EVOLUTION

Increase in predator-prey size ratios throughout the Phanerozoic history of marine ecosystems

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The escalation hypothesis posits that predation by increasingly powerful and metabolically active carnivores has been a major driver of metazoan evolution. We test a key tenet of this hypothesis by analyzing predatory drill holes in fossil marine shells, which provide a ~500-million-year record of individual predator-prey interactions. We show that drill-hole size is a robust predictor of body size among modern drilling predators and that drill-hole size (and thus inferred predator size and power) rose substantially from the Ordovician to the Quaternary period, whereas the size of drilled prey remained stable. Together, these trends indicate a directional increase in predator-prey size ratios. We hypothesize that increasing predator-prey size ratios reflect increases in prey abundance, prey nutrient content, and predation among predators.

Predators play a major role in structuring present-day ecosystems (*1*) and are thought to have played an important role in critical evolutionary transitions such as the origin of eukaryotes (*2*) and the Cambrian explosion of skeletonized animals (*3*). The escalation hypothesis (*4*, *5*) postulates that top-down pressure from increasingly powerful and metabolically active predators has driven evolutionary trends toward increased motility, burrowing, and defensive armor in many prey lineages. This highly influential hypothesis has proven challenging to evaluate, partly because of the difficulty of reconstructing ancient trophic interactions. Long-term trends in energetically important aspects of trophic structure such as predator size and predator-prey size ratios (*1*, *6*) remain largely unknown.

We used the fossil record of drill holes in marine shells to reconstruct Phanerozoic trends in the sizes of drilling predators, drilled prey, and predator-prey size ratios. Drill holes, produced by a variety of extant and extinct carnivorous groups, primarily gastropods (table S1), provide a direct record of individual predator-prey interactions. These trace fossils are abundant and widespread in the geological record, occurring in a wide variety of prey taxa from ~750 million years ago to present (*7*, *8*).

To evaluate the relationship between predator body size and drill-hole size across drilling clades, we compiled 556 paired measurements of predator sizes and the outer diameter of the drill holes they produced. The compilation includes 14 extant families of drilling predators representing five phyla: Mollusca, Cercozoa, Arthropoda, Foraminifera, and Nematoda (table S1). Driller shell size and drill-hole diameter are strongly positively correlated (Fig. 1), and this relationship is insensitive to the choice of size metric, data filter, or regression model (figs. S1 to S5). Drill-hole size is thus a robust predictor of predator body size regardless of phylogenetic identity.

We examined Phanerozoic trends in drill-hole size, prey size, and predator-prey size ratios using data compiled from 6943 drilled specimens representing 362 marine taxon occurrences. This data set focuses on mollusk and brachiopod prey because these taxa numerically dominate the marine fossil record (*9*) and represent the primary source of paleontological data on drilling predation (*10*). The median size of drilled prey shells shows no Phanerozoic trend and is best explained by a stasis model (Fig. 2A and table S2) (*11*). In contrast, the median drill-hole diameter increased from 0.35 to 3.25 mm from the Ordovician to the Quaternary (Fig. 2B), with a trajectory best fit by an unbiased random walk model (Fig. 2B and table S3), suggesting that predator body size increased through time. Predator-prey size ratios, as estimated by the ratio of drill-hole size to drilled shell size, show a 67-fold increase from the Ordovician to the Quaternary period that is best fit by a directional trend model (Fig. 2C and table S4). A directional trend remains the best-fit model when considering other size metrics, taxonomic and ecological subsets of the data, or more complex models (tables S5 to S20). Ranges of drill-hole and prey sizes show no significant change through time (figs. S6 to S9), reinforcing the conlusion that the increase in predator-prey size ratio reflects a directional trend rather than an increase in variance. An increase in predator-prey size ratios is also supported by independent evidence that hypothesized early Phanerozoic drillers were significantly smaller than late Phanerozoic drillers (fig. S10 and tables S21 and S22). Although increasing predator size is the major component of the increase in predator-prey size ratios, there is also evidence of a shift in predator size selectivity: Similar-sized predators attacked relatively smaller prey in the Cenozoic than in the Paleozoic (fig. S11).

Temporal trends in the geographic and environmental distribution of drilled shells are unlikely to explain the rise in predator-prey size ratios. Although continental landmasses drifted to higher latitudes throughout the Phanerozoic (*12*), there is no significant difference in median predator-prey size ratio between tropical and extratropical settings in the Cenozoic (fig. S12) or in modern marine ecosystems (*1*). There is also no significant difference in median predator-prey

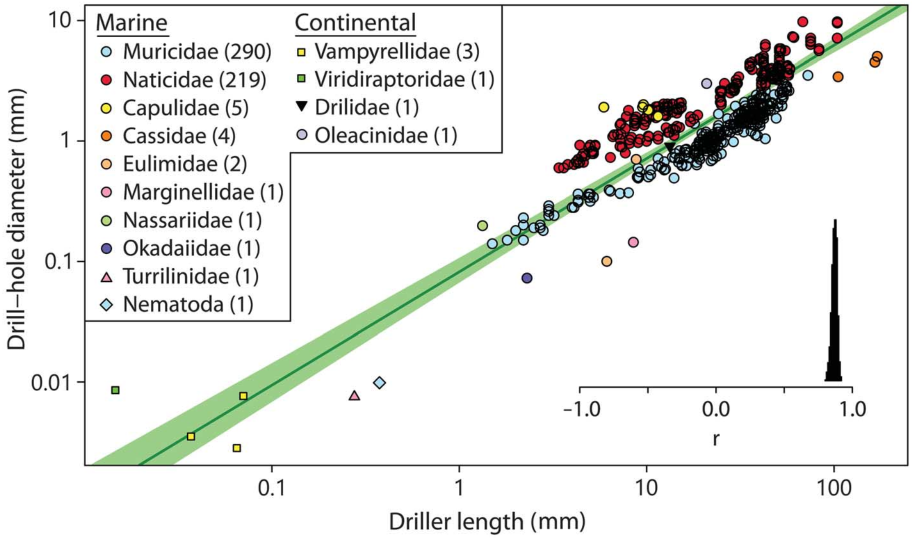

Fig. 1. Log$_{10}$-scaled outer drill-hole diameter versus shell length for modern drilling clades. Reduced major axis regression line supplemented by 95% bootstrapped confidence intervals and bootstrapped *r* values in histogram (both 1000 iterations). Driller family names are shown with sample sizes. Nematod family is not known. Circles, Gastropoda; diamond, Nematoda; triangle, Foraminifera; squares, Cercozoa; inverted triangle, Arthropoda. Log$_{10}$ slope = 0.94; intercept = –1.09.

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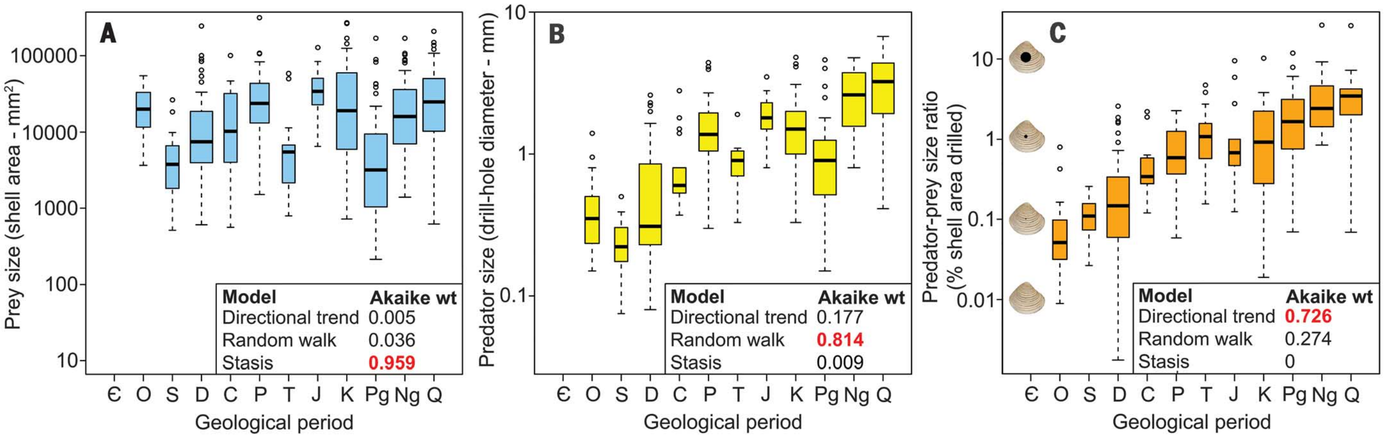

Fig. 2. Log$_{10}$-scaled boxplots of prey size, predator size, and the predator-prey size ratio in Phanerozoic brachiopods and mollusks. (**A**) Prey size (shell area). (**B**) Predator size (drill-hole diameter). (**C**) Predator-prey size ratio (= proportional to the percentage of shell area drilled). Boxplot widths are $\sqrt{n}$ (where n ranges from 13 to 54 per boxplot). (Inset) Support for three evolutionary models. The strict stasis model receives no support in any case. Geological periods: Ꞓ, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene; Q, Quaternary.

size ratio between lithified and unlithified sediments in the Cenozoic (fig. S13), ruling out lithification as an explanation for the trend. Paleozoic data are dominated by brachiopods and post-Paleozoic data by mollusks, raising the concern that our analysis may conflate temporal trends and taxonomic mixing effects, an issue that could be exacerbated by preferential dissolution of aragonitic mollusks (*13*). However, brachiopods and mollusks do not exhibit significant differences in predator-prey size ratio when both occur in the same collection (figs. S14 to S16). Moreover, permutations that preserve the taxonomic and temporal structure of prey occurrences and sizes but randomize drill-hole sizes within brachiopods, gastropods, and bivalves overwhelmingly produce trajectories best fit by a stasis model rather than a directional trend (fig. S17).

Because we use a broad definition of predators that includes macroparasites (*14*) and because modern drilling parasites are smaller relative to their hosts than predatory drillers are relative to their prey (fig. S18), a temporal rise in the proportion of strictly predatory drillers could produce an apparent increase in predator-prey size ratios. However, a predatory origin is likely for the majority of Paleozoic drill holes because parasitic gastropod drillers do not consistently co-occur with drilled prey (*14*, *15*), and attachment scars [often associated with parasitic drilling (*16*, *17*)] are not observed in even well-preserved Paleozoic prey (*15*, *18*). Last, the trajectory of predator-prey size ratios remains best fit by a directional trend model even when restricting the data set to strictly predatory drill holes (figs. S19 and S20 and table S14).

Our data provide direct evidence supporting a critical tenet of the escalation hypothesis: Drilling predators have become larger, and thus more powerful (*10*), throughout the Phanerozoic. Escalatory prey responses may include enhanced mobility or infaunalization, increase in defensive armor, or body size increase (*4*, *5*). No increase in prey body size is apparent either in our data (Fig. 2A) or in broader compilations of body size data (*19*), but the observed shifts toward more mobile and infaunal prey (figs. S21 and S22) are consistent with predator-driven evolution. Diversification of the relatively large infaunal naticid gastropod drillers since the Cretaceous may represent an example of a coevolutionary response to Mesozoic infaunalization of prey (*20*) but can also be interpreted as an escalatory escape strategy of naticids from their own epifaunal predators.

Predator-prey size ratios are not strongly influenced by environmental factors in modern marine ecosystems (*1*), and the Phanerozoic trajectory of predator-prey size ratios also does not correlate with environmental trends that influence metabolic scope, such as temperature and oxygen concentration (*21*, *22*). Instead, we hypothesize that dramatic changes in the energetic structure of marine ecosystems throughout the Phanerozoic (*23*, *24*) are the main drivers of the increasing predator-prey size ratios. Per-shell soft-tissue mass and nutritional content have increased as the ratio of mollusks to brachiopods has risen (fig. S14) (*25*–*27*) because brachiopods contain comparatively less soft tissue, have a lower tissue density, and have a higher inorganic tissue content than mollusks (*28*). The temporal shift in dominant prey type may thus account for the observation that similar-sized drillers selected increasingly smaller prey through time (fig. S11): Small molluscan prey in the Cenozoic may have been at least as nutritious as relatively larger Paleozoic brachiopods. Evidence for a transition in prey preference is provided by higher drilling frequencies on mollusks relative to co-occurring brachiopods since the Permian (*29*–*31*) and by experiments showing that predators prefer mollusks to brachiopods but feed on brachiopods once mollusks have been consumed (*32*). The overall abundance of prey animals at lower trophic levels also likely rose throughout the Phanerozoic, as suggested by increases in the proportional diversity of predators (*33*), the frequency and thickness of shell beds (*34*), and the inferred population density of benthic invertebrates (*35*). Eco-evolutionary models suggest that increases in predator-prey size ratio can be driven by both elevated prey abundance and by intensification of predation among predators (*36*). Predation among predators is likely to have risen throughout the Phanerozoic as ecosystems became increasingly dominated by active predators (*33*), an inference supported by increasing frequencies of confamilial predatory drill holes in the Meso-Cenozoic (*37*). The sustained increases in predator size and predator-prey size ratios throughout the Phanerozoic highlight the importance of biotic interactions, including the driving roles of both bottom-up and top-down processes on the evolving structure of marine ecosystems.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/356/6343/1178/suppl/DC1
Materials and Methods
Figs. S1 to S22
Tables S1 to S22
References (*38*–*109*)

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Bigger and badder

The escalation hypothesis posits that predator size has increased over time, leading to increased motility and defense in prey organisms. Although influential, the hypothesis has been difficult to test. Klompmaker *et al.* looked at predator drill holes in bivalve shells across 500 million years. Drill-hole size did increase, whereas prey size remained relatively constant. This changing predator-prey size ratio suggests that the number of prey consumed likely increased, a factor facilitated by greater complexity of food webs and availability of nutrient-dense prey.

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