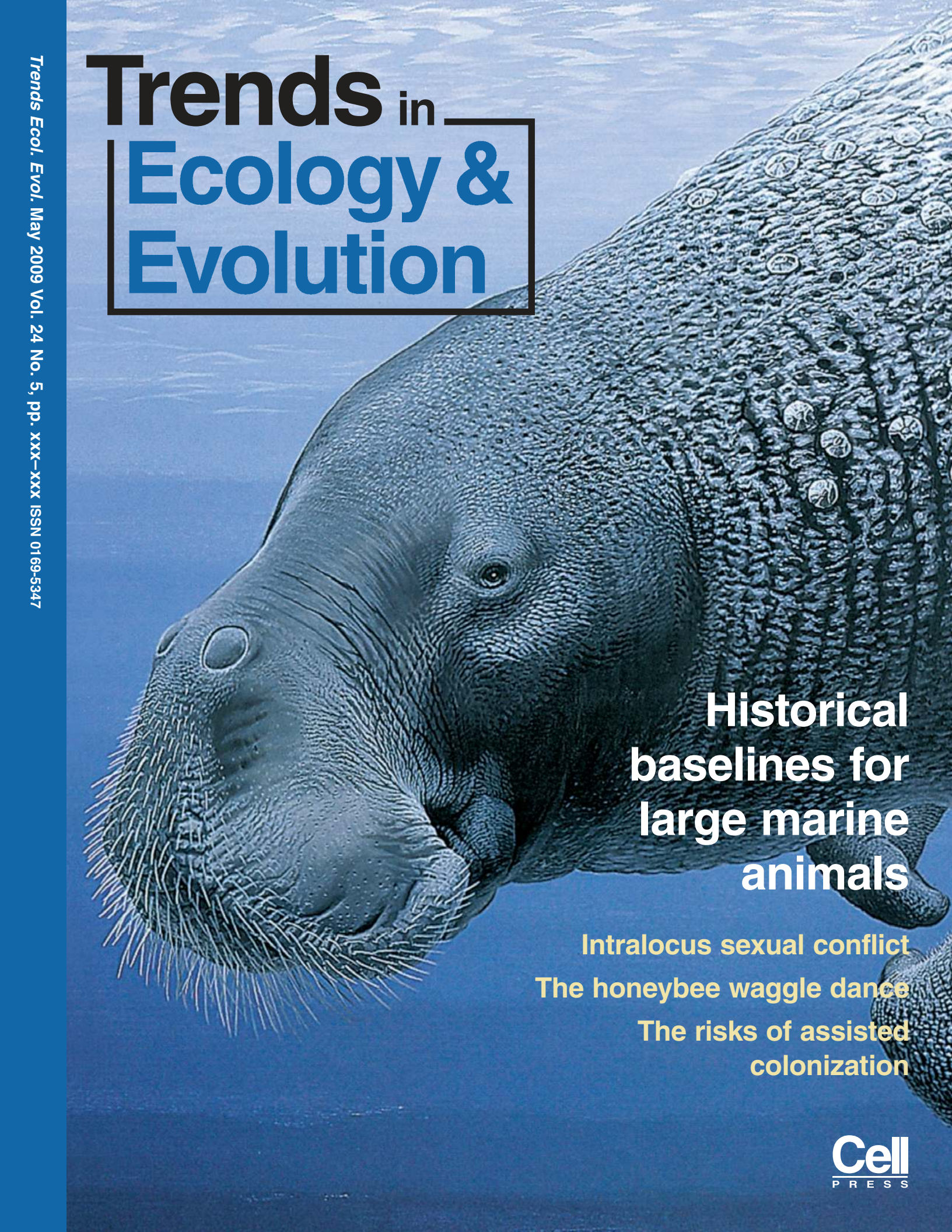


# Trends in Ecology & Evolution



**Historical  
baselines for  
large marine  
animals**

**Intralocus sexual conflict**  
**The honeybee waggle dance**  
**The risks of assisted  
colonization**

# 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 The search for historical reference points was partly initiated by Daniel Pauly's 1995 *Trends in Ecology and Evolution* paper [4], where he observed that most marine ecosystems were assessed by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 remark-

able 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.

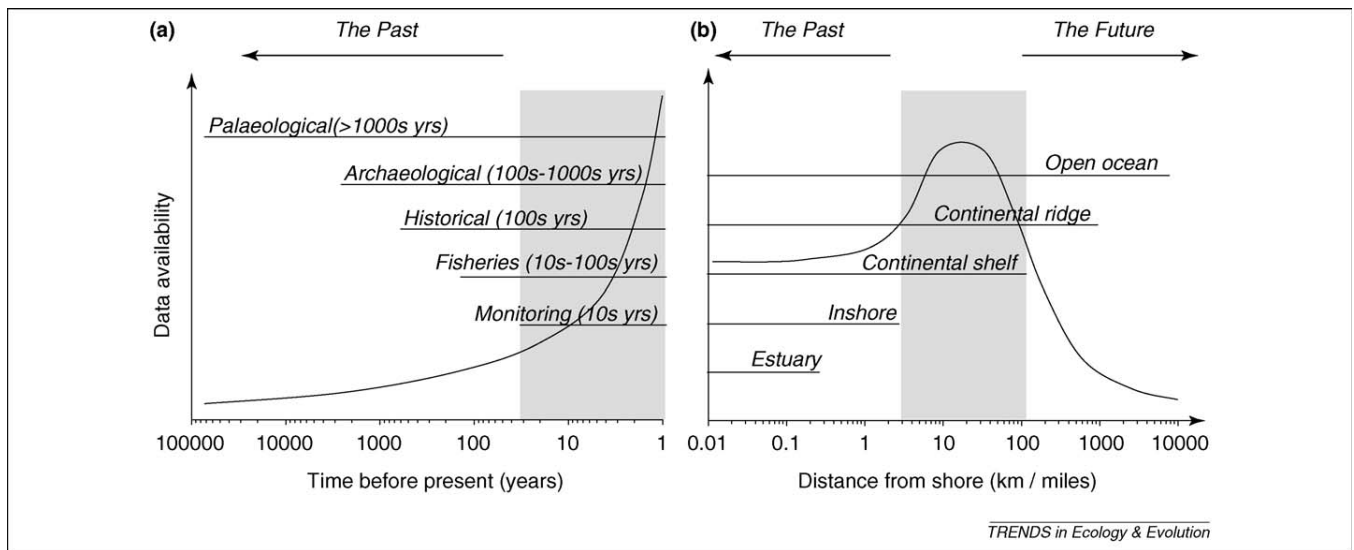
## Expanding the timeline

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,  $\delta^{15}\text{N}$  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-

### 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]).

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.

#### 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

are seen in archaeological records from southern Taiwan [23], the Wadden Sea [24], Great Britain [25] and the North Atlantic [26]. Historical records confirm a rapid expansion in marine fisheries in medieval Europe following a decline of freshwater and migrating fish resources [27].

An increasing number of archaeological studies document local resource depletions coinciding with growing human populations [8]. For example, relative abundance of large, nutritious species such as white sturgeon (*Acipenser transmontanus*) and several geese species decreased between ~2600 and 700 years ago in shell middens around San Francisco Bay, while smaller species increased [28]. During the same period, mean size and age of caught sturgeon declined, people traveled farther for hunting, and intense exploitation of cormorants (*Phalacrocorax auritus*, *P. penicillatus*) and sea otters (*Enhydra lutris*) collapsed local breeding colonies [28]. Similarly, middens in Puerto Marqués, Mexico revealed a decline and then loss of sea turtle (Cheloniidae) remains between ~5500 and 2300 years ago, and a shift from high to low trophic-level fish [29]. In New Zealand, archaeological remains indicated a >90% range contraction of fur seals (*Arctocephalus forsteri*) in the course of Maori hunting ~800–200 years ago [30]. In the southern Baltic Sea, European sturgeon (*Acipenser sturio*) remains dropped from ~70% of fish consumed in the 7th–9th centuries to ~10% in the 12th and 13th centuries [31]. Large aggregations of sturgeon were still reported until the 18th century, but annual catches declined to <500 individuals in 1900 and the fishery ceased in 1915 [32]. The species remains locally extinct today and is critically endangered across its range.

Not all archaeological records indicate resource depletion, and not all fluctuations are related to humans. Seabird remains on the Aleutian Islands, for example, showed long-term climate-driven fluctuations superimposed on local overhunting of accessible breeding colonies [33]. Likewise, many North Sea fish showed climate-related fluctuations over the past 9000 years which mirror recently observed shifts related to warming [34]. In summary, archaeological records suggest significant, but site-specific human impacts on local marine animal abundance, distribution and size long before the onset of commercial and industrial exploitation.

#### Historical records

Historical reports, maps, logbooks, catch records, even cookbooks and restaurant menus have been used to estimate the former distribution and abundance of whales, sea turtles and fish since the beginning of commercial exploitation. For example, whaling for North Atlantic right whales (*Eubalaena glacialis*) began around 1000 AD in the Bay of Biscay. Pre-whaling abundance was estimated at ~10 000 individuals, but populations on both sides of the Atlantic had been nearly exterminated by the early 20th century, with ~300 individuals (3%) remaining today [35]. Intensive whaling for southern (*Eubalaena australis*) and North Pacific right whales (*Eubalaena japonica*) commenced in the 19th century and rapidly expanded thereafter [36]. Historical catch data were used in a population model to estimate unexploited abundance of southern right

whales at 80 000 individuals [37]. The population was depleted to 0.1% of former abundance in the early 20th century, yet recovered to 7600 individuals (9.5%) following protection [13,37]. Other large, exploited whales show similar trajectories, depending on their value and ease of catch; North Pacific gray whales had declined by 90–96% in the early 1900s [38], North Atlantic humpback whales by 80–98% in the 1920s [39] and sperm whales by 73% in 1975 [40].

Another well-documented example concerns historical exploitation of sea turtles in the Caribbean. A comparison of historical and modern records from nesting beaches suggests that today's ~300 000 green (*Chelonia mydas*) and ~30 000 hawksbill turtles (*Eretmochelys imbricate*) both represent only ~0.3% of their historical abundance [41]. Similar data were used to document gradual range contraction and extinction of the Caribbean monk seal (*Monachus tropicalis*) [42]. Quantitative historical data for seabirds are sparse, but qualitative evidence indicates local extirpations following intense exploitation for food and feathers but also habitat loss, pollution and predator introductions [2,43,44]. Dwindling numbers of highly valued canvas-back ducks (*Aythya valisineria*), for example, could be traced by their increasing price on restaurant menus, rising fivefold from 1860 to 1918, after which the Migratory Bird Act prohibited its commercial sale [45].

For fish, historical records are often better than for other marine species. Based on records of bankers, financiers and tax collectors, Ravier and Fromentin [46] were able to reconstruct a 300 year time series of Mediterranean tuna catches from 1650 to 1950. Long-term fluctuations in trap catches appeared to be closely related to changes in temperature [47]. Since the 1950s, however, a 60% decline in spawning stock biomass has been attributed to over-exploitation [48]. In the Danish Wadden Sea, Holm [49] used fish inspectors' reports, archival information and tax records to reconstruct historical changes in inshore haddock stocks (*Melanogrammus aeglefinus*). In 1562, catches amounted to 1200 metric tons (mt) and remained roughly stable for a century before dropping to 500 mt by the 18th and to zero in the 20th century. Today, these stocks remain nonexistent and the fishery operates far offshore [49]. Similar inshore haddock stocks, as well as diadromous salmon, shad and sturgeon, were extirpated in the southern North Sea [24,43] and in other parts of the world [50] in the 19th and early 20th centuries. In summary, historical records imply that many highly valued large marine animals were severely depleted before the mid 20th century, and reached their low point decades to more than a century ago.

#### Fisheries data

Fisheries data separate into fisheries-dependent and -independent data. The former derive from commercial catch or effort data, the latter from research surveys that provide standardized abundance, size and life-history data of target and non-target species. Regularly collected survey data were rarely available before the 1960s, and typically lag the beginning of exploitation by decades if not centuries. In some cases, however, trawl surveys were performed

at or before the beginning of a large-scale fishery, providing insight into historical baselines. In the Gulf of Thailand, for example, overall fish biomass declined by 86% since the baseline survey in 1961 [51], and large predatory fish by 91% [52]. Similar declines for large fish were seen in research surveys from south Georgia (84%) and eastern Canada (90–92%) [52]. On the southeast Australian shelf, survey data indicate declines of 91% for the dominant target species, but other species declined less or even increased [53]. A contrasting pattern was seen in the Gulf of Alaska, where a 55% decline in total biomass from 1970 to the 1980s was followed by a sudden climate-related increase in the 1990s which more than compensated previous declines [54].

A macroecological approach was applied in the North Sea, where no surveys reach back to the beginning of exploitation. Here, size and biomass spectra from recent trawl surveys were used to project biomass of large fish under current and no fishing pressure. This indicated a 97% decline for 4–16 kg fish and >99% decline for 16–66 kg fish [55]. For the North Atlantic as a whole, ecosystem models were applied to predict past and present biomass of high trophic-level fish, suggesting a 90% decline since 1900 [56]. Other hindcasting approaches were used to predict former abundance of Atlantic cod (see Box 2).

In contrast to research surveys, fisheries-dependent data are biased toward commercial species and can be prone to gear-related changes, misreporting and other problems. In many cases, however, where survey data are absent, standardized commercial catch rates have been employed as a proxy for relative abundance. For example, using a global data set for the Japanese pelagic longline fishery, Myers and Worm [52] documented that catch-per-unit effort of large tuna and billfish declined by ~90% on average since the beginning of large-scale exploitation in the 1950s. This particular result has been very controversial, however, owing to uncertainties associated with changes in longline targeting, gear and effort distributions [57,58]. Where integrated stock assessments are available, they present a more varied picture. Southern bluefin tuna (*Thunnus maccoyii*), for example, is considered critically endangered, with spawning biomass estimated at 5–15% of pre-exploitation levels [58], whereas Pacific albacore (*T. alalunga*), yellowfin (*T. albacares*), skipjack (*Katsuwonus pelamis*) and bigeye tuna (*T. obesus*) adult stocks remain at 12–83% of estimated unexploited biomass [59]. Most scientists now agree that stocks of valuable, large target species (such as bluefin and bigeye tuna) have been severely depleted and are of management concern, whereas smaller species such as skipjack appear to be closer to their base-

### Box 2. Case study: historical baseline for Atlantic cod

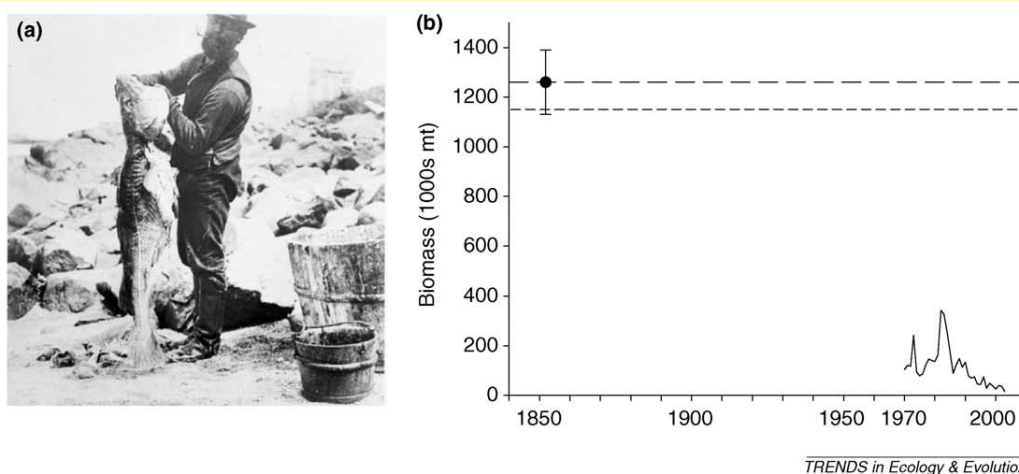
Atlantic cod (*Gadus morhua*) has been an ecologically and commercially dominant species throughout the North Atlantic. Archaeological data indicate that average size of cod fished in the Gulf of Maine remained similar (ca. 1 m; Figure 1a) over the past 5000 years until rapid declines in the later 20th century [1]. Since the 1500s, overall catches gradually increased, peaking in the 1960s, declining in the 1970s and collapsing in the 1990s, particularly in Eastern Canada [73,77].

Rose [77] used a surplus production model, based on reconstructions of cod catches in Newfoundland, to describe biomass dynamics from 1505 to 2004. Results suggest climate-related declines during the Little Ice Age (1800–1880), large declines in the late 1960s caused by overfishing and recent collapses in the late 1980s caused by both, leaving biomass at <3% relative to the average from 1500 to 1800.

Rosenberg *et al.* [9] reconstructed historical abundance of cod

stocks on the Scotian Shelf, Canada before the industrialization of fishing. They combined historical records on catch and effort from fisheries log books with population models to estimate 1.26 million mt of cod biomass in 1852. In comparison, cod biomass on the Scotian Shelf in 2000–2003 (NAFO Divisions 4X and 4VSW), estimated from research trawl surveys, was less than 40 000 mt or 3% of historical abundance (Figure 1b).

Spawner–recruit relationships were used to estimate the carrying capacity of 21 cod (*G. morhua*) populations across the North Atlantic [79,88]. Results suggest that current spawning stock biomass remains at 0.1–16% of carrying capacity, with ten populations falling below 2% [79]. For the Scotian Shelf, carrying capacity was estimated at 1.15 million mt, which is slightly lower than the abovementioned historical estimate but lies within the confidence interval (Figure 1) [9].



**Figure 1.** Estimating former abundance of Atlantic cod. (a) Photograph of a fisherman from Monhegan Island, Maine, USA with a codfish in the 1880s (courtesy of Robert Steneck). (b) Cod biomass on the Scotian Shelf as estimated from research trawl surveys in 1970–2003 (solid line), historical fisheries logbooks in 1852 (black dot, with confidence interval, and long-dashed line) and carrying-capacity analysis (short-dashed line). Reproduced, with permission, from Ref. [9].

line biomass, or might even increase owing to predatory release [58,59,60].

Estimating historical baselines for poorly assessed or non-target species is even more difficult. In those cases, it is particularly important to combine multiple data sources to alleviate concerns about any one source. For example, Ferretti *et al.* [61] combined several recreational and commercial fisheries and sighting records to track long-term declines of large sharks in the Mediterranean Sea. Using a meta-analytical approach, this analysis suggests 96–99% declines in large sharks. Similarly large declines were observed in large sharks in the northwest Atlantic [62], the Gulf of Mexico [63,64] and the tropical Pacific [60], independently of the specific data source used.

#### *Living memory*

Whether anecdotal information from living memory can be used for scientific inference has been of some debate. Yet, recent studies have provided valuable insights into historical changes and the aforementioned 'shifting baseline syndrome.' For example, structured interviews in the Gulf of California revealed that older fishermen had experienced higher catches and larger-sized fish than younger fishermen [10]. The number of fish caught in their best day's catch declined by 96% from 1940 to 2000. Similarly, perceptions of old, middle-aged and young fishermen in a traditional African coral reef fishery indicated that the number of groupers caught in the best day's catch was reduced by 75%, while maximum size had declined by 83% [65]. Older fishermen knew of more fish species that had declined (18 versus 8.5) over a longer period (15 versus 5 years), and reported an outward expansion of the fisheries to off-lagoon areas [65]. These studies suggest that older generations have experienced higher catches and larger sizes of valued fish than younger generations. Such information is particularly valuable for artisanal fisheries, and other data-poor situations.

#### *Ecological monitoring data*

Scientific monitoring programs quantify changes in abundance, distribution and size of marine species, with some surveys reaching back 20–50 years. These data are essential reference points for present-day conditions. Some scientists have recently employed field surveys across a spatial gradient of fishing pressure to evaluate the ecosystem effects of exploitation. Assuming that unpopulated and unfished ocean regions reflect pre-exploitation levels of marine fauna, such space-for-time substitution can approximate historical baselines. For example, dive surveys comparing the biomass of shallow reef fish assemblages between the remote northwestern and urbanized main Hawaiian Islands revealed that fish biomass was reduced by 72% over this gradient; however, large apex predators (primarily sharks and jacks) were reduced by 94% [66]. Virtually identical results emerged from two studies of the Line Islands, ~2000 km south of Hawaii [67,68]. Likewise, in American Samoa, biomass of large apex predators (>50 cm length) was reduced by 74% in high- compared to less-populated islands [69]. Including data from the Pacific Remote Islands area raised this estimate of depletion to 95% [69]. These studies indicate

that expeditions to ever more remote places might drastically change our perception of what was natural in these ecosystems.

#### *Molecular data*

The level of genetic diversity found in a population today can give insight into its average size over evolutionary times. Roman and Palumbi [70] used molecular markers to estimate pre-exploitation abundance of North Atlantic humpback, fin and minke whales. Their estimates suggest today's populations are at 4, 15 and 56% of their original size, respectively, far less than previous calculations based on current abundance and historical catch records [70]. Using similar methods, pre-whaling abundance of Pacific gray whales was estimated at three to five times higher than current levels [71]. This population had been thought fully recovered based on population reconstructions using catch records [71]. Marked differences among these estimates likely reflect methodological uncertainties, for example in the estimation of historical catch records or mutation rates, and are the focus of ongoing research [13].

#### *Piecing the puzzle together: a history of change*

So far, few studies have aimed at systematically piecing together results gained from different disciplines and periods in the past [2,3]. Such interdisciplinary studies provide synthetic, highly aggregated timelines that are based on hundreds of individual estimates, and allow broad comparisons across different regions and species groups. For example, across 14 coral reefs in the Atlantic, Red Sea and Australia, very similar trajectories of change have emerged. Following European colonization, large carnivores and herbivores were rapidly depleted well before smaller animals and architectural species [3]. A similar study on estuaries and coastal seas [2] found increasing resource depletions during the Roman Empire in the Mediterranean, during the medieval period in northern Europe and following European colonization in North America and Australia. All systems followed similar trajectories: slow changes over millennia, followed by rapid depletion over the last 150–300 years and some recovery in the 20th century, particularly for marine mammals and birds. Similarly, synthetic studies in the Benguela upwelling system [72], the Outer Bay of Fundy [44], Newfoundland [73], the Wadden Sea [24,43,74] and the Gulf of California [75] revealed a much longer history of change than previously assumed, and evidence for a temporal acceleration and spatial expansion of change over the last few centuries.

#### **Emerging patterns**

The increasing body of literature on historical change in the oceans not only provides insight into individual case studies but also a foundation to search for general patterns. In the following, we discuss such patterns as they emerged reviewing the studies described above and in Box 3.

#### *Finding baselines*

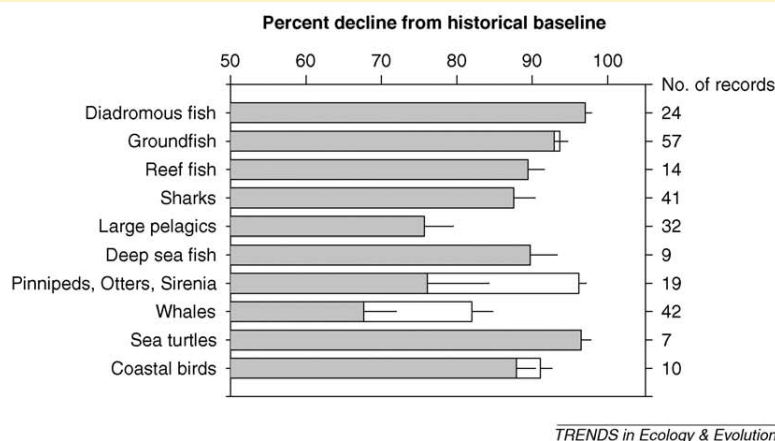
Finding a 'pristine' baseline is difficult because it is a moving target. First, there are climate-driven long-term fluctuations in animal abundance on scales of decades to

**Box 3. Population changes of large marine animals relative to their historical baseline**

We compiled studies estimating historical population changes for large marine animals (mostly >1 m maximum body length). Most species were highly valued and heavily exploited historically. We included studies that considered (i) extended time periods (100s to 1000s of years) in the deep past (mostly palaeontological, archaeological and historical studies), (ii) historical time series covering the effects of commercial exploitation, (iii) fisheries data starting at or before the onset of industrial exploitation, (iv) survey data across spatial exploitation gradients, (v) genetic analyses of former abundance or (vi) modeling approaches hindcasting pre-exploitation abundance. We aimed at covering different species groups and ocean regions to gain a general picture of historical change, yet our selection was limited by available historical studies. In total, we compiled 95 studies providing 256 estimates on historical declines in abundance, some of them for single species or stocks, others for

groups of species (see [supplemental data online](#)). From these records, we either used the estimated percent decline in absolute or relative abundance provided by the authors, or calculated the percent decline from the beginning to the low point (minimum) and to the recent end point of the data series.

Across all 256 records, populations on average declined by 89% ( $\pm 1\%$  SE) from their historical baseline to the low point in the data series (Figure 1). Whales, pinnipeds, otters, birds and some groundfish showed recent recovery (Figure 1). This lowered the estimated average population decline today to 84% ( $\pm 1.3\%$  SE) of historical abundance. Because the available data are mostly limited to highly valued, commercially important species, our estimates do not reflect average changes in marine species abundance *per se*, but should be interpreted for large, exploited species in particular.



**Figure 1.** Estimated declines of large marine animal populations from their historical baseline based on 256 records from 95 studies (see [supplemental data online](#)). The graph indicates the average decline and standard error for each species group to the low point in abundance (white bars) and to the most recent point in the data series (gray bars; in many cases the same as the low point). The number of corresponding records for each species group is shown on the right. Records can include estimates from different methods, stocks or regions for the same species; see [supplemental data online](#) for details.

centuries [14,33,76,77]. Exploitation is often superimposed on these fluctuations, leading to sharp and often sudden declines. Whereas the effects of climate variation and exploitation can often be separated quite clearly [33,77], they go hand in hand in other cases [12,77].

Second, many resource species have been affected throughout human history, and even low levels of subsistence exploitation had measurable effects [12,28,69]. This means that it is not always possible to trace records back to the beginning of exploitation. Where such records exist the observed magnitude of decline tends to be high, much of it occurring in the early years of exploitation [52,53]. Notably, this is partly intended by fisheries management to increase stock productivity [78]. These initial declines are missed if data series start later. In such cases, hindcasting virgin population levels or carrying capacity are valuable alternatives [55,77,79] (Box 2).

Finally, the relative value of the species in terms of nutrition, ease of catch, status or revenue is an important predictor for the magnitude of change over the baseline. Highly valued, large, coastal species were usually depleted first and most severely, with subsequent expansions to less valued or less accessible resources. These patterns have been documented equally in ancient [8,23,28] and recent times both on large [80] and small scales [65,81].

**Magnitude of historical change**

Individual estimates of historical change often have large uncertainties associated with the available data, proxy measurements or method limitations. Therefore, we aimed at comparing estimates across species, regions and approaches to evaluate whether there would be a more general answer to what the magnitude of change has been for particular groups of large marine animals (Box 3). Across 256 estimates from 95 studies (most of them described above), the average decline over the estimated historical baseline was 89%. Recent recovery of some species reduced that estimate to an 84% average decline today (Box 3). These figures correspond to threatened or endangered status following International Union for Conservation of Nature and Natural Resources (IUCN) criteria, and hence many (but not all) of the severely depleted species have been listed on national or IUCN red lists [20,61,79]. Results were reasonably consistent across different species groups (Box 3); diadromous fish, pinnipeds and sea turtles showed some of the sharpest historical declines, whereas recovery appeared most pronounced in mammals and birds (Box 3).

There are two important caveats to this analysis. First, aggregating results from the literature might be subject to publication bias because small or no changes in abundance

are less likely to be published than large, sweeping declines. Second, most historical studies so far have focused on large, valued and often heavily exploited species, for which historical declines are likely larger than they would be for a random sample of marine species. This might be different for modern fisheries and ecological data, where assessments are cast more broadly. Yet, a review of changes in abundance of 232 fish populations for which modern stock assessments were available indicated an average 83% decline from maximum breeding population size over 10–73 (average 25) years [82]. Similarly, an analysis of aggregated catch, abundance and size data for all exploited marine mammal populations suggested declines of 76% across all species and 81% for the great whales since the beginning of exploitation [38]. These figures are surprisingly similar to average declines observed in historical data and suggest a more general phenomenon.

#### *Spatial expansion*

A common response to local resource depletion has been the spatial expansion of exploitation to distant, previously unexploited resources. Such expansions and increasing reliance on offshore resources have been observed in archaeological records from California [22,28], Mexico [29], southern Taiwan [23], the Wadden Sea [24] and the North Atlantic [26]. Archaeological and historical records also explain the increase in marine resource use in medieval Europe as a consequence of declines in preferred freshwater and migrating fish [27]. Spatial expansions are also reflected in the history of the North Atlantic cod fishery that expanded from inshore Europe to continental shelves across the North Atlantic [27,73,77], and the global whaling history [36,38]. On a global scale (see Figure 1b), marine exploitation began in estuaries and along the coasts 100–1000 s of years ago, expanded across the continental shelves in the 19th and 20th centuries, moved into the open oceans in the mid 20th century and recently delved into the deep sea [24,52,80,83]. Past changes seen in rivers, estuaries and coastal seas might mirror some of the present changes seen offshore.

#### *Temporal acceleration*

Along with the spatial expansion, we can observe a temporal acceleration of change over time that is likely linked to technological advances and increasing human population and demand [2]. Whereas historical changes in many coastal regions unfolded over 100s–1000 s of years with simple tools and small boats [2,3], similar changes might have occurred on the continental shelves over the last 100–200 years [9,61,79], in the open ocean over the past 50 years [52,60] and in the deep sea over the last ~10–20 years [80,83]. During this time, fishing vessels have switched from sail to motor, and became larger, faster and more efficient. Yet, global catches have stagnated and decreased recently, likely indicating a limit to marine exploitation and a need for rebuilding lost resources [80].

#### *Lessons for recovery*

Management and conservation efforts in the 20th century have enabled some exploited populations to recover. Among

the reviewed 256 estimates of historical depletion, 40 populations experienced recovery in the 20th century, 33 of them marine mammals (Box 3). Likewise, there is evidence for recovery in marine bird populations [2,43,44] and some marine fish [82]. On average, recovery enabled populations to increase from 13 to 39% of their historical baseline; this often took several decades. Whereas conservation of mammals and birds has become generally accepted, recovery of exploited fish populations is still at the beginning, even where rebuilding plans exist [84]. Of 74 US fish stocks requiring recovery under the Magnuson-Stevens Act, half showed signs of increase by 2004, but less than 5% had reached the recovery target since 1996 [85]. Time might be a factor, as many long-lived fish require a decade or more to recover [84]. Recovery potential might also depend on the magnitude of previous depletion, among other factors [82]. For mammals and birds, reduced exploitation in combination with protection of breeding colonies and feeding grounds appeared to enable recoveries in most cases [2,20].

#### **Conclusions and future research**

Our review suggests that human impacts on marine ecosystems can now be traced back hundreds, sometimes thousands of years into the past. The new field of marine historical ecology has brought together scientists from diverse disciplines, yet different approaches often seem to yield similar results. The magnitude of historical population declines for highly valued, large marine animals, for example, typically seems to approach one order of magnitude (Box 3 [38,82]). Recovery is a more recent phenomenon and we can begin to learn from these successes, as well as from past failures. Many populations, particularly those of large, slow-growing species, remain at low abundance relative to historical baselines, and the number of IUCN-listed endangered species is growing [86]. Whereas exploitation and habitat loss have been primary drivers of historical population declines, climate variability has played a large role for long-term population fluctuations. As management agencies increasingly try to curb over-exploitation, and climate change intensifies, climatic factors might become critical for predicting the future of ocean ecosystems [87]. Historical research might benefit from a renewed focus on the consequences of past climate fluctuations, which might help anticipate future perturbations [33,34,77]. At the same time, we propose that historical approaches need to move beyond a focus on individual, highly exploited populations, and take an ecosystem approach wherever possible. Finally, we suggest that a better understanding of factors that enabled or impeded past recoveries will help managers to allocate limited resources wisely. In this respect, the ocean's past will continue to be an important reservoir of information needed to interpret current trends, predict future changes and inform management and conservation efforts.

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## Supplementary data

Supplementary data associated with this article can be found at doi:10.1016/j.tree.2008.12.004.

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