

## Primer

## Emergence of modern marine ecosystems

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The structure and function of marine ecosystems are not fixed. Instead, major innovations — from the origin of oxygenic photosynthesis, to the evolution of reefs or of deep bioturbation, to the rise of pelagic calcifiers — have changed biogeochemical cycles and ecosystem dynamics. As a result, modern marine ecosystems are fundamentally different from those in the distant past.

Marine ecosystems today reflect a series of evolutionary and ecological innovations that arose during the Mesozoic around 150–200 million years ago. This Primer considers three of these changes in the context of the last 300 million years of ocean history. They include the Mesozoic revolution in marine carbonate chemistry, in pelagic foodweb structure, and in predation (Figure 1). Why so many shifts in marine ecosystems occurred during the latter part of the Mesozoic is an open question, but they may be interrelated. Regardless of the cause, these revolutions have shaped modern ocean ecosystems and are key to understanding their dynamics.

**Revolution in ocean chemistry**

Plankton are the free-drifting organisms at the base of open ocean foodwebs. Two major clades of modern plankton have calcium carbonate shells or ‘tests’: coccolithophores and planktonic foraminifera. Coccolithophores are primary producers in the clade Haptophyta, and are the dominant group of planktonic calcifying algae in modern oceans. Planktonic foraminifera are mixotrophic to heterotrophic eukaryotes and are the free-drifting (i.e., planktonic) members of Foraminifera, a clade in the supergroup Rhizaria. Although individually microscopic in size,

together coccolithophores and planktonic foraminifera account for approximately half of the formation and burial of calcium carbonate in the global ocean today, with reefs accounting for most of the rest.

Planktonic calcification in these clades evolved in the early Mesozoic roughly around 200 million years ago but only rose to ecological prominence in the mid-Cretaceous between 150 and 200 million years ago (Figure 2). Both of these changes occurred surprisingly late in the history of marine biomineralization. Widespread biomineralization appears in the Early Cambrian (around 520–540 million years ago), with a range of taxa acquiring biomineralized skeletons, shells, or tests independently around this time. Calcification in marine plankton, by contrast, became a significant force in ecosystem engineering only around 350 million years later.

When it did occur, the rise of abundant pelagic calcification in the mid-Cretaceous profoundly changed marine chemistry by exporting roughly half of marine calcium carbonate to the deep sea. Prior to the evolution of pelagic calcification, effectively all marine carbonate was deposited in shallow marine environments, which are geologically unstable because sediments formed during sea-level high stands are eroded when sea level falls (for instance, during an ice age). The amount of space available for reef ecosystems is likewise contingent on sea level and plate tectonics, affecting the capacity of reefs to fix and bury calcium carbonate. The evolution of pelagic calcification diverted approximately half of the calcification away from these restricted and relatively volatile environments. The pelagic ocean is vast, and calcium carbonate can be buried in the deep sea regardless of sea level or plate tectonics. Thus, pelagic calcification added an important degree of redundancy for reef calcification by providing a second sink for calcium carbonate. Although large environmental perturbations can affect both shallow marine and open ocean environments, an open ocean carbonate sink can compensate for the reef carbonate sink (or vice versa) during such environmental perturbations.

The net effect of the evolution of pelagic calcification was to stabilize the marine carbon cycle on long timescales (many thousands to hundreds of thousands of years) and to increase the resilience of the marine environment to ocean acidification. By exporting calcium carbonate to the deep sea, pelagic calcifiers provided a deep sea carbonate reservoir that was responsive to changes in ocean carbonate chemistry driven by atmospheric CO<sub>2</sub> fluctuations: the dissolution of deep sea carbonates now acts as feedback on pCO<sub>2</sub> change. The effects of this feedback on ecosystem stability can be seen in the fossil record. Massive volcanic eruptions drove major mass extinctions prior to the rise of abundant pelagic calcifiers, but not afterwards.

**Evolution of pelagic foodwebs**

Coccolithophores were one of three major algal groups to increase in ecological prominence in the mid-Mesozoic. Together with the other two groups — dinoflagellates and diatoms — these algal innovators of the Mesozoic are the dominant eukaryotic primary producers in much of the modern ocean. Dinoflagellates are a diverse clade of marine eukaryotes unified by the possession of two flagella (one transverse, the other longitudinal), but are otherwise surprisingly variable and complex. Many dinoflagellates are mixotrophic and consume organic matter as well as undergoing photosynthesis. Diatoms, an algal clade encased in a two-valved silica shell known as a frustule, are particularly abundant in the productive regions due to their high growth rates, unusual nutrient requirements, and siliceous armor. Although all three groups first appear in the fossil record in the Mesozoic, diatoms rose to prominence relatively recently (roughly the last 30 million years) compared with coccolithophores and dinoflagellates (approximately the last 200 million years) (Figure 2).

The Mesozoic rise of these three major clades recently led Knoll and Follows (2016) to propose a Mesozoic revolution in pelagic foodwebs. In general, small algae should outcompete large algae due to higher growth rates and lower nutrient

requirements, given comparable losses (death and predation). However, dinoflagellates, diatoms, and coccolithophores all changed the rules of the game, colloquially speaking, by increasing nutrient uptake in oligotrophic conditions by mixotrophy (dinoflagellates), by having unusually high maximum growth rates for their size (diatoms, perhaps due to the siliceous frustule), and by reducing losses to predation (diatoms and coccolithophores, via biomineralized shells). Prior to the expansion of these three clades, green phytoflagellates were the dominant eukaryotic primary producers, a group notably lacking these strategies. As a result, more ancient oceans likely hosted a relatively greater fraction of small-bodied bacterioplankton than oceans today. The net effect of the innovations of diatoms, dinoflagellates, and coccolithophores may have been to shift the size structure of marine primary producers towards larger body sizes, increasing the amount of energy available for the top of the food chain by reducing the number of trophic transfers required. Increased body size and biomineralization are also tied to increases in the efficiency of organic matter export from the surface ocean to the deep sea (i.e., the biological pump).

Changes in foodweb structure and independent evidence for increased nutrient supply to Cretaceous oceans both suggest that the amount of energy available to large-bodied predators may have increased markedly in the late Mesozoic. This trend arguably accelerated with the environmental and ecological changes of the latter half of the Cenozoic (i.e., the last 34 million years), which include the onset of polar glaciation and the spread of productive pelagic ecosystems. With these late Cenozoic changes came the rise of diatom-based food chains and abundant, large-bodied filter feeders including sharks and whales that so characterize our modern oceans.

### The Mesozoic Marine Revolution

Closer to shore, the classic revolution of the Mesozoic occurred — the Mesozoic Marine Revolution (MMR). Geerat Vermeij famously noted the marked diversification during the



**Figure 1. Four major environmental changes in the Mesozoic set the stage of modern ecosystems.**

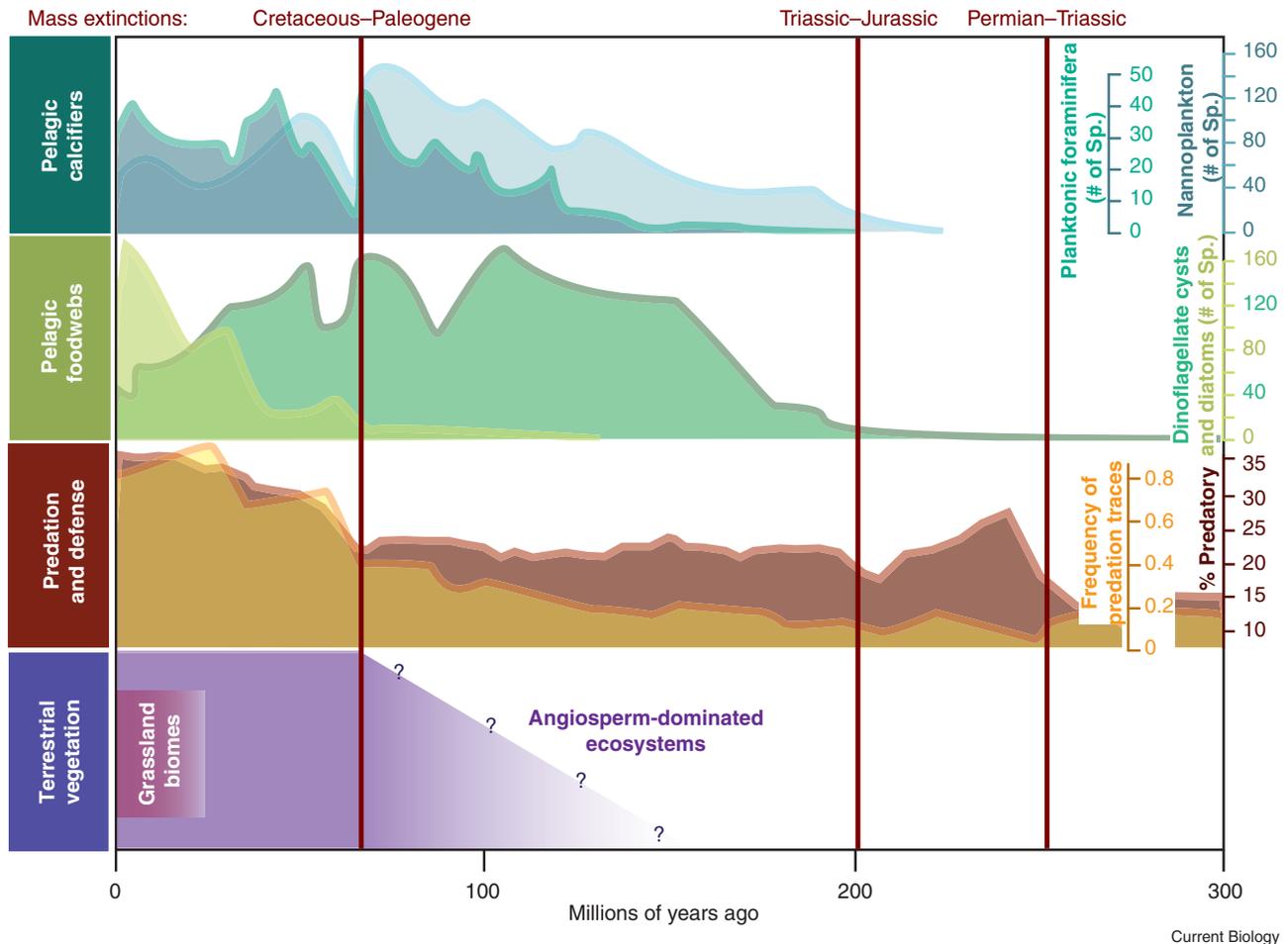
These environmental changes include the rise of calcareous plankton in the open ocean, a transformation in pelagic foodwebs, the escalation of predation pressure and defense strategies in marine benthic habitats, and the evolution and diversification of flowering plants (angiosperms) on land. Images: top left, Howard J. Spero, University of California, Davis; top right, Damián H. Zanette, Wikimedia Commons; bottom left, Brocken Inaglor, Wikimedia Commons; bottom right, Walter Jetz, Yale University.

Mesozoic of anti-predatory defenses in marine mollusks, including habitat and movement ecology, alongside evidence for the evolution of shell-crushing feeders in groups as diverse as crabs, stomatopods, lobsters, rays, and bony fishes. Vermeij thus described the MMR as an evolutionary arms race between predators and prey, with diversification and innovation in one trophic level leading to retaliatory innovations in the other and vice versa.

In the decades since Vermeij's landmark observations, widespread evidence has accrued to support the basic tenets of this hypothesis. In addition to the explosion of anti-predatory defenses in mollusks, groups like crinoids also show a switch from primarily sessile to primarily mobile life histories, a trend observed

across shelly marine invertebrates. Numerous studies have also subsequently documented an increase in: the incidence of predation attempts in Mesozoic and younger fossils (drill holes/chips and repair scars); the proportion of marine predators through time; and the average energetics of marine species (Figure 2).

At an ecosystem scale, predation matters because it changes energy and nutrient flows through the environment and can allow for greater local diversity. In addition to the increased ratio of calcium carbonate (or silica) to organic biomass in groups under siege, changes in dietary composition, foraging behavior, and activity levels in prey species in the presence or absence of predators are known to have pronounced effects on



**Figure 2. The ecological changes of the Mesozoic typically continue to the present day.**

Pelagic calcification, traced by the species richness of planktonic foraminifera and calcareous nannoplankton (the group containing coccolithophores), increased rapidly during the Cretaceous and provided a second open ocean sink for calcium carbonate, thereby stabilizing the carbonate cycle. Evolutionary innovations in eukaryotic algae, including dinoflagellates, diatoms, and coccolithophores (traced by the species richness of each group, respectively), may have shifted the size structure of open ocean foodwebs to larger body sizes and increased energy transfer to higher trophic levels. Around the same time, evidence for predation traces in marine invertebrates and the proportion of marine predators began to increase towards modern-day levels. Flowering plants (angiosperms) evolved around the earliest Cretaceous, but the timing of their rise to ecological dominance is uncertain, casting doubt on the link between the terrestrial and marine revolutions of the Mesozoic. The later rise of widespread grasslands does roughly coincide with the rise of diatoms (two groups linked by silica use), but a mechanistic link between the rise of grasses and diatoms is debated. Long-term trends presented in the top three panels are schematics and, in some cases, a hybridized combination of data presented in the following references: Bown (2005) *Micropaleontology* 51, 299–308 (nannoplankton species richness, diatom species richness from 0–65 Ma); Katz *et al.* (2004) *Annu. Rev. Ecol. Evol. Systemat.* 23, 523–556 (diatom richness extrapolated linearly from 65 Ma to age of oldest fossils from Katz *et al.* Figure 3); Fraas *et al.* (2015) *Annu. Rev. Earth Planet. Sci.* 43, 139–166 (Cretaceous planktonic foraminifera richness, roughly scaled to species richness of Ezard *et al.* by overlapping intervals); Ezard *et al.* (2011) *Science* 332, 349–351 (Cenozoic planktonic foraminifera richness); Huntley and Kowalewski (2007) *Proc. Natl. Acad. Sci. USA* 104, 15006–15010 (frequency of predation traces); Bambach *et al.* (2002) *Proc. Natl. Acad. Sci. USA* 99, 6854–6859 (% predatory marine metazoans). Please refer to the primary references for data if needed. The bottom panel is a schematic only and shows that the ecological dominance of angiosperms rose over the course of the Cretaceous (schematic of concept only; general inference from Lupia *et al.* (1999) *Paleobiology* 25, 305–340, and Crane and Lindgard (1989) *Science* 246, 675–678) and that grasslands, first C3 and then C4, are ecologically important systems by the latest Cenozoic (schematic of general timing only; from Edwards *et al.* (2010) *Science* 328, 587–591).

ecosystem functions, such as nutrient cycling and energy transfer. Also, predators often have large ranges relative to their prey and act to move nutrients and biomass across habitat boundaries.

Notably, the increase in predation and defense defining the MMR

continued throughout the Cenozoic to the present day (Figure 2). This occurred in spite of dramatic changes to other aspects of marine ecosystems, including a turnover in the composition of fish communities around 66 million years ago (from cartilaginous lineages to bony fish

lineages), the isolation of tropical ecosystems with the closure of the Isthmus of Panama and connections through the Red Sea, a tropical reef gap during the peak warmth of the Eocene (around 50 million years ago), and the shift towards rapidly growing coral taxa during the high amplitude

glacial–interglacial cycles of roughly the last 2 million years.

### Drivers of global ecosystem change

Why these revolutions occurred during the Mesozoic is a fascinating question because in each case the innovation in question could conceivably have occurred long before it did. For instance, Foraminifera were among the earliest biomineralizers to appear in the fossil record, so the evolution of abundant planktonic forms lags behind the evolution of benthic lineages by more than 400 million years. Since the Mesozoic, multiple independent origins of planktonic foraminifera from benthic foraminiferal ancestors have been documented, only adding to the mystery. The eukaryotic clade containing coccolithophores — Haptophyta — roots to the pre-Cambrian, but failed to evolve calcification at levels detectable in the body fossil record until the Mesozoic. Active predation by marine predators has comparably deep roots, but vastly increased in intensity in mid-Mesozoic and more recent times.

At present, the drivers of these innovations are still debated and a case can be made for likely feedbacks amongst nearly all of them. Two of the most encompassing drivers evoke a change in seawater chemistry. In the aftermath of the Permian–Triassic mass extinction (Figure 2) and long into the Jurassic, the carbonate saturation state of the open ocean (denoted as  $\Omega$ ) may have been extremely high ( $\Omega > 9$ ) and could have provided favorable conditions for the evolution of pelagic calcifiers and a calcification-driven arms race between predators and prey. In addition, once evolved, pelagic calcification stabilized the long-term carbonate saturation state of the ocean and reduced the frequency of large abiotic perturbations, potentially allowing for calcium-carbonate-intensive life histories to persist. Alternatively, or perhaps concordantly, other aspects of seawater chemistry may have changed, either providing seawater conditions that were favorable to coccolithophores, dinoflagellates, and diatoms and/or broadly increasing nutrient availability and biomass throughout marine foodwebs. Increasing marine productivity through some combination of nutrient

availability and foodweb structure (i.e., the rise of dinoflagellates, diatoms, and coccolithophores) would have increased the biomass of more — and more active — predators at higher trophic levels. Indeed, although siliceous protists appear long before the Mesozoic, the diversification of silica-armored clades in the Mesozoic also points to increased predation pressure at this time. Other hypotheses for major Mesozoic changes (e.g., selective reproduction, predatory arms race, and reef habitat availability) generally require an ultimate driver, such as an increase in the total productivity of marine ecosystems or a change in seawater carbonate chemistry, to start the process.

When it comes to the question of why major changes in seawater chemistry may have occurred during the latter half of the Mesozoic and on through the Cenozoic, it is notable that comparably large changes were occurring on land, with the rise of flowering plants and diverse insect communities (Mesozoic) and the rise of widespread grasslands (Cenozoic) (Figures 1 and 2). These terrestrial revolutions may have dramatically changed nutrient fluxes to the open ocean, although some have argued against linking marine and terrestrial changes because the potential driver (terrestrial change) appears to lag behind the effect (marine change) (Figure 2).

### Conclusions

Over the course of the Mesozoic, a series of evolutionary innovations and ecological revolutions reshaped marine ecosystems towards those we know today. The evolution of pelagic calcifiers changed the marine carbon cycle and left the ocean far more resilient to acidification and other perturbations to the carbon cycle. In addition, the rise of three major algal clades (coccolithophores, dinoflagellates, and diatoms) may have increased energy transfer to high trophic levels, possibly fueling an evolutionary arms race between marine predator and prey species. Whatever the cause, these directional changes in marine ecosystems over the last 300 million years have shaped modern ecosystems and their dynamics by changing the

sensitivity of marine chemistry to  $\text{CO}_2$  fluctuations, increasing energy availability to the top of the foodweb, and tightening the coupling between predators and prey.

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