EXTINCTION

Ecological selectivity of the emerging mass extinction in the oceans

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To better predict the ecological and evolutionary effects of the emerging biodiversity crisis in the modern oceans, we compared the association between extinction threat and ecological traits in modern marine animals to associations observed during past extinction events using a database of 2497 marine vertebrate and mollusc genera. We find that extinction threat in the modern oceans is strongly associated with large body size, whereas past extinction events were either nonselective or preferentially removed smaller-bodied taxa. Pelagic animals were victimized more than benthic animals during previous mass extinctions but are not preferentially threatened in the modern ocean. The differential importance of large-bodied animals to ecosystem function portends greater future ecological disruption than that caused by similar levels of taxonomic loss in past mass extinction events.

Terrestrial biodiversity is declining rapidly (1), and the oceans are poised to follow suit without intervention (2). This "sixth mass extinction" may approach or exceed the magnitude of the five major extinctions of the past 550 million years (My) if current loss rates persist (3). Because the effects of massive diversity loss are difficult to scale upward from laboratory experiments or local ecosystem disruptions (4), ancient extinction events provide critical information for forecasting the structure and function of the future biosphere. Previous attempts to contextualize present threats using past extinctions focused mainly on extinction intensity (rate and magnitude of taxonomic loss) [e.g., (3, 5)]. However, the distribution of losses across ecological functional groups (e.g., predators versus nonpredators) also strongly affects postextinction ecosystem function. Indeed, the preferential loss of dominant functional groups characterizes the two most important, era-bounding mass extinctions (6): the end-Permian event [252 million years ago (Ma)] exterminated all reef-building animals, and the end-Cretaceous (66 Ma) eliminated the nonavian dinosaurs.

The current distribution of extinction threat among functional groups has yet to be compared quantitatively to past extinctions, leaving unknown which events, if any, provide useful analogs for future ecosystems. The rich fossil record of marine animals provides an excellent opportunity to compare current trajectories of change with ancient patterns. Here, we use a database of 2497 extinct and living marine mollusc and vertebrate genera (fig. S1) to compare the projected inten-

sity and selectivity of future extinctions with previous mass extinction events and with background intervals. To ensure maximum correspondence between fossil and modern analyses, we conduct comparisons at the genus level and, for the modern oceans, include only extant genera also known as fossils, which ameliorates differences imposed by preservation. We classify extinction threat for modern taxa using assessments from the Inter-

national Union for Conservation of Nature (IUCN). We calculate extinction intensity as the percentage of genera that did not survive from one time interval to the next. We evaluate extinction selectivity via multiple logistic regression using four ecologically important predictors: body size (maximum length), habitat zone (pelagic or benthic), motility (motile or nonmotile), and feeding mode (predator or nonpredator) (7).

Predicted extinction intensity varies owing to the incomplete assessment of extinction threat for living species. In optimistic projections, we consider genera that lack IUCN-assessed species or are data deficient to be nonthreatened. Under these assumptions, projections for molluscs and vertebrates diverge, with vertebrates facing greater losses, because a large fraction of molluscs lack assessment whereas the vast majority of vertebrate genera in the data set contain at least one assessed species (Fig. 1). Pessimistic scenarios, in which only IUCN-assessed species are analyzed and all genera containing species categorized as vulnerable or worse are lost, predict the extinction of 24 to 40% of genera overall (table S1), with similar loss levels in vertebrates and molluscs (Fig. 1 and fig. S2). The lower value is twice the background rate, and the higher is comparable to the end-Cretaceous mass extinction (Fig. 1).

Extinction threat to living genera is most strongly associated with body size (Fig. 2). The odds [i.e., $q/(1 - q)$, where q is the probability of
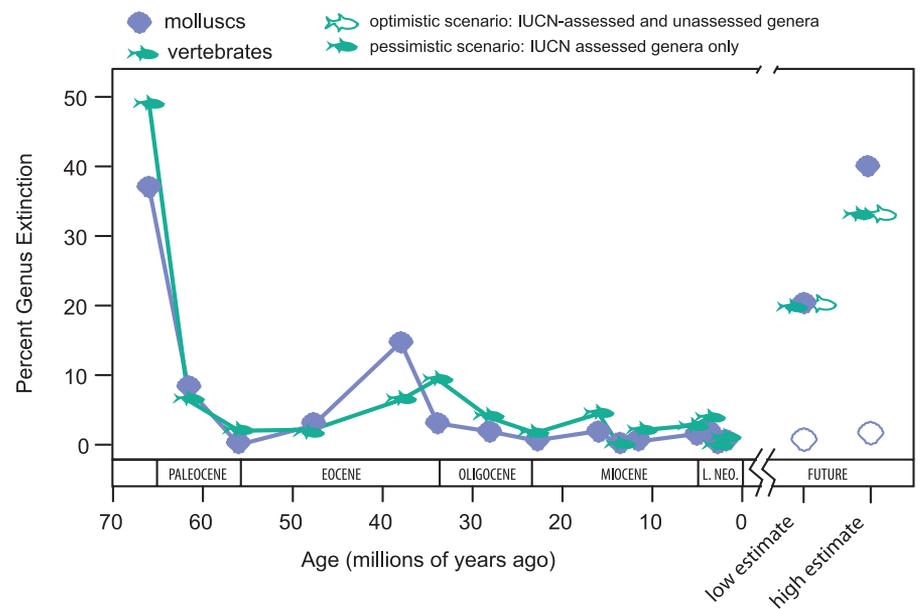
Fig. 1. Historic genus extinction intensity and modern predictions for marine molluscs and vertebrates. Extinction intensity has generally not exceeded 10% for either molluscs or vertebrates since the end-Cretaceous extinction. The proportion of modern genera with near-threatened species exceeds background extinction rates in most data treatments. The only exception is in molluscs under the assumption that genera lacking assessed species are entirely at low threat of extinction. Upper estimates approach the magnitude of the end-Cretaceous mass extinction. For future predictions, closed symbols indicate results from a pessimistic scenario based only on genera containing IUCN-assessed species; open symbols indicate results from an optimistic scenario in which genera lacking assessed species were included and assumed to be nonthreatened. Both scenarios include only living genera with fossil records to maximize comparability with extinction intensity for ancient events. Genera were classified on the basis of either the least- or most-threatened member species (low and high estimate, respectively). L. Neo., Late Neogene.

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being threatened with extinction] increase by a factor of 13 for each order of magnitude increase in body length (calculated by exponentiation of the coefficient in Fig. 2A) under our primary data treatment, in which genera lacking assessed species are assumed not to be threatened. This strong size bias holds in a wide range of data treatments, such as the exclusion of genera lacking assessed species (fig. S3), variation in the threat level used to distinguish threatened versus non-threatened genera (fig. S4), and the inclusion of living genera lacking fossil records (fig. S5). The size bias is present within both vertebrates and molluscs and most constituent classes (figs. S6 and S7). Motility is positively associated with extinction threat (Fig. 2C), although this result is sensitive to data treatment (figs. S3 and S5). Habitat zone and feeding mode are not correlated with threat (Fig. 2, B and D).
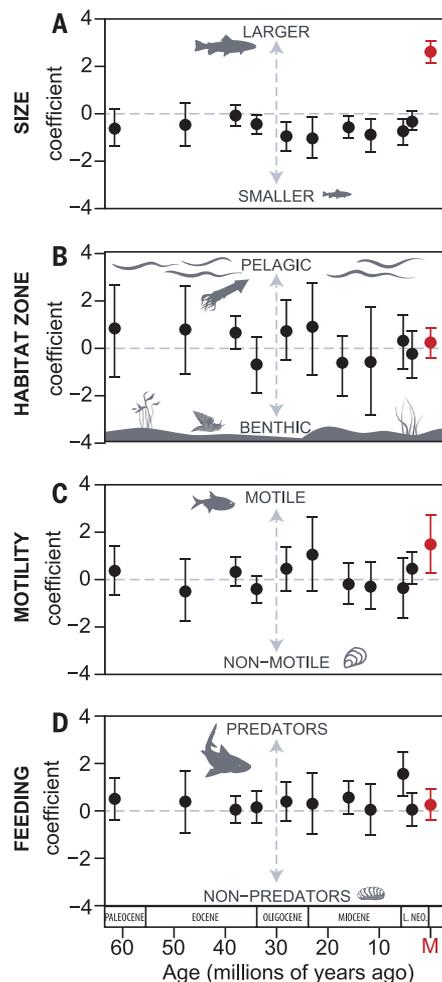
The ecological distribution of present-day extinction threat has no precedent in the fossil record. During the past 66 My, background extinction was generally associated moderately and inversely with body size and was independent of other predictors (Fig. 2). During previous mass extinctions, body size was inversely associated or not associated with extinction probability (Fig. 3). This result is robust to the exclusion of all genera smaller than 2 cm in maximum length and to the restriction of the analysis to narrower taxonomic groupings (figs. S8 to S10). Our finding that ancient extinctions were rarely selective with respect to body size is also largely consistent with previous analyses of fossil marine animals, although previous studies were taxonomically and temporally more restricted and generally did not adjust for other ecological predictors (7). Motility was inversely associated with extinction during the end-Cretaceous extinction but is generally positively associated with threat in the modern oceans (Fig. 3). Pelagic genera were preferentially lost in all previous mass extinctions, whereas modern threat is not preferentially associated with the pelagic habitat zone (Figs. 2 and 3). These results are also robust to alternative data treatments, such as the exclusion of genera smaller than 2 cm in maximum length (fig. S10).

A principal component analysis of the regression coefficients shown in Figs. 2 and 3 illustrates the unique selectivity of the emerging mass extinction (Fig. 4). None of the previous mass extinctions or background intervals plot near the modern extinction threat, reflecting differences in the coefficients of association for body size and habitat zone. The extreme bias against large-bodied animals distinguishes the modern diversity crisis from all potential deep-time analogs.

The association between body size and modern extinction threat is reflected in descriptions elsewhere of elevated threats to large-bodied marine animals and overfishing-induced population declines (8, 9). It is consistent with the tendency for fisheries to first exploit species at higher trophic levels and subsequently move down the food web (10), as animals at higher trophic levels are typically larger than their counterparts

at lower trophic levels (11). Size-biased vulnerabilities operate within species as well (12, 13), reflecting a unique human propensity to cull the largest members of a population (14). Humans also heavily influence small-bodied species (15), but these impacts have yet to register in global threat profiles. These pressures on large-bodied marine animals are mirrored in patterns of terrestrial defaunation (16), which are also distinct from background patterns spanning the past 66 My (17).
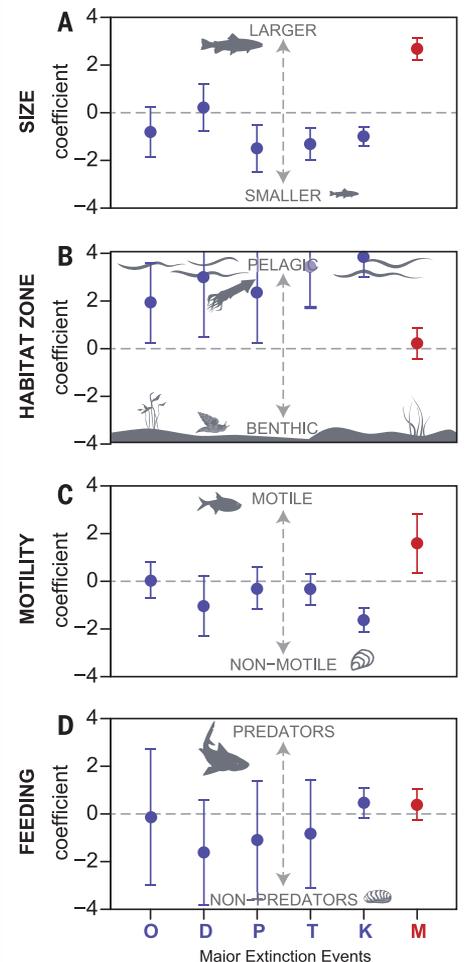
Although climate and ocean chemical responses to anthropogenic CO_2 emissions can be predicted by historical episodes of climate warming and ocean acidification [reviewed in (18)], climate change does not appear to be the dominant driver

of extinction threat for the taxa examined here. Rather, human fishing and hunting define the dominant threat to modern marine fauna (2, 19, 20). Although we observed no contemporary association between threat and habitat zone in these taxa, others have documented preferential and widespread modern declines in benthic marine microfauna resulting from nutrient pollution and oxygen deprivation in bottom waters (21). The sustained proliferation of dead zones associated with nutrient pollution (22) may eventually leave a similar, global mark on the macrofaunal groups that we examined. If climate change ultimately surpasses fishing in shaping extinction threats, patterns of selectivity would likely converge with earlier mass extinctions.

Fig. 2. Extinction threat in modern oceans is uniquely biased against larger-bodied animals. Ecological selectivity of extinction risk in the modern oceans (red symbols) and background extinction selectivity in the Cenozoic Era (66 Ma to present) based on the fossil record (black symbols). The vertical axis represents the coefficient associated with the predictor averaged across all subsets of the full multiple regression model. Error bars represent 95% confidence intervals on estimated coefficients.


Fig. 3. Ecological selectivity of extinction threat in the modern oceans is unlike any previous mass extinction. Previous mass extinction events (blue symbols) preferentially eliminated pelagic genera and, sometimes, smaller genera, whereas the modern extinction threat (red symbols) is strongly associated with larger body size and moderately associated with motility. Error bars represent 95% confidence intervals on estimated coefficients. O, Late Ordovician; D, Late Devonian (Frasnian/Famennian); P, end-Permian; T, end-Triassic; K, end-Cretaceous; M, modern extinction threat.

Fig. 4. Unique ecological signature of the emerging marine mass extinction. The first two principal components from a principal component analysis of the logistic regression coefficients presented in Figs. 2 and 3, illustrating the distinctive selectivity pattern of the modern extinction threat relative to the past 66 My of background extinction and the five main mass extinctions in the fossil record (letter and color scheme as in Fig. 3). Black dots represent Cenozoic background intervals. The first two principal components explain 79% of the variance.
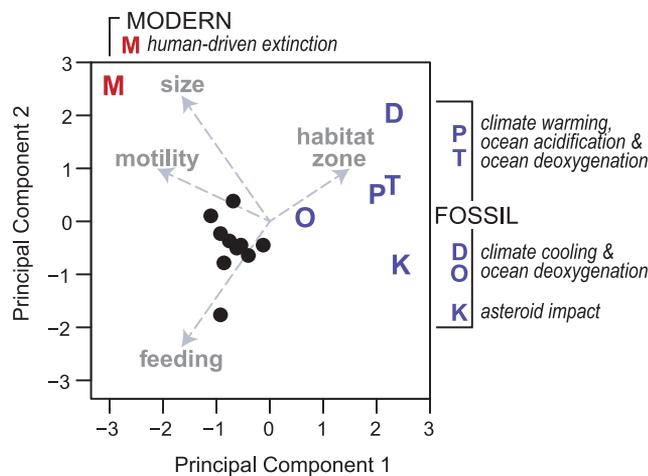
The preferential threat to large-bodied marine animals poses a danger to ecosystems disproportionate to the percentage of threatened species. Large-bodied animals are critical to ecosystem function because of their preferential position at the top of food webs (*11, 23*) and importance to nutrient cycling (*24*) and bioturbation of sediments (*25*). Removal of large-bodied predators can also trigger trophic cascades affecting many other species [e.g., (*26*)]. Although previous mass extinctions did not preferentially remove the largest taxa, the sheer magnitude of loss across the body-size spectrum entailed the extinction of many of the largest species, and surviving genera may have become smaller as well (*27*). The loss of large taxa may have caused more ecological disruption than the loss of comparable numbers of smaller taxa; indeed, loss of large animals may explain in part the multimillion-year delays in ecosystem recovery following these catastrophes. The preferential removal of the largest animals from the modern oceans, unprecedented in the history of animal life, may disrupt ecosystems for millions of years even at levels of taxonomic loss far below those of previous mass extinctions. And, unfortunately, the lack of correlation between the proportion of species assessed within higher taxa (phyla, classes, and orders) and the proportion considered threatened for marine animals (*28*) suggests that the pessimistic projection of future genus losses (Fig. 1) may more closely approximate the true threat level than the optimistic projection. Without a dramatic shift in the business-as-usual course for marine management, our analysis suggests that the oceans will endure a mass extinction of sufficient intensity and ecological selectivity to rank among the major extinctions of the Phanerozoic (541 Ma to present). Such an event would usher the world not only into a new geological epoch (Anthropocene) but also into a new period (Anthropogene) or even a new era (Anthropozoic) (*29, 30*).

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