

REVIEW SUMMARY

VERTEBRATE EVOLUTION

Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene

Neil P. Kelley^{1,2*} and Nicholas D. Pyenson^{1,3}

BACKGROUND: More than 30 different lineages of amphibians, reptiles, birds, and mammals have independently invaded oceans ecosystems. Prominent examples include ichthyosaurs and mosasaurs during the Mesozoic (252 to 66 million years ago) and penguins and sea otters during the Cenozoic (66 million years ago to the present). In today's oceans, marine tetrapods are ecologically important consumers with trophic influence disproportionate to their abundance. They have occupied apex roles in ocean food webs for more than 250 million years, through major changes in ocean and climate, and through mass ex-

tinctions. Major paleontological discoveries in the past 40 years have clarified the early land-sea transitions for some marine tetrapods (e.g., whales, sea cows), although the terrestrial origins of many lineages remain obscure. Incipient invasions appear frequently in marine tetrapod history, but such early transitions account for only a small proportion of the total fossil record of successful marine lineages, which in some cases persist for hundreds of millions of years.

ADVANCES: Marine tetrapods provide ideal models for testing macroevolutionary hypotheses because the repeated transitions between

land and sea have driven innovation, convergence, and diversification against a backdrop of changing marine ecosystems and mass extinctions. Recent investigations across a broad range of scales—from molecules to food webs—have clarified the phylogenetic scope, timing, and ecological consequences of these repeated innovations. Studies of the physiology and functional morphology of living species have illuminated the constraints and tradeoffs that

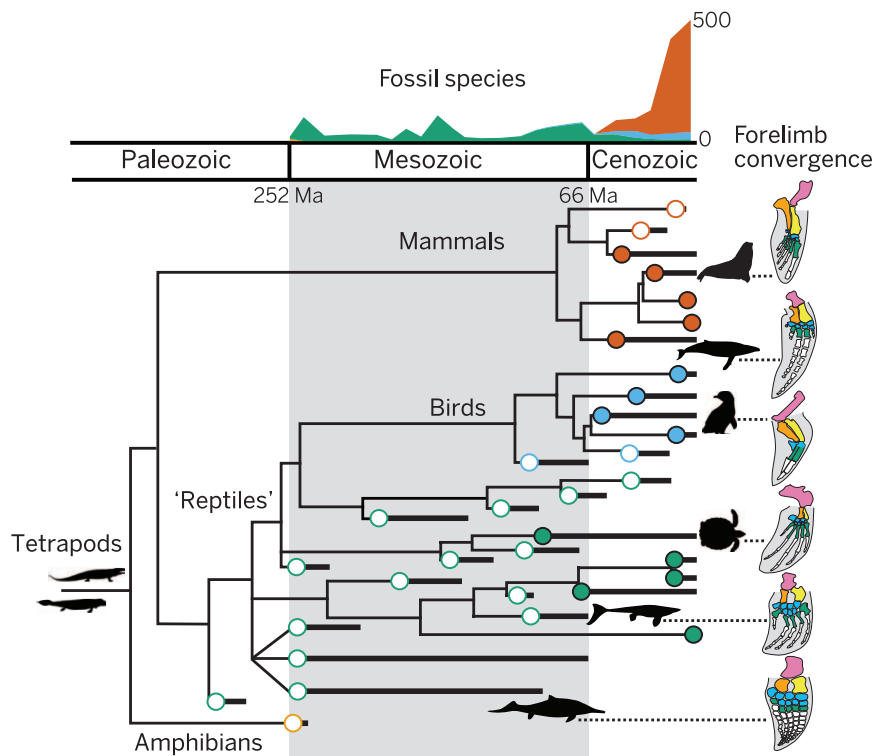
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shape the pathway of initial marine invasions. Comparative studies on muscle myoglobin concentration or the evolution of sex determination mechanisms, for example, have revealed

rampant convergence for these adaptive traits in the marine realm. Exceptionally preserved fossils have also revealed insights into reproductive biology, soft tissue structures, and trophic interactions. Fossils provide critical baselines for understanding historical changes in marine communities and diversity through time, and these baselines remain vital for evaluating the ongoing and severe anthropogenic disturbance to marine tetrapod populations and marine ecosystems as a whole.

OUTLOOK: Technological advances in remote sensing and biologging will continue to provide crucial insights into the macroecology of marine tetrapods below the water's edge. Field data, when combined with extensive vouchers represented in museum collections, provide the basis for integrative models of the function and ecology of these logistically challenging organisms. Placed in a phylogenetic comparative framework, these data can enable tests of hypotheses about macroevolutionary patterns. Although perpetually incomplete, new fossil discoveries continue to improve our understanding of the early land-sea transitions in lineages and reveal past ecologies that could not have otherwise been predicted. Emerging imaging, molecular, and isotopic techniques provide an opportunity to expand the investigational scope for studying extinct taxa and to inform our understanding of how living species evolved. Lastly, resolving the full evolutionary scope of marine tetrapod history provides context for the origins of modern ecological patterns and interactions, which are fundamentally being altered by human activities. ■



A unified view of marine tetrapod evolution. Circles mark initial invasions of marine tetrapod groups. Extinct and extant lineages are denoted by open and solid circles, respectively (yellow, amphibians; green, nonavian reptiles; blue, birds; red, mammals). Top curve summarizes marine tetrapod fossil richness through time. Schematic limb drawings demonstrate convergent hydrodynamic forelimbs in marine tetrapods (top to bottom): sea lion, whale, penguin, sea turtle, mosasaur, ichthyosaur. Ma, millions of years ago.

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Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene

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Many top consumers in today's oceans are marine tetrapods, a collection of lineages independently derived from terrestrial ancestors. The fossil record illuminates their transitions from land to sea, yet these initial invasions account for a small proportion of their evolutionary history. We review the history of marine invasions that drove major changes in anatomy, physiology, and ecology over more than 250 million years. Many innovations evolved convergently in multiple clades, whereas others are unique to individual lineages. The evolutionary arcs of these ecologically important clades are framed against the backdrop of mass extinctions and regime shifts in ocean ecosystems. Past and present human disruptions to marine tetrapods, with cascading impacts on marine ecosystems, underscore the need to link macroecology with evolutionary change.

More than 30 lineages of tetrapods (amphibians, reptiles, birds, and mammals) independently invaded marine ecosystems during the Phanerozoic (Fig. 1). Such repeated transitions from terrestrial or freshwater to marine habitats are generally uncommon in other clades (1). Reconfigurations in morphology, physiology, life history, and sensory systems characterize each transition. For example, differential constraints on movement between these realms—gravity on land versus drag in water—led to similar locomotory adaptations in marine tetrapods (2) (Fig. 2).

Sequences of fossil cetaceans (3) and sirenians (4) from Eocene rocks provide the best examples of major morphological transformations following marine invasions. Both groups show pelvic decoupling from the vertebral column and subsequent reduction of the pelvis and hindlimbs; later specializations included forelimb streamlining, tail propulsion, and posterior migration of the nostrils. Unfortunately, the early histories of most other marine tetrapod lineages remain obscure. For example, the freshwater carnivoran *Puijila darwini* provides clues about the origins of pinnipeds (5), but it is geologically younger than other marine stem pinnipeds (6) and is thus not likely a direct ancestor of modern pinnipeds. Likewise, semi-aquatic Permian reptiles, initially proposed to represent plesiosaur ancestors (7), are not closely related to plesiosaurs in recent analyses (8); the Early Cretaceous turtle *Santanachelys* (9) was once viewed as a stem predecessor to mod-

ern sea turtles, but this position is no longer supported (10). Thus, origins of several important marine tetrapod groups remain essentially unknown, with the oldest known fossil representatives exhibiting derived morphologies without obvious terrestrial antecedents. Prominent examples include penguins (11) and ichthyosaurs (12), although the recently described basal ichthyosauriform *Cartorhynchus* may clarify the origins of the latter (13).

The history of terrestrial-marine transitions reveals links between Earth system changes and marine tetrapod invasions, modulated by ecology and physiology. Marine transgressions and warming episodes coincided with Mesozoic and Early Cenozoic marine tetrapod invasions (3, 4, 14–18). Modern marginal marine tetrapods are concentrated in low-latitude mangroves, estuaries, and archipelagos (19). The paleoenvironmental context of marginal marine tetrapod fossils (7, 20) likewise indicates that warm, shallow marginal marine habitats provide favorable settings for terrestrial-marine transitions, especially in ectotherms. Conversely, mid-Cenozoic cooling and increases in marine productivity—particularly in the North Pacific and Southern Ocean—coincided with bird and mammal invasions (21, 22), and these regions remain hotspots of marine mammal diversity (23). However, such relationships are not always rigid throughout the history of a clade: Cetaceans evolved in shallow equatorial seas (18) but now thrive in high-latitude oceans; the origin of penguins preceded Southern Hemisphere cooling by several million years (24).

Studies of living marginal marine species illuminate ecological (25, 26), functional (2, 27–29), and physiological (30–32) pathways that facilitate transitions. A common theme is the high degree of plasticity in ecologically marginal taxa (26, 28, 31). Isotopic investigations of fossils suggest similar

patterns, demonstrating mixed habitat and resource use (33). Repeated independent invasions among some clades suggest that certain ecologies and/or body plans may predispose groups to marine transitions. Independent adaptation to marine lifestyles among close relatives simultaneously or in close succession would complicate efforts to decipher and enumerate transitions in the fossil record (34, 35).

Convergent evolution from molecules to morphology

Marine tetrapods provide canonical illustrations of evolutionary convergence (Fig. 2) (36), widely regarded as repeated solutions to problems imposed by physical contrasts between land and water. Simple visual comparisons, however, cannot fully decipher the processes that shape evolutionary convergence. Apparent similarities can mask differences in functional performance (37), and mechanical convergence can be achieved with alternative morphological solutions, often constrained by phylogeny (38). Thus, the dorsoventral caudal propulsion of cetaceans derives from the bounding locomotory mode of terrestrial mammalian ancestors (2), while the lateral caudal propulsion of ichthyosaurs evolved from the locomotion of lizard-like predecessors (39).

Quantitative functional morphology provides a means to quantify and compare performance and functional trade-offs, particularly in species that spend time both on land and in the water, such as snakes (29) and pinnipeds (40). Functional trade-offs can ultimately drive specialization and steer evolutionary convergence, as with repeated loss of flight among seabirds specialized for aquatic locomotion (41). In vivo studies of feeding performance provide similar insight into functional trade-offs and specialization (42–44), which shaped convergence in marine tetrapod feeding systems (45).

Increased bone density evolved repeatedly in coastal marine tetrapods for stability and buoyancy regulation (46–51). Conversely, decreased bone density has evolved among many pelagic groups, reducing the costs of sustained swimming, or as a consequence of increased growth rates (50). Some lineages, such as cetaceans (48, 49), ichthyosaurs (13, 49), and sauropterygians (51), transitioned through these contrasting phases sequentially, with increased bone density during early evolution followed by reduced bone density after open marine adaptation. The evolution of insulating structures in marine mammals follows a similar progression, with thick fur in coastal invaders replaced by thick insulating fat for energy storage and streamlining in more oceanic marine mammals (52). Fossil anatomy reveals the evolution of countercurrent heat exchange in penguins (53), convergent with similar systems in marine mammals.

The scope of recent studies of convergent evolution extends beyond morphology to include molecular physiology (54), metabolism and thermoregulation (55, 56), and life history (56, 57). Genomic investigations have revealed convergent genetic origins of important innovations, such as

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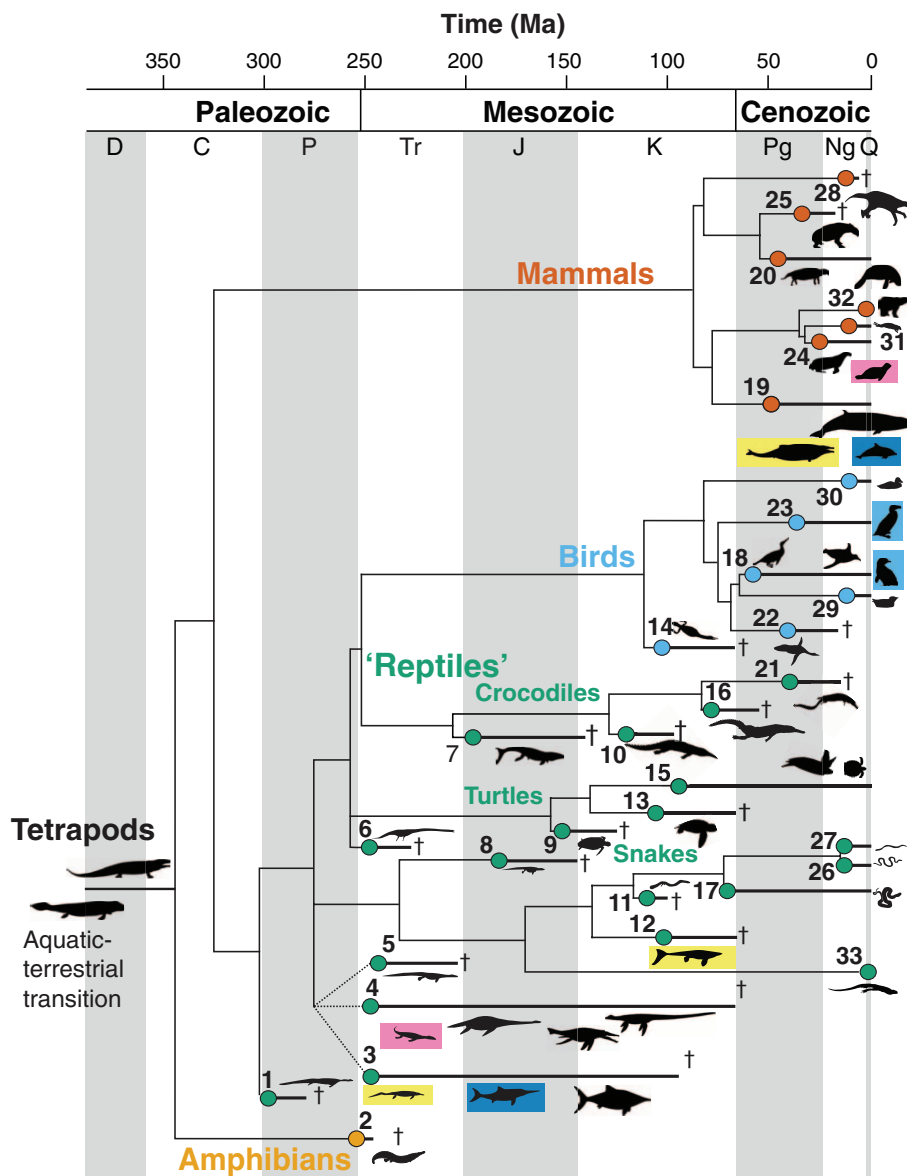


Fig. 1. Temporal and phylogenetic distribution of marine tetrapod groups. Circles indicate first appearance datum (FAD) for each lineage based on fossils, or divergence estimates for groups lacking a fossil record (136); daggers denote extinctions. Marine tetrapod taxa are numbered in order of appearance in the fossil record: (1) Mesosauria, (2) Trematosauria, (3) Ichthyosauromorpha, (4) Sauropterygia, (5) Thalattosauriformes, (6) Tanystropheidae, (7) Thalattosuchia, (8) Pleurosauridae, (9) Plesiochelyidae, (10) Pholidosauridae, (11) Simiolophiidae, (12) Mosasuroidea, (13) Protostegidae, (14) Hesperornithiformes, (15) Chelonioidea, (16) Dyrosauridae, (17) Acrochordoidea, (18) Sphenisciformes, (19) Cetacea, (20) Sirenia, (21) Gryposuchinae, (22) Pliopteridae, (23) Alcidae, (24) Pinnipedimorpha, (25) Desmostylia, (26) Laticaudini, (27) Hydrophiini, (28) *Thalassocnus*, (29) *Pelecanoides*, (30) *Tachyeres*, (31) *Enhydra*, (32) *Ursus maritimus*, (33) *Amblyrhynchus*. Colored boxes match convergent taxa shown in Fig. 2. A to D, Ma, millions of years ago. (Silhouettes from phylopic.org; see supplementary materials for usage and attribution details.)

sex determination mechanisms (58), myoglobin adaptations facilitating deep diving (54), and echolocation (59). Stable isotopes from fossils elucidate parallel histories of habitat shift in early cetaceans and sirenians (33) and convergent evolution of endothermy in Mesozoic marine reptiles (53). Recent breakthroughs in fossil pigment reconstruction have resolved structural and pigment adaptations in fossil seabird feathers (60) and have revealed widespread dark coloration in

fossil marine reptiles, possibly for temperature regulation or ultraviolet light protection (55).

Exceptionally preserved fossils (57, 61, 62) document convergent reproductive adaptations in marine reptiles. Recently discovered early ichthyosaur fossils (62) extend the history of viviparity in this group back to the Early Triassic and indicate that viviparity evolved in terrestrial fore-runners as an enabling factor for, rather than an adaptive response to, aquatic life. Fossils sug-

gest that some marine reptiles converged upon K-selected life histories observed among marine mammals (57). Aquatic birth evolved early in cetacean and sirenian evolution, but these transitions are so far only partly constrained by fossils (63).

Causes and consequences of convergence, innovation, and radiation

In addition to external drivers, convergent evolution is shaped by the underlying genetic and developmental pathways that give rise to convergent structures. Thus, repeated evolution of hydrodynamic limbs (Fig. 2E) (64) and axial modifications (65) likely exploited parallel developmental mechanisms. Such shared pathways may extend to the level of gene regulation linking genomic and phenotypic convergence and innovation. Recent work on marine mammal genomic convergence has questioned the prevalence of such linkages (66); however, more work is needed to evaluate potential scaling of convergence from gene to phenotype.

Innovations facilitate and constrain downstream evolution, as illustrated in the discrete pathways from drag-based to lift-based swimming in limb- and tail-propelled aquatic mammals (2). Likewise, independent innovation of aquatic birth in multiple marine reptile and marine mammal lineages removed the constraints of terrestrial locomotion, enabling limb and skeletal modification to increase swimming performance, as well as gigantism in some clades. Convergent evolutionary pathways [e.g., the emergence of tail-driven locomotion in ichthyosaurs, mosasaurs, and whales (Fig. 2A)] might follow similar tempos across groups (67), but this hypothesis awaits further testing.

Particularly diverse clades have frequently been characterized as adaptive radiations facilitated by new ecological opportunities after marine invasions (68). However, external factors may be equally important in shaping and pacing these radiations (69). Although diverse clades are often ecologically and morphologically disparate, as predicted under adaptive radiation models (70), diversity and disparity are not tightly coupled in other radiations (71).

Diversification can be triggered by innovations that occur well after initial invasions. For example, echolocation and baleen—two key innovations that evolved tens of millions of years after whales first entered the oceans—mark the emergence of crown cetaceans (72), the most species-rich marine tetrapod clade. Hydrophiine sea snakes, which entered marine environments in the last 6 million years and now comprise at least 60 species (71, 73), provide a key example of a marine tetrapod group in the midst of major radiation. Even within this group, diversity is heterogeneously distributed within subclades and linked to specific intraclade innovations, rather than simply reflecting rapid niche expansion after initial marine invasion (71).

Iterative evolution and ecological turnover

Marine tetrapods first diversified during the restructuring of marine ecosystems that followed

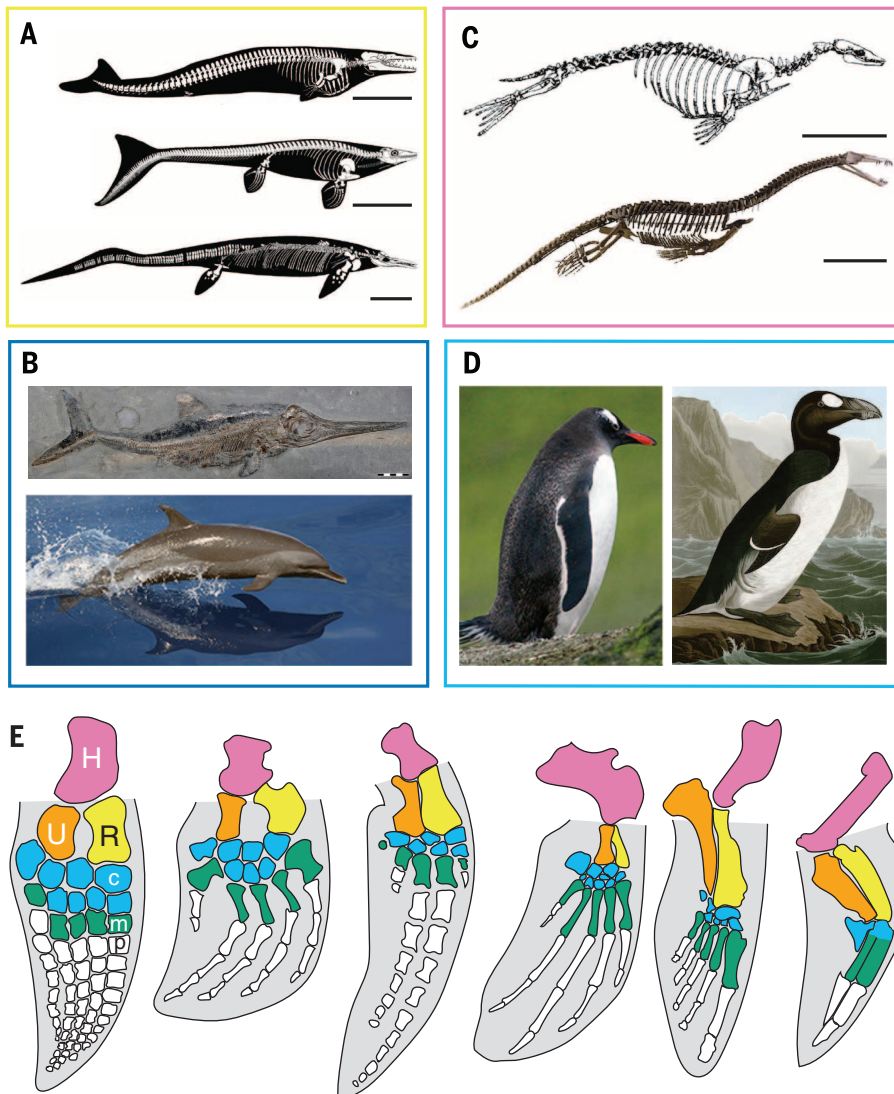


Fig. 2. Convergent morphology in marine tetrapods. Similar anatomy evolved among lineages that independently adopted marine lifestyles. From top to bottom: (A) early whale *Dorudon*, mosasaur *Platecarpus*, ichthyosaur *Cymbospondylus* (scale bars, 1 m); (B) ichthyosaur *Stenopterygius*, dolphin *Stenella*; (C) early seal *Acrophoca*, sauropterygian *Nothosaurus* (scale bars, 50 cm); (D) penguin *Pygoscelis* (left), great auk *Pinguinus* (right). (E) Forelimbs of select marine tetrapods (from left to right: ichthyosaur, mosasaur, whale, sea turtle, sea lion, penguin) showing anatomical convergence reflecting limb streamlining [adapted from (36, 64)]. Colors identify homologous elements labeled on ichthyosaur: H, humerus (pink); R, radius (yellow); U, ulna (orange); c, carpals (blue); m, metacarpals (green); p, phalanges (white). Phylogeny and contrasting locomotory patterns account for finer scale differences, such as proportionally longer humeri in forelimb-driven swimmers (sea turtle, sea lion, penguin) relative to tail-driven swimmers (ichthyosaur, mosasaur, whale). See supplementary materials for image sources.

the end-Permian mass extinction, and the rise of the so-called “Modern Fauna” (74). Their appearance has been characterized as a final step in the bottom-up reassembly of marine ecosystems after a delayed recovery (75, 76). However, the early appearance of predatory marine tetrapods in the Triassic has recently been cited as evidence that recovery was not delayed after all (77). Although later Mesozoic and Cenozoic invasions replaced these early groups, marine tetrapods have remained a persistent fixture of marine ecosystems since the Triassic. Some replacements coincided with mass extinctions (Fig. 1) (78);

others were staggered across intervals of gradual faunal change (78, 79).

Persistent biological processes such as competition (“Red Queen”) and stochastic environmental factors (“Court Jester”) (80) may regulate marine tetrapod community structure and diversity at different time scales (81). Pelagic habitats are typically dominated by one or two cosmopolitan marine tetrapod clades with long histories [e.g., ichthyosaurs from the Triassic to Cretaceous (78), plesiosaurs from the Jurassic to the Cretaceous-Paleogene (K-Pg) boundary (78), cetaceans since the Eocene (3)]. Near-shore communities often

host more lineages with higher endemism and frequent turnover (16, 82–84). Specific spatial and temporal successions hint at competitive interactions, as among flightless seabirds and marine mammals competing for shore space (22), replacement of herbivorous desmostylians by sirenians in the North Pacific (82), and replacement of phocids by otariids in South America (83).

These episodes of replacement between lineages are mirrored by iterative patterns within lineages. For example, evolution of herbivory and durophagy (feeding on hard-shelled prey) drove repeated convergent feeding morphologies in living and fossil sea turtles (85). Similarly, independent invasions of freshwater ecosystems by different odontocete lineages gave rise to a convergent “river dolphin” morphotype (86). Ecological interactions among sympatric relatives also drive iterative evolution. Multispecies fossil sirenian assemblages show parallel patterns of ecomorphological partitioning (82), contrasting with the relictual and disjunct distribution of living species. Sympatric or parapatric ecomorphs observed in widely distributed odontocetes (87, 88) have arisen through niche differentiation and onshore-offshore partitioning. Cryptic speciation and iteration is common among sea snakes, with repeated parallel evolution of morphotypes (7). Iterative evolution and resource partitioning may account for contrasting morphotypes in co-occurring fossil taxa (82, 89) and repeated evolution of certain morphotypes, such as polyphyletic “pliosaurs” (90).

Marine tetrapods themselves constituted an important trophic resource for other species in Mesozoic ecosystems beginning in the Triassic (76). Intriguingly, although hypercarnivory evolved repeatedly among Cenozoic marine mammals (91, 92), many lineages later specialized on resources at lower trophic levels. Hypercarnivorous species that regularly consume other tetrapods are comparatively rare in modern oceans, represented only by killer whales, leopard seals, and marginal marine crocodiles, all generalist predators that also feed regularly at lower trophic levels (42, 88). The comparative rarity of hypercarnivorous marine tetrapods in modern oceans may reflect different structuring of Mesozoic, Early Cenozoic, and modern marine food webs.

Contrasting Mesozoic and Cenozoic patterns of fossil richness

Patterns in raw marine tetrapod fossil species richness (Fig. 3) resemble those observed in the marine invertebrate record (93–95). Fluctuating Mesozoic diversity reflects repeated extinctions of incumbent clades (Fig. 1) followed by diversification of new groups (78) as well as geologic biases on the marine tetrapod fossil record (14). Contrasting patterns between coastal and pelagic Mesozoic marine tetrapod groups (14, 15) point to “common-cause” dynamics, whereby geologic processes that affect marine diversity also control sedimentary rock accumulation (95). The pronounced drop in richness at the K-Pg boundary corresponds to the simultaneous extinction of mosasaurs, plesiosaurs, and other lineages (Figs. 1 and 3).

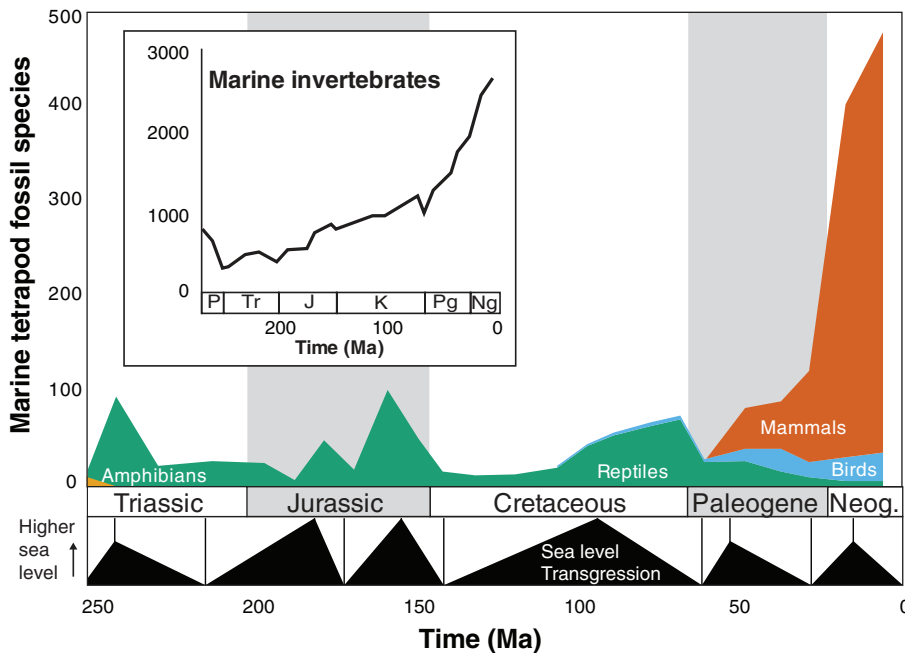


Fig. 3. Marine tetrapod fossil richness. Raw marine tetrapod fossil occurrence binned at intervals of ~10 million years [from (81)] and marine invertebrate genera [from (94)]. Both groups show episodic variation in fossil richness during the Mesozoic ending with abrupt drop at the K-Pg mass extinction, followed by continually increasing richness during the Cenozoic. Partial correspondence with marine transgression/regression [second order, cycles of ~10 to 100 million years, from (134)] suggests influence of sea level on shallow marine diversity and/or rock record bias, particularly in the Mesozoic.

After the K-Pg mass extinction, Early Cenozoic diversification of cetaceans (3), sirenians (96), and penguins (24, 97) brought Paleogene marine tetrapod richness back to peak Mesozoic levels. The emergence of crown cetaceans (72) and the invasion of pinnipeds (21), along with other groups, coincide with a marked increase in fossil richness to even higher levels. The apparent Cenozoic marine tetrapod diversity increase, like marine invertebrate richness (94), may be inflated by preservation biases (e.g., “pull of the recent”). However, recent investigations of fossil invertebrates (93) and marine mammals (98, 99) propose that increasing Cenozoic richness largely reflects a real biological signal. Fossil bias has been evaluated for some marine tetrapod groups (14, 98), but integrated comparisons of biases across the Mesozoic and Cenozoic are still needed.

Changes in ocean productivity regimes (100) and ecological escalation (101) may help to explain the differing trajectories of Cenozoic and Mesozoic marine tetrapod diversification. Exceptional diversification rates of eutherian mammals (102) might also account for increasing Cenozoic diversity, given the repeated marine invasions of placental mammals during the Cenozoic. However, other groups with elevated diversification rates, including Neoaves and squamates, also invaded marine ecosystems with varying degrees of success, indicating that phylogenetic differences alone cannot account for these differences.

Increasing marine tetrapod diversity since the Mesozoic also tracks increasing marine resources and expanding niches. Clear evidence of herbivory is unknown among marine reptiles until herbiv-

orous sea turtles evolved, coincident with the first seagrasses in the Cretaceous (85), which is consistent with “delayed herbivory” in other marine clades (103). Likewise, there is no evidence for pelagic suspension-feeding marine tetrapods in the Mesozoic (104) and little evidence for deep-diving mesopelagic feeders until the Jurassic (37). These absent ecologies suggest that Early Mesozoic marine food webs were less complex than modern equivalents.

Shifted baselines and marine tetrapod macroecology since the Pleistocene

Marine tetrapod and hominid ecological interactions began at least by the Late Pleistocene, with evidence for Neandertal (*Homo neanderthalensis*) exploitation of marine mammals in Gibraltar, Spain (105). Humans have continued to directly and indirectly interact with marine ecosystems ever since this time (106). Although these impacts have lagged behind profound human perturbations to terrestrial ecosystems, technological innovation has escalated their rate and magnitude in recent centuries (107).

The extinction of Steller’s sea cow (*Hydrodamalis gigas*) marks the first well-documented marine mammal species extinction in historic times (108). Hunting brought some cetacean species perilously close to extinction (109) and exterminated at least two pinniped species (110, 111). Historically, several marine mammal species were thought extinct until refugial populations were rediscovered (112, 113). Seabirds have been similarly vulnerable to human hunting, with historic and prehistoric extinctions of large flightless

seabirds (114–116) and others critically endangered (117). Many living marine reptiles also risk extinction—including six of seven sea turtle species—largely because of human exploitation and habitat alteration (117). The conservation status of many marine tetrapod species is poorly known because of the difficulties of studying wild marine populations.

The only cetacean extinction at human hands, the Yangtze River dolphin (*Lipotes*), was largely caused by habitat degradation (118). Before the end of this decade, another cetacean, the vaquita (*Phocoena sinus*), may be driven extinct through by-catch in small-scale fisheries in the Gulf of California (119). Such indirect impacts are a growing concern, with recent attention turning to ship collisions (120), shipping noise (121), military sonar (122), microplastics (123), and human-borne pathogens (124), among other emerging threats (107).

Anthropogenic climate change is already driving changes in marine tetrapod populations, particularly in polar ecosystems (125). Shrinking sea ice and changing ocean thermal gradients are also driving range shifts, most strikingly documented by repeated recent dispersal from the Pacific into the Atlantic by gray whales (*Eschrichtius*) via an ice-free northwest passage (126), potentially anticipating a recolonization of the Atlantic following extirpation four centuries ago (127). Global warming may have major impacts on ectothermic marine reptiles, potentially altering range limits, activity levels (128), and even the sex ratio in species with temperature-dependent reproduction (129). Potential feedbacks between anthropogenic warming and complex climate dynamics such as El Niño—known to trigger marine tetrapod population collapses (130)—suggest that impacts of climate change on marine tetrapods may be abrupt, episodic, and difficult to predict (100).

Anthropogenic declines in marine mammal populations also have downstream effects on marine food webs (131) via trophic cascades, for example, with killer whale–sea otter–mysticete interactions off southeast Alaska (132) and mysticete–seal–penguin interactions in the Southern Ocean (133). Emerging technologies such as animal-borne recording devices (used in biologging) promise to reveal new details about marine tetrapod ecology (134) and the state of the oceans themselves, such as information about ocean currents provided by biologging data (135).

Conclusions

Despite their status as conservation icons, major questions remain concerning marine tetrapod macroecology, morphology, and even alpha taxonomy. New discoveries and new techniques are helping to frame and test hypotheses about marine tetrapod evolution. Realizing the full potential of these advances requires integrating data sets from disparate disciplines to address unifying questions in ecology, evolutionary biology, and Earth systems history. Marine tetrapods have been ecologically influential members of ocean food webs since the end-Permian mass extinction, persisting through later mass extinctions, anoxic

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