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Alternating regimes of shallow and deep-sea diversification explain a species-richness paradox in marine fishes

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The deep sea contains a surprising diversity of life, including iconic fish groups such as anglerfishes and lanternfishes. Still, >65% of marine teleost fish species are restricted to the photic zone <200 m, which comprises less than 10% of the ocean's total volume. From a macroevolutionary perspective, this paradox may be explained by three hypotheses: 1) shallow water lineages have had more time to diversify than deep-sea lineages, 2) shallow water lineages have faster rates of speciation than deep-sea lineages, or 3) shallow-to-deep sea transition rates limit deep-sea richness. Here we use phylogenetic comparative methods to test among these three non-mutually exclusive hypotheses. While we found support for all hypotheses, the disparity in species richness is better described as the uneven outcome of alternating phases that favored shallow or deep diversification over the past 200 million y. Shallow marine teleosts became incredibly diverse 100 million y ago during a period of warm temperatures and high sea level, suggesting the importance of reefs and epicontinental settings. Conversely, deep-sea colonization and speciation was favored during brief episodes when cooling temperatures increased the efficiency of the ocean's carbon pump. Finally, time-variable ecological filters limited shallow-to-deep colonization for much of teleost history, which helped maintain higher shallow richness. A pelagic lifestyle and large jaws were associated with early deep-sea colonists, while a demersal lifestyle and a tapered body plan were typical of later colonists. Therefore, we also suggest that some hallmark characteristics of deep-sea fishes evolved prior to colonizing the deep sea.

fishes | deep sea | coral reefs | ecological filters | speciation rates

Significance

Most fish species live in shallow waters despite >90% of habitable ocean occurring in the deep sea. We show that present-day diversity patterns are the outcome of alternating phases over 200 million y that differentially favored shallow water or deep-sea fishes. The remarkable richness of shallow fishes is explained by rapid speciation during a time of extreme warm temperatures and continental flooding. Deep-sea colonization and speciation peaked twice throughout Earth's history during colder periods, suggesting "windows of opportunity" for deep-sea fishes. Lineages with traits beneficial for food-limited environments (large jaws) and efficient swimming (tapered tails) were more likely to colonize the deep sea, indicating these are preadaptations to deep-sea life. Marine biodiversity today retains signatures of ancient evolutionary events.

Most fishes live in shallow waters. Between 65% and 80% of marine teleost species are restricted to the photic zone, or habitats <200 m in depth (1–3). However, depths below 200 m (the "deep sea") represent >90% of the volume of the ocean (4, 5). Shallow habitats encompass a diverse range of complex coastal ecosystems (e.g., intertidal zone, coral reefs, kelp forests, seagrass beds) as well as the epipelagic zone of the open ocean, and are thought to have been cradles of evolutionary and ecological innovation through time (6–9). In contrast, the deep sea is characterized by a lack of solar light, cold temperatures, high pressure, large expanses of space, and food limitation (10). Despite the tremendous environmental differences between the deep sea and photic zone, causes of the differences in species richness between these two habitats can be distilled into three core processes: speciation, extinction, and habitat transitions (11, 12). These are the only processes that directly change species richness of any habitat. To explain the disparity in richness we must understand how these three processes varied over evolutionary timescales.

The dedicated study of deep-sea fishes dates to the early 19th century (13). Some authors thought the deep sea contained slowly evolving "living fossils" that were outcompeted from the shallow realm (14). The Challenger Expedition from 1872 to 1876 expanded the number of described deep-sea fishes from 37 to 385, and this number has been rapidly growing since (13). By the mid-20th century ichthyologists recognized distinct ecological and evolutionary guilds (10, 15). They also noted that the diversity of deep-sea fishes, which we now know comprises at least 20% of marine fish species, was higher than expected given the seemingly few barriers to dispersal and limited niches in this vast, dark environment (1). Moreover, recent studies using phylogenetic comparative methods now suggest rapid speciation and morphological evolution of deep-sea fishes (3, 16–19), falsifying the 19th century hypothesis that deep-sea fishes are living fossils (14).

The accumulation of knowledge of deep-sea fishes over the last century (13), coupled with recent advances in phylogenetic comparative methods (20, 21) and the availability of densely sampled molecular phylogenies of fishes (17), now allow us to address the richness disparity between shallow marine and deep-sea fishes from a macroevolutionary perspective. Differences in species richness may not be explained simply by

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faster speciation rates in the richer habitat (17). Instead, a holistic approach that examines variation in rates and timing of colonization and speciation gives a more complete picture of the drivers of present-day richness patterns (12, 22–25).

Here we test three nonmutually exclusive hypotheses for the higher richness observed in shallow marine habitats compared to the deep sea. First, we hypothesize that there has been more time for speciation in the shallow realm, potentially because of shallow habitats being ancestral and deep-sea habitats being derived (26). An onshore–offshore pattern, with higher taxa originating nearshore and nested taxa moving offshore, is well-known in fossil marine invertebrates (6, 27) and Paleozoic fishes (9). Trends within teleosts, the dominant group of living fishes, are less clear. For example, the spiny-rayed fishes (Acanthomorpha), the clade containing most reef fishes, has been inferred to have a deep-sea ancestor (3). Therefore, inferring ancestral depths across the teleost phylogeny is a necessary precursor to testing the time-for-speciation hypothesis.

Second, we hypothesize that speciation and net diversification rates differ between the shallow realm and the deep sea. A recent study suggested there was no overall difference in rates between shallow and deep-sea ray-finned fishes (17). In this study we consider whether differences in diversification rates by habitat are more nuanced. For example, fast rates may be specific to individual shallow water (28) and deep-sea clades (16, 17). A binary shallow and deep categorization may be too broad to capture rate variation driven by habitat. For example, diversification rates seem to be fast on coral reefs (29) and deep benthic habitats (30). In contrast, pelagic fishes, whether shallow or deep, experience few barriers to dispersal, which could limit opportunities for speciation (31). Another alternative is that the high diversity of shallow habitats is due to rapid speciation in the past (8, 32), a signature that is difficult to detect from molecular phylogenies (33). These influences on diversification rates may contribute to the present-day shallow–deep richness disparity in ways that are not straightforward.

Third, we hypothesize that transitions from shallow to deep habitats are a limiting factor on deep-sea richness. Deep-sea transitions are not exceptionally rare among fishes; many lineages have independently colonized the deep sea (3, 34). The ways that habitat transitions limit richness may be more nuanced than simple asymmetric transition rates. For example, the timing of transitions matters; if transition rates were low in the past but increased near the present, the rate shift may be too recent to accumulate high richness (22). In addition, fishes that live in the deep sea are often highly modified for life at depth (3, 10), and the adaptations required may act as ecological filters that prevent some shallow lineages from ever becoming deep-sea colonists. For example, herbivory is impossible in the deep sea (35). Deep-sea fishes tend to be elongate rather than deep-bodied, which is presumably related to lower-energy undulatory swimming (36). It is possible that successful shallow-to-deep transitions occur most often in lineages with phenotypes that are already well-adapted for life in the deep sea. This possibility has never been considered, yet is potentially a viable explanation for the shallow–deep richness disparity.

In this study we measure the influence of time-for-speciation, diversification rates, and transition rates for explaining higher shallow marine richness in teleost fishes. We also combine biogeographic models with ecological and morphological data to assess whether ecological filters limit shallow-to-deep colonization. Our results suggest that present-day richness patterns among marine fishes are explained by complex and dynamic periods of colonization and diversification within shallow and deep-sea habitats over time, potentially driven by abiotic and biotic factors.

Results

Diversification Rates and Habitat. To compare diversification rates across marine fishes, we began by using the most comprehensive time-calibrated molecular phylogeny of teleosts at the time of writing (11,507 species) (17). We collected and cleaned depth occurrence records from public databases (2, 37) using a multistep procedure that included corroboration with the literature (*SI Appendix, Extended Methods*). We found that 3,988 marine species (71.5%) were restricted to the shallow zone (0 to 200 m), 1,240 species (22.2%) were found in both shallow and deep seas, and 349 (6.3%) were restricted to the deep sea (>200 m) (*SI Appendix*, Table S1).

We first used BAMM (Bayesian analysis of macroevolutionary mixtures) (21) and STRAPP (structured rate permutations on phylogenies) (38) to test if speciation, extinction, and net diversification rates varied with depth, using three alternative measures of a species' depth (maximum depth, mean depth, and a binary shallow/deep category). STRAPP analyses were not significant, no matter the variables used (*SI Appendix*, Fig. S1 and Table S2).

We conducted a literature search to identify marine species as pelagic (swimming in water column) or demersal (on or near bottom). Within these categories, we further divided demersal species as benthic (resting on bottom) or benthopelagic (swimming near bottom). We divided pelagic species into inshore and offshore categories. We then used phylogenetic ANOVA (39) implemented using the geomorph R package (40) to test if tip-associated speciation rates from BAMM differed among seven depth-life habit combinations (shallow benthic, shallow demersal, shallow pelagic inshore, shallow pelagic offshore, deep benthic, deep demersal, deep pelagic). Speciation rates broadly overlapped among these categories (phylogenetic ANOVA $P = 0.82$) (*SI Appendix*, Fig. S2 and Table S3).

Biogeographic Model Fitting. Testing the time-for-speciation hypothesis requires an understanding of how long lineages have occupied each habitat. Biogeographic models (20) are well-suited for this purpose because these models allow species to occur in multiple areas (treating depth range as a biogeographic range but in vertical, not horizontal space). We used the R package BioGeoBEARS (20) to fit six alternative models of depth evolution (*SI Appendix*, Tables S4 and S5). We recorded each marine species as present or absent in shallow or deep zones of the ocean (*SI Appendix*, Table S1). While ocean depth is not relevant to freshwater species, we included these species in order to identify the timing of transitions into marine habitats (i.e., colonization time of shallow habitats).

The best-fitting model was BAYAREA+J (Akaike weight = 1) (*SI Appendix*, Table S5). The BAYAREA class of models (41), which we suggest is the class most applicable to marine organisms, differs from alternative models by allowing a widespread parent lineage to split into two widespread daughter species (*SI Appendix, Extended Biogeographic Results and Discussion*). This is important because most deep-sea fishes span both shallow and deep zones of the ocean (*SI Appendix*, Table S1). We found that bathymetric range expansion (i.e., a shallow species widening its depth range to include the deep sea) was overwhelmingly the most common mode of colonizing the deep sea as opposed to founder events ("jump" dispersal in the sense of ref. 20) (*SI Appendix, Extended Biogeographic Results and Discussion*). The

deep sea was colonized independently by teleosts almost 300 times (*SI Appendix*, Fig. S3), although ∼60% of deep-sea species are derived from speciation within just 14 independent colonizations (*SI Appendix*, Table S6).

Ancestral Depth Ranges. Our inferences of temporal patterns of habitat occupancy depend on the time calibration of molecular phylogenies, which are inferences themselves. Unlike Rabosky et al. (17), Alfaro et al. (42) found two pulses of rapid diversification using a phylogeny of ultraconserved elements (UCEs): one during the Late Cretaceous and another near the K–Pg boundary. We used the phylogeny of Alfaro et al. (42) as a reference to redate the phylogeny of Rabosky et al. (17) using the congruification approach (43), giving us an alternative divergence-time hypothesis without losing the dense species sampling of the original tree. Since the Alfaro et al. (42) phylogeny only includes spiny-rayed fishes (Acanthomorpha), we also reduced the original tree to the clade Acanthomorpha as a third option in order to more directly compare the two dating schemes. We refer to the two dating schemes hereafter as "RAB dates" (for all teleosts and Acanthomorpha alone) and "ALF dates" (for Acanthomorpha).

Using the RAB phylogeny of teleosts (Fig. 1), ∼36% of branches were reconstructed as shallow (≤200 m), 11% were reconstructed as widespread shallow and deep, and only 2.8% were limited to deep sea habitats (with the remaining branches limited to freshwater) (*SI Appendix*, Table S1). The most likely state of the ancestor of teleosts was shallow marine (Fig. 1 and *SI Appendix*, Fig. S4). However, the ancestor of Neoteleostei was inferred to have a widespread shallow and deep range, and this range was inherited by the ancestor of Acanthomorpha. This widespread ancestor was consistent across all phylogenies, although this node state had greater probability using the phylogeny of all teleosts (>0.90) than using trees of Acanthomorpha alone (<0.90) (*SI Appendix*, Fig. S4). Early divergences within Percomorpha were reconstructed in the shallow marine state (≤200 m). This implies that the contraction of a widespread depth range was an important event in the early evolution of percomorphs, a clade that now contains ∼90% of reef fish species (44).

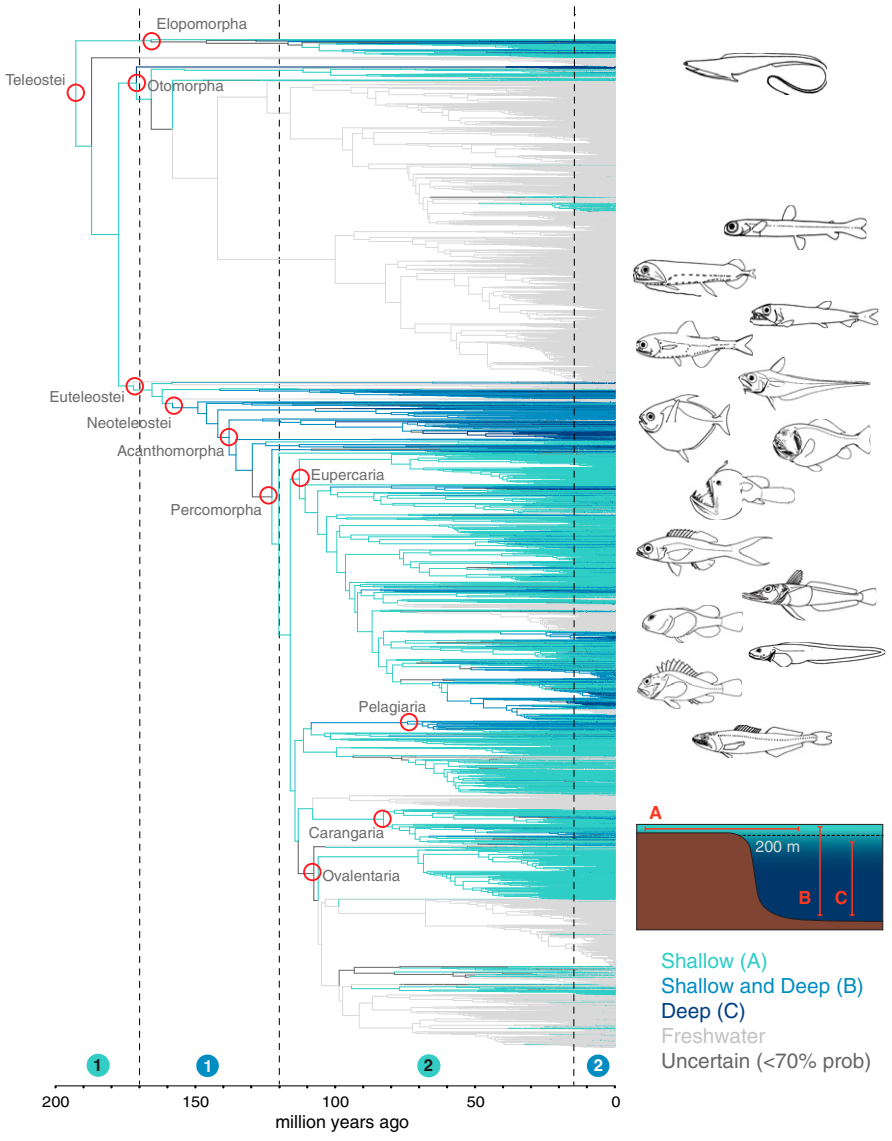

Fig. 1. Ancestral depth range based on BioGeoBEARS analyses using a phylogeny of teleost fishes (17). The proportion of branches reconstructed in each state is presented in *SI Appendix*, Table S1. See *SI Appendix*, Fig. S4 for results from alternative phylogenies. Phases are numbered as in Fig. 2. Fish images were digitized from Food and Agriculture Organization guidebooks (115, 116).

Time Series of Colonization and Speciation. We used the output of biogeographic stochastic mapping (45) based on the BAYAREA+J model to construct timelines of lineage accumulation and speciation rates in shallow and deep seas, as well as rates of deep-sea colonization and extirpation (constriction to shallow zone). We combined shallow+deep and deep-sea–only states for these analyses, corresponding to the classic definition of a deep-sea fish as having a maximum depth below 200 m (13). We initially built these timelines for each of the three aforementioned phylogenies (with two dating schemes), as well as for individual deep-sea groups representing independent colonizations (*SI Appendix*, Figs. S5–S7 and Table S6). These biogeographic time series (46) revealed dynamic phases in the evolution of shallow and deep-sea diversity. In general, time periods that favored shallow marine diversification did not favor deep-sea diversification and vice versa.

Shallow habitats began accumulating diversity earlier than deep-sea habitats since the ancestor of teleosts lived in shallow waters (Figs. 1 and 2*A*). However, a pulse of deep-sea colonization and speciation occurred near the Jurassic–Cretaceous boundary (~145 Ma) (Fig. 2 *B*–*D*). This pulse corresponds to independent colonization by several lineages (*SI Appendix*, Figs. S3 and S5), although it was primarily driven by diversification within a single lineage that colonized the deep sea via expansion of the bathymetric range (*SI Appendix*, Table S6). Living descendants of this lineage include eight orders (Aulopiformes, Myctophiformes, Polymixiiformes, Zeiformes, Gadiformes, Stylephoriformes, Lampriformes, and Beryciformes) (*SI Appendix*, Fig. S5) and potentially a ninth (Ophidiiformes) (*SI Appendix*, Fig S4 and Table S6). In contrast, shallow speciation rates were inferred to be slow at this time. Consequently, the ratio of shallow-to-deep teleost diversity appeared more balanced ~120 Ma compared to today (Fig. 2*B*).

After 120 Ma, deep colonization and speciation rates slowed while shallow speciation rose, corresponding to diversification within Percomorpha. Both dating schemes suggest an inflection point at ~100 Ma, at which shallow teleost diversity exceeded deep-sea diversity (Fig. 2*A*). This disparity in richness was maintained over much of the Cenozoic (Fig. 2*B*), accounting for much of the shallow diversity seen today.

A long period of shallow lineage accumulation from ~120 to 15 Ma is consistent among the alternative trees (Fig. 2*A*), but there are differences in the speciation-rate dynamics involved. ALF dates suggest a second pulse of shallow diversification near

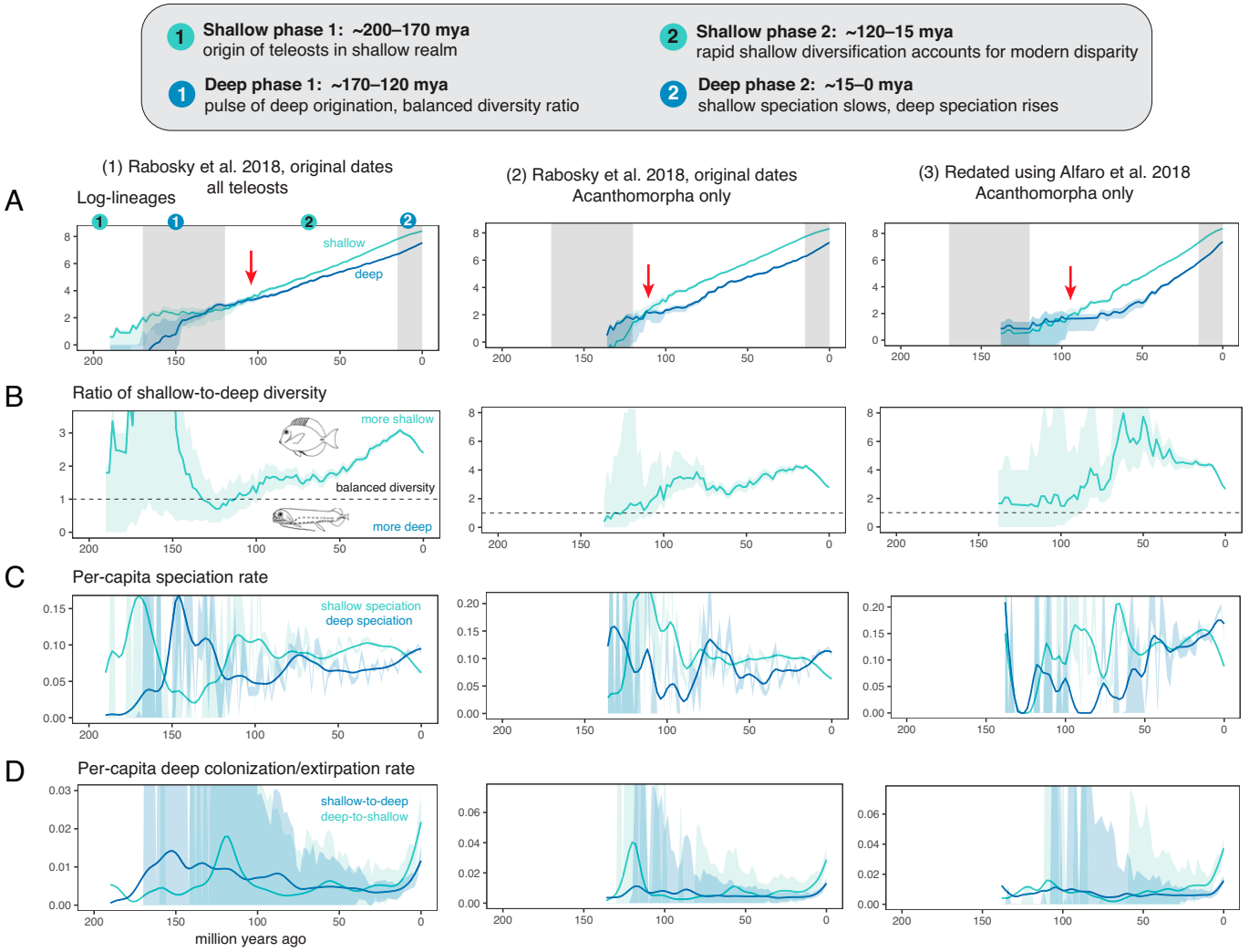

Fig. 2. (*A*–*D*) Time series of shallow and deep-sea lineage accumulation based on three phylogenies. The deep-sea category includes all branches reconstructed with a maximum depth >200 m. We suggest alternating phases with significance for shallow water (white panels in log-lineage plots) or deep-sea diversification (gray panels). Red arrow in log-lineage plots indicate the inflection point where shallow diversity no longer fell below deep-sea diversity. Time series were constructed from BSM following Xing and Ree (46). Bold lines indicate means among 100 BSMs (lines were smoothed for clarity in panels C and D); shading represents the 5 to 95% quantile interval among maps. See *SI Appendix*, Figs. S8 and S9 for results from additional phylogenies.

the K–Pg boundary followed by consistently high rates through the Early-Middle Cenozoic. However, RAB dates instead suggest protracted speciation and a steady accumulation of diversity after the initial pulse. The trees also differ in dynamics of deep-sea evolution during this time. ALF dates tend to suggest younger colonizations than RAB dates for the deep-sea clades within Acanthomorpha (*SI Appendix*, Fig. S5). RAB dates suggest a small deep-sea speciation event near the K–Pg followed by reduced speciation rates for much of the Cenozoic, while ALF dates suggest that shallow and deep speciation rates were similar after ~50 Ma.

Finally, during the most recent 15 million y, deep-sea speciation rates increased while shallow speciation rates decreased (Fig. 2*C*). Transition rates in both directions between shallow and deep habitats were high (Fig. 2*D*). Many new deep-sea colonists were single species, possibly because the newest colonists have not had time to diversify or were prevented from diversifying by competition with incumbents (*SI Appendix*, Fig. S3). Among those clades already present in the deep sea (*SI Appendix*, Fig. S5), speciation rates were highest in Sebastidae, Zoarcidae, and Notothenioidei (*SI Appendix*, Fig. S6). Consequently, the disparity in richness between shallow and deep seas is actually narrower today than in the past (Fig. 2*B*).

We also constructed timelines using four additional phylogenies of teleosts and one additional for Acanthomorpha. These published trees vary in taxonomic sampling strategies (focus on higher taxa versus species), molecular data (Sanger versus next-generation sequencing), and fossil calibration schemes (*SI Appendix*, Table S7). Four trees differ from the Rabosky et al. phylogeny (17) by using Paleozoic fossils as calibrations. Rabosky et al. (17) excluded Paleozoic calibrations in response to a reappraisal of early ray-finned fish fossils (47). The differences in timelines among trees reflect these alternative decisions. These four trees show a much older origin of Teleostei and subsequently an earlier onset of deep-sea diversification (>180 Ma) (*SI Appendix*, Fig. S8). The signal of recent (<15 Ma) deep-sea speciation was reduced in trees where key deep-sea families (Sebastidae, Zoarcidae, notothenioids) were poorly sampled relative to other clades (*SI Appendix*, Fig. S8 and Table S7). The two-burst pattern found by Alfaro et al. (42) was attenuated using the UCE tree of Ghezelayagh et al. (48) (*SI Appendix*, Fig. S9).

Outside of these differences, six features in the time series were remarkably consistent among the phylogenies used in this study despite differences in tree-building and time calibration (*SI Appendix*, Table S7). These features were: 1) a period during the Mesozoic where deep-sea speciation rates exceeded shallow rates; 2) an inflection point around 100 Ma where shallow diversity overtook the deep sea due to a burst in speciation rates; 3) a decline in shallow speciation rates toward the present; 4) deep-sea speciation rates higher or equal to shallow rates near the present; 5) an increase in shallow-to-deep colonization rates toward the present; and 6) a higher ratio of shallow-to-deep diversity in the past compared to the present (Fig. 2 and *SI Appendix*, Figs. S8 and S9). Alternating regimes of shallow and deep diversification are thus a persistent feature across published phylogenies of teleost fishes.

Ecological Filters on Deep-Sea Colonization. We compared our biogeographic results to ancestral state reconstructions of morphology (3, 49–51) and pelagic/demersal life habit (*SI Appendix*, Table S1) to test if deep-sea colonization was related to preexisting ecology and how these relationships changed over time. Early deep-sea colonizations were pelagic (e.g., Argentiniformes, Stomiatiformes) (Fig. 3 and *SI Appendix*, Fig. S5).

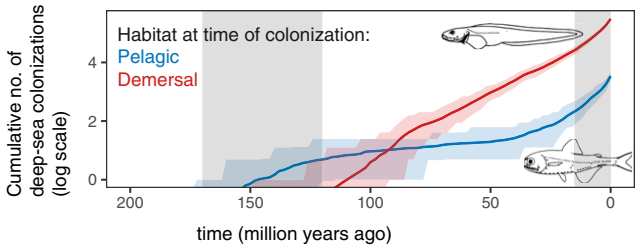

Fig. 3. Time series of shallow-to-deep colonizations (maximum depth >200 m) according to habitat. Bold lines indicate means among 100 BSMs; shading represents the 5 to 95% quantile interval among maps. Results shown here for Rabosky et al. phylogeny (17); see *SI Appendix*, Fig. S10 for alternative trees. Gray shading represents phases as in Fig. 2.

However, beginning ~120 Ma, pelagic shallow-to-deep colonization halted and colonizers were instead demersal. Rates of demersal colonization have been stable since then (e.g., Pleuronectiformes, scorpaenoids, notothenioids, liparids, zoarcoids) (Fig. 3 and *SI Appendix*, Fig. S5), with an increase over the most recent 15 million y. Pelagic shallow-to-deep colonization rates rose again during the mid-Cenozoic and are presently high, as are deep-sea colonization rates in general (Fig. 2 and *SI Appendix*, Fig. S3). These trends were consistent among RAB and ALF dates (*SI Appendix*, Fig. S10).

Of eight functionally relevant body shape measurements, two that were related to deep-sea colonization were lower jaw length (associated with large prey) and minimum caudal peduncle depth (a feature of the tail; a small peduncle is associated with low-energy swimming) (3). The importance of these traits changed through time (Fig. 4 and *SI Appendix*, Fig. S11 and Tables S8–S10). Colonists from 200 to 56 Ma tended to have larger lower jaws than noncolonizers, while colonists from 56 to 15 Ma tended to have shallower caudal peduncle depths than noncolonizers. The morphology of recent colonizers (15 to 0 Ma) did not appear significantly different from noncolonizers based on subsampling tests (*Materials and Methods* and *SI Appendix*, Tables S8–S10), consistent with reduced barriers to deep-sea colonization.

Discussion

In this study we aimed to explain the richness disparity between shallow marine and deep-sea habitats by testing three hypotheses centered around variation in rate or timing of the three processes that directly change species richness. These hypotheses were: 1) that shallow and deep-sea lineages differ in speciation rates; 2) the shallow realm was occupied longer, allowing more time for speciation; or 3) transitions from shallow-to-deep are too infrequent to counterbalance differences in speciation rate and timing. Our results show that all three hypotheses are relevant for explaining the richness disparity. Some hypotheses were only supported after considering that diversification and colonization patterns were quite different in the past. In fact, the richness disparity itself was wider in the past, peaking at 15 Ma or earlier depending on the phylogeny used (Fig. 2*B* and *SI Appendix*, Figs. S8 and S9). In addition, using ecological and morphological data we revealed some potential mechanisms for colonization rate variation across time and clades.

Support for Three Hypotheses. Differences in speciation rates were not apparent when comparing shallow versus deep rates at present (*SI Appendix*, Figs. S1 and S2), as is typically done in many studies (17, 24, 25, 28). One might expect speciation

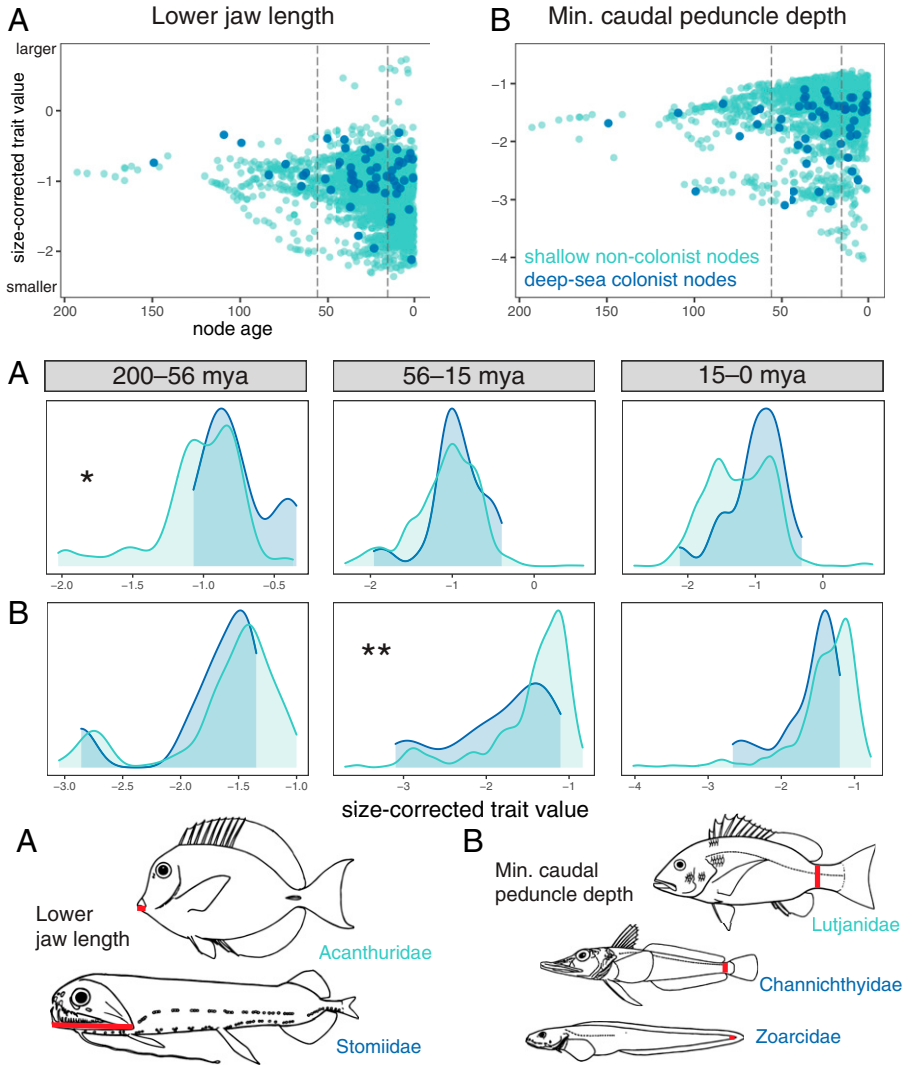

Fig. 4. Filters on shallow–deep-sea colonization (maximum depth >200 m) based on (*A*) lower jaw length and (*B*) minimum caudal peduncle depth. (*Top*) Morphology reconstructed on nodes of the phylogeny (17) through time. (*Middle*) Distribution of shape values reconstructed at shallow-to-deep colonization nodes (dark blue) versus shallow noncolonization nodes (light blue). Panel with an asterisk (*) indicates 50 to 70% of subsampling iterations were significant; panel with a double asterisk (**) indicates >70% of iterations were significant (*SI Appendix*, Tables S8–S10). See *SI Appendix*, Fig. S11 for all eight traits from Price et al. (49). (*Bottom*) illustration of measurements on representative shallow and deep-sea families. Fish images were digitized from Food and Agriculture Organization guidebooks.

rates to be higher in the shallow zone because of the complexity and provinciality of coastal habitats, such as coral and rocky reefs. However, the deep sea also has complex and patchy benthic habitats, namely continental margins, hydrothermal vents, and seamounts (5, 52) that may have similar influence on speciation. Shallow speciation rates were higher in the past, especially during the early diversification of Percomorpha (Fig. 2*C* and *SI Appendix*, Figs. S8 and S9). This event was responsible for growing the richness disparity in favor of shallow habitats at a remarkably consistent inflection point of ∼100 Ma, and is arguably the most important driver of the disparity. The rapid diversification of percomorphs was already known from molecular (42, 53) and fossil data (32, 54–57), but this study is unique in showing its importance for the present-day shallow–deep sea richness disparity.

Biogeographic reconstructions found that the ancestral habitat of teleosts was shallow marine (Fig. 1 and *SI Appendix*, Fig. S4). This shallow origin, when viewed in isolation, might suggest that the shallow realm is more diverse due to greater "time-for-speciation" than the deep sea (26). However, deep-sea colonization and diversification during the Mesozoic eroded the benefit of earlier colonization of the shallow realm (Fig. 2*B*). Instead, the modern-day richness disparity formed during the Cretaceous. Still, relative time for speciation matters for the richness disparity in the sense that a shallow-biased disparity has been maintained for the past 100 million y. While there were at least two periods where deep-sea speciation rates exceeded shallow rates (∼150 Ma, present day) (Fig. 2*C*), these periods were too brief or too recent to counterbalance the long-term speciation of shallow percomorphs. Thus, we suggest that the combination of fluctuating diversification rate dynamics and long-term accumulation of diversity formed the modern richness disparity between shallow and deep seas.

The integration of traits to explain why some clades undergo major habitat transitions and some do not (58) could potentially reveal mechanisms for species-richness patterns. Since teleosts originated in the shallow realm, shallow-to-deep colonization is a necessary precursor for deep-sea richness to ever exceed shallow richness. We found that shallow-to-deep colonization rates varied through time, hinting at a role of oceanic history (Fig. 2*D*). In addition, not only did successful colonization depend on preexisting ecology and morphology (eliminating

the deep sea as a potential habitat for some clades), but the favored traits shifted through time (Figs. 3 and 4). We suggest that abiotic and biotic filters on shallow-to-deep colonization helped maintain unbalanced richness during the formation of the shallow–deep richness disparity 100 to 15 Ma by discouraging new colonizations that would have added to deep-sea diversity. These filters have lasting effects on the distribution of today's biota despite currently high deep-sea colonization rates (*SI Appendix*, Fig. S3). Our results also suggest that some of the hallmark characteristics of deep-sea fishes, specifically long jaws and a narrow tail (10), evolved prior to colonizing the deep sea, and are thus exaptations.

Alternating Regimes of Shallow and Deep Evolution. In 1935, Andriashev (13, 15) argued for two groups of deep-sea faunas. The "ancient" fauna (Mesozoic) were higher taxa endemic to the deep sea, and tended to have large jaws and stomachs, bioluminescence, and cosmopolitan distributions due to a pelagic habit. The "secondary" fauna (Cenozoic) belonged to groups that originated in the shallow realm, tended to be demersal, and were less "modified" for deep-sea life compared to the ancient fauna. Although Andriashev's classifications were based on early phylogenetic groupings, some of which are no longer recognized (59), we find general support for his idea of evolutionary phases using modern approaches.

Below, we describe four phases of marine teleost evolution (Fig. 2). We also suggest putative abiotic and biotic drivers and discuss evidence from the fossil and paleoceanographic record. In general, deep-sea colonization and diversification were favored during periods of cool temperatures and lower sea level, while shallow diversification was favored during warm temperatures and higher sea level.

Shallow phase 1 (Triassic or Early to Middle Jurassic): Teleost origin. This period simply marks the origination of modern teleosts in shallow marine habitats (Figs. 1 and 2*A*), which is supported by molecular phylogenetics (Fig. 1) and the fossil record (34, 60).

Deep phase 1 (Early or Middle Jurassic to Early Cretaceous): The ancient deep-sea fauna. While the timing of this event varies among phylogenies, there is consistent phylogenetic evidence for faster deep-sea than shallow speciation (Fig. 2*C* and *SI Appendix*, Figs. S8 and S9). We found that early deep-sea colonists were pelagic and were likely to have large jaws (Figs. 3 and 4 and *SI Appendix*, Fig. S11). The fossil record shows that early teleosts were pelagic (57, 61, 62), consistent with our phylogenetic inferences. The earliest known body fossils for deep-sea teleosts appeared in the Late Cretaceous; fossils for many living families appear in the record simultaneously (13, 14, 55, 56). The combined phylogenetic and fossil evidence supports a diversification scenario of stem lineages in the Jurassic and crown lineages in the Cretaceous. Large jaws were present among these fossils suggesting this phenotype has long been successful in the deep sea (63).

Independent evidence for developing deep-sea ecosystems best supports a mid-to-late Jurassic onset of this phase (170 to 150 Ma), more consistent with RAB dates (Fig. 2) than other phylogenies (*SI Appendix*, Fig. S8). Pangaea began to break up and the Atlantic Ocean formed (64). This period corresponds well to the lowest Phanerozoic point in global $^{87/86}$Strontium ratios at 150 Ma (65), indicating high hydrothermal activity but low nutrient input from continents (66). The period ~174 to 120 Ma was punctuated by cooling intervals, which improved deep-ocean circulation and efficiency of the biological pump (the process in which particulate organic carbon sinks from surface to the seafloor) (64, 67, 68). The Tithonian-early Barremian Cool Interval (~150 to 120 Ma) was the only period in the Mesozoic cool enough to support ice caps (global temperatures below 18 °C) (64). Coccolithophores and dinoflagellates diversified, which could support new deep-sea food webs (69, 70). The deep sea became a carbonate sink, as evident by the first carbonate oozes (71). Many invertebrates found on seeps and vents today have their first fossil occurrences during this time (72). The invertebrate fossil record overall shows a diversification shift from epicontinental seas to open-ocean facing coastlines, where the deep sea would have been an accessible habitat (73).

Shallow phase 2: 120 to 15 Ma (Early Cretaceous to Middle Miocene), rise of shallow percomorphs. This dynamic period accounts for the modern unbalanced diversity disparity (Fig. 2*B*). The origination of Acanthomorpha in deep-sea environments is supported by all phylogenies used (Fig. 1 and *SI Appendix*, Figs. S4, S8, and S9) and anecdotally by fossil occurrences (74, 75). We found that the shallow diversification of Percomorpha, a clade within Acanthomorpha, was associated with a depth constriction (Figs. 1 and 2*D*). This corresponds well with geologic evidence of severe deep-sea anoxia ~120 Ma driven by warming temperatures, rising sea level, and eutrophication from increased nutrient input from continents (27, 64, 65, 76). At 93 Ma global temperatures reached their highest point since the End-Permian Extinction (28 °C or 10° higher than Jurassic cool intervals), and sea level rise caused ~33% of continental area to be underwater (64). The fossil invertebrate record shows that these oceanic changes increased marine diversity overall (65) but at the expense of extinction of deep-sea taxa (27). Interestingly, some of the deep-sea fish clades inferred to have survived these events (the ancient deep-sea fauna) (*SI Appendix*, Fig. S5) are tolerant of anoxia today (77). Still, oxygen-minimum zones may have discouraged new shallow-to-deep colonizations (34) and limited speciation by depth parapatry (31). The Paleogene–Eocene thermal maximum (~56 Ma) brought on warm temperatures and anoxia once more, corresponding to fossil evidence of depth extirpations in fishes and invertebrates (78–80). New isotopic evidence suggests deep ocean temperatures fluctuated greatly between 65 and 50 Ma, reaching peaks of ~24 °C (81).

Epicontinental seas were the site of shallow diversification (57, 64, 78). These seas were less than 100 m in depth as a rule (73), which precluded deep-sea colonization as a simple diffusion effect of increased shallow diversity. Evolution on reefs was likely critical for the formation of the modern shallow–deep diversity disparity in fishes (32, 53, 57). Interestingly, an analogous shallow–deep diversity disparity in marine invertebrates is also driven by reefs (7).

Most deep-sea colonists during this period were demersal instead of pelagic (Fig. 3 and *SI Appendix*, Fig. S10). The first fossil appearance of a tapered body plan among teleosts was in the Late Cretaceous (77), and a narrow caudal peduncle was also unobserved in our ancestral state reconstructions until ~100 Ma (Fig. 4). A trend toward lower trophic levels among deep-sea colonizers (Fig. 4) may reflect the ecological diversification of demersal teleosts in general (57, 61, 62). Today, there is more diversity in dietary guilds among deep-sea demersal fishes than deep-sea pelagic fishes (35).

Deep phase 2: 15 to 0 Ma (Middle Miocene to present), recent diversification in the deep sea. Shallow speciation rates slowed, possibly reflecting the latitudinal constriction of reefs (8, 82). Conversely, deep-sea speciation rates rose (Fig. 2*C*), driven by high-latitude clades such as Sebastidae, Notothenioidei, and Zoarcidae (*SI Appendix*, Fig. S6). Depth transition rates also

rose in both directions (Fig. 2*D* and *SI Appendix*, Figs. S3, S8, and S9). This transition-rate pattern was previously found during this time period in Pelagiaria (83) and fossil invertebrates (84, 85). Speciation rates were similarly increasing within deep-sea invertebrates (86) and plankton (87).

This period corresponds well to the Middle Miocene Climactic Transition, which began ∼16 Ma with the closure of the Tethys Ocean. This resulted in changes in ocean currents and circulation, cooling the deep sea toward its present-day low of ∼0 °C (81, 82). Diatoms supported shorter food chains, corresponding to the rise of mysticete whales and oceanic lanternfishes (69, 78, 79). Cooler temperatures increased the efficiency of the biological pump creating the modern twilight zone ecosystem (88, 89).

Caveats and Future Directions. We have proposed abiotic and biotic explanations for alternating regimes in shallow and deep-sea teleost diversification. These putative explanations should be revisited as fossil and phylogenetic evidence improves. Two areas of high priority are: 1) the construction of molecular phylogenies with robust topologies, improved taxonomic sampling and more accurate time calibration; and 2) more directly integrating the fossil record with these molecular phylogenies to infer diversification dynamics. There is uncertainty in the timing of "regime shifts" among phylogenies caused by differences in fossil calibration choices (Fig. 2 and *SI Appendix*, Figs. S8 and S9 and Table S7). Efforts in systematic paleontology are needed to resolve the placement of controversial early fossils that have large effects on time calibration (47, 90). Time-calibration choices affect recent nodes too. For example, a previous phylogenetic study found increasing speciation rates in lanternfishes (Myctophiformes) around ∼15 Ma (16), suggesting they diversified during deep phase 2. Yet, inferences using the Rabosky et al. (17) phylogeny show declining speciation rates in lanternfishes (*SI Appendix*, Figs. S7 and S12). Branch lengths are quite different between these two phylogenies (*SI Appendix*, Fig. S12), demonstrating that accurate time-calibration remains a priority.

There is corroborating fossil, geologic, and paleoceanographic evidence for each proposed regime of marine evolution, including the invertebrate and planktonic record (see above). Still, diversification patterns deeper in time are more difficult to infer from molecular phylogenies than recent trends and should be interpreted with caution (91, 92). One persistent, yet perplexing, phylogenetic pattern we report here is balanced shallow-and-deep water lineage diversity prior to ∼100 Ma. Neoteleostei mostly contains deep-sea higher taxa with exception of Percomorpha (Fig. 1) (59), a long-recognized systematic pattern that demands explanation. One possibility is that the richness disparity did favor shallow habitats in the Jurassic as it does today, but deep-sea neoteleosts were more successful at avoiding extinction and are now disproportionately represented among extant taxa. This possibility is only testable using the fossil record (93, 94).

Comparing shallow and deep-sea diversity using fossils has its own biases. Here we list some challenges that future researchers must overcome. First, comparison of fossils to living relatives is used as evidence for the paleobathymetry of a preserved assemblage. Practitioners should avoid circular logic by using independent lines of evidence to determine the depth of fossils (95). Second, preserved assemblages often contain combinations of fossils from a range of depths. Bodies are moved after death or preservation via sinking, current action, or allochthony to form assemblages of ecologically disharmonious species, the depth of which are impossible to determine reliably (96, 97). Third, deep-sea fossil fishes are exceedingly rare because of their delicacy and the geologic and eustatic circumstances needed to make these fossils discoverable. This has wide-ranging consequences. Deep-sea fossils are often much younger than the inferred deep-sea colonization times from molecular phylogenies (55, 96, 97), representing diversification long after colonization. A comparison of shallow versus deep diversity would be heavily biased by shallow fossils; for example, there is no deep-sea teleost fossil record at all until the Cretaceous (13, 14, 55). There are fossils of living deep-sea clades from shallow settings (79, 95, 98), suggesting that modern species' depths may not be representative of ancestral lineages. However, the majority of deep-sea fishes today have wide depth ranges that includes depths <200 m (*SI Appendix*, Table S1). The shallow portion of a depth range is more easily discovered for both living and extinct species. Fossils represent incomplete snapshots of a fish's life; in contrast, we have the option of inferring depth ranges of living species based on many catches and in situ observations.

There is evidence that the balanced shallow–deep diversity during the Jurassic is a genuine representation of crown teleost evolution. The fossil record shows that crown teleosts were not the dominant clade on reefs until ∼90 Ma (53, 57, 61), around the time when we inferred a dramatic rise in shallow marine diversity. Instead, the stem teleost Pycnodontiformes occupied niches during the Jurassic similar to percomorphs today (32, 99). Morphometric and diversity-through-time analyses using fossils suggest pycnodontiforms displaced teleosts to marginal habitats until their decline in the Late Cretaceous (99). The extinction of incumbents and the subsequent expansion of teleosts on reefs together may be the inciting events forming the modern shallow–deep richness disparity.

Beyond sensitivities from the lack of fossils, we do not expect our results to be overturned based on model identifiability or sampling. Diversification dynamics based on models have identifiability concerns (100); however, the method used here is not model-based and simply reflects branch lengths (46), an approach that remains useful as diversification-rate methods are scrutinized (28, 92). While diversification dynamics based on branch lengths are sensitive to taxonomic sampling, we found no evidence of biased species sampling associated with depth in the Rabosky et al. (17) phylogeny (*SI Appendix*, *Extended Methods*). Finally, while there are many undescribed deep-sea species, there is also much undescribed diversity on coral reefs (101), and so the proportion of described shallow-to-deep species should not change dramatically (4).

Conclusions. In this study we aimed to explain the species richness disparity between shallow marine and deep-sea habitats within teleost fishes. The modern richness disparity is ∼100 million y old and was caused by an early burst of diversification in the clade Percomorpha, not recent speciation. We describe alternating regimes that favor shallow or deep-sea speciation, and we propose that these regimes changed in conjunction with changes in sea level and temperature. Finally, we combined ecological and morphological traits with biogeographic reconstructions to show that there were time-variable ecological filters on deep-sea colonization, which served to exclude shallow groups from the deep sea and maintain the richness disparity. These results also show that some hallmark characteristics of deep-sea fishes (i.e., large jaws and narrow tails) are exaptations.

Materials and Methods

Phylogenetic Sampling and Depth Ranges. Our main analyses use the molecular phylogeny of Actinopterygii developed by Jonathan Chang and published by Rabosky et al. (17), the most comprehensive at the time of writing

(11,638 tips). We excluded 48 species that were not teleosts and 83 tips that were unresolved or duplicates, leaving 11,507 species. We began by classifying each species into one of four aquatic types (marine, freshwater, euryhaline, and diadromous) using recent compilations (24, 102). While ocean depth is not relevant to freshwater species, these species are needed in the ancestral state reconstructions to identify the timing of transitions into marine habitats.

We collected data on depth of occurrence for each marine species using a multistep procedure (details in *SI Appendix, Extended Methods*). The procedure was designed to minimize errors associated with public databases (103) while maximizing taxonomic sampling. We obtained vetted depth records for almost all marine species in our phylogeny (5,148 species or 96.1%). Of those species missing records, we could still code the coarse-grain presence and absence in shallow or deep oceans using Priede (13) for the purpose of BioGeoBEARS analyses. Only 40 remaining species did not have enough information to assign them to shallow or deep habitats and were removed from biogeographic analyses. Note that we found no evidence that shallow species were more likely to be sampled in the molecular phylogeny than deep-sea species (details in *SI Appendix, Extended Methods*).

Demersal and Pelagic Life Habit. Deep-sea communities fall into two general categories: pelagic and demersal (13). To test for differences in diversification and colonization by life habit, we performed a literature search to assign species to either pelagic or demersal states. A total of 53 literature sources were used to assign life habits to all 5,541 marine species in the phylogeny (*SI Appendix*, Table S1; see references in *SI Appendix*). We also considered whether finer ecological categories than these were more appropriate (i.e., benthic versus demersal and pelagic inshore versus pelagic offshore; details in *SI Appendix, Extended Methods*).

Comparing Diversification Rates by Depth Using BAMM. We began by using BAMM (21) and STRAPP (38) to test if diversification rates varied with depth. BAMM detects shifts in diversification rates across a phylogeny independent of a priori hypotheses based on habitats or clades. STRAPP estimates a test statistic between a chosen focal variable and diversification-rate regimes estimated by BAMM. This test statistic is then compared to a null distribution generated by permutating the rate regimes across the phylogeny. As input for STRAPP, we used the output of two independent time-variable BAMM analyses performed by Rabosky et al. (17). These diversification-rate regimes were estimated based on the full phylogeny, including all marine and freshwater ray-finned fish species with genetic data, not a pruned subset limited by the availability of depth records.

We used STRAPP to test for a relationship between diversification rates and three alternative measures of depth for each species based on Ocean Biogeographic Information System (OBIS) records. These were the maximum depth, the mean depth, and a binary shallow versus deep categorization (shallow species were restricted to 0 to 200 m). For each depth measure, we tested for significant differences using three alternative rate types (speciation, extinction, and net diversification) using either raw or log-transformed rate values, and using results from one of two independent BAMM runs, for a total of 36 tests. Tests were performed using the "traitDependentBAMM" function in BAMMtools v2.1.7 (104).

We also tested if rate differences were associated with specific depth-habitat combinations. We used the function "getTipRates" in BAMMtools to obtain tip-associated speciation rates from the BAMM output. We compared rates among seven depth-habitat categories: shallow benthic, shallow demersal, shallow pelagic inshore, shallow pelagic offshore, deep benthic, deep demersal, and deep pelagic. We tested for differences in log-transformed speciation rates by habitat using phylogenetic ANOVA (39) implemented using the "procD.pgls" function in the geomorph R package v4.0.1 (40). This function implements a residual randomization permutation procedure (10,000 iterations) from the RRPP R package (105).

Biogeographic Model Fitting. To reconstruct ancestral depth ranges, we used biogeographic models (20), which allow species to be coded as present in more than one area (depth zone). We recorded each marine species as present or absent in shallow (0 to 200 m) and deep-sea habitats (>200 m). The boundary of 200 m for the deep sea is widely accepted. At this depth, photosynthesis is no longer possible and the continental shelf breaks into the slope in many parts of the world (13). Freshwater species (n = 5,625) were coded as occurring in a third "freshwater" region. An additional 665 brackish species were coded as occurring in both marine and freshwater zones. We excluded diadromous species (n = 265) because diadromy is a distinct lifestyle and not a transitionary state between freshwater and marine habitats (102). Some deep-sea species undergo daily migrations from depths to near surface at night to feed [e.g., myctophids (13)]. These species were considered to occupy both shallow and deep oceans because the shallow realm remains of principle ecological importance. In total, 11,202 species were included in biogeographic reconstructions, with 5,228 species present in shallow marine habitats, 1,589 in the deep sea, and 6,276 in freshwater (*SI Appendix*, Table S1).

We used the package BioGeoBEARS v1.1.2 (20) to fit alternative models. We eliminated unobserved range combinations from the state space (i.e., a species in freshwater and the deep sea but not shallow marine) leaving six possible area combinations. The maximum range size was set to three, because this was the maximum range observed among species in our dataset (14 teleost species were found in freshwater or brackish, shallow marine and deep-sea habitats) (*SI Appendix*, Table S1). The root of teleosts was restricted to the marine state in accordance with the fossil record (94) but could occur in any depth. We input a dispersal matrix that enforced ordered transitions among depths (i.e., to move from freshwater to the deep sea, lineages must first pass through the shallow zone) (*SI Appendix*, Table S4). We compared the fit of six alternative models using Akaike weights (106). These were: DEC (107), DIVA-LIKE (108), BAYAREA-LIKE (41), and their equivalents with the +J parameter (cladogenetic dispersal) (20). See *SI Appendix, Extended Biogeographic Results and Discussion* for detailed comparison of these models in the context of bathymetric range.

Time Series of Speciation and Colonization. We used the explicitly biogeographic approach of Xing and Ree (46) to estimate speciation and colonization rate changes through time. To do this, we first performed 100 simulations of biogeographic stochastic mapping (hereafter "BSM") (45) using the best-fit model. This allowed us to visualize uncertainty associated with the reconstruction. In these analyses, we defined deep-sea lineages as those with a maximum depth below 200 m, combining branches reconstructed as widespread shallow+deep with those restricted to the deep sea (states B and C of Fig. 1). We did this because: 1) this is the most widely accepted definition of a deep-sea fish and the one used in most studies (3, 13) and 2) <3% of branches in the phylogeny were reconstructed in the deep sea alone, consistent with the observation that most deep-sea species have a wide bathymetric range (*SI Appendix*, Table S1). We used the output of BSM to construct time series of: 1) the number of shallow water and deep-sea lineages, 2) the ratio of shallow-to-deep water lineages, 3) per-capita speciation rates within shallow and deep habitats, 4) per capita shallow-to-deep colonization rates, and 5) per capita deep extirpation rates (constriction to shallow zone). The number of lineages were counted as the number of branches reconstructed in either habitat per rolling 2-million-y time bin. The ratio was simply the number of shallow divided by the number of deep-sea lineages in each time bin. The per capita speciation rate was calculated for each habitat as the number of splits (nodes) reconstructed in that habitat within the focal time bin, divided by the number of lineages in the habitat in the preceding time bin (the number of lineages that could have potentially speciated). The shallow-to-deep colonization rate was the number of deep colonizations in the focal time bin divided by the number of shallow lineages in the preceding time bin (the number of lineages that could potentially colonize the deep sea). Similarly, the deep extirpation rate was the number of losses of the deep zone in the focal bin divided by the number of deep-sea lineages in the preceding bin. We constructed these time series for all teleosts, as well as for individual deep-associated lineages (*SI Appendix*, Figs. S6 and S7 and Table S6).

Additional Phylogenetic and Temporal Hypotheses. To test how our time series would change according to differing molecular dating hypotheses, we first used the congruification approach (43). This method uses a reference phylogeny, which is a tree containing few exemplar tips representing higher taxa, to time-calibrate a target phylogeny with shared higher taxa but denser species-level sampling. The reference phylogeny is usually constructed with genomic approaches (more base pairs but fewer species). We used the phylogeny of Alfaro et al. (42) for Acanthomorpha, which is based on 1,100 UCE loci across 120 species, as a reference to redate the phylogeny of Rabosky et al. (17), which is based on 27 loci across 11,000+ species (*SI Appendix*, Table S7). We trimmed the original phylogeny to the clade Acanthomorpha, then implemented the congruification using the function "congruify.phylo" in the R package geiger

v2.0.7 (109). The function uses TreePL (110) to time-calibrate the target tree. We then used the redated phylogeny to construct time series of colonization and diversification as described above. To test for effects on biogeographic inferences caused by reducing from all teleosts to acanthomorphs, we constructed a third time series using the trimmed tree and the original dating scheme (before congruification).

We also constructed speciation timelines using five additional phylogenies built from different molecular datasets. These phylogenies had different taxonomic sampling strategies, gene sampling, topologies, and time calibration schemes than either Rabosky et al. (17) or Alfaro et al. (42) (*SI Appendix*, Table S7). These were: the 1,105 gene phylogeny from Hughes et al. (111) with 34- and 31-fossil calibration schemes [with and without controversial fossils (90)], the summary tree from Betancur-R et al. (112), the phylogeny used by Medeiros et al. (113) to test if genome size increased with ocean depth, and the UCE phylogeny of Acanthomorpha by Ghezelayagh et al. (48).

Effect of Life Habit on Deep-Sea Colonization. We constructed timelines of deep-sea colonization based on demersal or pelagic life habit. We performed a maximum-likelihood ancestral state reconstruction of life habit on each of the three phylogenies (see above) implemented with the function "ace" in the package ape v5.4-1 (114). Three character states were included with the reconstruction as defined above: pelagic, demersal (including benthic species), and freshwater. We did not attempt to code life habit for freshwater species because it was not clear how comparable our definitions are in the deep sea versus freshwater habitats. We allowed transition rates to differ between demersal and pelagic states. We enforced a single marine-to-freshwater rate and a single freshwater-to-marine rate regardless of demersal or pelagic state because a model with all rates differing had problematic parameter estimates.

We previously identified deep-sea colonization-associated nodes (see above). We matched colonization nodes to the ancestral reconstruction of life habit to identify the lineage as pelagic or demersal at time of colonization. We then estimated a timeseries of the number of pelagic versus demersal deep-sea colonizations as the count of these events per 2-million-y time bin.

Effect of Morphology on Deep-Sea Colonization. We tested whether successful shallow-to-deep colonists are overrepresented by particular morphologies (i.e., if there are exaptations for life in the deep sea). Conversely, this would imply that some shallow clades do not colonize because they have body plans ill-suited for life in the deep sea. We tested this hypothesis using a morphological dataset spanning teleost fishes based on museum specimens (49, 50). This dataset includes eight functionally relevant linear measurements: standard length, maximum body depth, maximum fish width, head depth, lower jaw length, mouth width, minimum caudal peduncle depth, and minimum caudal peduncle width. We size-adjusted the variables using log-shape ratios following recommendations of Price et al. (49). The log-shape ratio was the measurement divided by size (the geometric mean of standard length, maximum body depth, and maximum fish width) and then log-transformed. The log-shape ratio of standard length, for example, can be considered a measure of body elongation (49). We performed a maximum-likelihood ancestral state reconstruction of the eight size-adjusted variables individually using the "fastAnc" function in phytools. We then obtained the trait values reconstructed at colonization-associated nodes. To facilitate node matching, we reperformed biogeographic model fitting using a reduced phylogeny with sampling matching the morphological dataset (5,741 species versus 11,202 species). We identified deep-sea colonization nodes as those with $\geq$70% probability of including the deep sea and an ancestor with <70% probability.

To test if the morphological context of deep-sea colonization varied through time, we separated colonization-associated nodes into three categories: 200 to 56 Ma (root of teleosts through the K–Pg boundary and shortly after), 56 to 15 Ma, and 15 Ma to present. The first age category is broader than the phases shown in Fig. 2 for practical reasons, representing the origin of teleosts through the K–Pg mass extinction and shortly thereafter, because there were few deep-sea colonization nodes to compare when looking further back in the phylogeny (*SI Appendix*, Fig. S3). The phase 15 Ma to present is consistent with Fig. 2 and represents an increase in deep-sea colonizations toward the present.

Within each of the three time periods, we compared the morphological states at colonization-associated nodes with contemporary shallow nodes (shallow lineages in the same period that did not colonize the deep sea). If there is ecological filtering on body shape in the deep sea, we would expect the trait values at colonization nodes to differ in mean and/or variance from those of shallow contemporaries (i.e., trait values skewed toward large or small values). Sample sizes differed greatly between colonization and noncolonization nodes because colonization is less frequent than in situ speciation. For each time bin we subsampled the shallow nodes to match the number of colonization nodes, then performed a *t* test (comparing means) and a Levene's test (comparing variances). We performed 10,000 sampling iterations per trait and per time bin.

Data, Materials, and Software Availability. Data and R scripts have been deposited in a Dryad repository, https://doi.org/10.5061/dryad.s1rn8pkc5, (117).

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