Opinion piece


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Palaeontology

Understanding modern extinctions in marine ecosystems: the role of palaeoecological data

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Because anthropogenic impacts on ecological systems pre-date the oldest scientific observations, historical documents and archaeological records, understanding modern extinctions requires additional data sources that extend further back in time. Palaeoecological records, which provide quantitative proxy records of ecosystems prior to human impact, are essential for understanding recent extinctions and future extinction risks. Here we critically review the value of the most recent fossil record in contributing to our understanding of modern extinctions and illustrate through case studies how naturally occurring death assemblages and Holocene sedimentary records provide context to the plight of marine ecosystems. While palaeoecological data are inherently restricted censuses of past communities (manipulative experiments are not possible), they yield quantitative records over temporal scales that are beyond the reach of ecology. Only by including palaeoecological data is it possible to fully assess the role of long-term anthropogenic processes in driving modern extinction risk.

1. Millennial scale context of extant ecological systems

Palaeoecological data, despite their shortcomings, can provide multi-millennial ecological records required to contextualize modern extinctions [1–5] and thus complement other types of data used to assess extinctions and extinction risks. While real-time instrumental records are the highest precision records and quantitative ecological research is best able to test mechanisms, their temporal scope is inadequate ([1], figure 1). Written records of exploitation deliver priceless insights further back in time, but they are typically qualitative [2]. Zooarchaeological data represent critical records of human harvesting activities [3]. By contrast, palaeoecology integrates biological, sedimentary and geochemical records to derive diverse quantitative data about ecological systems prior to, as well as during, human occupation and impact [4,5,7].

Palaeoecological research alone cannot completely document human-driven ecological changes because it relies primarily on restricted census data types (figure 1) and unlike written historical and midden records, palaeoecological research only correlates ecological changes with changing human activities. Ecological studies can take advantage of real-time instrument records and experimental manipulations to enable mechanistic understandings of ecological changes. Consequently, quantifying anthropogenic impacts necessitates a holistic approach—a synthesis of ecological, historical, archaeological and palaeoecological data—that provides more realistic assessments of anthropogenic changes and modern extinction risks (figure 1). Only then can we separate extinctions due to human impacts from those likely driven by natural causes. Of note, deep-time palaeoecological studies are becoming increasingly relevant for assessing current extinction risks (e.g. [8]). However, such studies represent macroevolutionary
approaches fundamentally different from those discussed here. Near Recent palaeoecological records are particularly valuable as they typically contain extant, albeit locally or regionally extirpated, species in an essentially modern geographical and environmental context.

While humans occupied continents and substantially impacted faunas and floras prior to Western colonization and industrialization (Medieval/Early Modern and Early/Late Modern transitions in figure 1), these represent substantial increases in anthropogenic pressures exerted on biological populations (e.g. [2,6]). Here we outline opportunities afforded by Recent palaeoecological data (i.e. surficial death assemblages and buried Late Quaternary sedimentary records) when assessing extinction risk in the context of human cultural development. We also outline some of the challenges in using these records for assessing extinction risk.

2. Recent palaeoecological records
(a) Naturally occurring shell assemblages sampled from surface sediment
Surficial accumulations of biomineralized skeletal material, or death assemblages, represent globally available historical
records of marine communities. These death assemblages yield demographic and ecological data somewhat analogous to human graveyards, including a comparable suite of biases. Naturally occurring death assemblages typically contain skeletal material produced over decadal to millennial timescales [7]. The composition of a death assemblage reflects the live community that produced it and provides strong evidence of species occurrence and abundance [5,7]. When death assemblages and living assemblages disagree, the cause is often attributed to recent anthropogenic change in the living community [5,7], although this requires the death assemblage to pre-date the change in the living community [7]. This is because death assemblages are evolving records of biological productivity and will eventually reflect an altered community state. Despite their potential biases, surficial skeletal assemblages represent an accessible record of past communities.

Because shell assemblages archive the pre-impact communities, they can be used to directly assess population declines and the efficacy of restoration efforts. The ecosystems of the Colorado River delta, which deteriorated drastically following construction of numerous dams, offer an apt example. Surveys and numerical dating of shell accumulations indicated clams were at least 20 times more abundant and remarkably stable over the last millennium, prior to human alteration of the river flow [9]. These data also demonstrate that restoration efforts have not returned the local benthic productivity to its pre-industrial levels. Geochemical and palaeoecological data also indicate that growth rates and trophic structure of shelly invertebrates have changed [10,11]. Similarly, isotopic indicators from fish otoliths [12] suggested that the pre-industrial river flow helped commercially important fish species to more rapidly attain large body size. Oxygen isotopes from pre-dam shells have been used to provide quantitative estimates of the water flow levels required to restore natural salinity levels in the delta [13]. Shell assemblages have also been used to strengthen litigation against industry, as exemplified by taphonomic and trace elements data from freshwater mussel shells, which provided direct evidence linking mussel extirpation to mercury pollution rather than other causes (e.g. [14]).

3. Key challenges
(a) Preservation and sampling
Palaeoecological data are subject to taphonomic biases associated with fossilization. Most obviously, organisms with robust skeletons typically yield more fossil remains than those without. However, taphonomy is just a special case of sampling bias. All data-gathering techniques have biases, and some taxa may be over/under represented by different sampling/observation techniques (e.g. [21,22]). As with ecological sampling, a species’ absence may reflect its true absence during the sampling period or the failure of a particular sampling methodology to sample it. A variety of commonly used methods can control for such sampling effects, and taphonomic processes are increasingly well understood (see [5,7,21,23] and references therein).

(b) Cores, excavations and buried palaeoecological remains
Sediment cores are increasingly recognized as valuable archives of past ecosystems. For example, cores were used effectively to document the role of fisheries in the decline of Tasmanian molluscan communities. The threefold decline in diversity and fourfold decline in abundance of molluscs observed in cores closely mirrored fishery activities in space and time, while actively harvested species declined relatively more abruptly [15]. While fishing and direct exploitation are linked to the decline of Tasmanian molluscs [15], introduced species have played an equally important role in reshaping these coastal marine systems, with 83% of live molluscan biomass collected in 1997–1999 belonging to introduced taxa [16]. While harvesting rarely drives marine species to extinction, the indirect impacts of fishing, introduced species, and other anthropogenic impacts have the potential to drive species locally if not regionally extinct [16]. To the extent that marine protected areas (MPAs) can represent control sites, most Tasmanian MPAs have existed for fewer than 20 years and the oldest temperate MPA has been active for just 40 years [16,17]. While the global increase in MPAs is laudable, it is important to recognize that indirect effects appear on decadal or longer timescales and that MPAs are not immune from anthropogenic impact [17,18]. Biominalized remains from sediment cores are the only long-term data source for most MPAs. Population collapses are not always a result of human activities. Fish scales, used to reconstruct a 1700-year history of sardine abundance off the California coast, documented nine major collapses and recoveries, demonstrating that sardine population crashes occurred naturally prior to the start of the fishery, and indicated an average recovery time of approximately 30 years [19].

Cores can provide a much longer temporal perspective than surficial shell assemblages (figure 1). Core data demonstrated that benthic communities of the northern Adriatic changed notably in the most recent centuries despite persevering virtually unchanged during the previous 125,000 years [20]. This exemplifies the value of palaeoecological core data in demonstrating differential responses of marine communities, which may be resilient to naturally occurring major climate perturbations, but vulnerable to recent human impacts.

(b) Chronology and time-averaging
While Holocene sediments enclosing fossils can be dated using a number of methods, using sedimentary dates implicitly assumes that fossils and sediments are coeval. Even when this is the case for the median fossil age, sediment derived ages cannot estimate the variance around the median age, termed time-averaging, which quantifies the time over which the fossils accumulated (e.g. [23,24]). Time-averaging can be quantified by numerical dating of individual fossils. Advances in amino acid racemization, carbon-14 and uranium–thorium disequilibrium dating have significantly reduced the costs, making it possible to date hundreds rather than a handful of specimens (see [7,18,23,24] and references therein). Estimates of time-averaging are critical when comparing palaeoecological to ecological data, so the differences in the timespan of sampling and temporal resolution of resulting data can both be assessed. For example, the above-mentioned River Colorado delta study [9] quantified time-averaging and corrected palaeoecological estimates of productivity to allow direct comparisons with ecological surveys of the modern fauna.
Fossil assemblages with highly precise chronologies and low amounts of time-averaging are most analogous to ecological samples. However, a highly time-averaged assemblage is valuable precisely because it provides long-term (often millennial scale) estimates of the relative importance of species in local communities. The essential chronological requirement is to place data in the temporal context of human impacts: does the assemblage pre-date or post-date the onset of substantial anthropogenic change?

4. Conclusion
To make meaningful contributions to policy and scientific understanding, conservation scientists must be able to move beyond simple observations of decline. The IUCN Red List is dominated by charismatic terrestrial organisms [25] because scientists have more data for those organisms. While the number of documented marine extinctions pales in comparison to terrestrial extinctions, this is in part an artefact of a lack of quantitative data on marine invertebrate abundances, ranges, habitats, dispersal and population dynamics [26]. While most palaeobiological/historical studies document population declines and extinctions at local and regional scales, these local and regional declines have a profound impact on communities and will have important implications for their extinction risk. Palaeoecological data inform us about past biospheres and are thus suited for generating testable mechanistic hypotheses regarding ecosystem changes, extinction threats and extinctions.

Ethics. No experiments involving animals were conducted during the course of this research.

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