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Historical baselines for large marine animals

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Current trends in marine ecosystems need to be interpreted against a solid understanding of the magnitude and drivers of past changes. Over the last decade, marine scientists from different disciplines have engaged in the emerging field of marine historical ecology to reconstruct past changes in the sea. Here we review the diversity of approaches used and resulting patterns of historical changes in large marine mammals, birds, reptiles and fish. Across 256 reviewed records, exploited populations declined 89% from historical abundance levels (range: 11–100%). In many cases, long-term fluctuations are related to climate variation, rapid declines to overexploitation and recent recoveries to conservation measures. These emerging historical patterns offer new insights into past ecosystems, and provide important context for contemporary ocean management.

Why we need historical baselines

For thousands of years, humans have settled along coastlines to make use of living marine resources for food, clothing, fuel, medicine and ornaments [1–3]. Only recently, however, did scientists start to unravel the long-term effects of humans on marine animal populations – essentially asking: where do we come from, and how did we get here? The search for historical reference points was partly initiated by Daniel Pauly's 1995 *Trends in Ecology and Evolution* paper [4], where he observed that most marine ecosystems were assessed by scientists only after many species had declined. He hypothesized that historical amnesia has contributed to a 'shifting baseline syndrome,' where our perception of 'what is natural' shifted toward more degraded ecosystems.

Therefore, it is difficult to evaluate the current state of marine ecosystems or to make future projections without knowing about the history, magnitude and drivers of past changes [5–7]. Until recently, marine ecology, conservation and management focused largely on the last 20–50 years of scientific monitoring data but rarely provided historical reference points that reach back to the beginning of exploitation, or other impacts. Historical reference points are critical, however, to measure and interpret long-term changes, and to set meaningful targets for management, restoration and recovery [5–7].

The emerging field of marine historical ecology aims to fill this gap. Over the past decade, researchers from various disciplines have engaged in reconstructing past ecosystem changes (e.g. [1–3,8–11]). To find historical baselines, and to understand drivers of change, they have used a remarkable diversity of data sources, ranging from palaeontological and archaeological evidence to molecular markers, historical records and fisheries statistics. To date, these studies have built a sufficient foundation to critically review what we have learned from marine historical ecology.

The value of using a diversity of data sources for historical studies has been reviewed elsewhere (e.g. [8,11,12]). Here we attempt to review and summarize available quantitative estimates of historical population changes to derive a more general picture of historical baselines in the sea, and to sketch a history of change. Our focus is on large (above 1 m maximum body length) marine fauna including whales, pinnipeds, large fishes and sea turtles, most of which have been the subject of intense historical exploitation. These species are a nonrandom yet important sample of marine biodiversity. Many of them have been of historical value to humans; today they include prominent resource species, as well as species of heightened conservation concern. Estimates for some of these populations have been controversial owing to inadequacies of available data and uncertainties associated with proxy measurements (see e.g. Ref. [13]). However, when comparing results across many studies, we found that several patterns emerged independently of the methods used.

In the following, we first highlight insights from different disciplines and analytical approaches used to reconstruct the past. We then compare the emerging patterns across species groups and studies to draw more general conclusions about the approximate magnitude of historical changes.

Expanding the timeline

Expanding ecological timelines into the past typically involves a range of records that provide estimates for different historical time periods (Figure 1a). A range of analytical approaches is available to compare present with past data and make inferences about the magnitude of historical changes (Box 1).

Palaeontological records

Palaeontologists work with sediment or coral reef cores that contain isotopes, trace elements, fossils, fish scales, shells and plant seeds in distinct layers across time, often spanning thousands of years. These are used as proxies to reconstruct past changes in climate, productivity and species occurrence. For example, $\delta^{15}N$ isotopes in sediment cores revealed large shifts in abundance in North Pacific sockeye salmon (*Oncorhynchus nerka*) over the past 2200

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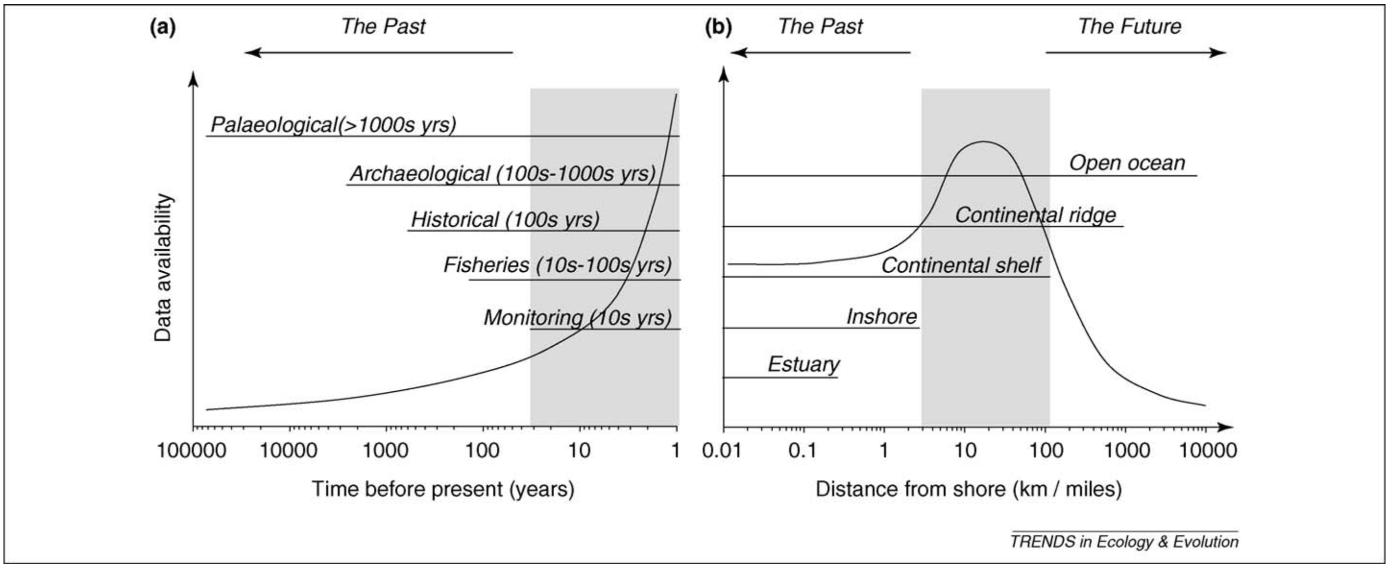

Figure 1. Temporal **(a)** and spatial **(b)** availability of modern scientific data (gray bars) covering the last 20–50 years. Including different disciplines enables us to expand the timeline into the past (a). Moreover, what has occurred in coastal regions (rivers, estuaries, inshore) in the past might reflect current changes on the continental shelves and future changes in the open ocean and deep sea (b).

years [14]. These shifts were linked to natural changes in climate and ocean productivity and provide a baseline for natural, long-term variation. Chronological sediment core data from estuaries [2] and coral reefs [15] revealed long-term stability followed by rapid declines in coastal water quality in the course of human settlement, including increased sedimentation, eutrophication and loss of vegetated habitat. Hence, palaeontological records have helped distinguish directed anthropogenic change from fluctuating baseline conditions.

The fossil record has also been used to estimate background rates of extinction at 0.1–1.0 marine species per millennium over evolutionary timescales [16]. This adds context to the current rate of species extinctions, which is thought to be ~1000 times higher [16]. Past mass extinctions were probably linked to sudden changes in climatic or environmental conditions [17]. In comparison, marine extirpations and extinctions in the 19th and 20th centuries were mostly caused by exploitation and habitat loss, with lesser impacts of pollution, species invasion, disease or climate change [2,18–20]. Overall, palaeontological records can identify natural long-term changes and their drivers, placing more recent anthropogenic changes into context.

Box 1. How to reconstruct historical baselines

Temporal comparison

Most studies compare point estimates of past and present species abundance, distribution or size; this is sometimes referred to as a then-now comparison (e.g. [1,41,60]). Although providing some valuable insight, this method ignores temporal variability. It is also difficult to judge whether the past estimate represents a true baseline given its historical context.

Time series analysis

Time series of absolute or relative abundance can indicate trends and fluctuations over time, which can be analyzed statistically, along with putative drivers such as fishing or climate records (e.g. [52,59,61]). Time series can be combined into longer or more robust series, or compared meta-analytically in search of general patterns. The length (10 s, 100 s or 1000 s of years) and historical context of the series needs to be considered when making inferences about baselines.

Hindcasting

If we have estimates on present species abundance, historical catch data and some information on life history such as recruitment, growth rate or natural mortality, we can backcalculate former abundance using simple population models [13]. Other, related approaches include the calculation of virgin biomass or carrying capacity based on spawner–recruit relationships [79,88], surplus production models to describe former stock dynamics [77] or stock reduction analysis [38]. Past abundance estimates can also be calculated based on historical habitat availability or past extractions [44] or ecosystem configuration [56]. Abundance–body mass relationships (size spectra) have also been used to estimate the potential abundance of marine animal populations under unexploited conditions [55].

Space-for-time comparisons

Unexploited regions in the ocean should reflect former abundance, size and species composition in exploited regions, assuming that other conditions are similar. Surveys across spatial gradients of exploitation can therefore provide insight into how exploitation changes population abundance and ecosystem structure (e.g. [66–68]).

Archaeological records

Animal remains in archaeological sites, such as bones, shells, teeth or hair, help us trace past species occurrence. At some former settlements, animal remains were deposited over 100s–1000s of years in layered garbage heaps, or ‘middens.’ Prehistoric hunters, fishers and gatherers had simple tools and relatively small populations, yet evidence is mounting that such subsistence exploitation had significant impacts on marine mammals, birds, turtles and fish [8]. For example, over the past 11 000 years, coastal people on San Miguel Island, California deposited bones and shells of >150 species, some of which are extinct today [21]. Intertidal shellfish and nearshore finfish were of greatest importance, followed by marine mammals. Over time, fishing increased in importance as human populations grew and technology improved. About 1500 years ago, fisheries expanded into deeper waters targeting larger offshore species [22]. Similar trends toward increasing reliance on marine fish and spatial expansion of fishing