Review

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Extinctions in ancient and modern seas

Paul G. Harnik[1], Heike K. Lotze[2], Sean C. Anderson[3], Zoe V. Finkel[4], Seth Finnegan[5], David R. Lindberg[5,6], Lee Hsiang Liow[7], Rowan Lockwood[8], Craig R. McClain[1], Jenny L. McGuire[1,9], Aaron O'Dea[10], John M. Pandolfi[11], Carl Simpson[12] and Derek P. Tittensor[2,13,14]

[1] National Evolutionary Synthesis Center, Durham, NC 27705, USA
[2] Department of Biology, Dalhousie University, Halifax, NS, B3H 4R2, Canada
[3] Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada
[4] Environmental Science Program, Mount Allison University, Sackville, NB, E4L 1A5, Canada
[5] Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, CA 94720, USA
[6] Center for Computational Biology, University of California, Berkeley, CA 94720, USA
[7] Center for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, Blindern, N-0316 Oslo, Norway
[8] Department of Geology, College of William and Mary, Williamsburg, VA 23187, USA
[9] School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA
[10] Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Republic of Panama
[11] Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, The University of Queensland, Brisbane, QLD 4072, Australia
[12] Museum für Naturkunde, Leibniz Institute at the Humboldt University Berlin, 10115 Berlin, Germany
[13] United Nations Environment Programme World Conservation Monitoring Centre, Cambridge, CB3 0DL, UK
[14] Microsoft Research Computational Science Laboratory, Cambridge, CB3 0FB, UK

In the coming century, life in the ocean will be confronted with a suite of environmental conditions that have no analog in human history. Thus, there is an urgent need to determine which marine species will adapt and which will go extinct. Here, we review the growing literature on marine extinctions and extinction risk in the fossil, historical, and modern records to compare the patterns, drivers, and biological correlates of marine extinctions at different times in the past. Characterized by markedly different environmental states, some past periods share common features with predicted future scenarios. We highlight how the different records can be integrated to better understand and predict the impact of current and projected future environmental changes on extinction risk in the ocean.

The past as a key to understanding the present and future

For millennia, the oceans of the world have harbored a great diversity of life and have provided humans with a variety of ecosystem goods and services [1]. Humans, in turn, have greatly impacted marine species and ecosystems through the direct effects of exploitation and habitat degradation, and the indirect effects of greenhouse gas emissions on ocean temperature, pH, and sea level [2–4]. To understand the present and potential future consequences of these impacts on marine ecosystems, scientists increasingly look at the oceans' past. By leveraging information archived in ship logs, tide gauges, sedimentary cores, and shell middens, the historical trajectories of marine organisms and the environments that they inhabit have been reconstructed at annual to millennial scales [5]. Such time series provide valuable baselines against which

contemporary conditions can be compared, and have been used to model conditions in marine ecosystems for the near future [3,4].

However, current understanding of how organisms will respond to projected future environmental conditions is limited. Over the coming century, marine organisms will be confronted with a suite of environmental conditions that have no analog in human history [6,7]. Predicted changes in ocean temperature and chemistry [3] can amplify the effects of overexploitation, habitat degradation, and other impacts on marine ecosystems [8,9]. Therefore, there is an urgent need to determine which marine species have the capacity to endure or adapt to these novel conditions or, alternatively, are likely to go extinct [4,10].

Although marine species are commonly assumed to be less susceptible to extinction than terrestrial species [11], extinctions are ubiquitous in the marine fossil record [12,13] and contemporary risk is considerable (e.g., corals [14]; marine mammals [15], cartilaginous fishes [16], tunas and billfishes [17], seagrasses [18], and mangroves [19]). There are few well-documented examples of global marine extinctions in recent centuries [20,21], but many marine species have declined in abundance and are regionally and/or functionally extinct [2]. This calls the presumed resilience of marine species into question and highlights the need for better understanding of marine extinctions and extinction risk.

Which biological and environmental factors lead to elevated extinction risk among marine organisms? In addition, in the absence of long-term monitoring of most marine species, is it possible to predict their current and future extinction risk? We address these questions by comparing the patterns, drivers, and biological correlates of marine extinctions in fossil and historical records with information on modern extinction risk. Paleontological and

Corresponding author: Harnik, P.G. (paulharnik@nescent.org).
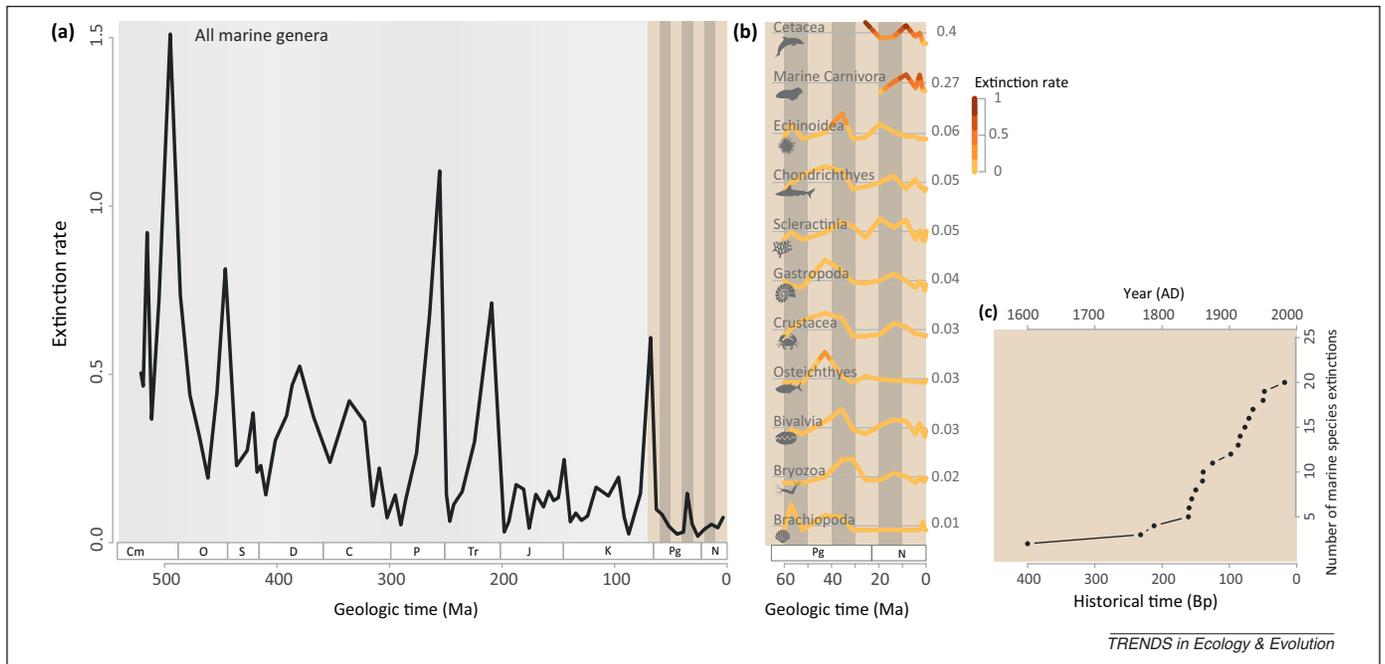
Figure 1. Evidence of marine extinctions in the fossil and historical records. **(a)** Extinction rate of all marine genera in the Phanerozoic [past 550 million years (Ma)] and **(b)** by major clades in the Cenozoic (past 65 Ma); horizontal gray lines and corresponding numerical values in (b) are the mean Cenozoic extinction rates. **(c)** Cumulative number of global extinctions of marine species in historical times (1500–2000 AD). Fossil data are from the Paleobiology Database (http://paleodb.org). Historical extinctions reproduced, with permission, from Dulvy *et al.* [20]. See Box 1 for details regarding the calculation of fossil extinction rates and tabulation of historical extinctions. Abbreviation: Bp, before present.

historical data offer insights into marine extinctions over multiple scales and under different environmental conditions, some of which are partly comparable to predicted future environmental states. Our comparisons reveal the many opportunities and challenges of combining data for ancient and modern organisms in an effort to better understand and predict the impact of current and future environmental changes on extinction risk in the sea.

Extinctions in ancient and modern seas
The fossil record
Extinctions are a primary feature of the marine fossil record (Figure 1a). Although mass extinction events were important drivers of macroevolutionary change [22], most marine organisms (>90%) went extinct during intervals

characterized by 'background' extinction rates (Figure 1a; Box 1) [12,13,23]. This long record of extinctions provides many opportunities to assess the environmental conditions and biological characteristics that can lead to elevated risk.

One conspicuous trend in the marine fossil record is the overall decline in background extinction rates towards the present-day (Figure 1a). This decline reflects the loss of extinction-prone lineages, which, combined with variation in origination rates, led to marked changes in the composition of marine ecosystems over time [24]. Recovery from the end-Permian [251 million years ago (Ma)] and end-Cretaceous extinctions (65 Ma) involved the diversification of clades that are the major constituents of marine communities today. Thus, because of their ecological and evolutionary similarities, data for the past 65 million years

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Box 1. Calculating extinction rates and extinction risk

Fossil record
The calculation of fossil extinction rates relies on compilations of taxon occurrences over geologic time. Several methods exist to calculate fossil extinction rates [82]; however, per-capita rates based on the census of taxa at specific moments in time are increasingly used because of their insensitivity to several potential biases [82,83]. These survivorship-based rates are calculated as $-\ln(N_{bt}/N_b)$, where N_{bt}/N_b describes the proportion of taxa censused at the beginning of an interval (N_b) that are still extant at the end of an interval (N_{bt}), assuming that extinctions are exponentially distributed through the interval [80,82]. Geological stages (average duration approximately 7 million years) are the intervals commonly used in studies of global extinction rates in the fossil record. The per-capita rates presented in Figures 1a,b, and 2a (main text) were calculated using global data for marine genera in the Paleobiology Database (http://paleodb.org).

Historical record
The assessment of historical extinctions largely relies on assembling reported examples in the published literature [29]. They are generally distinguished between global extinctions (Figures 1c and 2b, main

text [20]), where species completely disappear from the planet and local or regional extirpations (Figure 2b, main text [11]), where species become extinct in only part of their geographic range. Generally, the last known date of occurrence is provided together with a reason for the loss. Although some extinctions are certain, others are debated and there are examples of species believed to be extinct that have been rediscovered later on, or locally extirpated species that have recolonized an area after decades of absence [30].

Modern record
The IUCN uses five criteria to evaluate whether a species belongs in one of the three threatened categories: critically endangered (CR), endangered (EN), or vulnerable (VU) [38]. These include: (i) the magnitude of population decline measured over the longer of 10 years or three generations; (ii) the geographic range (extent of occurrence and area of occupancy); (iii) small population size and decline; (iv) very small or restricted populations; and (v) the probability of extinction in the wild [38]. The IUCN also reports the number of assessed species, the number of data-deficient species, and whether taxonomic groups are completely assessed (Figure 2c, main text).

might be most informative for understanding current and future extinction risk.

Extinction rates varied considerably over the past 65 million years (Figure 1b), with congruent extinction peaks at some times for some clades (e.g., elevated rates 34 Ma for several groups associated with a transition from greenhouse to icehouse climates [25]), and incongruent peaks at other times. On average, extinction rates differ markedly among major clades, with marine mammals [cetaceans and marine carnivorans (pinnipeds and aquatic mustelids)] going extinct at rates more than ten times those of most invertebrates (Figures 1b and 2a). Extinction rates also vary among invertebrates: the mean extinction rate for scleractinian corals is approximately twice that of bivalves and five times that of brachiopods (Figures 1b and 2a). This temporal and phylogenetic heterogeneity in rates provides an opportunity to dissect the factors associated with elevated extinction risk among past marine organisms [26–28]. Moreover, when integrated with paleoenvironmental data, these rates can be used to predict the susceptibility of marine clades to extinction under different scenarios of current and future environmental change.

Historical extinctions and extirpations

During historical times (approximately 1500 AD to today), at least 20 marine species are recorded to have gone globally extinct (Figures 1c and 2b; Box 1) [20]. In addition, at least two seabird species known only from archaeological records

became globally extinct in prehistoric times [29]. Despite this small number of documented global extinctions, there are increasing records of local- to regional-scale extirpations (i.e., the loss of populations from a portion of the former geographical range of a species). Dulvy *et al.* [11] reported 133 marine extirpations and extinctions (Figure 2b), most of them local extirpations during the 19th and 20th centuries. Although some of these have been disputed [30], others have been confirmed or added [20,31]. Moreover, historical assessments of estuaries, coastal seas, and coral reef ecosystems worldwide show dramatic declines in the abundance of many species over past decades and centuries [32,33]. Several species have reached such low abundance that they can be considered ecologically, functionally, or economically extinct. However, not all local extirpations are permanent and some have been reversed by natural or assisted reintroduction [34,35]. Whether global or local, ecological, or economical, extinctions and extirpations often have strong consequences for the ecological structure and resilience of marine ecosystems as well as for ecosystem functions and services to human well-being [34,36,37].

Current extinction risk

An increasing number of marine species are currently threatened by extinction (Figure 2c; Box 1) [38]. At least 830 marine species have been classified as critically endangered, endangered, or vulnerable and at least 1538 as data deficient [38]. Overall, the assessment of marine
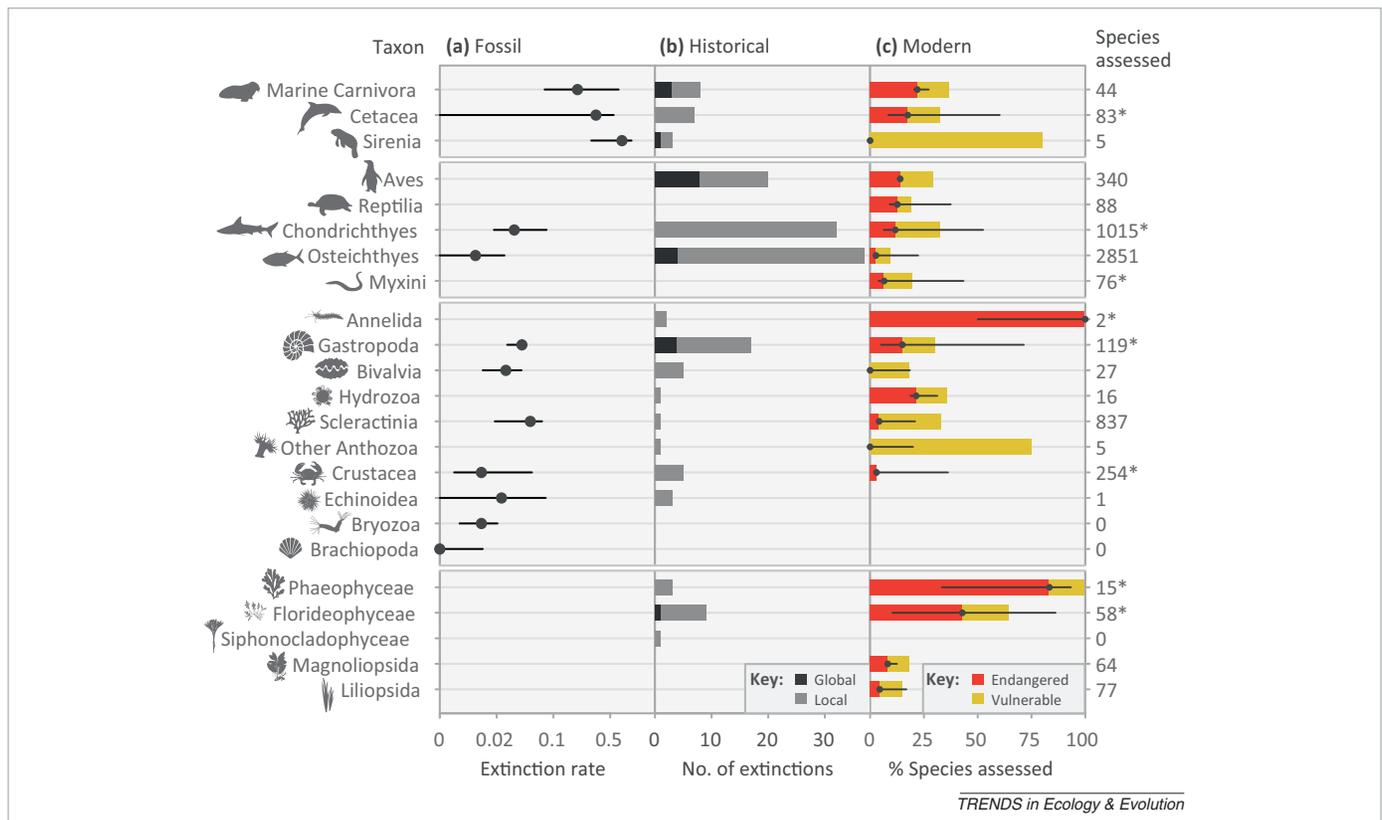
FIGURE 2. Comparison of extinction rates in the Cenozoic fossil record, the number of extinctions in the historical record, and current extinction risk among marine taxa. **(a)** Extinction rates over the Cenozoic (Box 1); median (circles) and 1st and 3rd quartiles (lines) derived from time series in Figure 1b. **(b)** Number of historical global extinctions (dark gray) and local (light gray) extirpations (based on [11,20] with two additional species from [64]) (Box 1). **(c)** The percentage of modern species assessed in the International Union for the Conservation of Nature (IUCN) Red List [64] as endangered or critically endangered (red) and vulnerable (yellow), excluding data-deficient species (Box 1). Taxonomic groups are mammals (top), followed by other vertebrates, invertebrates, and plants (bottom). Numbers on the right indicate the number of modern species assessed by the IUCN for each taxonomic group. Asterisks indicate taxonomic groups with >50% of assessed species considered data deficient. Line segments in (c) indicate upper and lower estimates of the fraction of endangered species if all data-deficient species were classified as endangered or not endangered, respectively.

species lags behind that of terrestrial species: out of the 41 500 assessed species in 2007 only 1500 were marine, with another 1500 marine species added by 2008 [38]. This included complete assessments of sharks and rays, groupers, reef-building corals, seabirds, marine mammals, and sea turtles (Figure 2c). Since then, assessments for all mangroves [19], seagrasses [18], and tunas [17] have been completed (Figure 2c), and the International Union for the Conservation of Nature (IUCN) aims to have 20 000 marine species assessed by 2012 [38]. Nevertheless, assessments for many groups are incomplete or entirely lacking (Figure 2c).

Comparing extinctions through time
Although overall background extinction rates have declined throughout the fossil record, there have been many periods of enhanced extinction rates (Figure 1). Currently, the Earth is again in a period of increased extinctions and extinction risks (Figures 1 and 2), this time mainly caused by human factors (see below). Unfortunately, only a few groups have sufficient information from two or all three periods to enable one to compare their records of extinction over time (Figure 2). Marine mammals (carnivorans, cetaceans, and sirenians), bony fishes (Osteichthyes), and scleractinian corals have information on current risk and fossil extinction rates and, interestingly, the same rank order of extinction vulnerability, with marine mammals being most and bony fishes least vulnerable. Yet, bony fishes have the highest number of recorded local extirpations in historical times. For other groups (e.g., seabirds and plants), there are relatively good assessments of current risk and some records of historical extinctions, but little information on fossil extinction rates (Figure 2). By contrast, fossil extinction rates are well known for several invertebrate groups (e.g., echinoids, bryozoans, and bivalves) for which current risk assessments are either data deficient or lacking, but some records on historical

extinctions exist. These discrepancies reflect the selective historical exploitation and current conservation of vertebrate megafauna [39,40] and the greater fossilization potential of invertebrates with biomineralized elements. As invertebrates comprise most of the marine metazoan diversity, are key components of marine food webs, and provide critical ecosystem services, improving the assessment of their current risk would greatly enhance understanding of the resilience of marine ecosystems and how current and potential future extinction risks compare with those in the geologic past.

Current threats and past extinction drivers
The degree to which current extinction threats differ from past extinction drivers is an important question when considering the utility of fossil and historical records for understanding current and predicting future extinction risk. Even if the ultimate drivers of extinctions have changed over time, the proximal effects experienced by organisms might be similar. For example, ultimate sources of elevated atmospheric CO_2 differ between the late Permian (volcanic activity) and present day (burning of fossil fuels), but in both instances marine organisms have had to contend with the proximal effects of acidification and warming (Table 1) [41]. Similarly, large changes in the area of shallow benthic habitat have occurred throughout geologic time (e.g., via sea-level fall due to the growth of continental ice sheets), which might bear similarities to human-driven habitat degradation and loss today (Table 1). Below, we compare the similarity and relative importance of current threats and ancient drivers of marine extinction, and consider synergistic effects among multiple drivers.

Overexploitation
Overexploitation is one of the principal threats to marine organisms today [38,42] and in the historical record

Table 1. Past drivers of extinction in the ocean and current threats[a]

Time period[b]	Drivers and Threats[c]						
	Acidification[d]	Anoxia[e]	Warming	Cooling	Habitat Loss[f]	Overexploitation	Pollution
Ordovician-Silurian (~444 Ma)		○	○	●	●		
Late Devonian* (Frasnian-Famennian; ~374 Ma)		●	○	●	●		
End Permian* (~251 Ma)	●	●	●	○	●		
Early Triassic (~245 Ma)	○	●	○	○	○		
Triassic-Jurassic* (~202 Ma)	●		●				
Early Jurassic* (Pliensbachian-Toarcian; ~183 Ma)	●	●	●	●			
Aptian-Albian (~112 Ma)	●	●		○	○		
Cenomanian–Turonian (~93.5 Ma)	●	●	○				
Cretaceous–Paleogene (~65.5 Ma)	●		○	●	○		
Paleocene–Eocene Thermal Maximum* (~56 Ma)	●	○	●				
Eocene–Oligocene (~34 Ma)				●	○		
Mid–Miocene Climatic Optimum (~14.7 Ma)			●		○		
Historical (~10 Ka)			○		●	●	○
Modern	●	●	●		●	●	●

[a]Table generated using references in 'Current threats and past extinction drivers' section of the main text and [95].

[b]Periods in bold indicate mass extinctions and asterisks indicate global reef crises [27].

[c]Solid circles highlight confident and open circles less confident drivers.

[d]Causes of acidification include volcanism, bolide impacts, and methane clathrates in the past and burning of fossil fuels currently.

[e]Causes of anoxia include warming, eutrophication, and ocean stratification in the past and eutrophication currently.

[f]Causes of habitat loss include sea-level fall in the past and habitat degradation and coastal development currently.

[11,33,43], followed by habitat loss and, to a lesser extent, pollution and climate change (Table 1). Of 168 marine, estuarine, and diadromous (i.e., migrating between fresh and salt waters) species listed or considered for listing under the US Endangered Species Act (ESA) in 2004, 81% were affected by overexploitation [42]. Historically, exploitation was associated with 55% of local extirpations and global extinctions [11] and 96% of depletions and extirpations in estuaries and coastal seas [33]. Although human-initiated overexploitation is well understood, extending back through the Pleistocene [44], identifying definitive examples of predator-driven extinction in the fossil record is more elusive, despite potential candidates. One example comes from the Neogene, where declining mysticete whale diversity coincided with the occurrence of carcharodontid sharks [45] and sperm whales [46]. Although these predators fed on mysticete whales during the Neogene [46,47], it is challenging to determine from the fossil record whether predation was directly responsible for the extinction of mysticete species. However, it is known

from modern data that predation can accelerate extinction in taxa that are already at risk [48]. Nevertheless, overexploitation stands out as a major threat for historical, current, and potentially future extinctions without a strong analog in the fossil record.

Habitat loss
Habitat loss or degradation is another primary factor associated with elevated extinction risk today, historically, and in the fossil record (Table 1), although driven by different ultimate causes. Kappel [42] showed that 76% of current ESA-listed marine, estuarine, and diadromous species were affected by habitat loss or degradation and 61% by pollution. For seagrasses and mangroves, habitat loss is the most important threat, followed by pollution and sedimentation [18,19]. Historically, habitat loss and degradation were important drivers for 37% of extirpations around the world [11] and 42% of extirpations in estuaries and coastal seas [33]. Large-scale losses of three-dimensional habitats, such as seagrass beds and coral reefs, can

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Box 2. Case studies: drivers of extinction through time

The geologic records of sea level, temperature, and ocean chemistry are being increasingly used to investigate the conditions associated with marine extinction. Climatic drivers have had a role in many ancient extinctions events, but not in all. The following examples illustrate how examination of the fossil record can help address the drivers of biological changes in marine ecosystems and distinguish the impacts of climate change from other impacts [84].

Reefs
Reefs have suffered five episodes of global-scale biodiversity loss or cessation of reef growth, termed 'reef crises' [27], over geologic time. The four most recent crises coincided with ocean acidification and rapid global warming, including three of the 'Big 5' mass extinctions (Figure I) [27]. Comparing the extinction rates of unbuffered (i.e., taxa that secrete carbonate skeletons, with limited or no circulatory system, and low metabolic rates [27,63]) versus other taxa points to

an important role for rapid increases in acidification in causing extinctions (Figure I) [27,28]. The most recent reef crisis (approximately 56 Ma) was characterized by rapid sea surface temperature rise and a similar order of magnitude of CO_2 increase as at present [54]. However, although a marked faunal shift occurred on continental carbonate platforms [85] at this time, reef assemblages in some other settings were relatively unaffected [86].

Nearshore marine environments
Nearshore marine environments during the past 2.5 Ma were characterized by substantial and rapid climate change, consisting of more than ten glacial–interglacial cycles (Figure II). Yet, extinctions among nearshore marine taxa in the Northeastern Pacific were minimal (Figure II) [53,87], and many species responded by shifting their geographic ranges to track preferred temperature, productivity, and other environmental gradients [88].
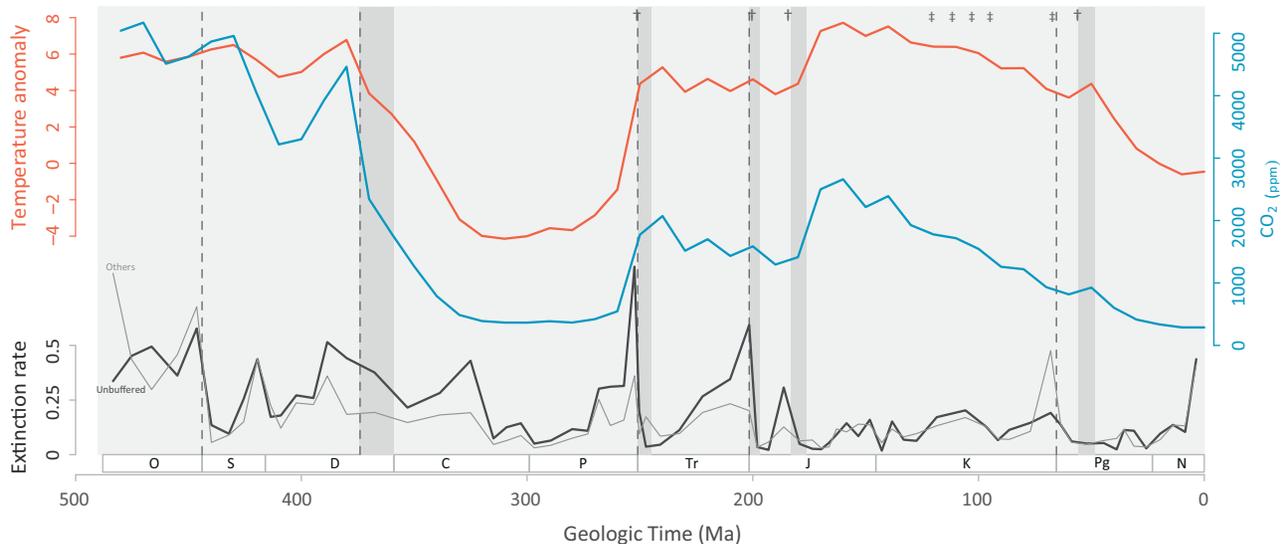
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Figure I. Rates of extinction for physiologically unbuffered versus other marine organisms and their association with global environmental change over geologic time. Unbuffered groups include calcareous algae, calcareous foraminifers, hypercalcified sponges, corals, calcareous brachiopods, calcifying bryozoans, and pelmatozoans. Vertical broken lines indicate mass extinctions and vertical gray bars indicate reef crises. Ocean acidification events from [27] indicated by † with additional candidate ocean acidification events from [89] indicated by ‡. Abbreviations: Ma, million years; ppm, parts per million. Reproduced, with permission, from [4] using extinction rates from [27].
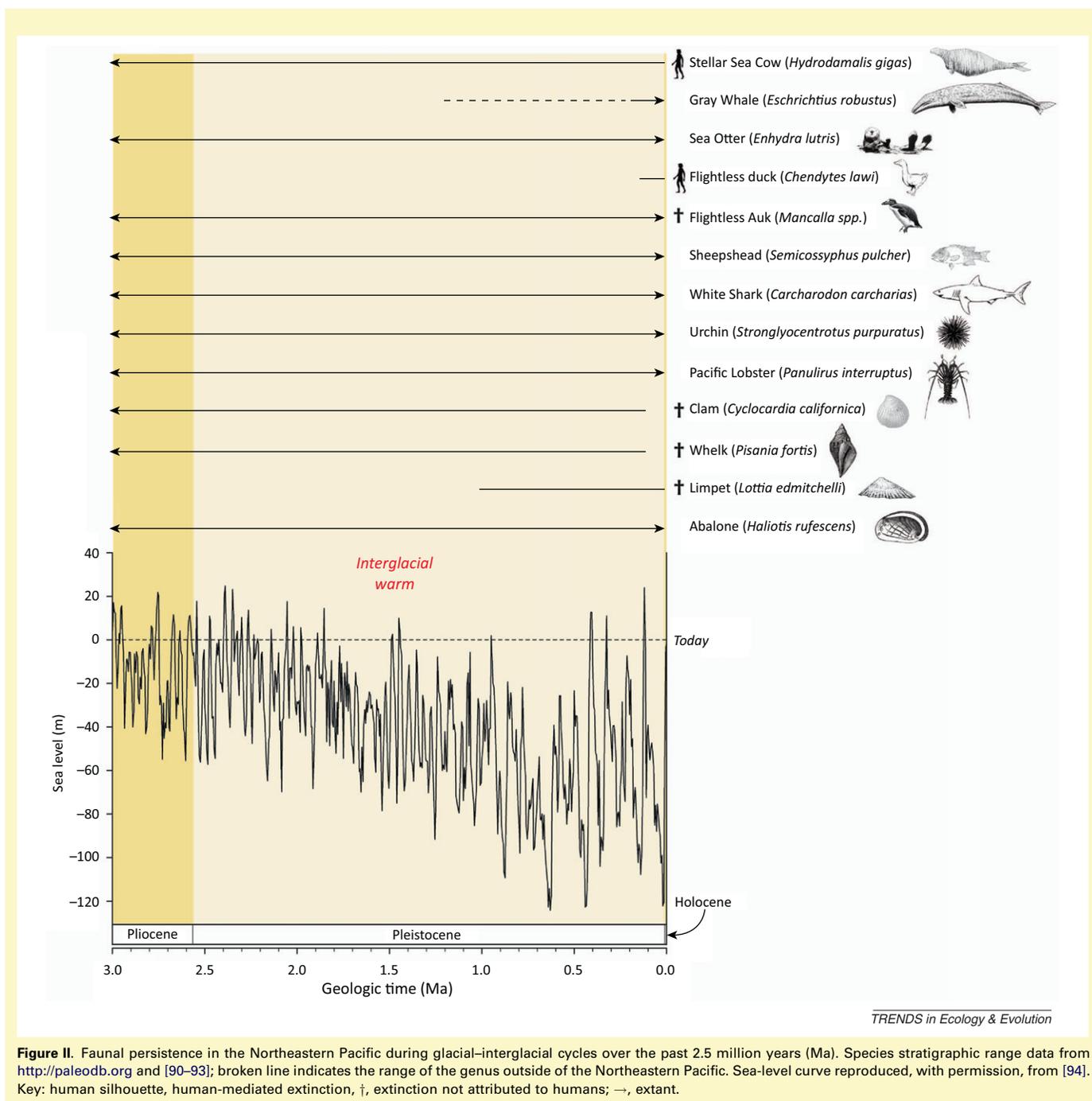
Figure II. Faunal persistence in the Northeastern Pacific during glacial–interglacial cycles over the past 2.5 million years (Ma). Species stratigraphic range data from http://paleodb.org and [90–93]; broken line indicates the range of the genus outside of the Northeastern Pacific. Sea-level curve reproduced, with permission, from [94]. Key: human silhouette, human-mediated extinction, †, extinction not attributed to humans; →, extant.

have particularly strong effects on associated species. In the Wadden Sea, for example, loss of such habitat contributed to 70% of the 25 species extirpations in historical time [34]. In the fossil record, the loss of shallow marine habitat due to falling sea level has been associated with elevated extinction rates [13] and biodiversity loss [49]. For example, sea-level fall driven by global cooling was associated with elevated extinction during the end-Ordovician (444 Ma) [50] and Eocene–Oligocene (34 Ma) [51] (Table 1), but not during the most recent glacial–interglacial cycles (1 Ma) [52,53] (Box 2). This might reflect a difference in starting conditions: the Late Ordovician and late Eocene were characterized by greenhouse conditions with extensive continental flooding, whereas the Pliocene–Pleistocene transition occurred in a world with minor

continental flooding that had already cooled considerably from the early Cenozoic.

Global warming and associated stressors
Global warming and ocean acidification, which are of growing concern today and for the future [3,4,38], were important factors in some ancient extinctions [27,28] but played little role in historical extinctions (Table 1, Box 2) [11,33,34]. Geochemical and paleontological evidence suggests that four of five global reef crises and three of five mass extinctions in the fossil record were associated with warming and acidification (Table 1, Box 2) [27]. However, not all organisms respond similarly to such conditions. For example, during the Paleocene–Eocene Thermal Maximum (approximately 56 Ma; Table 1), 30–50% of

deep-water benthic foraminiferan species went extinct, whereas other microfossil groups were relatively unaffected [54]. Today, climate warming and acidification pose increasing threats to corals [4,14,55], warming and sea-level rise to seagrasses and mangroves [18,19], and many species show range shifts, local extirpations, and invasions in response to changes in ocean temperature [56,57].

Anoxia and pollution

Anoxia is another important driver of extinction risk in both modern and ancient seas (Table 1). In addition to direct toxicity, oxygen depletion of bottom waters can lead to large-scale habitat loss [58]. In historical and modern times, bottom-water anoxia driven by excessive nutrient loading and decomposition of organic matter has led to some extirpations in estuarine and coastal waters [11,33,42]. Widespread anoxia is also associated with several major extinctions in the fossil record (Table 1), triggered by elevated atmospheric CO_2, global warming, diminished thermohaline circulation, and eutrophication [59]. Other forms of pollution (e.g., pesticides and toxic algal blooms) have also contributed to historical extinctions and current risk [11,15,33,38,42], but identifying definitive examples of these in the fossil record is challenging.

Synergistic effects

In the near future, most human impacts in the ocean will increase, and the effects of climate change will interact with existing threats, such as overexploitation and habitat loss [4,10,60]. There is great uncertainty about how these cumulative impacts will interact to affect marine species and ecosystems; if already severely stressed, their resilience to further change can be greatly reduced [8,61,62]. Historical assessments show that multiple human impacts were involved in approximately 40% of extirpations in the Wadden Sea [34] and 42% of extirpations in estuaries and coastal seas worldwide [33]. This usually involved the combination of overexploitation and habitat loss and, to a lesser extent, pollution. In the fossil record, many extinction events were associated with multiple stressors that might have acted synergistically. For example, the end-Permian extinction is associated with warming, acidification, and anoxia [27,28,41]. Further study of past extinctions caused by the interacting effects of warming, acidification, and anoxia might be especially informative for understanding future risk under projected climate change and environmental impact scenarios.

Biological correlates of extinction

Extinctions depend not only on extrinsic drivers, but also on the physiology and ecology of affected organisms. Consequently, biological characteristics have been widely used to assess extinction risk in ancient and modern seas [63,64]. However, are these biological correlates of extinction comparable over time?

Among contemporary marine mammals, greater body mass at weaning, fewer births per year, taxonomic group, small geographic range size, and small social group size are the major predictors of extinction risk globally [65]. In Canada, body size is the most important predictor of

extinction risk for marine mammals and age at maturity for marine fishes [66]. In addition, among 61 historical extirpations, large body size explained more than half (57%), followed by greater ecological specialization (28%) and small geographic range (7%) [11]. By contrast, in the marine invertebrate fossil record, geographic range size is the only biological characteristic consistently associated with elevated extinction risk [67–69]. The influence of other attributes, such as body size and feeding mode, varies according to extinction magnitude, duration, driver, and clade, and few attempts have been made to assess multiple correlates simultaneously [50,68–70]. Differences over time in the correlates of extinction risk might reflect the disproportionate current and historical impacts of exploitation relative to other threats, such as habitat loss, as well as differences between vertebrates and invertebrates, which are the focus of most paleontological analyses. In addition, the processes responsible for short-term population declines might not scale up to the 10^5–10^6-year timescales at which extinctions are observable in the fossil record. Thus, understanding biological correlates of risk in both modern and ancient seas requires additional investigation into how correlates vary with threats, timescales, and among clades.

Predicting future extinction risk: integrating paleontological, historical, and modern data

Predicting future extinction risk in the ocean is inherently difficult, given uncertainties regarding the relative importance of different drivers, potential interactions among drivers, a lack of long-term monitoring or basic assessment for many marine species, and spatial uncertainty in climate projections. However, integrating the lessons learned about extinction rates, drivers, and biological correlates from fossil, historical, and modern records can aid in making more meaningful future projections.

First, whereas recorded historical extinctions have largely affected economically important target species, mostly vertebrates, current and future risk extends to non-target species, including many invertebrates and plants. Here, information about fossil extinction rates could be used to project future risk among the many non-target species for which current assessments are lacking (Figure 2). A recent study of corals [71] provides support for such an approach, showing that those species at elevated risk today are related to species that suffered elevated rates of extinction and regional extirpation during the Plio–Pleistocene. This suggests that some biological attributes that confer resilience and risk are phylogenetically conserved [72,73] and that information about the past vulnerability of related species might provide meaningful predictions of current and future risk.

Second, although overexploitation and habitat loss are the primary drivers of historical extinctions and current extirpations, in the near future drivers such as warming and acidification implicated in extinction events in the deep past are expected to become more important. Thus, the fossil record provides important lessons on the responses of different groups of organisms to different climate change scenarios and to different rates of environmental change. For example, comparing episodes of past

warming and acidification can identify threshold rates below which carbonate saturation was well buffered (>10 000 years) [6] and warming and acidification had little effect on reef diversity and growth versus episodes of more rapid change associated with reef declines and extinction (Box 2) [4].

Third, in terms of the biological correlates of marine extinctions, it appears that body size has been strongly associated with historical and current risk, whereas geographic range has been one of the strongest correlates in the fossil record. These different patterns probably reflect vulnerability to different selective pressures. Body size has been an important trait of harvested species, with larger species under greater exploitation pressure. By contrast, the marine fossil record shows that large- and small-bodied taxa are equally at risk during times of large-scale environmental change, whereas taxa with small range sizes are at greater risk [74]. As such, extinction risk in the future might shift from larger-bodied species to those with restricted geographic ranges as marine ecosystems respond increasingly to habitat loss and the environmental disturbances associated with climate change.

Finally, a variety of modeling approaches have been developed to estimate future risk based on modern species distributions, including species diversity–area relations, species distribution and habitat suitability models, and ecophysiological models [75]. These methods are promising but have rarely been applied to marine systems [56], and do not yet consider the capacity for species to adapt. Another limitation is that these models tend to consider a single extinction driver rather than synergistic effects of multiple drivers, so expected extinction rates might be gross underestimates. Historical and fossil data could be used to evaluate how well these models perform and what environmental and biological data are most relevant [76].

Outlook: research challenges and future directions

Recent reviews have highlighted the tremendous value of multidisciplinary research in understanding past and current changes in marine ecosystems [32,33,43], as well as the role of historical and fossil records in understanding ecological and evolutionary responses to future environmental change [77]. Fossil, historical, and modern records of marine extinction and extinction risk offer considerable insights into the trajectories of marine ecosystems in the near and long-term future. Yet, taxonomic, temporal, and geographic scaling issues offer serious challenges for comparing fossil, historical, and modern data sets.

Taxonomic challenges include the fact that marine taxa have received relatively little attention compared with terrestrial species and, among marine groups, vertebrates have received disproportionate attention in modern and historical records. This might have led to the underestimation of historical extinctions and modern risk in other groups, such as invertebrates [21,38]. Therefore, enhanced assessments of current risk for invertebrate groups that have fossil records are essential to better understand similarities in risk over time, extinction rates on different timescales in the historical and fossil records, and how extinction rates vary with different rates and drivers of environmental change.

For both fossil and modern records, spatial and temporal sampling can be patchy, hindering direct comparisons. Fossil records are not available for all regions of the modern ocean, and many areas are undersampled with respect to both modern and ancient marine biodiversity. Some ocean habitats, such as the deep sea for current, historical, and macrofossil species records [78,79], are also chronically undersampled. Moreover, preservation and sampling of the fossil record is not uniform [49,80], leaving some time intervals under-represented in existing databases. Here, increased future sampling of under-represented areas and intervals could help fill important data gaps.

Finally, there are some methodological challenges to overcome. When comparing rates, the length of interval considered affects the calculated rate so that direct comparisons of extinction rates from the fossil record with those from historical or modern records still proves to be difficult [81]. However, many of these challenges can be addressed by careful sample selection, subsampling methods, modeling processes of sampling and preservation, and vigilance concerning the underlying assumptions and sources of error.

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