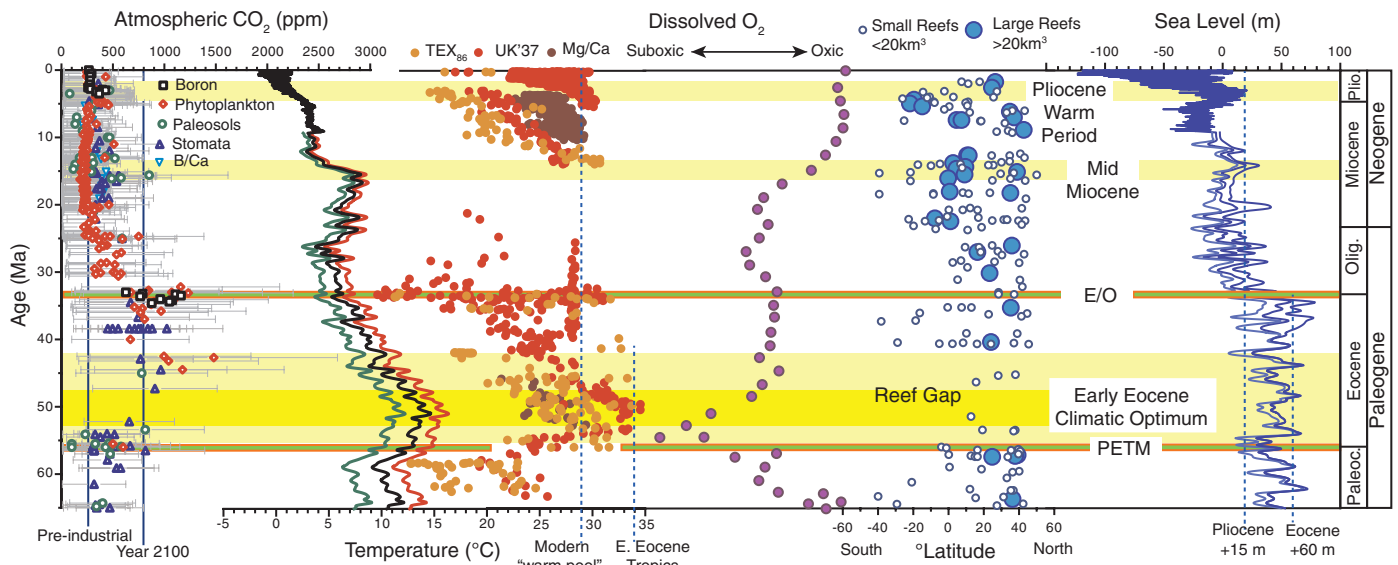


Fig. 2. Cenozoic record of major ecosystem drivers and responses. From left to right: Proxy evidence for atmospheric $p\text{CO}_2$ (14); vertical lines show the preindustrial $p\text{CO}_2$ (280 ppm) and estimated $p\text{CO}_2$ for year 2100 under a business-as-usual emissions scenario. Deep ocean temperature (15) estimated from oxygen isotope and Mg/Ca proxy evidence. Black line is long-term average for benthic foraminifera, red line is temperature adjusted for pH, and green line is temperature adjusted for seawater $\delta^{18}\text{O}$ effects. Compilation of surface ocean temperature estimates from multiple organic matter and Mg/Ca proxies (as indicated by different colors) (37, 90–98); data are plotted with their published

assumptions and age models. (Although the age models may differ slightly, these differences are not apparent at this resolution.) Dissolved O_2 is estimated from the Benthic Foraminifer Oxygen Index in a global compilation (99). Reef volume and temporal distribution (31); reefs with estimated volumes greater than 20 km^3 are plotted in large solid circles, smaller reefs as open circles. Sea level is estimated from combined benthic foraminifer $\delta^{18}\text{O}$, Mg/Ca, and the New Jersey sea-level record: long-term average (middle line) and uncertainty (maximum, minimum lines). Dotted vertical lines show the estimated average high stands for the Pliocene and Eocene.



pelagic predators (including the whales, seals, penguins, and tunas) began in the greenhouse world of the late Cretaceous and early Paleogene, their modern forms and greatest diversity were achieved later, as large diatoms emerged as important primary producers and food chains became shorter and more diverse in the icehouse world (Fig. 3).

Multiple lines of evidence suggest that early Paleogene (45 to 65 Ma) ecosystems differed from the modern with respect to the organic carbon cycle (23, 24). The greenhouse ocean was about as productive as today, but more efficient recycling of organic carbon led to low organic carbon burial (23, 25). There were also major radiations of midwater fish, such as lanternfish and anglerfish (26), and diversifications of planktonic foraminifer communities typical of low-oxygen environments between 45 and 55 Ma (27, 28) (Figs. 2 and 3).

Coral-algal reef systems existed throughout the low- to mid-latitude Tethys Seaway from ~58 to 66 Ma (Fig. 2) (29). During the very warm, high- $p\text{CO}_2$ interval between ~42 and 57 Ma, coral-dominated large reef tracts were replaced by foraminiferal-algal banks and shoals (30, 31). This “reef gap” was present throughout Tethys, Southeast Asia, Pacific atolls, and the Caribbean (29, 31–33). The timing of the Tethyan reef gap suggests that the loss of architectural reefs was related to some combination of unusual warmth of the tropics and hydrologic changes in sedimentation and freshwater input (34, 35). Notably,

many modern groups of reef fishes evolved before or during this time (26, 36), which suggests that the changing biogeography of metazoan reefs and extensively flooded continental shelves may have contributed to their evolution.

Icehouse World Physical Conditions

Atmospheric $p\text{CO}_2$, which had been ~700 to 1200 ppmv during the late Eocene, fell to 400 to 600 ppmv across the Eocene-Oligocene boundary (34 Ma) (37). The decline in greenhouse gas forcing caused tropical SSTs to fall to values within a few degrees of those in the modern “warm pool” western Pacific or western Atlantic (~29° to 31°C) by 45 Ma (37) (Fig. 2). At high latitudes, deep ocean temperatures declined to 4° to 7°C between 15 and 34 Ma, with further polar cooling over the past 5 million years (15).

Polar cooling and Antarctic ice growth between ~30 and 34 Ma occurred as CO_2 levels declined (38) and were accompanied by the tectonic separation of Antarctica from Australia and eventually South America (17). Establishment of the Antarctic Circumpolar Current increased the pole-to-equator temperature gradient, increased the upwelling of nutrients and biogenic silica production in the Southern Ocean, and initiated modern polar ecosystems (39, 40). The growth of polar ice at ~34 Ma produced a sea-level fall of ~50 m, and the later growth of Northern Hemisphere ice sheets at 2.5 Ma initiated a cycle of sea-level fluctuations of up to 120 m (41, 42). In the Arctic, the ecosystem evolved from a marine anoxic “lake”

to a basin with perennial sea ice cover by at least 14 Ma (43).

Icehouse World Ecosystems

By 34 Ma, an ecosystem shift occurred in the high southern latitudes (40) as better wind-driven mixing in the Southern Ocean supported diatom-dominated food chains. The resulting short food chains fueled a major diversification of modern whales (39, 44), seals (45), seabirds (46, 47), and pelagic fish (48) (Fig. 3). The onset of Southern Ocean cooling is closely timed with the appearance of fish- and squid-eating “toothed” mysticetes at ~23 to 28 Ma and the radiation of large bulk-feeding baleen whales beginning at ~28 Ma (49). It is hypothesized that tropical and upwelling diatom productivity—initiated by nutrient leakage out of the high latitudes—spurred the development of long-distance migration by the great whales in the past 5 to 10 million years (39). This interval also coincides with radiations of delphinids (50), penguins (46), and pelagic tunas (48) (Fig. 3). The diversification of Arctic and Antarctic seals also unfolded during the past 15 million years as polar climates intensified and sea ice habitats expanded (45).

Reefs expanded in low to mid-latitudes, particularly in the northern subtropical Mediterranean and western Pacific, by ~42 Ma (31). However, the major growth of large reefs mostly occurred from ~20 Ma to the present, with major expansions of reef tracts in the southwestern

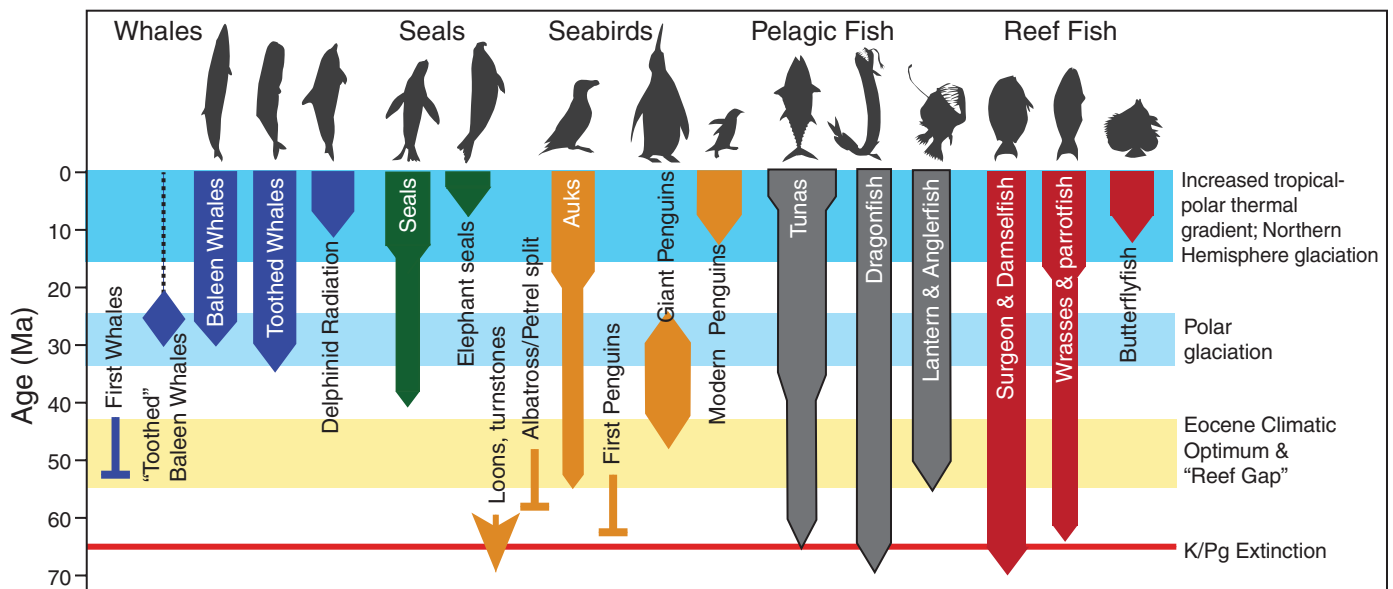


Fig. 3. Evolutionary events and diversification of selected marine vertebrate groups. Radiations of marine birds, tuna, mid-pelagic fish (e.g., dragonfish), and various groups of reef fish occur at or before the Cretaceous-Paleogene (K/Pg) mass extinction (65 Ma). The Eocene Climatic Optimum (45 to 55 Ma) is associated with the first whales (44), radiations of pelagic birds [albatrosses (100), auks (47), and penguins (46)], and diversification of midwater lanternfish and anglerfish (26).

With the onset of Antarctic glaciation (~34 Ma) and development of the Circum-Antarctic current, there is the major diversification of whales (49) and giant, fish- and squid-eating penguins (46). The differentiation of polar and tropical climate zones at ~8 to 15 Ma is associated with the extensive diversification of coastal and pelagic delphinids (50), Arctic and Antarctic seals (45), auks (47), modern penguins (46), pelagic tuna (48), and reef fishes (52, 53).

Pacific and the Mediterranean (31, 51). Several large groups of reef-associated fish, such as wrasses (52), butterflyfish (53), and damselfish (51), experienced radiations between 15 and

20 Ma (Fig. 3). These fishes include reef obligates, such as clades associated with coral feeding, that diversified along with the geographic expansion of fast-growing branching corals (53).

Sea-level variations in the past 34 million years had major impacts on shaping shallow marine ecosystems. The break in slope between the gentle shelf and the relatively steep slope

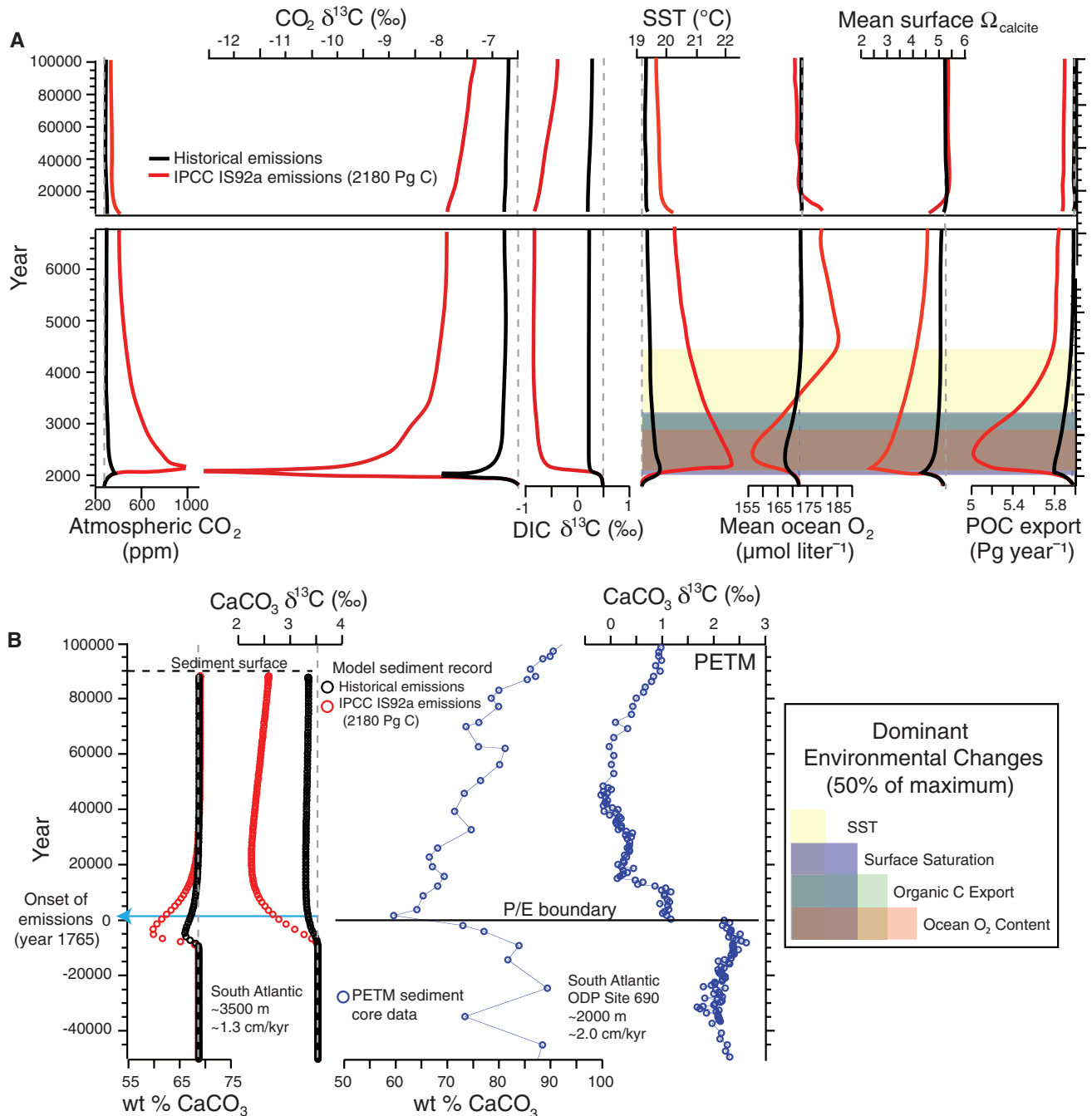


Fig. 4. Future Earth model. (A) 100,000-year simulations of historical anthropogenic CO₂ emissions (black lines) and the IPCC IS92a emissions (red lines). From left to right: the evolution of atmospheric CO₂, the δ¹³C of CO₂, the δ¹³C of dissolved inorganic carbon (DIC), SST, mean ocean O₂, surface ocean carbonate saturation with respect to calcite, and particulate organic matter (POC) export (modeled from a simple relationship with phosphate inventories). Note that some records such as the δ¹³C of DIC do not recover fully in even 100,000 years. Color bars highlight the interval in which each environmental variable (SST, mean ocean O₂, calcite saturation state, and organic C export) shows at least 50% of

the total change. (B) Modeled sedimentary expressions of the scenarios shown in (A) from a model site with a sedimentation rate of 1.3 cm per 1000 years (typical of the deep sea). Profiles show the weight percent CaCO₃ in sediments (left) and the δ¹³C of sedimentary carbonates (right). Although both scenarios were initiated in year 1765 (to simulate the start of the Industrial Revolution), dissolution of sea-floor carbonates and mixing by burrowers shifts the apparent start date substantially earlier than this. The PETM (blue lines, right) has a CaCO₃ minimum (101) and a δ¹³C minimum (102) comparable in duration, but larger in magnitude, than the simulated future.



occurs at ~100 m on most continental margins. In the later Pleistocene, glacially driven sea-level falls produced major decreases in shallow marine habitat area, fragmented formerly contiguous ranges of coastal species, and disrupted barrier reef growth (54–56). Sea level rose during glacial terminations at a pace of ~1 m per 100 years (57), a pace readily matched by the dispersal of benthic marine invertebrates and algae. However, Pleistocene sea-level rise was fast enough to trap sand in newly formed estuaries and create transient ecosystems such as marshes, sandy beaches, and sand-covered shelves over time scales of several thousand years (11, 55).

Lessons from Cenozoic Mean States

Past warm climates had warmer-than-modern tropics, extensively flooded continental margins, few architectural reefs, more expansive midwater suboxic zones, and more complete recycling of organic matter than now. Tropical oceans were likely as productive as today, but the productive waters expanded into the subtropics and supported long food chains based in small phytoplankton. Today, the inefficiency of energy transfer in picophytoplankton-dominated ecosystems limits the overall size of top predator populations and probably did so in the past. Although some of these conditions may recur in the future, tectonic boundary conditions are likely to prevent polar ecosystems from completely reverting to their past greenhouse world configurations in the near future. Hence, it seems unlikely that the Arctic “lake” will be reestablished or that wind-driven mixing will diminish enough in the Southern Ocean to destroy ecosystems founded on short, diatom-based food chains.

Past Transient Global Change Impacts: The Paleocene-Eocene Thermal Maximum

One of the best-known examples of a warm climate transient is the Paleocene-Eocene Thermal Maximum (PETM), a period of intense greenhouse gas–fueled global change 56 million years ago. The PETM is characterized by a 4° to 8°C increase in SSTs, ecosystem changes, and hydrologic changes that played out over ~200,000 years (58). Warm-loving plankton migrated poleward, and tropical to subtropical communities were replaced by distinctive “excursion” faunas and floras (35). Open-ocean plankton were dominated by species associated with low-productivity settings, whereas shallow shelf communities commonly became enriched in taxa indicative of productive coastal environments (59). Numerous in-

dicators suggest that toward the close of the PETM (100,000 years after it began), there was a widespread increase in ocean productivity (60, 61) and a transient rise in the carbonate saturation state above pre-PETM levels (62) due to intensified chemical weathering during the event (63).

The only major extinctions occurred among deep-sea benthic foraminifera (50% extinction) (35, 64). Surviving benthic foraminifera reduced their growth rate, increased calcification, and switched community dominance toward species accustomed to high food supplies and/or low-oxygen habitats (65). Deep-sea ostracodes also became dwarfed and shorter-lived, and many species vacated the deep sea into refugia for the duration of the PETM (35, 66). The preferential extinction of benthic foraminifera and temporary disappearance of ostracodes in the deep sea is attributed to a combination of a drop in export production associated with stratification in low and mid-latitudes, a marked drop in deep-sea dissolved oxygen concentrations related to transient ocean warming, and/or reduced carbonate saturation related to uptake of atmospheric CO₂ inventories (35, 64, 66, 67).

There are indications of a possible drop in carbonate saturation during the PETM, such as the common occurrence in a few species of malformed calcareous phytoplanktonoliths and planktic foraminifera (68). However, the evolution of reef ecosystems through the PETM argues against severe surface-ocean acidification. For instance, a Pacific atoll record does not record a distinct sedimentary change or dissolution event (69). In the Tethys Seaway, large coral-algal reefs disappeared prior to the PETM, but coral knobs persisted into the early Eocene amid the dominant foraminiferal-algal banks and mounds (34, 35). Hence, if there was surface-ocean acidification during the PETM, its effects were modest and did not precipitate a major wave of extinction in the upper ocean.

The Geologic Record of the Future: Diagnosing Our Own Transient

How representative are transient events like the PETM for Earth’s near future? We compared the PETM record to a modeled future of the historical record of CO₂ emissions (Fig. 4A, black lines) and the Intergovernmental Panel on Climate Change (IPCC) IS92a emissions scenario (peak emissions rate of 28.9 Pg C year⁻¹ in 2100; total release of 2180 Pg C) (Fig. 4A, red lines). The latter represents a conservative future, given the availability of nearly twice as much carbon in fossil fuels.

We used the Earth system model cGENIE, including representation of three-dimensional ocean circulation, simplified climate and sea ice feedbacks, and marine carbon cycling (including deep-sea sediments and weathering feedbacks) (70, 71). In both long-term (10,000 years) (10) and historical perturbation (72) experiments, cGENIE responds to CO₂ emissions in a manner consistent with higher-resolution ocean models. Experiments were run after a 75,000-year model spin-up, needed to fully equilibrate deep-sea surface sediment composition.

Under the IPCC IS92a emissions scenario, CO₂ peaks at ~1000 ppmv just after year 2100 (Fig. 4A). The emission of a large mass of fossil fuel carbon causes a ~6‰ drop in atmospheric δ¹³C and a ~1‰ drop in carbonate δ¹³C—an event less than half the size of the PETM anomaly (73). SSTs increase by 3°C, reaching a maximum just before year 2200, and remain elevated above preindustrial SSTs by almost 0.5°C for >100,000 years (Fig. 4A). Here again, the estimated PETM surface ocean temperature anomaly is larger, at 5° to 9°C (58, 73). In the future scenario, the CO₂ invasion of the surface ocean causes the mean calcite saturation state of the surface ocean (Ω) to drop to a minimum of 2 Ω just after year 2100,

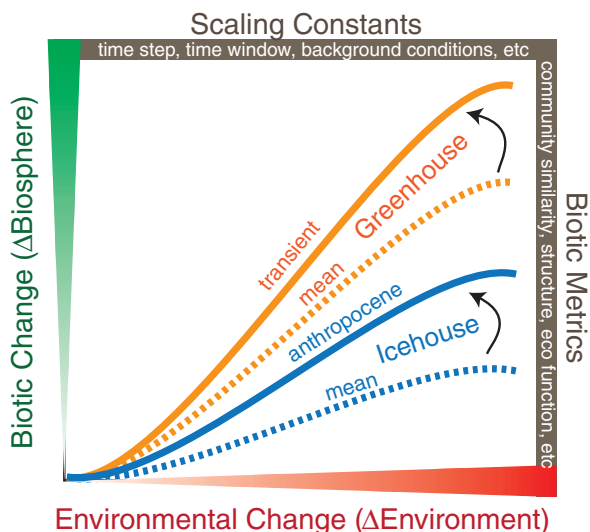


Fig. 5. Hypothetical biotic response to global change. Biotic sensitivity describes the response of ecosystems to a given amount of environmental change. It is currently unknown whether biotic sensitivity is constant in differing background conditions. For instance, here we illustrate the possibility that biotic sensitivity changes with climate state. This could occur if species exhibited broader environmental tolerances in icehouse climates, conferring greater biotic resilience across communities more generally. Modern global change is expected to change ecosystem structure in the direction of past greenhouse transient events. Additional research is needed to determine whether biotic sensitivity varies by taxa and ecosystem metrics (biotic metrics), sampling intervals, study durations, and background conditions (scaling constants). Our understanding of biotic sensitivity will determine our ability to predict future biotic changes over the next 50,000 to 100,000 years.

accompanied by a decrease in CaCO_3 export. The global average hides the extensive regions of the world ocean that will become undersaturated with respect to calcite and, in particular, aragonite (74)—with profound biological effects (75, 76), including the possible cessation of all coral reef growth (77). Eventually, a temporary buildup of weathering products leads to an overshoot in Ω beginning around year 13,500 that persists through the remaining 100,000 years—an effect also observed after the PETM (78, 79). Mean ocean oxygen concentration is modeled to drop to a minimum at year 2500, return to preindustrial levels a thousand years later, and then increase above modern values for ~12,000 years as a result of the resump-

tion of strong ocean overturning and decreased export of particulate organic carbon. Both a drop in O_2 and export production also occurred in the early stages of the PETM (35).

The modeled sedimentary expression of the future is broadly similar to the PETM (Fig. 4B). The decrease in carbonate $\delta^{13}\text{C}$ and weight percent CaCO_3 is greater for the PETM than for the modeled future, consistent with a greater mass of carbon injected during the PETM than in the conservative future emissions scenario of 2180 Pg C. A striking aspect of the modeled future record is that the onset of the $\delta^{13}\text{C}$ excursion does not appear notably more rapid than for the PETM. Both sediment mixing (bioturbation) and carbonate dissolution act to shift the apparent onset of a

transient event into geologically older material and reduce the apparent magnitude of peak excursions (80, 81).

Biotic Sensitivity and Ecosystem Feedbacks

Ecological and environmental records from past oceans provide guideposts constraining the likely direction of future environmental and ecological change. They do not, however, inform key issues such as the likelihood that ecosystems will change or how they may mitigate or amplify global change. These are all questions of biotic sensitivity and ecosystem feedbacks.

Biotic sensitivity describes the equilibrium response of the biosphere to a change in the environment (Fig. 5). There is tantalizing evidence that ecosystem responses scale with the size of transient warming events in the same way that surface temperature scales with $p\text{CO}_2$ concentrations [i.e., climate sensitivity (82)]. Specifically, Gibbs *et al.* (83) found that change in nanoplankton community structure (Σ_{CV}) scaled with the magnitude of environmental change (as measured by $\delta^{13}\text{C}$) during a succession of short-lived global change events between 53.5 and 56 Ma. This result suggests that “background” biotic sensitivity can predict responses to much larger perturbations. Additional studies of biotic sensitivity in deep time are urgently needed to test whether this type of scaling exists across taxa and different ecosystems or with changes in background conditions, time scale, or time step (Fig. 5).

Ecosystem feedbacks have the potential to mitigate or amplify the environmental and ecological effects of current greenhouse gas emissions. For instance, the greenhouse gas anomaly of the PETM is drawn down more quickly than would be expected by physical Earth system feedbacks alone (60, 84). Widespread evidence for a burst in biological productivity in the open marine environments (60, 61) and indirect evidence for increased terrestrial carbon stores during termination of the PETM (84) support the hypothesized importance of negative ecosystem feedbacks in driving rapid carbon sequestration. Species-specific responses to environmental perturbation—including growth rates (85), dwarfing (86), range shifts (87), or loss of photosymbionts (88)—can affect the structure and function of entire ecosystems. For instance, ecological interactions are hypothesized to have an important influence in setting the carbonate buffering capacity of the world’s ocean (70, 71) and in driving Cenozoic-long trends in the carbonate compensation depth (89), among many others. The geological record of transient events has the largely unexploited potential to constrain the type and importance of ecosystem feedbacks.

Lessons for the Future

The near future is projected to be a cross between the present climate system and the Eocene-like

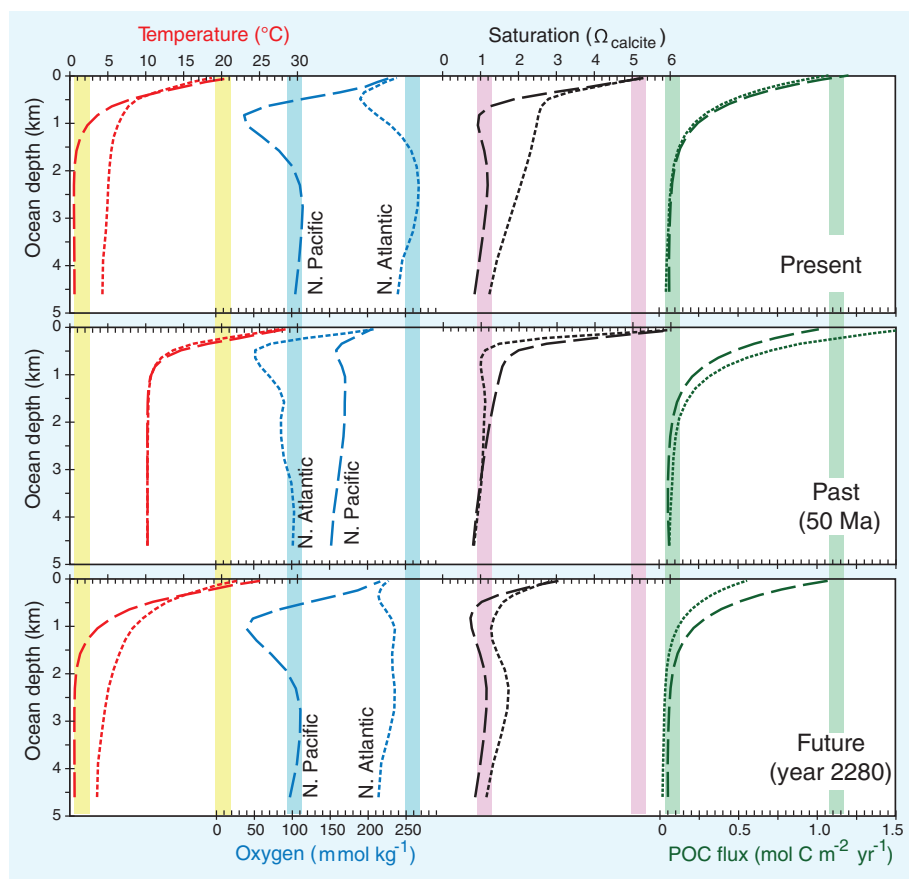


Fig. 6. Dynamics of past, present, and future oceans. Profiles of ocean temperature (red lines), oxygen saturation (blue lines), carbonate ion saturation (black lines), and particulate organic carbon flux (green lines) are shown for modeled averages of the North Pacific (long dashes) and the North Atlantic (short dashes). Note that the future (bottom panel) is a hybrid of the present (top panel) and the past (middle panel). Although the future SST resembles that at 50 Ma, the future deep ocean is much colder, reflecting the continued presence of polar ice and an Antarctic Circumpolar Current. Future oxygenation is reduced in the Atlantic relative to the present, but not as much as in the 50 Ma simulation. Notably, surface ocean carbonate saturation is much lower in the future relative to the present or past, reflecting ocean acidification. Eventually, acidified surface waters will be neutralized by reacting with deep-sea carbonates, reducing deep-sea carbonate concentrations by 10 to 20% (see Fig. 4B). POC flux is model-dependent but shows the expected drop in organic matter export in the future ocean. Colored vertical bands show the maximum and deep ocean minimum values for each parameter. Profiles were generated in cGENIE, with the future simulation the same as in Fig. 4A.



warmth of coming centuries (Fig. 6). Our future Earth model and analogies to the PETM show that a transitional, non-analog set of climates and ecosystems will persist for >10,000 years because of the slow response times of many parts of the biosphere. Over this interval, the oceans will continue to take up CO₂ (from fossil fuel combustion) and heat, causing a rise in sea level, acidification, hypoxia, and stratification. Lessons from the PETM raise the possibility that extinctions in the surface oceans due to greenhouse gas-driven Earth system change will be modest, whereas reef ecosystems and the deep sea are likely to see severe impacts (2). In addition, Earth now supports a much more diverse group of top pelagic predators vulnerable to changes in food chain length (9) than it did in the PETM. The severity and duration of ecosystem impacts due to human greenhouse gas emissions are highly dependent on the magnitude of the total CO₂ addition. If the CO₂ release is limited to historical emissions, ocean surface temperature and carbonate saturation will return close to background within a few thousand years, whereas the “conservative” modeled 2180 Pg C release produces impacts persisting at least 100,000 years (Fig. 4B). Although the future world will not relive the Eocene greenhouse climate, marine ecosystems are poised to experience a nearly continuous state of change lasting longer than modern human settled societies have been on Earth.

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