

Bottom-up controls, ecological revolutions, and diversifications in the oceans through time

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Abstract

Animal life originated in the oceans and evolved there for hundreds of millions of years before adapting to terrestrial environments. Today's oceans cover more than two-thirds of planet Earth and generate as much primary production as does land. The path from the first macrobiota communities to the modern menagerie of marine life involved parallel increases in terrestrial nutrient input, marine primary production, species' abundance, metabolic rates, ecotypic diversity, and taxonomic diversity. Bottom-up theories of ecosystem cascades arrange these changes in causal sequence. At the base of marine food webs, nutrient fluxes and atmosphere–ocean chemistry interact with phytoplankton to regulate production. First-order consumers (e.g., zooplankton) might propagate changes in quantity and quality of phytoplankton to changes in abundance and diversity of larger predators (e.g., nekton). However, many uncertainties remain about the mechanisms and effect size of bottom-up control, particularly as applied to the world's oceans and the entire history of animal life. Here, we distinguish and review modern and fossil evidence for hypothesized bottom-up pathways, and we assess the ramifications of these processes for four key intervals in marine ecosystems: the Ediacaran–Cambrian (635–485 million years ago [Ma]), Ordovician (485–444 Ma), Devonian (419–359 Ma), and Mesozoic (252–66 Ma). We advocate for clear articulation of bottom-up hypotheses to better understand

causal relationships and proposed effects, combined with additional ecological experiments, paleontological documentation, isotope geochemistry, and geophysical reconstructions. How small-scale ecological change transitions into large-scale evolutionary change remains an outstanding question for empirical and theoretical efforts to address.

Keywords: macroecology, nutrient cycles, primary production, marine food web, trophic cascade, predation, evolutionary arms race, Cambrian Explosion, Great Ordovician Biodiversification Event, Mesozoic Marine Revolution

Introduction

Identifying the factors that promote or limit biodiversity is key to understanding ecological and evolutionary change across timescales. Throughout modern biomes, predation pressure is cited as an important regulator of ecosystem structure, determining the abundance, size, and behavior of consumers at lower trophic tiers (“top-down control”)^{1,2}. When a trophic level or size class is free of predators, a common assumption is that food availability limits the abundance of that level or class instead³⁻⁵. Ultimately, all food resources are limited by the rate of primary production, which in turn is strongly influenced by nutrient concentrations.

Research on modern ecosystems frequently has assumed that the environmental conditions governing nutrient pathways are static or homogeneous (the “mean field approximation”)⁶⁻⁸. Where nutrient flux changes are noted, perturbations are often cyclic, with a phase of centuries at longest. Consequently, resource-driven ecological changes tend to be treated as reversible outcomes of brief environmental excursions. For instance, plankton productivity fluctuates partially in response to annual to decadal variation in polar climate⁹ and to decadal to centennial variation in the California Current System¹⁰. Although anthropogenic

nutrient redistribution is increasingly seen as a threat to biodiversity^{11,12}, loss of apex predators remains a primary focus of global change biology research, management, and conservation^{1,2,13}.

Over the more than 500 million years of animal evolution, however, the assumption of baseline environmental stasis is strongly violated. Widespread volcanism, planetary glaciation, and other dramatic perturbations to nutrient cycles lasted on the order of millions of years^{14,15}. Ecological changes close in time to some of these geologic events were similarly momentous. On global, geologic scales, the role of primary productivity might shift from passively limiting local abundances to actively driving diversification of species and ecotypes. Such “bottom-up controls” (Fig. 1) are hypothesized to have generated substantial evolutionary and ecological changes throughout Earth history¹⁶⁻²⁰.

We use the term “ecological change” in the most inclusive sense, encompassing shifts in biomass, population density, relative abundances, species diversity, metabolic rates, frequency distribution of functional traits, and more. Changes in behavior may also occur^{13,21,22}, particularly as a top-down effect, but this outcome is unobservable in most of the fossil record. Ecologists distinguish between species-level cascades vs. community cascades, and abundance cascades vs. diversity cascades^{6,23-25}. In contrast, most fossil studies aim to quantify only community or diversity responses, because it is harder to study individual species and absolute abundance from the rock record than in living systems.

Expansion of trophic tiering, acceleration of metabolic activity, and radiations of clades at many trophic levels are the outcomes of bottom-up controls discussed in the paleontological literature most often¹⁶⁻²⁰. Below, we briefly summarize examples of these and other ecological changes during four intervals of Earth history. We then synthesize theory and data from modern ecological studies as well as the fossil record to evaluate each proposed biological pathway of

bottom-up control. Other recent reviews cover the geological record of putative bottom-up cascades in more detail, including comparing time series of family-level diversity and geochemical proxies for weathering and organic carbon production and burial^{19,20,26}.

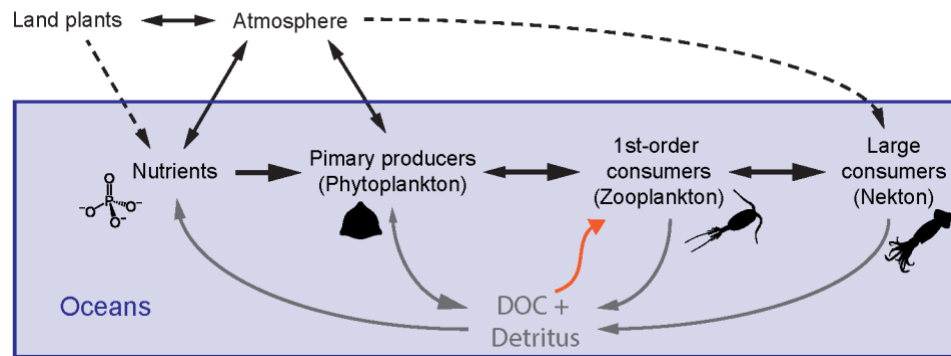


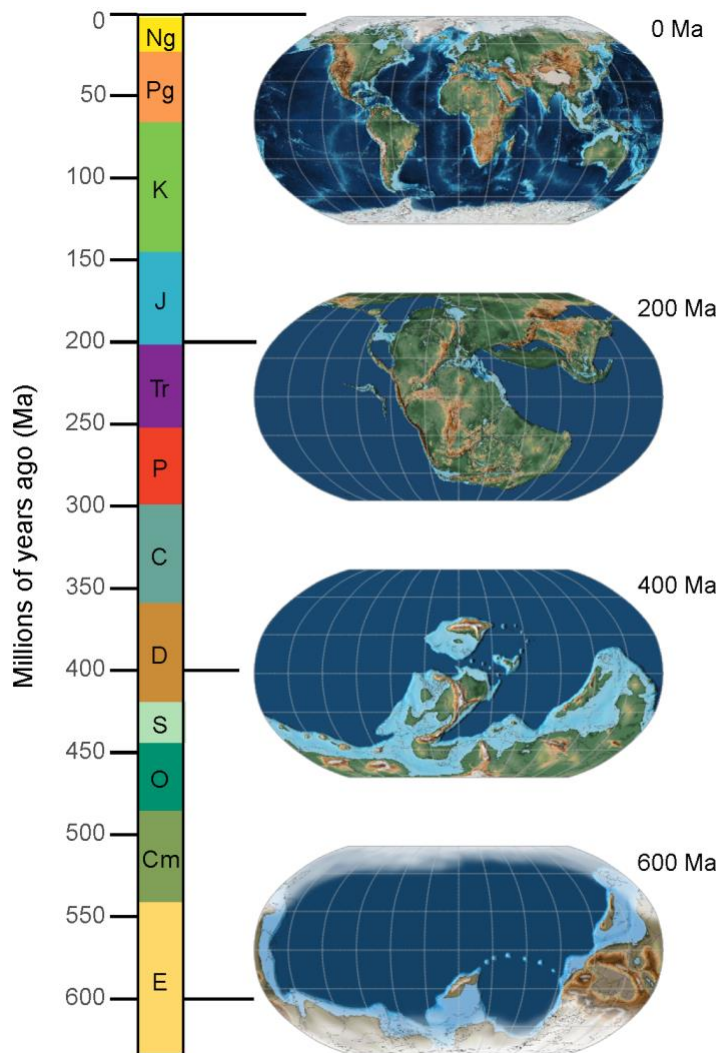
Figure 1. Components of marine ecosystems.

The abundance and diversity of marine primary producers, first-order consumers, and higher-order consumers depend on nutrient availability and atmospheric gas concentrations. Pelagic consumers can be coarsely divided into zooplankton and nekton; multiple tiers of consumers live on the benthos as well. All trophic levels leak organic carbon from food webs, in particulate form (detritus) or dissolved form (DOC). Substantial volumes of phytoplankton mass convert to DOC through cell death and viral lysis. The microbial loop (orange arrow) recycles some of this carbon to zooplankton via a chain of bacteria, nanoflagellates, and ciliate protozoans. Terrestrial ecosystems can affect marine ecosystems by eroding and weathering rock, altering the hydrologic cycle, and absorbing and respiring CO₂ and O₂ to the atmosphere. Thick arrows indicate the main candidate pathway for bottom-up ecosystem controls. Dashed arrows indicate pathways that may be weaker or of variable strength throughout Earth history.

History of marine ecosystems

Our ecological focus centers on oceans because the history of marine ecosystems is substantially longer and better known than that of terrestrial ecosystems. Notable environmental events since the appearance of animals include multiple glaciations in the Neoproterozoic and Paleozoic^{14,27}, superplumes and volcanism in the Ordovician and Cretaceous²⁸⁻³⁰, enhanced upwelling and runoff in the Jurassic³¹, and land plant evolution in the Devonian and Cretaceous³²⁻³⁴. Marine ecosystem revolutions have been said to have occurred in each of four intervals overlapping these geologic events: the Ediacaran–Cambrian (635–485 Ma)³⁵,

91 Ordovician (485–444 Ma)³⁶, Devonian (419–359 Ma)³⁷, and Mesozoic (252–66 Ma)³⁸. Biotic
 92 events during these intervals involved rapid speciation into previously unexplored or inaccessible
 93 areas of ecospace, such as the expansion of macroscopic life into the water column and the origin
 94 of metabolically-active predators throughout the Paleozoic³⁹⁻⁴¹.



96 **Figure 2. Continental configurations through time.**
 97 Reconstructions of continental positions, orientations, and topography are shown at 200-million-year
 98 intervals between the present day, Mesozoic, Paleozoic, and Neoproterozoic. Maps are plotted from
 99 PaleoAtlas data^{42,43}. E, Ediacaran; Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C,
 100 Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; N, Neogene. Quaternary
 101 not labeled.

Ediacaran–Cambrian Radiation

Few intervals remain as contentious among geobiologists as the Neoproterozoic–Cambrian (1,000–485 Ma), a time that perhaps witnessed both glaciation and oxygenation on global scales, alongside the origin and radiation of animals. Earth scientists have established that the planet froze repeatedly, first in the Sturtian glaciation (720–660 Ma) and again in the Marinoan glaciation (650–635 Ma)²⁷. Unlike the Pleistocene ice ages of the last few million years, ice covered even the equatorial zone and sea surface in these “snowball Earth” events. At least one more glaciation occurred, the Gaskiers (580 Ma), but this event may have been less temporally and geographically extensive than were the two preceding glaciations⁴⁴. Massive reconfiguration of continents overlapped the glaciation intervals. From 900–650 Ma the supercontinent Rodinia broke up; afterwards, the continents of East and West Gondwana collided into a new supercontinent, Pannotia (Fig. 2)^{45–47}.

Landmark evolutionary and ecological changes were interwoven with abiotic events in the Neoproterozoic. Molecular clocks place the evolution of animals before the first Neoproterozoic glaciation event, with metazoan–choanoflagellate divergence 1000–900 Ma and Metazoa origin *ca.* 800 Ma^{reviewed in 48}. Biomarker evidence indicates a pivotal turnover in marine primary production between the two snowball events: chlorophytes (green algae) and other primary endosymbiotic algae expanded from freshwater habitats to marine settings and displaced bacteria as the important primary producers in oceans⁴⁹. Eukaryotic algae have flourished as the main marine producers ever since, although component clades later turned over in abundance in the Phanerozoic (“Mesozoic Marine Revolution” below). The earliest known fossils of macroscopic animals (rangeomorphs) are dated at 574 Ma, placing them 5 Ma after the final, Ediacaran glaciation, the Gaskiers^{50,51}. Large multicellular organisms in the Ediacaran formed

ecologically complex communities upon the seabed surface and set the stage for unprecedented radiation of animal ecomorphology and clades⁵²⁻⁵⁵. By the Early to Middle Cambrian, 40–60 million years later, body plans had evolved for nearly every animal group ranked as a phylum^{35,56}, and trophic webs had attained the complexity of those in modern marine ecosystems⁵⁷. Note that molecular and body fossils set only minimum age constraints, and it is possible eukaryotic algae, macrobiota, and metazoan crown groups proliferated earlier than currently documented.

The broadly similar timing of such dramatic abiotic and biotic events has prompted a slew of causal explanations, many of which assume spikes in oxygen or phosphorus mediated Earth and life system changes⁵⁸⁻⁶². Unfortunately, the onset, duration, and magnitude of any Neoproterozoic Oxidation Event or phosphorus pulses are poorly constrained relative to glaciation events and the Ediacaran–Cambrian Radiation (ECR). One set of hypotheses posits glaciation (and deglaciation) released terrestrial nutrients such as phosphorus that fueled phytoplankton production, and thence oxygenation^{26,58,63}; uplift of Transgondwanan Supermountains might have shed nutrients into oceans with similar effect^{45,47}. Even if glacial or montane phosphorus input was transient, an associated sulfate increase could have jump-started the self-sustaining modern phosphorus cycle, recycling the nutrient for primary production⁶¹. A contrasting set of hypotheses reverses the order of causality and suggests plankton community restructuring caused a Neoproterozoic Oxidation Event and thence glaciation^{64,65}, just as the Great Oxidation Event had preceded snowball glaciation *ca.* 2.4 billion years ago⁶⁶. Another biotic change that could have transformed ecosystems indirectly via subsequent abiotic change was the innovation of bioturbating metazoans. Bilaterians with a through-gut disrupted coverage of microbial mats that had sealed the Ediacaran seafloor, thereby allowing new, burrowing

species to access the underlying sediment^{35,67}. It is even possible environmental change was irrelevant to the origins of multicellularity and metazoans; gene regulatory network innovations alone might have paced eukaryote evolution⁶⁸ but see ⁵⁶. For such multifaceted changes as the ECR entailed, any single trigger may be insufficient as an explanation^{35,48,52,56}. A “fire triangle” of oxygen, primary production (fuel), and favourable climate (temperature) together might have incited the ECR⁴⁸.

Great Ordovician Biodiversification Event

Ecological and evolutionary radiations continued after the Cambrian. Diversifications in the Ordovician were so pronounced as to be named the Great Ordovician Biodiversification Event (GOBE). The GOBE entailed an explosion of marine diversity: species increased both in raw count and in occupation of feeding, motility, and water-column ecotypes^{40,41,69}. The radiation and adoption of pelagic lifestyles in graptoloids (filter-feeding, colonial pterobranch hemichordates) exemplifies this diversification in both taxonomic richness and ecospace⁷⁰. In addition to these evolutionary and ecological changes, the body size and therefore inferred metabolic demand of several clades, including brachiopods and crinoids, increased during the Ordovician^{71,72}. Despite similar patterns across clades, the GOBE was not one synchronous event. Rather, it occurred as a series of diversifications, first in planktonic fauna, then in benthic communities, and finally in reefs³⁶. The first phase may have begun in the Cambrian with an increase in phytoplankton and zooplankton diversity⁷⁰. It is still inconclusive whether net primary production rose alongside producer diversity⁷³.

Nutrient enrichment may have instigated the many biotic changes associated with the GOBE^{70,72,74,75}. Putative nutrient sources in the Ordovician include mountain building⁷⁶; volcanic superplumes^{28,29,77}; strong upwelling along the western coasts of Laurentia and Gondwana⁷³,

possibly in response to global cooling⁷⁸; trace metal availability associated with a pulse of oxygenation⁷⁰; and non-vascular plant expansion on land^{36,79,80}. An increase in detritivore abundance, diversity, and burrowing depth also could have facilitated bottom-up cascades in the Ordovician^{20,81}. By recycling organic matter from sediment and reclaiming detritus from the water column, deposit- and filter-feeding animals can increase nutrient availability to other marine trophic tiers even without an increase in nutrient delivery to oceans from land. This same contribution of burrowers is also suggested as a contributor to the ECR, as discussed above^{35,67}, but could have played a reprise role in the GOBE and later Paleozoic as burrowing modes continued to deepen^{69,82}. Focusing entirely on biotic processes, some authors have argued for the general importance of competition in driving the GOBE⁸³. However, this idea is unsupported by several studies on specific taxa, which concluded Ordovician interactions were primarily non-competitive^{71,84}.

The GOBE was a complex and prolonged event that may have been a continuation of the ECR³⁶. Cambrian–Ordovician reorganization of phytoplankton remains a strong candidate for enabling radiations at higher trophic tiers later in the GOBE⁷⁵. Nevertheless, there are many additional putative causes for the GOBE, both biotic and abiotic, and a combination of factors might have been responsible for such varied evolutionary and ecological changes^{36,73,81,83}.

Devonian Nekton Revolution

The Ordovician ended in a mass extinction event, which severely curtailed species diversity but minimally pruned ecotypic diversity^{85,86}. Both types of diversity continued to accumulate in many taxa throughout the later Paleozoic, until the late Devonian, when two slightly more disruptive biodiversity crises occurred at *ca.* 383 and 376 Ma⁸⁵⁻⁸⁷. One interpretation of Paleozoic ecosystem change suggests that Ordovician species expanded into

pelagic habitats as passive drifters and filter feeders, whereas the fauna in the Devonian turned over to well-defended bottom-dwellers and active swimmers in the water column, including jawed fish^{18,37,88}. Both the processes and patterns of the so-called Devonian Nekton Revolution (DNR) have been contested, however. Chaetognaths, predaceous fish, and other nektonic groups originated before the Devonian, and some scholars have argued the mid-Paleozoic ecosystem change was too incremental to merit the title of revolution⁸⁹. In recent network analyses and machine learning classifications, the ECR, GOBE, and Mesozoic stand out for evolutionary radiations while the Devonian does not^{90,91}. Assuming some amount of ecotypic and evolutionary turnover did occur in the Devonian, bottom-up mechanisms might have contributed to this restructuring.

Rather than glacial melts as in the ECR⁶³, a top candidate source for nutrient enhancement during the Devonian is terrestrialization. Land plants might have increased nutrient input through mechanical weathering of rock, acceleration of the hydrologic cycle, or mobilization of phosphorus from soil acidification^{32,33,92,93}. Land plants are also proposed as drivers of the DNR through indirect effects on deep-water chemistry in the Devonian, with regional oxygenation or shifts from ferruginous to sulfidic anoxia^{93,94}. Burial of refractory plant material such as wood can increase partial pressure of oxygen in the atmosphere. Similar to proposals for the ECR, Devonian oxygen spikes might have enabled diversification of high-metabolism predators such as large fish⁹⁴, although this link is disputed⁹⁵. The net effect of terrestrial vegetation is not straightforward, however, because botanic land cover also protected surface particles from blowing into the ocean, transformed river morphology from dispersed streams to meandering channels, and perhaps lowered the threshold of atmospheric CO₂ required to maintain mass balance of carbon and other elements in Earth's surface system^{92,96,97}.

As a standalone event, the DNR was a lackluster revolution compared to the functional innovation and rapid speciation of the ECR and GOBE. In broader historical context, however, changes in the Devonian continued a Paleozoic trend of evolution in the water column and strengthened land plants as a lever on Earth surface processes that has persisted through the Mesozoic and Cenozoic.

Mesozoic Marine Revolution

The Paleozoic drama of the ECR, GOBE, and DNR—arguably a continuum of biotic changes rather than discrete events^{36,83,89}—involved progressive expansion into trophic and water column tiers for the first time. In the Mesozoic (252–66 Ma), taxonomic and functional compositions of marine ecosystems turned over more than expanded⁹⁸. Classically, this Mesozoic Marine Revolution (MMR) is discussed in reference to diversification of active hunting modes in predators and of defense strategies in prey⁹⁹. Crinoids evolved mobility at around the same time as their echinoid predators diversified and evolved stronger jaws¹⁰⁰, and gastropods evolved thicker, spinier shells³⁸. Burrowing bivalves radiated, and although infaunalization can be unrelated to predation pressure⁶⁹, hard-boring forms are linked to predation and diversified beginning in the Mesozoic¹⁰¹. These and other examples have been interpreted as top-down cascades, where grazers and carnivores exerted evolutionary pressure on lower trophic tiers. In addition to such top-down arms races, however, bottom-up mechanisms might have contributed to the MMR.

There are several possible sources of increased marine nutrient concentrations in the Mesozoic. Continental configuration may have played a role: over the course of the era, the supercontinent Pangaea split and the Tethys and then Atlantic ocean opened (Fig. 2). Submarine volcanism, long coastlines, wet conditions of interior seaways, and offshore upwelling from

circulation changes during this interval could have contributed to enhanced nutrient runoff into oceans^{19,31,77}. The radiation of angiosperms in the Cretaceous is also suggested to have increased terrestrial nutrient runoff^{16,17}. However, the impacts of floral turnover on biogeochemical cycling are not straightforward. Although angiosperms increased the recycling rates of some nutrients (e.g., via deciduous leaf-fall), it remains unclear whether Mesozoic flora turnover increased the net volume of nutrient input to the marine reservoir—and even if angiosperms did drive a net nutrient loss from land to oceans, much of this terrestrial abundance change might have occurred after its supposed effects in the marine realm³⁴. Abiotic processes alone could have fueled a surge in primary production across much of the Mesozoic¹⁹ regardless of whether land plants played a smaller role in marine nutrient increases than during the Paleozoic.

Additional bottom-up theories for the MMR center on a turnover in major phytoplankton taxa. Mixotrophic dinoflagellates radiated in the Jurassic, and their large cell size could have increased energy flow to top trophic tiers¹⁰²; in addition, diatoms radiated from the Cretaceous, and their efficient growth could have produced more biomass at the base of food webs¹⁰². Dinoflagellates, diatoms, and other secondary and tertiary symbiotic algae primarily derive plastids from red algae and use chlorophyll *c* or rarely *b* as an accessory pigment to chlorophyll *a*. Green algae use chlorophyll *b* as an accessory to chlorophyll *a*. Differences in host cell phenotypes and plastid origins lead to differential uptake of nutrients and trace metals¹⁰³. Chlorophyll *c* algae are denser than chlorophyll *b* algae in phosphorus, nitrogen, and the subset of trace metals that are more bioavailable in oxygenated waters, such as cadmium and cobalt¹⁰³. The Paleozoic–Mesozoic turnover of chlorophyll *b* to chlorophyll *c* algae therefore would have shifted the elemental stoichiometry of primary production, potentially increasing biomass quality at all trophic levels^{19,26}. Mesozoic oxygenation, evidenced by positive carbon isotope

excursions¹⁰⁴, would have rebalanced metal availability in oceans and might have ushered in the proliferation of chlorophyll *c* algae^{26,103}. Ultimately, both nutrient addition and phytoplankton evolution could have contributed to the morphological and taxonomic diversity of animal consumers that increased during the Mesozoic.

A framework for bottom-up mechanisms

Increased biomass, abundance, taxonomic diversity, feeding and motility modes, and metabolic rate are all discussed as outcomes of bottom-up processes^{16,17,19,77,105}. Although it is possible for these changes to occur in lockstep, different mechanisms likely underpin such disparate outcomes. We identify eleven potential stepping-stones in bottom-up ecological pathways (Fig. 3, Table 1), where each stepping-stone can lead to multiple knock-on consequences at a higher trophic tier. This framework connects nutrient concentrations to primary producers to first-order consumers to higher-order consumers (Fig. 1). In the pelagic realm, these three trophic tiers correspond roughly to phytoplankton (primary producers), zooplankton (pelagic consumers with passive dispersal), and nekton (active swimmers such as large predators). Multiple tiers of trophic consumers live above, on, and within the seabed as well.

A tripartite division is a simplification of marine food webs. Many organisms fall between these categories, such as facultative heterotrophs (e.g., some planktonic foraminifera) and the nektoplankton (weak swimmers, e.g., Euphausiacea, krill). In these cases, multiple of the mechanisms discussed for individual trophic tiers may apply. An additional influence of facultative heterotrophs is discussed in “Phytoplankton evolution” below. Other organisms fall beyond the above categories altogether, such as chemoautotrophs (e.g., many bacteria and archaea) and detritivores (e.g., Holothuroidea, sea cucumbers). Chemoautotrophs may avoid

dependence on marine food webs entirely, while detritivores can source organic material across every trophic tier (Fig. 1). Viruses and parasites also shape marine food webs^{106,107} but leave few traces in the fossil record.

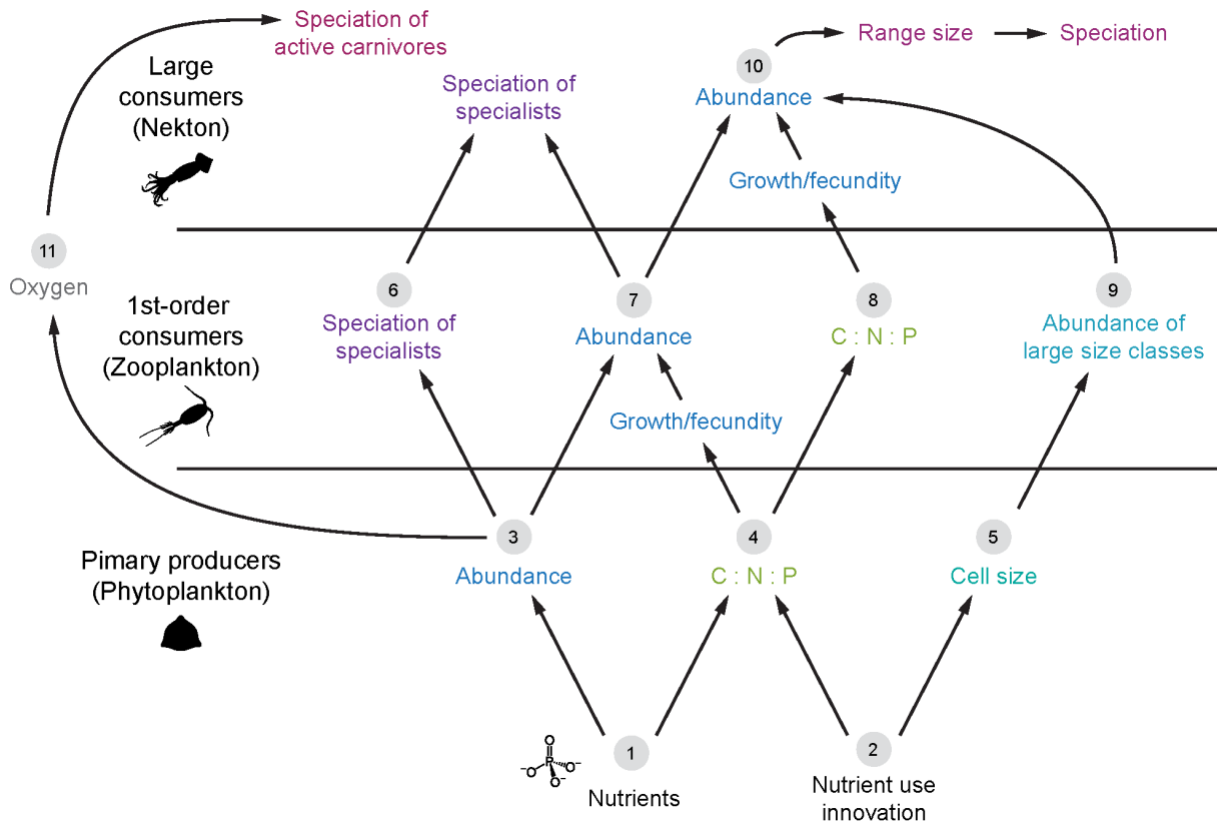


Figure 3. Bottom-up pathways in marine ecosystems.

Ecological variables that affect successive trophic levels are numbered as stepping-stones in this simplified flowchart of bottom-up pathways. Initial triggers of bottom-up change include increased nutrients (stepping-stone #1) or evolutionary innovation in nutrient acquisition or metabolism (stepping-stone #2). Subsequently, these nutrient-related changes affect primary producers, first-order consumers, and higher-order consumers. Times in Earth history where each step is thought to have taken place are listed in Table 1. Top-down pathways are not shown but can co-regulate abundances (stepping-stone #3 and #7) and influence prey behavior. Carbon, C; nitrogen, N; phosphorus, P.

Table 1. Stepping-stones in bottom-up pathways.

The bottom-up stepping-stones numbered in Fig. 3 are listed in order of increasing trophic level. Most effects are themselves the cause of subsequent changes, and the index numbers associated with these knock-on effects are included in parentheses. Time intervals where a given change is hypothesized to have occurred are listed at far right. Phosphorus, P; nitrogen, N; carbon, C; ↑, increase and ↓, decrease in count, concentration, or rate.

	Trophic level	Change	Direct effect(s)	Occurrences
1	Nutrients	↑ nutrient flux to oceans	↑ phytoplankton abundance (3) ↑ P and N relative to C in cells (4)	Cambrian, Ordovician, Devonian, Mesozoic
2	Phytoplankton	Key innovations in nutrient use and storage	↑ P and N relative to C in cells (4) ↑ cell size (5)	Cambrian, Mesozoic
3		↑ abundance	↑ zooplankton abundance (7) ↑ speciation of zooplankton specialists (6) ↑ O ₂ (11)	Cambrian, Ordovician, Devonian, Mesozoic
4		↑ P and N relative to C in cells	↑ P and N relative to C in zooplankton (8) ↑ growth, ↓ generation time, ↑ abundance of zooplankton (7) ↑ fecundity, ↑ abundance of zooplankton (7)	Mesozoic
5		↑ cell size	↑ abundance of large zooplankton (9)	Neoproterozoic, Mesozoic

6	Zooplankton	↑ speciation of specialists	↑ speciation of nekton specialists	Cambrian, Ordovician, Devonian, Mesozoic
7		↑ abundance (all size classes)	↑ speciation of nekton specialists ↑ abundance of nekton (10)	Cambrian, Ordovician, Devonian, Mesozoic
8		↑ P and N relative to C	↑ growth, ↓ generation time, ↑ abundance of nekton (10) ↑ fecundity, ↑ abundance of nekton (10)	Mesozoic
9		↑ abundance of large zooplankton	↑ abundance of nekton (10)	Mesozoic
10	Nekton	↑ abundance	↑ geographic range size, ↑ speciation	Devonian, Mesozoic
11	Atmosphere and oceans	↑ O ₂	↑ speciation of high-metabolism carnivorous nekton	Cambrian, Devonian

Nutrient flux

Approximately half of net primary production today takes place in the marine realm¹⁰⁸. Nutrients limit or co-limit production in many parts of the oceans, as evidenced by blooms after nutrient addition¹⁰⁹⁻¹¹¹. This relationship is illustrated in Fig. 3 as the link between nutrients (stepping-stone #1) and phytoplankton abundance (stepping-stone #3). There are many macronutrients and micronutrients, including essential elements such as iron, cobalt, and molybdenum. As mentioned in preceding sections, the greater availability of certain metals after

oxygenation pulses is hypothesized to have contributed to the ECR, GOBE, and MMR^{26,70,103}. In modern oceans, nitrogen is well documented to limit primary production in many local regions on the scale of days to weeks—but ultimately, it is phosphorus that limits marine production on large spatiotemporal scales¹¹²⁻¹¹⁴. Nitrogen concentrations dictate local population fluctuations about a long-term carrying capacity, while phosphorus concentrations set that capacity in many areas because there are fewer ways organisms can compensate for low phosphorus availability.

Marine organisms can source bioavailable nitrogen either from terrestrial runoff or from bacteria fixing atmospheric N₂ gas. However, runoff is the near-exclusive source of marine phosphorus. Ash-fall and wind-blown dust contribute a smaller volume of phosphorus on the global scale, and volcanos can enrich phosphorus concentrations locally¹¹⁵. Because terrestrial fluxes are so important to the phosphorus cycle, abiotic and biotic events on land have large potential to influence marine ecosystems. Additionally, some changes that enhance terrestrial delivery of phosphorus to oceans could also enhance delivery of nitrogen and trace metals, further nourishing oceans. In the mid-20th century, Helen Tappan wrote about this connection between terrestrial nutrients and marine productivity^{116,117}, thereby sparking much of the later inquiry into bottom-up controls across the Phanerozoic. As detailed above in the “History of marine ecosystems,” developments on land relevant to oceans included multiple phases of mountain building, glacial scouring and melting, and expansion of plant root networks. Before the establishment of soils, runoff was unimpeded, so Precambrian and Paleozoic glacial and volcanic activity could have had an impact on oceans disproportionate to any such change observable today¹⁵. Therefore, nutrient addition, especially of phosphorus, was a potentially strong contributor to the ECR and GOBE.

Unfortunately, although the sources and sinks of nutrient cycles are known in qualitative detail, it is difficult even in the present day to quantify net flux of phosphorus and other nutrients to oceans globally^{12,115}. Uncertainty stems in part from the complicated balance of burial vs. remineralization on the seafloor^{115,118} and from spatial heterogeneity in rates of weathering¹¹⁹ and of precipitation in rivers, estuaries, and shelves^{115,120}. Recently, plankton have been found capable of recycling phosphorus through reduced forms, which may be an important reservoir in the marine phosphorus cycle; however, it remains unknown how environmental conditions affect biologic production of these reduced compounds¹²¹. The cumulative imprecision in quantifying marine phosphorus availability is even greater in deep time, challenging efforts to estimate even the direction of change (e.g., whether more or fewer nutrients reached the open ocean at a given time), let alone the magnitude of change¹⁹. Substantial new geochemical research is needed to constrain the timing, duration, and location of nutrient addition to oceans both past and present.

Phytoplankton evolution

Even without an increase in nutrient flux to oceans, there are at least two ways to increase per-cell macronutrients in phytoplankton (stepping-stone #2). First, clades with denser macronutrient profiles could proliferate (stepping-stone #4). The relative amounts of phosphorus, nitrogen, and other elements are deeply conserved in algal lineages, and the clades with highest relative abundance today have lower carbon : nitrogen : phosphorus ratios (i.e., more phosphorus and nitrogen per unit dry mass) than clades that were most abundant during the Paleozoic^{26,102,103}. This compositional turnover took place in the Mesozoic, when chlorophyll *a* and *c* algae such as diatoms replaced green algae such as prasinophytes in abundance (“Mesozoic Marine Revolution” above). The richer nutrient profile of phytoplankton that resulted from algal

radiations has cascading consequences for consumer fitness (discussed in “Population abundance” below) and is suggested to have facilitated the ECR and MMR (Table 1)^{26,122}.

Second, cell size distribution could shift rightward, with more cells at larger size fractions (stepping-stone #5). Generally, organism size increases at higher trophic levels, and so raising the size of primary producers at the base of food chains might increase the carrying capacity of the largest zooplankton consumers (stepping-stone #9), effectively truncating the low-level consumer portion of food chains^{102,123}. Since energy transfer efficiency across trophic levels is low—usually less than 15%^{124,125}—bypassing low-level trophic tiers means a larger energy input to apex predators at the highest tiers (stepping-stone #10).

The size-based hypothesis is put forward as another bottom-up facilitator over marine ecosystem history, with initial cell size increases resulting from the evolution of mixotrophy in dinoflagellates during the Mesozoic and from fast-growing diatoms in the Cenozoic¹⁰². Ecosystem models suggest that mixotrophy does increase cell size and trophic energy transfer efficiency¹²⁶. At the same time, mesocosm experiments demonstrate that trophic energy transfer efficiency reciprocally affects food chain length: more efficient energy transfer can lengthen food chains, but the addition of higher-order consumers reduces the energy transfer efficiency of first-order consumption¹²⁴. It is difficult to directly estimate energy transfer efficiency in deep time, although trophic network properties derived from fossil and modern marine assemblages match closely^{57,127}. The evolution of mixotrophy and of diatoms are milestones in marine history, but there are too many trade-offs in ocean food web dynamics to assign these events singular importance in driving post-Paleozoic ecosystem change.

Evolution in microbes can and does occur independently of environmental change or predation pressure. In tens of thousands of generations of *Escherichia coli* cultured under

controlled laboratory conditions, growth rate and cell volume have increased steadily in every one of 12 replicate strains¹²⁸. There are both adaptive and non-adaptive explanations that may explain this size increase, which is linked to changes in other physical properties and gene expression patterns¹²⁹. A lesson to remember when considering the history of microbial life is that environmental change is sufficient but not necessary for traits to evolve that have repercussions for higher trophic levels.

Population abundance

Abundance of phytoplankton ties intimately to that of zooplankton and higher-order consumers (stepping-stone #7 and #10). Understanding the bottom-up influence of nutrients vs. top-down influence of zooplankton on phytoplankton biomass is of immense interest to biological oceanography in the Recent, because marine primary producers are a major carbon reservoir in the biosphere with an uncertain future trajectory^{9,108,130}. Since consumers represent a minor fraction of marine carbon, ocean and climate scientists sometimes lump together predator consumption, viral lysis, and other forms of phytoplankton losses under a single parameter⁹. However, to evaluate phytoplankton biomass increases as a candidate cause of ecological change in zooplankton and nekton throughout geological time, paleoecologists need estimates on the specific amount of phytoplankton consumed by higher trophic levels. Mesocosm and ocean fertilization experiments can address this question.

Experiments on living organisms demonstrate that zooplankton fed nutrient-rich phytoplankton become dense in nutrients themselves and pass these nutrients up to nekton (stepping-stone #8); conversely, in some cases nekton can become limited by the same nutrient as are phytoplankton^{124,131}. Animals have a partial ability to buffer this effect (“relaxed homeostasis”), particularly to raise their nutrient consumption when fed low-nutrient diets. For

instance, *Daphnia* forage with greater fervor when fed phosphorus-poor diets to burn off carbon while increasing phosphorus intake¹³². However, there may be fewer physiological mechanisms to mitigate diets with above-average nutrient density: phosphorus far in excess of levels to which consumers are adapted decreases growth and survival rates^{133,134}. Study of elemental stoichiometry as a control on growth rate and body condition, and thence generation time and fecundity, has grown into its own subfield, with applications from human aquaculture to paleoecology^{122,124,131,135}.

An experimental example of nutrient addition to marine food webs was an artificial phosphorus pulse made in an ultraoligotrophic patch of the Mediterranean¹¹⁰. This study stands out because it is one of few ocean fertilization experiments that monitored zooplankton population responses^{109,111}. As expected from bottom-up theories, copepods used the extra dietary phosphorus to produce substantially more eggs¹¹⁰. However, the route by which phosphorus reached zooplankton was unexpected. Rather than stimulating primary production, the phosphorus fertilization caused a decline in chlorophyll concentration and rise in bacterial production. The added phosphorus might have bypassed phytoplankton and instead travelled primarily through heterotrophic bacteria, to flagellates, to ciliates, to copepods (the microbial loop, Fig. 1). In addition or instead, both heterotrophic bacteria and phytoplankton could have stored the surplus phosphorus, increasing the quality rather than quantity of primary producer cells. This experiment holds several lessons for historians of life. First, the study demonstrates that the uses to which cells put nutrients are not always so straightforward as linear conversion of elements to biomass. Second, the results give greater importance to the quality than quantity of primary production, which might favor bottom-up hypotheses of phytoplankton evolution discussed in the previous section.

Nutrient addition experiments in a freshwater system led to similar conclusions of food quality determining ecosystem trajectories in deep time¹²². Researchers measured growth rate and survival of snail grazers along a gradient of phosphorus supplementation in a stromatolitic system, one of the closest modern analogues to Cambrian shallow ecosystems^{122,134}. Snails appeared limited by low nutrient density but not by mass of primary production. This result was interpreted as support for the hypothesis that a phosphorus flux might have enabled Cambrian metazoan diversification^{26,58}.

Short-term experiments can reveal complex pathways of energy flow, but the local community responses on the scale of weeks do not necessarily translate to species-level effects on the scale of millennia or longer. Authors of nutrient addition experiments themselves have been quick to point out the dangers of spatiotemporal extrapolation^{110,122}. In the Mediterranean, for instance, the results documented might be specific to seasonal conditions of aeolian nutrient pulses, which cause phosphorus to be limiting for bacteria¹¹⁰. There is a clear need for nutrient addition experiments on intergenerational scales, to approximate steady-state population responses rather than individual plasticity in reaction to transient perturbations. In one such longer-term study, researchers transplanted guppy populations between predation-controlled and food-limited habitats¹³⁶; they found lags in population evolution that would have been overlooked by a shorter study but were consistent with theory for life-history trait evolution.

Even if more laboratory and fertilizer experiments scale up in time, they will still be limited in space. There is a gap between the small spatial scale of manipulation and the larger scale at which both bottom-up and top-down effects can manifest in ecosystems². Limnologists have long been aware that a phytoplankton species' response to predation in a mesocosm may be opposite to that in a whole lake, for instance¹³⁷. Nevertheless, it is possible to generate results in

mesocosms that concur with those found in the broader ecosystems they replicate, in both terrestrial and marine settings. The vital qualities for experimentation are (1) identification of fundamental mechanisms (e.g., herbivore behavior response to predators), which can be scale-independent; (2) careful design of enclosures (e.g., ensure relative dimensions do not curtail fish growth); and (3) measurement in both field sites and mesocosms to corroborate results^{8,13,22}. In fossil studies it is also important to recognize the role of both temporal variability and spatial variability—a shift from evaluating “diversity through time” towards “diversity through time and space” as advocated by Benson and others in this special issue¹³⁸.

Consumer speciation

There are both direct and indirect ways elevated productivity could increase speciation rate at higher trophic tiers. Directly, when a population increases in abundance it might expand geographically, become isolated across dispersal barriers, and undergo allopatric speciation (stepping-stone #10). Indirectly, an increase in the biomass within a trophic level could make it viable for new consumer species to specialize on resource types from that level (stepping-stone #6). At the core of both ideas is the question: how do ecological changes at the individual and population level translate into evolutionary changes within and between lineages?

Consumer abundance responds to primary production quality and quantity, as discussed in the previous section. In turn, abundance is strongly correlated with geographic range size, and so range expansion is a plausible outcome of population growth—although exceptions may occur if a species is limited by habitat availability or if niche breadth is ultimately the common cause of both abundance and geographic range size^{139,140}. Since the number of peripheral populations and the chance of intersecting a geographic dispersal barrier both increase with range size, some biologists postulate a positive relationship between distribution area and speciation

probability^{141,142}. However, traits that promote broad distributions (e.g., fast dispersal rates) could also make it harder for populations to become isolated; therefore, the distribution–speciation relationship could be negative^{143,144}. Empirical work in marine animals supports a negative distribution–speciation relationship¹⁴⁵ yet finds weak concurrence between dispersal rate and range size¹⁴⁶. Accommodating these conflicting ideas and data, some authors propose a unimodal relationship between geographic range size and probability of successful speciation: species of intermediate distribution may split the most^{19,147}. In summary, population growth could cause geographic expansion, but a larger range area might either increase or decrease speciation rate, perhaps depending on the absolute range area.

The abundance–distribution–speciation relationship (the “speciation cycle”) has been put forward as a major mechanism linking primary production to diversifications across the history of life, including the revolutions described above¹⁹. The merit of this idea is its explicit elaboration of every causal step, which may allow robust empirical tests in future. A challenge to the importance of the speciation cycle is the difference in timescale between its cause and effect. Phytoplankton and zooplankton abundances respond to environmental change on the scale of weeks to months, and all plankton, including planktonic larvae of benthic organisms, can ride currents across the planet on the scale of years. In contrast, the timescale of evolutionary radiations has been clocked at millions of years or more; for instance, the successive diversifications of planktonic, benthic, and reefal species in the GOBE spanned 40 million years³⁶. Although abundance-driven speciation may be a weaker explanation of this prolonged change than previously thought, an increase in primary production could still have facilitated past diversifications via opening ecospace.

Paleobiologists have identified a notable increase in marine ecospace occupation throughout the half a billion years since animals evolved, e.g., burrowing deeper into the sediment and swimming higher into the water column^{41,105}. One explanation for this pattern is that an increase in the number or size of prey at a trophic level made it possible for specialized predators to evolve at the trophic level above. The “more specialization” hypothesis posits generally that specialists evolve whenever a category of food resource attains sufficient energetic density to sustain them¹⁴⁸⁻¹⁵⁰. Resource expansion thereby can support the existence of a new species in communities, but the actual process of speciation could be due to any number of selective pressures or chance events, e.g., sexual selection, character displacement, or the emergence of a geographic barrier.

Adaptive radiation and niche construction are two areas of theory that seek to explain why species diversify into areas of niche space. Each idea helps structure thinking about causal processes behind speciation but is difficult to demonstrate empirically. Evolutionary biologists invoke adaptive radiations frequently to explain rapid tree-branching, yet definitively eliminating alternative explanations for historical branching events can prove difficult or even insurmountable^{151,152}. The strength of adaptive radiation literature lies in linking macroevolutionary patterns to evolutionary developmental biology. In recent formulations, ecological opportunity is rarely the first step in adaptive radiations but instead the last, lagging behind the initial steps of (1) potentiating or permissive mutations, (2) actualization or appearance of a novel trait, and (3) adaptive refinement of that trait¹⁵¹⁻¹⁵³. In contrast to adaptive radiation, niche construction theory links population genetics to ecosystem changes as simultaneous processes, arguably as important as natural selection¹⁵⁴⁻¹⁵⁶.

The salient feature of niche construction theory is that when organisms change their environment, they also change the evolutionary landscape of selective pressures on their own species and others. Niche construction theory applies equally well when ecosystem change occurs in food chains as in the abiotic environment¹⁵⁴ and has also been applied in archeology to describe human modification of the natural environment, e.g., the origins of agriculture¹⁵⁷. Niche construction is effectively synonymous with ecosystem engineering but is used in contexts that emphasize the evolutionary ramifications of ecosystem change. Detractors argue that although niche construction undoubtedly occurs, it fails to generate either specific, testable predictions or explanatory power beyond what classical theory can provide¹⁵⁵⁻¹⁵⁷.

Labels of adaptive radiation and niche construction have been applied to many radiations including those of the ECR and GOBE. However, critics say ascribing the enormity of morphological changes in so many Cambrian taxa to adaptive radiation “stretches the bounds of that term beyond recognition”^{151, p. 5}. In contrast, Neoproterozoic oxygenation can be considered ecosystem engineering that could easily influence evolutionary pressures across marine clades^{35,158}. Discussions of niche construction for the GOBE tend to be more implicit than for the ECR, but commentary is often couched in this interpretatione.g., ⁷⁴. Before evolutionary biologists can test any hypothesis for a given radiation, the assumptions and causal steps involved must be elaborated—explanations should be explicit. Ultimately, the relative contributions of adaptive radiation, niche construction, species selection, sexual selection, and other evolutionary processes may vary with every clade and historical context.

Body mass and metabolism

Alongside intervals of diversification, paleontologists have suggested body mass and metabolic rate have risen through time^{16,19,105}. These latter traits are grouped under the category

of energetics for their tight correlation. Paleontologists infer changes in ecosystem energetics in deep time by measuring fossil body size, which can be substituted into metabolic rate scaling equations calibrated on modern descendants. This approach has demonstrated that after many animal clades suddenly appeared in the earliest Cambrian deposits, their body mass seems to have remained equivalent through the period⁷², at least in minimum and maximum size¹⁵⁹. During the GOBE, however, there were increases in body size, abundance, and species count in brachiopods—a major component of the benthic fauna^{71,72,160-162}. Trilobite species that originated or survived into the end of the period tended to be larger than their predecessors and may have occupied a higher trophic level⁷¹. Brachiopods, trilobites, and crinoids continued to grow in body mass until at least the Early Devonian^{72,160,162}. Across the Mesozoic, gastropod metabolic rates are estimated to have increased by 150%¹⁶³. Gastropods have been a prominent taxon in discussions of the MMR because of their vulnerability to crushing predators and their evolution of shell defenses during this era³⁸. Drilling gastropods in particular have grown in size consistently from the Ordovician to the Recent¹⁶⁴.

Although many clades studied for their size evolution over the Phanerozoic are primarily filter-feeders and detritivores, predators such as many fish and marine mammals have also increased in mean body size through time¹⁵⁹. Many large chordates are active predators, and their size is again theorized to be affected by phytoplankton production, because hunting incurs a high metabolic cost. The proportion of carnivorous taxa decreases in progressively lower-oxygen habitats today, and therefore ubiquitous anoxia or suboxia may have precluded active hunters prior to the Neoproterozoic Oxidation Event³⁹. Primary producers are strongly responsible for regulating O₂ and CO₂ concentrations in the atmosphere on geologic timescales (stepping-stone #11), and so aerobic facilitation of apex predators could be considered another kind of bottom-up

control. In addition to the ECR, the middle Paleozoic has been suggested as another interval where oxygenation facilitated evolution of the huge, metabolically-active animals of the time^{94,159}, although oxygen limitation after the Cambrian is more contentious.

Increased primary production has been proposed as a direct cause of energetic escalations across taxa in the Paleozoic and Mesozoic regardless of oxygen levels^{16,18,72,163}. The biological mechanisms underlying this link remain elusive, however. Why would greater resources lead consistently to larger body mass instead of to faster growth rate and earlier reproduction, for instance? Of course, it is possible for all these outcomes to co-occur: in living bivalves, faster growth leads to both faster maturation and larger adult size across a latitudinal gradient of temperature and food availability¹⁶⁵. Either faster maturation or greater fecundity associated with larger adult size would then increase population abundance as well (stepping-stone #7 and #10), with further ecosystem consequences as discussed in previous sections.

Energetic effects of phosphorus, oxygen, and primary production volume should be considered in concert because they might have increased in lockstep. Low primary production may be essential to maintaining low atmospheric oxygen concentration, e.g., during low-phosphate spans of the Proterozoic^{166,167}. In modern marine ecosystems, independent limitation of oxygen and food are both associated with small body size and non-carnivorous feeding modes, and therefore it may not yet be possible to differentiate the relative importance of tightly correlated oxygen and primary production amounts for consumer body size and metabolic rate increases across life history⁴⁸.

The evolution of growth rate, body size, fecundity, and other life history traits involves many trade-offs, including the balance of competing for resources vs. surviving predation¹³⁶. The history of body size evolution is particularly troublesome to disentangle because size has so

many correlates and causes, both biotic and abiotic¹⁶⁸. Nevertheless, evidence suggests the orders-of-magnitude increase in Phanerozoic animal size reflects change in community composition rather than parallel evolution to larger size within many lineages^{159,161}. In other words, radiation seems to occur preferentially in clades with larger ancestors. To understand this macroevolutionary pattern will require testing frameworks such as adaptive radiation and niche construction theory (summarized in the previous section).

Other mechanisms of change

Many types of biological processes operate in parallel and interactively to generate ecological and evolutionary diversity. The focus of this article is clarification of occurrences of bottom-up control across the history of life and their potential mechanisms, but bottom-up processes alone cannot explain fully the variety and richness of ecosystem history. Top-down controls, sexual selection, global-scale ecosystem engineering, Earth surface processes, extraterrestrial impacts, and other mechanisms should be considered as well when interpreting past ecological change.

In modern ecosystems top-down and bottom-up controls are known to interact with each other strongly and synergistically¹⁶⁹, although some communities are exceptions²⁵. For instance, to predict phytoplankton blooms over months, unraveling the balance of top-down vs. bottom-up control is cited as a key area for further research⁹. On geologic timescales over which species evolve, a compounding interaction between top-down and bottom-up control could take place: once bottom-up processes increase predator abundance, diversity, or energetics, arms races with prey species could ensue⁹⁹. In this way, bottom-up processes could stimulate top-down processes that then unfold concurrently.

In addition to interactions among ecological processes, reciprocal relationships occur between life and Earth systems. In sections above, we have noted repeated instances of volcanic, tectonic, and other geologic events leading to sustained ecological change^{77,78}. We have also discussed examples of biotic events affecting geologic processes, such as oxygenic photosynthesizers changing ocean chemistry and land plants accelerating weathering⁹². However, biological and Earth processes have mutually buffered and enabled each other in myriad ways since life arose; these couplings occur across scales of space, time, and biological organization^{155,158,170}. Perhaps nowhere are these interactions more apparent than in tracing the modern carbon cycle, which encompasses feedbacks between primary production, biomass, respiration, detritus, soil, atmospheric composition, global temperature, ice volume, calcium carbonate concentration, sediment burial, rock formation, weathering, wildfires, and now human emissions¹³⁰.

Conclusions and outlook

The history of animal life in the ocean has involved parallel increases in marine nutrients, primary production, abundance, diversity, niche space occupancy, and metabolic rate. Rather than a monotonic, lockstep increase, these changes have varied in pace through time and relative to each other. Notable intervals of concerted change were the ECR, GOBE, DNR, and MMR. These events share similarities but also differ in both putative causes and outcomes (Table 1). An increased rate of nutrient delivery from land is theorized for all four events, leading to increased primary production in oceans. However, the source, magnitude, and duration of primary production increase are specific to a given time interval.

Empirical knowledge of the ECR remains insufficient to state the extent to which radiation in animal diversity, trophic tiering, and water column occupancy were due to nutrient

addition, oxygenation, both, or neither. Multiple interpretations of available data are plausible. Many lines of study can contribute to disentangling Ediacaran–Cambrian events, including geochemical and geophysical research on Neoproterozoic glaciations, paleomagnetic reconstructions of continent position and configuration, and taxonomy and systematics of Ediacaran and Cambrian faunas. Physiological experiments on living organisms would complement these Earth science approaches, particularly with regard to the synergistic stresses of the metazoan fire triangle—low oxygen, restricted primary production and food supply, and warming climate⁴⁸.

The GOBE and DNR continued filling the water column and sediment depths after the Cambrian. The Ordovician was a time of especially rapid diversification of species and ecotypes^{40,41,69}. Infaunalization during the Paleozoic may have been key to recirculating more nutrients back into food webs^{20,81}, although a succession of volcanism, mountain building, land plant evolution, and glaciation also could have input nutrients to oceans^{14,33,76,77}. We have focused on increases in functional and taxonomic diversity, but it is also interesting to consider the end-Ordovician and late Devonian mass extinctions with respect to primary production. Phytoplankton booms might facilitate population growth and speciation at higher trophic levels, yet nutrient addition and carbon burial beyond a threshold could tip the oceans into a eutrophic state, drive subsurface anoxia, and cool the global climate into icehouse conditions^{33,87,92}. Hence, for the middle Paleozoic, nutrients and primary production might explain extinctions more than they do diversification.

Many lines of evidence place the MMR as a strong example of bottom-up ecological cascades, independent of strong top-down controls that probably occurred synchronously. Nutrient pulses related to continental fission, and possibly angiosperm evolution, are candidate

triggers of phytoplankton biomass increase¹⁹. The evolution and proliferation of chlorophyll *a* and *c* algae groups, such as dinoflagellates and diatoms, could have increased per-cell nutritional content^{26,102}. Based on results from ecological experiments, algal quality changes might exert stronger leverage on ecosystem complexity than do quantity changes, but as yet there is insufficient evidence to make this claim for the Mesozoic.

Strong theoretical and empirical links exist between nutrient concentrations and phytoplankton production. However, it becomes more difficult to predict the importance of bottom-up mechanisms at higher trophic levels. Nutrient addition experiments demonstrate the feasibility of cascades in biomass quantity and stoichiometry, from phytoplankton through to nekton¹²⁴, but there are many caveats to extrapolating the results of such studies in space and time. The data gap between micro scales (days to years, mesocosms to ocean patches) and macro scales (millennia to millions of years, ocean basins to biosphere) remains a black box for mechanisms of diversification, particularly in evolutionary diversifications interpreted as adaptive radiations or involving body size increases¹⁵¹. Future studies should work to close this gap from both sides. In living systems, insight into intermediate scales is attainable by extending the duration of nutrient addition experiments to multiple generations and all trophic levels, including secondary-or-higher predators like fish^{124,136}. Using the fossil record, studies can examine the record of basins with high sedimentation rates and anoxic seabeds, where it is possible to reconstruct historical pelagic ecology on decadal to centennial scales¹⁰.

Aquatic ecologists originally led the way in quantifying the relative importance of bottom-up and top-down controls, and terrestrial ecologists eventually adopted this view of co-regulation^{6,7}. In considering the whole of animal history, it is important to continue this holistic line of thinking. Unfortunately, it is no small feat to tease apart the relative contributions of

bottom-up and top-down controls to speciation events and abundance changes that took place up to hundreds of millions of years ago. Further complicating inferences, any specialization in predators that involved adaptations such as enhanced sensory perception and agility could have contributed to (and been amplified by) sexual selection processes¹⁷¹. One aid to cut through such generalizations is to articulate mechanistic hypotheses rather than treat bottom-up processes as a monolith. The more that scholars specify the pathways they invoke, for instance by referencing particular stepping-stones itemized here (Fig. 3), and embed discussions in the historical context of specific past environments (e.g., Table 1), the more fruitful ensuing hypothesis-testing and interpretation will be.

Mechanistic investigations of ecosystem history hold deep import for human understanding of how our world came to be. If future studies confirm that nutrient fluxes or phytoplankton stoichiometry changes incited more than one marine revolution, then ecological diversification may be more deterministic than previously thought⁶⁷. However, regardless of the strength of bottom-up controls, there remains scope to invoke other causal and stochastic Earth and life processes in shaping ecosystems through time.

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