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Food for Thought

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Geohistorical insights into marine functional connectivity

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Abstract

Marine functional connectivity (MFC) refers to the flows of organic matter, genes, and energy that are caused by the active and passive movements of marine organisms. Occurring at various temporal and spatial scales, MFC is a dynamic, constantly evolving global ecological process, part of overall ecological connectivity, but with its own distinct and specific patterns. Geological and historical archives of changes in the distributions, life histories, and migration of species can provide baselines for deciphering the long-term trends (decadal to millions of years) and variability of MFC. In this food-for-thought paper, we identify the different types of geohistorical data that can be used to study past MFC. We propose resources that are available for such work. Finally, we offer a roadmap outlining the most appropriate approaches for analysing and interpreting these data, the biases and limitations involved, and what we consider to be the primary themes for future research in this field. Overall, we demonstrate how, despite differences in norms and limitations between disciplines, valuable data on ecological and societal change can be extracted from geological and historical archives, and be used to understand changes of MFC through time.

Keywords: palaeontology; archaeology; historical ecology; geology; sclerochronology; genetics

Introduction

Marine functional connectivity (MFC) encompasses all of the movements of marine organisms, both active and passive, that drive flows of organic matter, genes, and energy, and create functional interdependence between habitat patches, distinct areas, and ecosystems (Darnaude et al. 2022). The recent emergence of this ecological concept moves beyond structural or seascape connectivity, which solely considers physical connections between marine habitats and regions (Tischendorf and Fahrig 2000; Table 1). MFC describes how living organisms respond to environmental variations throughout their lifespan by moving between habitat patches over various spatial and temporal scales (Tischendorf and Fahrig 2000). As such, MFC is largely determined by structural connections

Table 1. Examples of changes in MFC that might be observed over long (>decadal) timescales associated with their long-term drivers.

Long-term driver	Environmental changes	Consequences for MFC	Examples
Climate	– Ocean temperature – Sea-level – Ice cover – Seawater salinity – Ocean pH	– Changes population connectivity as species distributions shift due to: a) their thermal/salinity/pH/oxygen tolerance and b) physical disconnection of habitats as ice sheets contract (for polar species) or sea level rises (for coastal/shelf species)	– Migration of small pelagic fishes from the Atlantic into the Mediterranean changed in the historical past following the different phases of the North Atlantic Oscillation and the Atlantic Meridional Oscillation (Alheit et al. 2014, Tsikliras et al. 2019).
Palaeogeography controlled by tectonics and volcanism	– Marine gateways size – Coast and shelf areas sizes and physical connectivity	– Population connectivity changes – Migration routes closed with the restriction of marine gateways – Changes dispersal pathways	– Opening of Bering Straits led to Early Pliocene trans-Arctic interchange and homogenization of Pacific and Atlantic mollusc fauna by facilitating larval dispersal (Vermeij 1991). – Formation of the Isthmus of Panama hindered dispersal between Caribbean and Pacific (O'Dea et al. 2016).
Ocean circulation	– Water-column stratification – (De)oxygenation	– Changes population connectivity due to species distribution contraction in response to deoxygenation – Stratification inhibits vertical migration of zooplankton and fishes – Changes plankton and larval dispersal pathways – Changes seasonal latitudinal migration routes (for animals depending on currents)	– Expansion of marine molluscs in the Southern Ocean after the establishment of the Antarctic Circumpolar Current (Beu et al. 1997, Hodell et al. 2021).
Biogeochemical cycles over geological timescales	– C, N, S, P, and O availability and distribution in the oceans	– Changes in migration routes driven by nutrient availability – Vertical migration patterns controlled by changing productivity at surface	–Change in nutrient supply during the Early Oligocene drove lanternfishes to deeper waters, potentially initiating their diel vertical migration (Schwarzhans and Carnevale 2022).
Evolution		– Organismal traits associated with MFC (e.g. larval dispersal capacity) may be favoured or not by the evolutionary process	–The evolution of herbivory-related traits of coral reef fishes favored Miocene–Pleistocene expansion of their lineages and thus of coastal-to-deep connectivity (Siqueira et al. 2019).

(Lough et al. 2017). However, the biology and ecology of organisms can often lead to divergence from structural connectivity, sometimes even resulting in linkages that could not be achieved by passive fluxes (McInturf et al. 2019).

While climate change and human activities affect both structural and functional connectivity, it is functional connectivity that ultimately determines the demographic, ecological, and evolutionary interdependency of populations and communities (Cowen and Sponaugle 2009, Lamberti et al. 2010), and may attenuate or amplify the ecological effects of environmental change (Marcos et al. 2021). MFC varies in space and through time, since it may be caused by temporary or permanent movements of individuals during their lifespan, but also because it depends on the evolutionary stability of the related organism traits (Auffret et al. 2015). Therefore, changes in MFC may occur over timescales from several centuries to hundreds of millions of years, and, importantly, MFC evolves through time as individuals, populations, and species respond to progressive or episodic environmental changes (Wood et al. 2022).

Geological, archaeological, and historical archives (together referred to here as 'geohistorical') are useful for describing the past distributions, life histories, and migratory behaviour of marine species, (Fig. 1), revealing past functional connections between populations, communities, and ecosystems, both at sea and the land–sea interface. This paper results from the discussions at the international workshop 'Geohistorical perspectives on functional connectivity patterns' (Sesimbra, Portugal—25 May 2023) and aims to provide food for thought and a research roadmap for using geohistorical data to study MFC. Specifically, we focus on identifying: (1) the types of geohistorical data that can be used to study past MFC patterns; (2) the resources available for such work and their limitations; and (3) how they might be used to understand MFC. In order to illustrate how geohistorical records can provide information on MFC, we present three case studies: (a) population connectivity during the Pleistocene glacial–interglacial cycles; (b) the Mediaeval and early modern hunting of marine mammals; and (c) the formation of the Isthmus of Panama and its cascading effects of ocean connectivity loss. We conclude with a set of best-practice guidelines and a series of open questions that we believe should be the focus of future research on this topic, highlighting the importance of advances in recovery methods and of the taxonomic

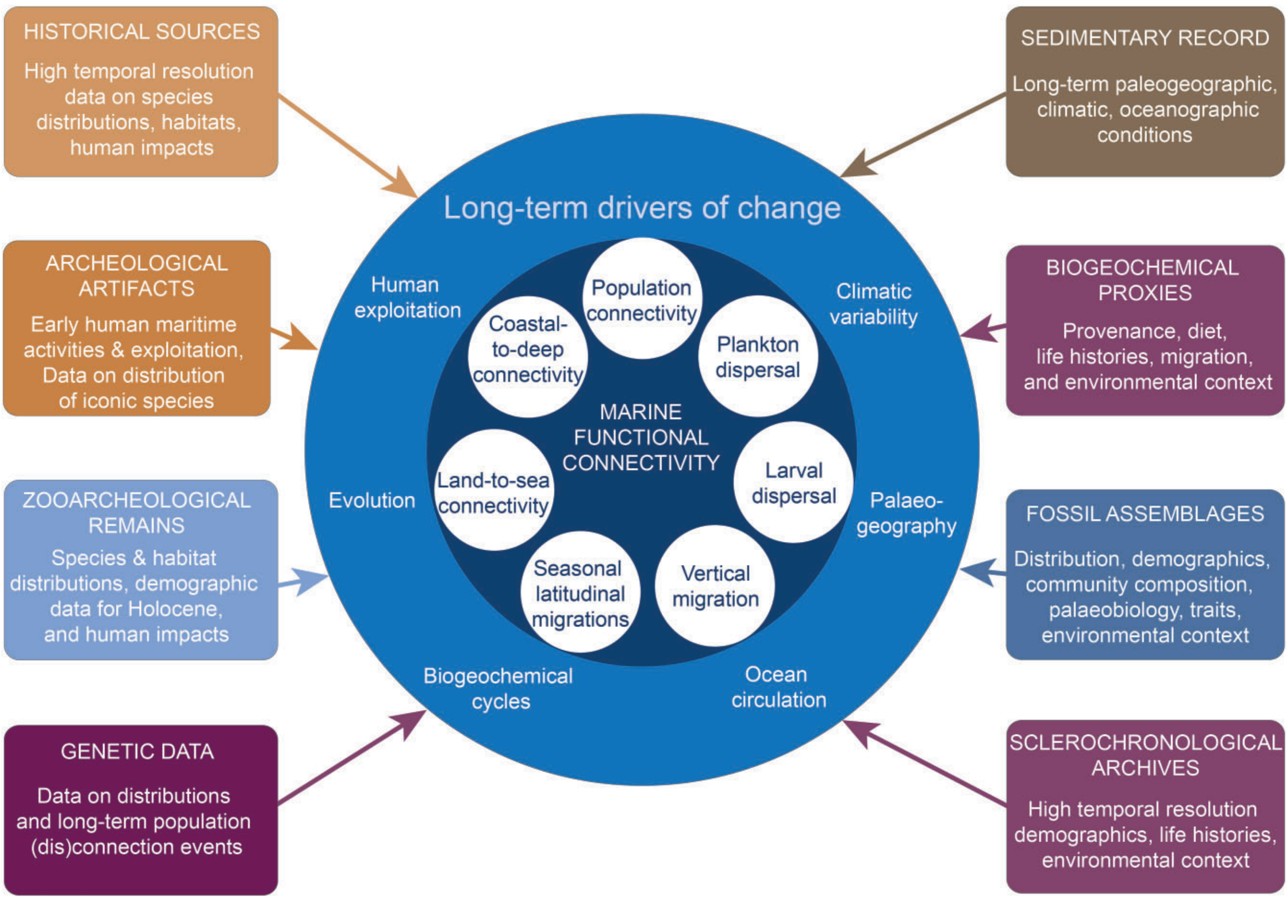

Figure 1. Overview of MFC processes, their long-term drivers, and how geohistorical data can help unravel their changes over time. The boxes reflect the methods and materials used: human sources and archaeological artifacts are remains from human activities; zooarchaeological remains and fossil assemblages are the preserved (mostly hard) parts of organisms; biogeochemical proxies, sclerochronological archives and genetic data derive from the application of methods to a wide range of organismal remains.

identification of fossil and zooarchaeological material for the correct interpretation of the results.

MFC processes and their long-term drivers

Active migrations

Functional connections between the land and the sea, and between coasts and the deeper ocean are formed by the migrations of many marine birds, mammals like seals, and diadromous fishes such as salmons, sturgeons, or eels (Fariña et al. 2003, Wagner and Reynolds 2019, Hentati-Sundberg et al. 2020, Benkwitt et al. 2022). Changes in the life history and behaviour of these species led to past changes in land-to-sea (e.g. D'Amore et al. 2011, Whitfield et al. 2017, Sturrock et al. 2019) and coastal-to-deep connectivity (Gorlova et al. 2012).

Past warming and ocean acidification are expected to have reduced the capacity of marine organisms to perform seasonal latitudinal migrations. For instance, changing migration patterns of small pelagic fishes in the Atlantic and the Mediterranean Sea in the historical past have been associated with different phases of the North Atlantic Oscillation and the Atlantic Meridional Oscillation (Alheit et al. 2014, Tsikliras et al. 2019). Another example is the Northeast Arctic cod, whose spawning distribution has shifted northwards in the last century (Martínez-García et al. 2022). On the other hand, in deeper time, the stable oxygen isotopic composition of barnacles has been used to determine the seasonal migration routes of whales and turtles in the past, and their changes that are associated with climate (Bianucci et al. 2006) and sea-level change (Pyenson and Lindberg 2011, Taylor et al. 2019).

Although direct evidence of past vertical migrations is difficult to obtain, as many of the organisms performing these migrations today do not usually fossilize (e.g. copepods and jellyfishes), much information can be obtained about mesopelagic fishes. Palaeoclimate drove seawater temperature, oxygenation, and circulation, and ultimately controlled the geographic distribution, abundance, and functional traits (e.g. body size and feeding behaviour) of mesopelagic fishes that perform daily vertical migrations (Agiadi et al. 2011, 2018, 2023, Lin et al. 2023).

Plankton and larval dispersal

Pelagic larval dispersal capacity (measured as either duration or distance of dispersal until settlement) has been used to explain the distribution of extant and extinct species of gastropods and corals based on genetic and fossil occurrence data (Henry et al. 2014, Hongo and Montaggioni 2015), but the duration of pelagic dispersal alone does not always explain the observed species ranges and size distributions (Ludt and Rocha 2015, Nanninga and Manica 2018). Plankton dispersal may have been instrumental in the rapid re-establishment of marine biota after major palaeoenvironmental perturbations (Bulian et al. 2022a, b).

Global warming can impact larval life cycles and dispersal (Munday et al. 2009, Gerber et al. 2014). Oceanic circulation then controls seawater temperatures, salinity, and oxygenation that can determine the capacity of water bodies to facilitate larval transport (Strugnell et al. 2008). Through its effects on water-column stratification and sea level, climate in the past regulated oceanic circulation, and thus the flows of nutrients and genes (Beu et al. 1997, Fraass et al. 2019, Fenton et al. 2023). On geological timescales, the effects of paleogeographic changes on plankton and larval dispersal can be observed indirectly through the expansion or contraction of the biogeographic distributions of the species. Large-scale changes in dispersal pathways have been attributed to the opening and closure of marine gateways: the opening of the Drake Passage leading to the onset of Antarctic Circumpolar Current (31–26 Ma; Beu et al. 1997, Hodell et al. 2021); the opening of the Fram Strait (17.5 Ma) and the Bering Strait (4.8–7.4 Ma) that ventilated the Arctic (Jakobsson et al. 2007, Yasuhara et al. 2019); the closing of the Tethys Seaway (Lo et al. 2014, Agiadi et al. 2021, Li et al. 2021, Carolin et al. 2022); the formation and closure of the Central American Seaway (200–154 Ma and 3.5 Ma, respectively; Beu 2001, Teske et al. 2007, although Miura et al. 2011); and the stepwise restriction and reopening of the Atlantic–Mediterranean gateway that enabled establishment of the present-day water exchange between the two basins at Gibraltar (5.97 Ma and 5.33 Ma, respectively; Mancini et al. 2021, Bulian et al. 2022a, Agiadi et al. 2024).

Population connectivity

Recurring periods of climatic and hydrological changes in the past led to extreme changes in the oceans including warming, changes in thermohaline circulation, acidification (Zachos et al. 2005, Marcott et al. 2014, Penman et al. 2014, Babila et al. 2018), deoxygenation (Dickson et al. 2012, Praetorius et al. 2015, Rohling et al. 2015, Yasuhara et al. 2019), and salinification (Krijgsman et al. 1999, Fenton et al. 2000, Arz et al. 2003; Table 1). Such changes were detrimental for many marine taxa, driving defaunation and habitat degradation, destruction and fragmentation, and increasing the isolation of populations and communities (McCauley et al. 2015). Variations in the Earth's orbital movements (Milankovitch cycles) that drive climate over 105–106 years (Hays et al. 1976) directly affected the geographic distributions of species, connecting and disconnecting populations and driving evolution (Dynesius and Jansson 2000).

Palaeogeographic reconfigurations, eustatic changes, and changes in sea ice-cover prevented or enabled physical connectivity between habitats (i.e. structural connectivity), and therefore affected MFC patterns over evolutionary timescales. The opening and closure of marine gateways, as oceans formed and died, controlled the connectivity of populations of marine species between the seas (Zaffos et al. 2017, Rossi et al. 2023, Agiadi et al. 2024). Critical for the MFC of cosmopolitan species at low–mid latitudes were the Tethys Sea (closing at 13.8 Ma) and the Central American Seaway (closing at 2.8 Ma), which affected population connectivity of shallow and deep-water species (Harzhauser et al. 2007, Lessios 2008, Rahiminejad et al. 2011, Leprieur et al. 2016, O'Dea et al. 2016). Furthermore, the formation of epicontinental seas has been instrumental in facilitating or hindering MFC in the geological past. The Paratethys is a characteristic example of how changing paleogeography has altered MFC particularly for neritic organisms, ultimately determining the evolution of many important clades. The Paratethys formed at ∼34 Ma and spread across most of Central–Eastern Europe and the western part of Asia; its remnants are the Aral Sea, the Caspian Sea, and the Black Sea (Palcu et al. 2017, Hoyle et al. 2021). Because of its complex history, numerous fresh, brackish, and marine endemic species originated in the Paratethys: the transient connections between its adjacent seas allowed species to disperse increasing regional marine diversity (Agiadi et al. 2017, 2021, Schwarzhans et al. 2020).

There is ample evidence that the large sea-level changes occurring during the Pleistocene glacial–interglacial cycles affected population connectivity between land and sea, coastal, and deeper habitats (Erlandson et al. 2007, Pellissier et al. 2014, Ludt and Rocha 2015), which likely in turn influenced the fluxes of matter and energy in coastal areas. Finally, deep-time records (e.g. Vermeij and Roopnarine 2008, Iba et al. 2011) can provide insights into how the future opening of polar corridors in the Arctic and the increasing connectedness in the Antarctic can impact MFC.

The impact of preindustrial human activities on MFC

Although recent human activities and climatic change disrupting MFC patterns today are relatively well-known, evaluating the long-term impacts is challenging due to the lack of preimpact baselines and their unprecedented nature. Connectivity between the early human populations themselves, which exchanged technologies and experiences, enhanced their impacts on the marine environment and MFC (e.g. Pawlik 2021; Table 2). The archaeological record shows evidence of human exploitation of marine populations over millennia (Desse and Desse-Berset 2002, Erlandson and Rick 2008, Orton 2016). However, establishing to what extent human exploitation impacted MFC in the distant past is typically difficult to infer due to the spatially and temporally patchy nature of archaeological sites and preserved materials, as well as written historical sources.

The scale and sustainability of harvesting practices through time, the quantities and nature of marine products traded and their trade routes, and the potential implications for marine populations, have been interpreted from archaeological data using techniques such as allometry, growth-increment ageing, and stable isotope signatures (Desse and Desse-Berset 1999, Barrett et al. 2011, Betts et al. 2014, Orton et al. 2014, Welker and Morales 2022). Comparisons between archaeological materials and present-day exploitation can also provide clues to e.g. the distribution and size of species harvested, and their relative abundance through time as exploitation or the environmental conditions changed (Desse and Desse-Berset 2002, Limburg et al. 2008, Maschner et al. 2008, Morales Muñiz and Roselló Izquierdo 2008). These data are essential for estimating human effect on MFC in the past.

In more recent time periods (i.e. the Mediaeval period to the present day), evidence of human impacts on marine species and habitats, typically from exploitation but including habitat transformation and degradation, coastal development, pollution, and disease, exist in the historical record (Table 3). Collation of information from historical sources (which

Table 2. Examples of changes in MFC that might be observed over long (>decadal) timescales associated with human drivers.

Human driver	Environmental changes	Consequences for MFC	Examples
Coastal urbanization	−Habitat loss, deterioration, and fragmentation −New artificial habitats (sea defences, offshore infrastructure, and ship wrecks) −Construction of canals creates new connections −Construction of weirs, dams, and other constructions on rivers that affect flow or create a physical obstruction	−Disconnects populations/communities −Isolates habitat-forming species and organisms that inhabit them	−The spawing and migration of catadromous and anadromous fish (e.g. eel, sturgeon, salmon, and alewife) have been impacted by alterations to rivers for millennia (D'Amore et al. 2011, Sturrock et al. 2019, Lenders et al. 2016, Mattocks et al. 2017)
Anthropogenic transport (hitchhikers on hulls or within ballast tanks, aquarium trade, and aquaculture)		−Connects or disconnects populations/communities −Makes novel connections between species and populations (natural and genetically modified) −Introduces diseases	− Marine non-native species have been transported since at least 1200 (Crosby 2004, Lotze et al. 2014, Hoffmann 2023).
Historical biomass removal	−Destroys, damages, or fragments seafloor habitats, including biogenic coral, bryozoans, and oyster reefs	−Connects or disconnects populations/communities −Deteriorations in population demographics	−Substantial historical removal of fish and shellfish biomass impacted population size and demographics (Clements et al. 2017), and caused extirpations (Caribbean monk seal (Baker 2008, Brito and Vieira 2016,Vieira and Brito 2017, Vieira et al. 2019).

include written materials, iconography and cartography, artefacts, and verbal transmission of knowledge) can be used to infer changes in MFC resulting from human activities spanning decades to centuries. This can include evidence for the loss of functionally important habitat-forming species and resulting fragmentation of biogenic habitats (the presence of which enhances ecological functions such as nutrient cycling and energy capture and promotes biodiversity) through the use of fishing gears or coastal development (e.g. Zu Ermgassen et al. 2012, Alleway and Connell 2015), declines or extinction of populations targeted for their meat, oils, or fur (i.e. local and global whaling activities, exploitation of seals, sea otters, sea cows, and sea turtles; e.g. Springer 2003, Brito and Vieira 2016, Vieira and Brito 2017, Letessier et al. 2023), and the transport and introduction of non-native species into new habitats (Albano et al. 2018). Specifically, the impacts on MFC can include the disruption or loss of community structure, both physical (i.e. habitat fragmentation, loss or changes in the dominant habitat-forming species)—which may impact the survivability of particular life stages or influence their migration patterns—and demographic e.g. the loss of older sexually mature individuals or subsets of the population that are more vulnerable to exploitation due to specific behaviours, such as site fidelity (Engelhaupt et al. 2009).

The impacts on MFC may also include changes in behaviour, for example, the migrations of a targeted species may be disrupted due to the loss of knowledgeable older individuals (i.e. evidence of whales loss of culture; Clapham et al. 2008, Sremba et al. 2023) or the loss of meta-populations. Changes in whale population composition and size can also be detected through historical analyses, depending on the techniques employed and the studied period (e.g. Prieto et al. 2013, for 20th-century sperm whale hunting in the Azores). For example, intense targeting of females (in earlier periods) may have impacted population dynamics, while the persecution of males or larger animals (in recent times) impacted the body size of individuals and led to the shrinking of populations (Clements et al. 2017). Species responses to wider environmental change may lead to the loss of meta-populations or even adaptation by adopting novel behaviours. For example, human alterations of the physical environment e.g. the placement of dams, weirs, or other structures that reduce riverine flow or prevent movement, can also create physical impediments to MFC i.e. the movement of diadromous fish (Lenders et al. 2016, Mattocks et al. 2017), meaning subpopulations are quickly lost. Pressure from human exploitation, can also induce shifts in size or age at sexual maturity, and altered behaviour in the target species i.e. favouring the survival of individuals that are more hook-shy or who use alternative migratory routes (e.g. Monk et al. 2021).

Geological and historical resources: utility and limitations

Understanding the multiple dimensions of MFC is conceptually challenging, in terms of the breadth and scale of data required versus what is available (Menegotto and Rangel 2018, Canonico et al. 2019), the complexity of ocean connectivity, and deficiencies in understanding of organism life history and ecological connections over broad spatial and temporal scales (Hillman et al. 2018, Townsend et al. 2018). Many different approaches are being employed to understand both structural and functional connectivity, including harnessing data on ecological-niches, biophysics, genetics, geochemical signatures, and the physical tagging of animals. These approaches vary in utility, across taxa, spatio-temporal scales, the underlying hypotheses, and assumptions (Bryan-Brown et al. 2017, Darnaude et al. 2022). The challenges differ as we move deeper into the past, where the organisms' life histories and ecological connections cannot be observed

Table 3. Resources that can be used to infer long-term changes in MFC, the type of data provided (that is relevant for MFC), how it can be used for studying MFC, its limitations, and references for examples from the literature. Taphonomy includes all the processses involved in fossilization.

Resource	Type of observational data provided	Derived information for studying MFC?	Limitations and biases	Example references
A. Sedimentary record Timescales covered: $10–10^9$ *Sediments and once lithified sedimentary rocks*	• Sediment or rock type (lithology) and sedimentary structures can be used to infer depositional environments • Bulk element geochemistry (total organic carbon, inorganic carbon, nitrogen, sulfur, and elemental ratios) and mineralogy provide information on environmental conditions • Analyses of lipid biomarkers provide information on the source of organic matter (terrestrial versus marine origins)	• Geological and environmental context that is necessary for interpreting most geohistorical archives • Combined with macrofossils, lithology used to map biogenic habitat extent • Shifts in the source of organic matter imply changes in land-to-sea connectivity	• Temporally incomplete due to hiatus or erosion • Availability declines with time • Biomarkers may degrade, but degree of degradation and interference may be independently determined • Habitat bias	Adame et al. (2012), López-Merino et al. (2015), Bernhardt et al. (2017), Butiseacă et al. (2022)
B. Frozen remains Timescales covered: $10^2–10^4$ *Ice cores and frozen animal remains*∗ ∗aDNA and approaches for other fossils may be used	• Species presence and abundance • Body size • Morphological characteristics related to modes of movement • Soft tissue for extraction of aDNA • Living conditions, burial conditions	• Past species distribution (population connectivity) • Identify refugia • Body size as a proxy of migration capacity • Species traits related to movement and migratory behaviour derived from morphology	• Temporally limited (∼800 000 y BP) • Sometimes seasonal resolution • Accumulation varies by location with rate of snowfall. Where snowfall is very low, the uncertainty can be >1000 years • Environmental context important for interpretations	McMahon et al. (2006), Meiners et al. (2012), Kohlbach et al. (2016)
C. Fish bones, scales, or denticles Timescales covered: $10^2–10^8$	• Species presence and abundance • Body size • Morphological characteristics related to modes of movement • Age and growth rates (sclerochronology)	• Past species distribution (population connectivity) • Identify refugia • Body size as a proxy of migration capacity • Species traits related to movement and migratory behaviour derived from morphology and sclerochronology	• Taphonomic bias • Time-averaged • Availability declines with time • Scales are more degradable than fish bones •Preservation may be incomplete •Material may be transported •Environmental and geological context important for interpretations	Dillon et al. (2017), Salvatteci et al. (2022)
D. Fish otoliths Timescales covered: $10^2–10^8$	• Species presence and abundance • Body size • Age and growth rates (sclerochronology) • Oxygen and strontium isotopes • Morphological characteristics associated with modes of movement	• Reconstruct past species distribution (population connectivity) • Body size as a proxy of migration capacity • Isotopic composition and sclerochronology evidence fish migrations across temperature and salinity gradients • Species traits related to movement and migratory behaviour derived from morphology and sclerochrnology	• Taphonomic bias • Time-averaged • Availability declines with time • Preservation may be incomplete • Material may be transported • Environmental and geological context important for interpretations	Morrongiello et al. (2019), Tanner et al. (2019), Denechaud et al. (2020), Agiadi et al. (2011, 2018, 2023)

Table 3. Continued

Resource	Type of observational data provided	Derived information for studying MFC?	Limitations and biases	Example references
E. Fish, mammal or reptile teeth Timescales covered: 10^2–10^8	• Species presence (and abundance under conditions) • Body size • Oxygen and strontium isotopes • Age and growth rates (sclerochronology)	• Past species distribution (population connectivity) • Identify refugia • Isotopic evidence of latitudinal migrations • Body size as a proxy of migration capacity	• Taphonomic bias • Time-averaged • Availability declines with time • Fish/shark teeth are rarer than scales or denticles • Preservation may be incomplete • Material may be transported • Environmental and geological context important for interpretations	Clementz et al. (2014), Taylor et al. (2021)
F. Macrofossils Timescales covered: 10–10^8 *Body fossils of macroscopic taxa (>0.5 mm) not already considered above. Might represent the only preservable element for some taxa (e.g. polychaete jaws).*	• Species presence and abundance • Body size • Morphological characteristics related to modes of movement • Larval stage duration and development • Shell chemical and isotopic composition • Age and growth rates (sclerochronology) • Assemblage composition is used to reconstruct palaeoenvironmental conditions	• Past species distribution (population connectivity) • Identify refugia • Body size and morphology as a proxy of dispersal/migration capacity • Larval stage duration as a proxy of dispersal capacity • Shell chemistry is used to reconstruct migrations along environmental gradients • Combined with lithology, macrofossils used to reconstruct biogenic habitat extent • Environmental context that is necessary for interpreting most geohistorical archives	• Taphonomic bias • Time-averaged • Availability declines with time • Material may be transported • Geological context important for interpretations	Caswell and Coe (2013), Kidwell and Tomašových (2013), Schöne (2013), Nützel (2014), Kidwell (2015), Harnik et al. (2017), Friedman and Carnevale (2018), Fuksi et al. (2018)
G. Disarticulated or fragmented fossil remains of other taxonomic groups Timescales covered: 10–10^8 *e.g. sponge spicules*	• Species presence (and abundance under conditions) • Assemblage composition is used to reconstruct palaeoenvironmental conditions	• Past species distribution (population connectivity) • Identify refugia • Environmental context that is necessary for interpreting most geohistorical archives	• Remains may not be identifiable to species level • Taphonomic bias • Time-averaged • Availability declines with time • Very often material is be transported • Geological context important for interpretations	Thomka et al. (2012), Mancosu et al. (2015), Łukowiak (2020)
H. Microfossils Timescales covered: 10^2–10^8 *Coccolithophores, dinoflagellates, diatoms, foraminifera, and radiolarians*	• Species presence and abundance • Body size • Assemblage composition, elemental and isotopic biogeochemical proxies are used to reconstruct palaeoenvironmental conditions	• Past species distribution (population connectivity) • Body size as a proxy of dispersal capacity • Environmental context that is necessary for interpreting most geohistorical archives	• Taphonomic bias • Time-averaged • Geological context important for interpretations	Falkowski et al. (1998), Rita et al. (2019)

Table 3. Continued

Resource	Type of observational data provided	Derived information for studying MFC?	Limitations and biases	Example references
I. aDNA + sedaDNA Timescales covered: 10^2–10^6 *aDNA from recent fossilized + nonfossilized organic residues and sediments (sedaDNA)*	• Species presence and abundance • Evolutionary relationships	• Past species distribution (population connectivity) • Identify refugia • Evolutionary patterns provide evidence of the persistence (and resilience) of MFC patterns and traits over long timescales	• sedaDNA is biased towards abundant taxa • Limited by variable preservation: SST, salinity, and sediment type affect preservation of sedaDNA • Very sensitive to contamination • Sampling and analysis are expensive	Rodrigues et al. (2016), Der Sarkissian et al. (2017, 2020), Gómez-Cabrera et al. (2019), Kjær et al. (2022), Barrenechea-Angeles et al. (2023)
J. Zooarchaeological remains Timescales covered: 10^2–10^5 *Shell middens, bones, teeth, shells, scales, skin, hair, and feathers** *aDNA approaches can be used on many of these materials	• Species presence and abundance • Body size • Morphological characteristics related to modes of movement • Age and growth rates (sclerochronology) • Larval stage duration and development • Chemical and isotopic composition • Human behaviour (e.g. gear used for the exploitation) • Cultural value of species inferred from type of processing applied	• Past species distribution (population connectivity) • Identify refugia • Body size as a proxy of migration capacity • Human transport of nonindigenous species evidences new functional connections • Species traits related to movement and migratory behaviour derived from morphology and sclerochronology • Larval stage duration as a proxy of dispersal capacity • Chemical and isotopic evidence of migration along environmental gradients • Exploitation history to infer impacts of human activities on MFC	• Taphonomic bias • Time-averaged • Availability declines with time and requires human presence • For earlier periods almost strictly coastal • Human filter: remains only reflect resources extracted by humans • Location data for exploited species may be coarse • Sampling bias reduces with advancements in zooarchaeology in specific periods/region • Cultural and environmental context important for interpretations	Wheeler and Jones (1989), Desse and Desse-Berset (1992), Owen and Merrick (1994), Rodrigo García (1994), Van Neer et al. (1999), Leach and Davidson (2001), Reitz (2001), Borge et al. (2007), Hunt et al. (2011), Çakirlar (2014), Bernal-Casasola et al. (2016), Butler et al. (2019)
K. Archaeological remains Timescales covered: 10^2–10^5 *Tools, clothing, adornments, dwellings, and vehicles*	• Human presence and culture • Fishing practices, gear, effort, and yield (boat design, number of fishermen) • Storage vessels (food residues reflect human diet) • Evidence of trade • Timescale of exploitation	• Cultural context that is necessary for interpreting most geohistorical records • Trade may be linked to human transport of nonindigenous species	• Preservation bias • Time-averaged • Availability declines with time • Environmental context important for interpretations	Colley (1987), Theodoropoulou (2023)
L. Prehistoric art and iconography Timescales covered: 10^2–10^5 *Cave paintings, mosaics, sculpture, and ornaments*	• Human presence and culture • Species presence and abundance • Body size estimates • Fishing practices, gear, and yield • Cultural value of species inferred from location and way of representation	• Past species distribution (population connectivity) • Body size as a proxy of migration capacity • Cultural context that is necessary for interpreting most geohistorical records	• Preservation bias • Body size representations are highly subjective • Qualitative data • Location data for species may be coarse • Taxonomic identifications are uncertain • Cultural context important for interpretations • Biased to iconic, charismatic or exploited species	Ballester (2018), Delorme and Roux (1987), Kokkini (2016), Tribot et al. (2021)

Table 3. Continued

Resource	Type of observational data provided	Derived information for studying MFC?	Limitations and biases	Example references
M. Written archives Timescales covered: 10^2–10^3 *logbooks, fish market records, government records, import/export records, newspapers, periodicals, journals, expedition logs, fisheries surveys, books, letters, diaries, and naturalist books natural history and philosophy treatises*	• Biogenic habitat extent • Species presence and abundance • Body size • Fishing effort, gear, catch, and bycatch • Aquaculture efforts • Data from historic fish/mammal tagging work, telemetry, and biologging • Larval stage duration, development, ecology, and distribution • Information on diseases that could impact migration capacity or provide environmental context • Evidence of trade • Timescale of exploitation • Evidence of ecosystem degradation	• Cultural and environmental context that is necessary for interpreting most geohistorical records • Past species distribution (population connectivity) • Body size as a proxy of dispersal/migration capacity • Trade may be linked to human transport of nonindigenous species • Species and larval movements • Larval stage duration as a proxy of dispersal capacity • Direct evidence of dispersal and migration	• Spatial and temporal resolution highly variable and gaps are frequent • Biased to species of commercial value, larger, and iconic species • Historical context important for interpretations	Brito and Vieira (2016), Thurstan (2022), Rodrigues et al. (2019)
N. Nautical charts & maps Timescales covered: 10^{-1}–10^3	• Biogenic habitat extent • Species presence • Trade links and human infrastructure	• Past species distribution (population connectivity) • Direct evidence of migration • Trade may be linked to human transport of nonindigenous species • Direct evidence of biogenic habitat extent	• Quality and coverage vary with developments in cartography • May be biased to iconic and charismatic species, exploited stocks, or those forming reefs • Cultural and historical context important for interpretations	Rankin and Holm (2019), Thurstan (2022)
O. Local or traditional ecological knowledge (LEK) Timescales covered: 10^{-1}–10^2 *Accounts from present-day fishers, the families of deceased fishers, or recorded accounts (oral histories)*	• Biogenic habitat extent • Species presence and abundance • Body size • Fishing effort, gear, catch, and bycatch • Aquaculture efforts • Information on diseases that could impact migration capacity or provide environmental context • Timescale of exploitation evidence of ecosystem degradation	• Past species distribution (population connectivity) • Body size as a proxy of dispersal/migration capacity • Direct evidence of biogenic habitat extent • Human transport of nonindigenous species evidences new functional connections • Environmental context that is necessary for interpreting most geohistorical records	• Qualitative, rarely quantitative • Often biased towards exploited or iconic species and varies through time (favouring extremes) • Important observation bias • Cultural amnesia can lead to both over- and underestimation (e.g. of catches) • Cultural and historical context important for interpretations	Beller et al. (2020), REDMAP (2023); NOAA (2023)
P. Historical imagery Timescales covered: 10^2–10^3 *Paintings, book illustrations, sculpture, tapestries, photographs, stamps, shipwright plans, images of gear, and architectural plans*	• Species presence and abundance • Body size • Species economic and cultural value • Fishing effort, gear, and catch • Evidence of ecosystem degradation • Information on diseases that could impact migration capacity or provide environmental context • Evidence of trade • Timescale of exploitation	• Past species distribution (population connectivity) • Body size as a proxy of migration capacity • Human transport of nonindigenous species evidences new functional connections • Environmental context that is necessary for interpreting most geohistorical records • Exploitation history to infer impacts of human activities on MFC	• Qualitative • Location data may be coarse • Artistic license: very subjective, reflecting personal perspective and cultural values • Often biased to species of commercial value, larger, and iconic species • Cultural and historical context important for interpretation	Beller et al. (2020)

Table 3. Continued

Resource	Type of observational data provided	Derived information for studying MFC?	Limitations and biases	Example references
Q. Historical collections of animal remains Timescales covered: 10^2–10^3	• Species presence and abundance • Body size • Morphological characteristics related to modes of movement • Larval stage duration and development • Shell chemical and isotopic composition • Age and growth rates (sclerochronology) • Soft tissue can be extracted for aDNA • Information on diseases that could impact migration capacity • Type and extent of human exploitation • Trade links • Timescale of exploitation	• Past species distribution (population connectivity) • Body size as a proxy of dispersal/migration capacity • Species traits related to movement and migratory behaviour derived from morphology and sclerochrnology • Larval stage duration as a proxy of dispersal capacity • Human transport of nonindigenous species evidences new functional connections • Chemical and isotopic evidence of migration along environmental gradients • Exploitation history to infer impacts of human activities on MFC	• Location data may be coarse • Biased to iconic, charismatic, or exploited species • Availability declines with time	Gallmetzer et al. (2017)
R. Historical collections of human artefacts Timescales covered: 10^2–10^3 *Tools, vehicles, clothing, engravings, and ornaments (scrimshaw)*	• Fishing practices, gear, and effort (boat design, number of fishermen) • Type and extent of skeletal materials used from marine taxa • Evidence of trade • Timescale of exploitation	• Cultural context that is necessary for interpreting most geohistorical records • Human transport of nonindigenous species evidences new functional connections • Exploitation history to infer impacts of human activities on MFC	• Location data may be coarse • Qualitative • Biased to exploited species • Cultural and historical context important for interpretations	Barrett (2019)
S. Trace fossils (ichnology) Timescales covered: 10^2–10^4	• Ichnospecies presence • Body size • Palaeoenvironment can be reconstructed based on the presence of particular ichnofossil types	• Past ichnospecies distribution (population connectivity) • Body size as a proxy of dispersal/migration capacity • Direct evidence of movements near/on/inside the sea bottom • Environmental context that is necessary for interpreting most geohistorical records	• Taphonomic bias • Time-averaged • Species identification uncertain (or even some times impossible), because the ichnofossil confirms only the presence of a behaviour • Availability declines with time	Caswell and Herringshaw (2023)
T. Remains of terrestrial / freshwater organisms Timescales covered: 10^2–10^8 *e.g. pollen*	• Pollen, plant remains, dendrochronology, and other palaeoclimate proxies • Palaeoenvironment can be reconstructed based on the species presences and abundance	• Evidence of land-to-sea connectivity pathways (e.g. rivers, deltas) • Environmental context that is necessary for interpreting most geohistorical records	• Taphonomic bias • Time-averaged • Geological context important for interpretations	Ye and Peters (2023)
U. Phylogenetics Timescales covered: 10^3–10^8	• Evolutionary relationships and events derived from analysis of DNA in modern tissue or morphology	• Inferred gene flow between populations	• Pinpointing events in time requires verification with fossils • Morphological approaches have problems with cryptic species • Environmental and geological context can aid interpretations	Leprieur et al. (2016)

Figure 2. Fragment of the mosaic discovered at the 'Sea front villa' in Hippo, dating from 210 and 260 AD (photo taken by Ali Becheker, 2023).

directly, but must instead be inferred. We identify here eight types of records that provide evidence of past MFC: sedimentary records, biogeochemical proxies, fossil assemblages, sclerochronological archives, genetic data, zooarchaeological remains, archaeological artefacts and representations, and historical sources (Fig. 2).

Sedimentary records

Sediments record the conditions of past environments, including sedimentological and geochemical evidence of the physical connectivity between marine basins and climate contexts (Table 3A). Sedimentary structures reflect the level of energy in the depositional setting and the direction and strength of currents (Bernhardt et al. 2017). The chemical and isotopic composition of the sediments, especially in conjunction with fossil assemblages provide evidence of past connectivity. For example, the total organic carbon in marine sediments reflects organic carbon burial and hence the combination of production and the biological carbon pump efficiency, including through the diel vertical migration performed by zooplankton (e.g. Li et al. 2023).

Changes in continental arrangement, extent of sea-ice cover, ocean primary production, and terrestrial vegetation can also be detected from sediments, fossils, and their geochemical signatures: providing the environmental context needed for determining past local, regional, and global changes in structural connectivity, functional connectivity, and its drivers.

Mapping the extent of important habitats and ecosystems in the past such as seagrass meadows, reefs, and deep-sea geothermal vents can be achieved using sedimentological data, which in turn can help reconstruct their structural and functional connectivity.

Biogeochemical proxies

The elemental and isotopic composition of marine fossils provide direct evidence of the movements and migration of marine organisms (Gorlova et al. 2012, Trueman et al. 2016, Taylor et al. 2019). Unlike studies of present-day MFC patterns that can benefit from the analysis of the soft tissues of organisms (e.g. muscle, blood, and skin), only hard tissues (e.g. shells, bones, teeth, otoliths, and microfossil tests) are usually preserved as fossils and can be used to reconstruct palaeoenvironmental conditions and life histories in historical and geological times (Table 3B–H). The composition of hard tissues depends on the elemental availability and isotopic ratios in the ambient water. Taxon- and tissue-specific fractionations control the final incorporation of the elements and isotopes into these tissues during biomineralization. The main premises in using biogeochemical proxies for reconstructing long-term MFC patterns are that: (a) the concentration of the measured element or the isotopic ratio differs between the marine environments the organism (was suspected to) occupy; (b) the fractionation of the measured element or isotopes between the ambient seawater and the targeted tissue can be determined (preferably for the target species, or at the lowest possible taxonomic level in case of extinct species); (c) any vital effects on the fractionation are insignificant or well-constrained; and (d) the preservation of the fossil is good and any possible effects of diagenesis (i.e. all the physical and chemical alteration taking place after the organism remains have been buried) have been excluded prior to analysis.

Elemental and isotopic ratios from the remains of skeletal elements, e.g. fish otoliths, mollusc shells, corals, and calcareous microfossils (such as foraminifera and ostracods) have already been used as proxies in long-term (decadal–millions of years) MFC studies. The Mg/Ca, Sr/Ca, Ba/Ca, and Na/Ca ratios are strongly controlled by ambient water temperature and salinity allowing the reconstruction of the movements of marine organisms across thermal and salinity gradients (Eggins et al. 2003, Amekawa et al. 2016). On the other hand, movements may be inferred by a change of provenance because of the differences in the Li content of seawater between sites (Thibon et al. 2022). Life histories of organisms moving between environments of different salinities are commonly reconstructed based on $^{87}Sr/^{86}Sr$ of their hard tissues (Koch et al. 1992, Kocsis et al. 2007, Glykou et al. 2018), but this proxy is also used in deep-time studies to test hypotheses about the connectivity of aquatic settings (e.g. Andreetto et al. 2021, Hoyle et al. 2021). The $^{15}N/^{14}N$ ratio is a commonly used proxy for trophic position: in the case of migrating animals, a dietary shift may also indicate a change in migration potential, patterns or routes (Hesslein et al. 1991). The analyses of $^{13}C/^{12}C$ and $^{18}O/^{16}O$ in fossil and modern enamel (Clementz et al. 2014, Taylor et al. 2021), otoliths or invertebrate shells (Zazzo et al. 2006, Lukeneder et al. 2010, Geffen et al. 2011, Stevens et al. 2015, Immenhauser et al. 2016) provide evidence of ontogenetic and (sub-)seasonal migration patterns in the deep past, especially when combined with the record from other, nonmigratory organisms or other proxies (Amekawa et al. 2016). The Branched and Isoprenoid Tetraethers index, an organic geochemical proxy, defines the terrigenous versus aquatic components of organic inputs into a basin (Butiseacă et al. 2022), reflecting the degree of land-to-sea connectivity. Similarly, glomalin, a protein produced by fungi, is transported to the sea through rivers and groundwater, and is detected in varying amounts in reefs, mangroves and seagrasses (Adame et al. 2012, López-Merino et al. 2015).

Fossil assemblages

Fossils allow us to map the distributions (or biogeographic ranges) of species and how they have changed through time (e.g. Smith et al. 2023), inferring connectivity and evolutionary dynamics (e.g. Vermeij 1991, Vermeij and Roopnarine 2008, Iba et al. 2011, Dunne et al. 2014, Leprieur et al. 2016, O'Dea et al. 2016, Agiadi et al. 2018, Friedman and Carnevale 2018, Reddin et al. 2018, Caswell and Herringshaw 2023).

The potential for making such inferences about MFC depends upon the species studied, their preservation potential, and the conditions of burial. This could range from near-complete soft tissue preservation as found in conservation lagerstätten (e.g. the Burgess Shale and the Solnhofen Limestone) to accumulations of disarticulated and transported skeletal materials. The fossil record is spatially patchy and incomplete and tends to be biased towards lower energy marine environments with reasonable sediment accumulation rates and organisms with hard parts that have higher preservation potential. This can be supplemented by trace fossils that record the behaviour of animals. Exceptionally preserved materials, although rare, can yield valuable biological information on individual species and on MFC (Table 3F).

Biological traits that are related to MFC can also be reconstructed from particular fossilized skeletal remains. For instance, fish body size and morphology, which are directly correlated to the fish's mobility, can be reconstructed from fossil otoliths, teeth, and other bones (Table 3C–E; Agiadi et al. 2023). Similarly, shark denticles reflect body morphology and behavioural traits (Dillon et al. 2017, Cooper et al. 2023). Fish scales, both fossilized and nonfossilized, may also yield valuable information on species distribution, population size and demographics, traits, and the response of fish to environmental and anthropogenic changes (e.g. Salvatteci et al. 2022). Data on marine invertebrates can be extracted for species with good preservation potential (e.g. molluscs, crustacea, and echinoderms) and linked with changes in the environment (e.g. Caswell and Coe 2013, Fuksi et al. 2018, Rita et al. 2019; Table 3F). Changes in invertebrate traits can be interpreted based on the principles of functional morphology and comparison with modern analogues (Kroh and Nebelsick 2003, Caswell and Frid 2013), for those with incremental structures, growth life history can be reconstructed, and for some (e.g. molluscs), the larval shell may be preserved on the adult and so fossils may provide information on larval behaviour, including dispersal (Landau et al. 2009, Nützel 2014, Harnik et al. 2017). In others (e.g. echinoids), features of the adult skeleton may be used to infer larval development modes (e.g. Cunningham and Jeffery Abt 2009).

The temporal resolution of MFC reconstructions that can be achieved through the study of fossil assemblages cannot be lower than the range of time-averaging, which depends on abiotic and biotic factors (Kidwell 1997, 2001, Kowalewski et al. 2018, Albano et al. 2020, Agiadi et al. 2022, Ritter et al. 2023, Tyler and Kowalewski 2023). Abiotic factors include the sedimentation rate, paleodepth, substratum, the level of mixing, and other factors specific to the depositional environment. Biotic factors are the marine production, the type of skeletal material and its preservation potential, the presence of organisms that disturb the sea bottom through burrowing, and so on. Usually, fossil assemblages are time-averaged at centennial–millennial ranges (e.g. Scarponi et al. 2013, Terry and Novak 2015, Tomašových et al. 2015, Albano et al. 2020), but there are notable exceptions, where temporal resolution can even be decadal (e.g. Kowalewski et al. 2018).

Sclerochronological archives

Sclerochronology is the study of physical and chemical variations in the hard tissues of organisms, focusing primarily on growth patterns and the variety of environmental factors influencing growth (Oschmann 2009). Analogous to the study of tree rings, sclerochronology aims to reveal individual life-history traits and reconstruct environmental changes through time and space.

Marine taxa producing sclerochronological archives range from mammals and fishes, bivalves, and gastropods (shells) to corals and coralline algae (Table 3C–E) (Baglinière et al. 1992, Panfili et al. 2002, Trofimova et al. 2020).

Different resources can be exploited as sclerochronological archives to obtain information on past MFC patterns over timescales ranging from decades to millennia. These include zooarchaeological samples obtained from middens, fossil samples from sediment cores, and more recent collections archived in fisheries institutes (e.g. otolith from research survey programs) and museums (e.g. biological material archived from past expeditions to remote locations). The growth increments of sclerochronological archives provide two types of information relevant to MFC: (i) life-history parameters and events and (ii) past climate and environment, including human impacts. Individual age and/or size at death is a key parameter that is readily obtained from sclerochronological archives and for some taxa can be complemented with information on important life-history traits, such as metamorphosis and settlement, age or size at maturity, growth pattern, and longevity, which can be used to infer dispersal duration and timing as well as movement behaviour (Campana and Thorrold 2001). Sclerochronological archives, in particular the shells of long-lived bivalves (e.g. *Arctica islandica*), have been successfully employed to create multicentury composite records of climate (e.g. Schöne 2013), which can be used to infer habitat characteristics and suitability for hindcasting species distribution. Sclerochronological archives are also useful tools to investigate human impacts on marine environments, in particular comparing preindustrial and modern environmental conditions and rates of exploitation. Archaeological fish otoliths from the mid- to late-Holocene period indicated larger size of individuals in the past, which may be related to more recent fishing practices, introduced species and habitat degradation (Disspain et al. 2012). Covering up to a century, otolith-increment-based chronologies have enabled researchers to assess the impact of both climate change and fishing on many different species around the world (e.g. Morrongiello et al. 2019, Tanner et al. 2019, Denechaud et al. 2020). Finally, sclerochronological archives from zooarchaeological sites can be used to determine the season of capture, which is of broad interest to archaeologists, but may also provide information on fish migration timing (Desse and Desse-Berset et al. 1992, Van Neer et al. 1999, Çakirlar 2014, Butler et al. 2019).

Genetic data

In the last decades, the potential of ancient DNA (aDNA) analysis in marine conservation has been widely recognized. The advancement of high-throughput DNA techniques has revolutionized the field of palaeogenomics, enabling the extraction and analysis of aDNA from fossil shells and skeletal remains recovered from sediment cores (Der Sarkissian et al. 2017, 2020, Nguyen et al. 2021; Table 3I). For example, through aDNA analysis of fossil bones and baleen from museum specimens, Borge et al. (2007) demonstrated that bowhead whale populations from the North Atlantic and North Pacific were connected in the Early Holocene, and raised questions about current whale stocks in the Arctic. Sedimentary ancient DNA (*seda*DNA) can also be used for reconstructing palaeoecological communities and inferring changes in past environments (De Schepper et al. 2019, Nguyen et al. 2021). While most studies are currently restricted to the Holocene, this technique has the potential for reconstructing communities dating back over a million years (Kjær et al. 2022). By providing snapshots of historical genetic diversity and community composition at different points in time, this technique allows the reconstruction of changes in marine assemblages, which can shed light on historical biodiversity loss and patterns of migration and dispersal for both species and communities (Gómez-Cabrera et al. 2019, Shaw et al. 2019, Barrenechea-Angeles et al. 2023). These records of biotic change can describe how populations have been connected or isolated over historical periods, and can give useful insights for future marine conservation and management.

Zooarchaeological remains

The remains of marine organisms found in archaeological sites (specifically sites of human occupation) comprise the hard parts of marine mammals and birds, fishes, molluscs, and other invertebrates (e.g. mostly crustaceans, stony corals, sea urchins, and cephalopods) (Colley 1987, Wheeler and Jones 1989, Claassen 1998, Theodoropoulou 2023), which can be used to infer changes in MFC patterns in historical times (Table 3J). Despite certain limitations, these archives may provide valuable information, especially during periods for which other lines of evidence are lacking. Viewed over short spatial and temporal scales, they can reflect local conditions and small-scale changes in coastal areas close to past human habitations. Over longer timescales, they can provide information on human pressures on living resources or their body size that led to shifts in species distributions, population connectivity, and/or seasonal migration patterns of these animals (e.g. Allen et al. 2001, Leach and Davidson 2001, Desse and Desse-Berset 2002, Bernal-Casasola et al. 2016, Béarez et al. 2016). They can also be correlated with known climatic events and the coastal geomorphological record to infer changes in structural connectivity between populations, habitats, or ecosystems due to sea-level change or habitat degradation (e.g. Owen and Merrick 1994, Rodrigo García 1994, Johnsson 1995, Reitz 2001, Desse and Desse-Berset 2002, Cortés Sánchez et al. 2008, Hunt et al. 2011, Béarez et al. 2012, Rodrigues et al. 2016).

Archaeological artefacts and representations

Artefacts related to fishing, whaling, and other extractive practices are occasionally found in archaeological sites and may inform us directly on the fishing techniques used and the social organization of these activities, as well as indirectly on the species/quantities/habitats targeted (e.g. Buchholz and Joehrens 1973, Colley 1987, Cleyet-Merle 1991, Leach 2006). It is important to keep in mind that, depending on the region, usually only the hard parts of the fishing tackle (e.g. hooks, harpoon points, and net weights) are preserved in the archaeological sediment, while equipment made from perishable plant or animal materials (e.g. nets, floaters, lines, and baskets) will only survive in extreme environmental conditions (dry, waterlogged, anaerobic, or frozen, e.g. Pedersen 1995; Table 3K). Ideally, these should be compared with the results from historical evidence and also from faunal analyses (Table 3J), although the two may not always occur within a single archaeological site (e.g. Davidson and Leach 1996, Pickard and Bonsall 2004, Leach 2006, Michael 2023).

Pictorial evidence may also provide information on the presence of marine species at a specific time/region, their size and abundance, as well as the seasonal migration routes followed by these organisms. Representations of marine organisms (Fig. 2) date back to the Palaeolithic (Cleyet-Merle 1991, Cleyet-Merle and Madelaine 1995) and provide valuable information on extinct and extirpated species. Some ancient civilizations recorded a wealth of information (e.g. Delorme and Roux 1987, Kankeleit 2003, Kokkini 2016), such as the mosaics widely distributed along the coasts of the ancient Roman Empire depicting images of fishing and fish species (Fig. 2) up to the European art pieces that can provide evidence of ecological variations and sociocultural drives and consequences (Tribot et al. 2021; Table 3L). For instance, the c. 11 000 year old El Medano rock art found along the Atacama Desert coast in Chile shows in great detail the species hunted, the techniques and devices employed to catch them and the social organization around such activities (Ballester 2018). However, caution must be made regarding these representations as they often provide a distorted, i.e. exaggerated, displaced or misunderstood, image of marine ecosystems, or marine organisms are misidentified or nonrecognizable.

Historical sources

Historical sources that can potentially be used to track changes in MFC include documents such as natural history treatises, diaries, logbooks, correspondence, legal documentation, governmental enquiries or statistical accounts, newspapers and popular books, early scientific written observations (Table 3M), maps, and nautical charts (Table 3N). Knowledge or skills held by individuals and communities (i.e. information passed among generations verbally or via other forms of nonwritten expression; Table 3O), as well as multiple art and religious manifestations (Table 3P) can also hold information on human-induced changes to marine populations and habitats (Máñez et al. 2014, Engelhard et al. 2016, Barrett 2019, Brito 2023). Evidence collated from these sources can inform on past human activities, human perceptions and practices, and their ecological outcomes, and be used to track the pathways, rates, and consequences of species distributions and movements at decadal to millennial timescales (Bekker-Nielsen 2005, Jacobsen 2005, Orton et al. 2014, Brito and Vieira 2016, Lenders et al. 2016). Additionally, they provide information on how human activities have contributed to functional connections and disconnections. For instance, the transport of nonindigenous species along shipping routes ('hitch-hikers' on wooden hulls), and for aquaria and aquaculture, has been documented from at least the 1200s (Lotze et al. 2014, Holm et al. 2022a, Hoffmann 2023). This is particularly relevant to East–West Atlantic connections, and Northern–Southern hemispheres connections, since early European expansions and colonization of peoples, water, and territories, through processes of geographic globalization, ecological imperialism, and oceanic teleconnections (Crosby 2004, Holm et al. 2022b). As well, the more recent construction of physical connections, such as the Suez Canal, has led to unprecedented rates of biological invasion (Por 1971, Albano et al. 2021).

Historical sources may provide evidence of changes through, for example, historical accounts of species behaviour or habit that are not observed in the modern day, or their historical presence in locations that are outside of its known geographic range today (or, in the case of nonindigenous species above, their notable absence in the historical record or the timing of when they became a social or economic issue). Historical data on human exploitation can also provide evidence of the drivers of the observed changes i.e. the scale and intensification of historical increases in fishing effort, the introduction of new gears or hunting techniques, of demand, taste and preference, the opening of new extraction grounds, trade routes, and new locations or species being exploited (Vieira et al. 2019, van den Hurk et al. 2023, Vieira 2023). These typologies of historical sources can and should be complemented with other types of documentation, such as visual and cartographic sources, material evidence and remains, objects or art, combining a number of different data sources and information (e.g. as described in Table 3M, N, P–R) can improve confidence.

The biases and limitations of using geohistorical records to reconstruct past MFC

Whatever the source, utilization of geohistorical data and information for understanding MFC needs to account for the historical, cultural, environmental, and geological contexts of their production, and therefore requires a critical interpretation of the information (Table 3). In the past decades, methodological advances now allow extracting information to create high-resolution records of ecosystem change, with variable timescales (Table 3), which cover the last c. 540 million years of MFC (Dietl and Flessa 2011, Kidwell 2015). Central to the issue of the resolution of geohistorical data is the dating (absolute or relative) of the records, because it is necessary for constructing time-series of change, ordering events, and calculating rates of change.

Additionally, integrating data of different types requires an understanding of dynamic processes across spatial (local, regional, and global) and temporal scales both for marine organisms and human populations. Employing the principle of consilience, we can weave together the separate evidence into a coherent, temporally and spatially resolved picture of social–ecological system states and changes. Temporal correlation between materials from different sources is critical to building a timeline of change. Mapping those changes over spatial scales is essential for understanding structural and functional connectivity.

Historical, archaeological, and geological data are incomplete and discontinuous in time and space. This is also true for ecological data, as natural and environmental scientists sample the environment to detect spatial and temporal patterns and the relationships that drive them. However, the sampling in the case of geohistorical materials is more opportunistic and determined by what materials are available and well-preserved. For one, with few exceptions, only the hard tissues of organisms are preserved in the fossil and archaeological record, creating a gap in knowledge of micro- and mesozooplankton and marine plants that do not contain hard parts. Organisms such as jellyfishes, which play a critical role in the marine ecosystem are virtually unknown to us from the past. For those organisms that do leave hard parts, marine faunal assemblages are more or less available depending on the period (e.g. few Pleistocene sites have provided such remains; increasingly they are more available from the early Holocene down to Antiquity, and are also quite common in the Medieval period) and region (e.g. available in the Mediterranean, European Atlantic coasts, circum-Arabian peninsula, Indian Ocean, Australia, and few studies from coastal Africa).

The quality and resolution of geological records is strongly affected by anthropogenic factors, and human bias exists both because of exploitation and during investigation. This is because the processes that govern the preservation of these resources can be affected both positively (increased quality and resolution) or negatively (decreased quality and resolution) by human activities (Nawrot et al. 2024 and references therein). Many archaeological and historical records are also biased according to human interest in the species and the long-term conservation potential of their tissues (Table 3): often the best represented species are those that were exploited as a source of food or for other uses, e.g. those that provide ecosystem services. This is also true for the larger, more visible and iconic species that were spiritually and culturally valued by humans. For instance, the amount of geohistorical evidence of marine animal migrations increased with the onset of human settlement that allowed documentation of such patterns (Damm et al. 2022), and with advancements in fishing and fish processing practices that facilitated the detection of migrations (Avery and Underhill 1986, Boethius et al. 2021). Additionally, the retrieval and recovery methods in both Archaeology and Palaeontology have vastly advanced in the last 200 years: indeed, many records from older expeditions were quite coarsely resolved. Refined sampling methods during excavation, namely sieving, are required, otherwise the sample may be biased towards larger taxa or larger/intact anatomical parts (Theodoropoulou 2023; Table 3J). Using data from diverse geohistorical sources can provide a more complete picture that includes other species, e.g. using data on fisheries by-catch, naturalists accounts, creative writing, other imagery, and death assemblages (Table 3).

These materials will almost always be time-averaged, and the extent of this averaging determines the temporal resolution achievable for a time series constructed from these materials (Table 3). These time-averaged records, being temporally coarser than modern ecological records, do not preserve short-term variations. However, they have been shown to be more powerful for detecting ecological patterns over long timescales and large spatial scales (Kidwell and Tomašových 2013). Time-averaged materials may actually be better for detecting rare species, metacommunity structure (i.e. the regional species pool), identifying changes in biogeographic distributions, and evaluating historic habitat use. Specifically, Kidwell and Tomašových (2013) showed that fossil death assemblages capture 20% more regional diversity than life assemblages because of time averaging. For instance, they may be used to confirm species absences, document the presence of rare species, identifying biogeographic range changes, describing past habitat use, metacommunity size and structure, community states, and shifted baselines. Many of these ecological attributes are key for investigating MFC and how it changes with natural and human drivers (Kidwell 2009, Kidwell and Tomašových 2013). Additionally, methods exist today to assess the completeness of the fossil record, how faithfully death assemblages reflect living assemblage (Table 3) and to unravel the postmortem and postburial processes they have been subjected to (which itself can also yield valuable context, e.g. Tomašových et al. 2021).

In some cases, the data represent only temporal snapshots of the past: this may be the case with isolated fossilized or nonfossilized remains in middens and material collections, fossil lagerstätten, genetic data, much of the archaeological data, and some historical sources (e.g. imagery, oral histories). These windows into the past can provide an, albeit punctuated, perspective on a population, habitat, or community and yield valuable biological or ecological information on extinct species, contributing information on species distributions, human activities, and impacts. In combination with other sources, they can be used to extract quantitative data that can be embedded into time series constructed from other resources (Table 3).

Emerging approaches using aDNA and sedaDNA are significantly affected by the environment of preservation, potential sample contamination, and are biased towards the more abundant taxa, but as the technology advances they have strong potential for providing direct information on species distribution ranges, migratory life cycles and niche shifts, on the changes in the structure of local communities over time and on the evolutionary processes that modulate this functional connectivity through time. However, obtaining reliable sedaDNA data from marine organisms remains challenging in many ways (Nguyen et al. 2021). One of its main limitations is that sample collection requires specific technological instruments to collect long cores while avoiding contamination, leading to very expensive oceanographic campaigns (Nguyen et al. 2021). The acquisition of viable samples is limited to certain environments, as environmental and physical factors such as temperature, salinity, and sediment type influence the preservation of DNA in the sedimentary records (reviewed in Nguyen et al. 2021). In addition, the prevalence of sedaDNA in the environment is related to the species-specific abundance, and thus low-abundance organisms as top predators will be hardly identified in these records (Kjær et al. 2022).

Finally, an important distinction should be made between palaeontological and zooarchaeological material. Where fossil assemblages offer both qualitative information (taxa, morphology based on skeleton, season of capture, and exploited habitats) and quantitative data (relative frequencies and body size) on the entire marine fauna and flora, assemblages from archaeological sites can be considered as ancient exploitation archives. They mostly represent the resources extracted, i.e. caught or collected, by humans. In this sense, they are not considered direct proxies of past MFC. They indirectly reflect the available habitats, but not the entire range of ecosystems. The latter is even more relevant for earlier periods, when humans exploited almost strictly coastal resources.

Case studies

Population connectivity during the Pleistocene glacial–interglacial cycles

The Pleistocene glacial–interglacial cycles recorded recurring shifts in the geographic distributions of many marine species, whose ranges retracted (Kiessling et al. 2012, Scarponi et al. 2022) or expanded (Girone et al. 2006, Agiadi et al. 2018, Melo et al. 2022) leading to the fragmentation (Rödder et al. 2013) or reconnection (Sabelli and Taviani 2014) of their populations, respectively. The resulting dynamic pattern of MFC is especially prominent in marginal and semienclosed seas, such as the Mediterranean Sea. The most recent example of such distribution shifts can be found in the Last Interglacial marine isotope stage (MIS) 5e (ca 135–116 ka), which represents one of the most recent climate analogues for the coming decades (Yin and Berger 2015). During MIS 5e, the geographic ranges of tropical molluscan species ('warm guests') from the West African coast expanded into the Mediterranean, and they regressed to the tropical belt during the subsequent glaciation (Sabelli and Taviani 2014). Conversely, 'cold invaders' were commonly found in the Mediterranean during glacial periods, but retracted during interglacials. Cold-water fish (Girone et al. 2006, Agiadi et al. 2011, 2018, Lin et al. 2017), bivalve (Rossi et al. 2018), and even planktonic foraminifera (Marino et al. 2018, Quillévéré et al. 2019, Girone et al. 2023) species have been repeatedly found in sediments deposited in the Mediterranean during glacial periods, especially those corresponding to the last 1.5 million years, when climate started to shift towards its modern state (McClymont et al. 2023). In addition to restricted seas, biogeographic shifts in response to Pleistocene glacial–interglacial cycles have been recorded in the Pacific and North Atlantic Oceans as well, with examples from ostracods (Yasuhara et al. 2012, Yasuhara and Okahashi 2015, Huang et al. 2018), shallow- (Mitsui et al. 2023), and deep-water fishes (Lin et al. 2023).

Mediaeval and early modern hunting of marine mammals

Marine mammals are among the largest migratory organisms in the oceans today, and a group for which geohistorical records have much to contribute. Whaling is a paradigmatic case of human exploitation, dominance, and impact on marine wildlife, leading to disconnected populations and the contraction of biogeographic ranges and changes in the trophic structure of marine ecosystems. It is estimated that between 1900 and 1999, nearly 2.9 million large whales were killed and processed globally by industrialized whaling (Rocha Jr et al. 2014). However, the history of whaling encompasses the entire history of human life as a practice of biomass and energy removal from the oceans. The fishing of several species of cetaceans is reported since the first settlement of human populations in coastal areas and extends globally, e.g. from the Atacama Desert coast in Chile from c. 11 000 years ago (Ballester 2018) to the littoral mountain of Arrábida, 30 km south of Lisbon in Portugal up to 106 000 years ago (Zilhão et al. 2020). Data from environmental history and historical ecology studies have been combined to describe the changes and assess the ecosystem impacts of the removal of whales. The analysis of historical documents related to preindustrial whale exploitation (covering several centuries of data) can help track changes in whale species and populations' geographic distributions, behaviour, and their contributions to seasonal/latitudinal and vertical MFC.

Very illustrative examples are found in records of Mediaeval whaling in Europe that led to the extirpation of North Atlantic whales' populations and to the early modern whaling in the South Atlantic. From the Roman period to the late Middle Ages, data from historical documents and zooarchaeological records show that baleen whales and toothed whales were valued and consumed in Europe (Teixeira et al. 2014, van den Hurk et al. 2021, 2023). The main targets of exploitation were three species of baleen whales: the North Atlantic right whale (*Eubalaena glacialis*), nowadays only extant in western Atlantic waters, and listed as 'critically endangered' by the IUCN (Cooke 2020); the grey whale (*Eschrichtius robustus*) assessed as 'regionally extinct' in European waters (IUCN SSC Cetacean Specialist Group 2007); and the bowhead whale (*Balaena mysticetus*) with a currently increasing population trend. In the last few decades, with a growing number of archaeological and historical studies it has become possible to infer the relative abundance of these species in the past (e.g. van den Hurk et al. 2023). As a result, we can now better understand changes in the structure and functioning of Arctic ecosystems, since the extirpation of bowhead whales' from the Svalbard Archipelago is believed to have led to large increases of zooplankton biomass due to the reduced grazing pressure (Rodrigues et al. 2019). The ecosystem structure switched from dominance by whale biomass, prior to the start of commercial exploitation in 1596, towards a system dominated by pelagic fishes, and their predators (piscivorous seabirds, seals, and whales; Weslawski et al. 2000).

As humans began to understand that the number of whales available for hunting in European coastal seas was decreasing, new perceptions began to emerge on the abundance of whales and other marine mammals (and the consequent potential for gaining wealth) in America's (North and South) coastal waters. This was the case for several aquatic species of Brazil within a colonial context of nature commodification, confirming that early modern catch data, even if fragmentary, can provide information on species occurrences and distribution (Vieira 2023). Historical data allows us to map species past geographic distributions and realized niches, for instance southern right whales (*Eubalaena australis*) that were hunted at lower latitudes, outside the current species ranges or, inversely, for West Indian manatees (*Trichechus manatus*) that previously occupied higher latitudes than nowadays (Vieira and Brito 2017). Also, historical accounts on the spatial distribution and abundance of monk seals (*Monachus monachus*) in the Caribbean prior to exploitation have been used to model reef productivity and suggest that the extirpation of this species, as a major predator in the reef ecosystems, had an ecological effect across the entire Caribbean region (Baker 2008). The continued exploitation and biomass removal of such species of marine mammals through the centuries had significant impacts that are reflected in the extirpation of populations and the current conservation status of these species, and most probably had an important impact on MFC.

The formation of the Isthmus of Panama and the cascading effects of ocean connectivity loss

Prior to formation of the Isthmus of Panama, Miocene fossil records reveal taxonomic, ecological, and environmental similarities across the entire Tropical American marine region as large amounts of energy, biomass, and genes were exchanged between the Pacific and Caribbean (Leigh et al. 2014, Yasuhara et al. 2022). When the isthmus formed and this link finally severed, the biodiverse tropical marine faunas underwent major ecological, evolutionary, and biogeographic disruption. The most striking consequence of this was the ultimate cessation of gene flow between marine populations in either ocean, which occurred around 2.8 Ma (O'Dea et al. 2016). But Isthmus formation began more than 20 million years earlier (Farris et al. 2011), and the movement of water, nutrients, and energy from the Pacific into the Caribbean had been substantially reduced by the late Miocene and Pliocene as documented in serially sampled isotopic analysis of shells (Grossman et al. 2019), which eventually created the oligotrophic Caribbean we know today. Quantitative analyses of near-shore fossil assemblages of molluscs, corals, bryozoans, urchins, fish teeth, and fish otoliths reveal how the ecological structure of these diverse tropical communities responded. In the Caribbean, filter feeders reliant on high planktic nutrients declined by a third, large-bodied predatory sharks declined 50% giving way to small, bottom-dwelling demersal fishes, and in the benthos predatory gastropods were replaced by herbivorous snails (O'Dea et al. 2016). Cumulatively these changes demonstrated decreasing MFC between the oceans, a decline in population connectivity within the Caribbean, and the consequential switch of the dominant source of energy in the Caribbean from widely distributed pelagic to spatially limited benthic origins. Detailed measurements of the size and shape of fossilized larval shells revealed that animals with long-lived planktonic-feeding larvae that connected the two regions, became substantially rarer as feeding became more challenging in the oligotrophic water column (Landau et al. 2009). The consequence was a further reduction in MFC, which ultimately contributed to an increase in provinciality in the Caribbean (Leigh et al. 2014).

While the majority of these biotic responses to the environmental changes were linear and predictable, others were nonlinear. For example, Caribbean species that were poorly adapted to the new, low nutrient conditions diminished at first, but were able to cling on in small, isolated populations until their eventual demise a million years later (O'Dea and Jackson 2009). This pattern can be best explained as isolated metapopulations in deteriorating conditions (Nee and May 1992), and reflects the model of 'extinction debt' where the final loss of a species lags long after the ultimate cause (Tilman et al. 1994).

The proliferation of the Caribbean coral reefs and seagrasses also lagged a million years or more behind the formation of the Isthmus and the collapse in planktonic productivity, as observed in the rapid increase in abundance of seagrass-specific lucinid bivalves and a sharp increase in coral abundances and reef growth in the early to middle Pleistocene

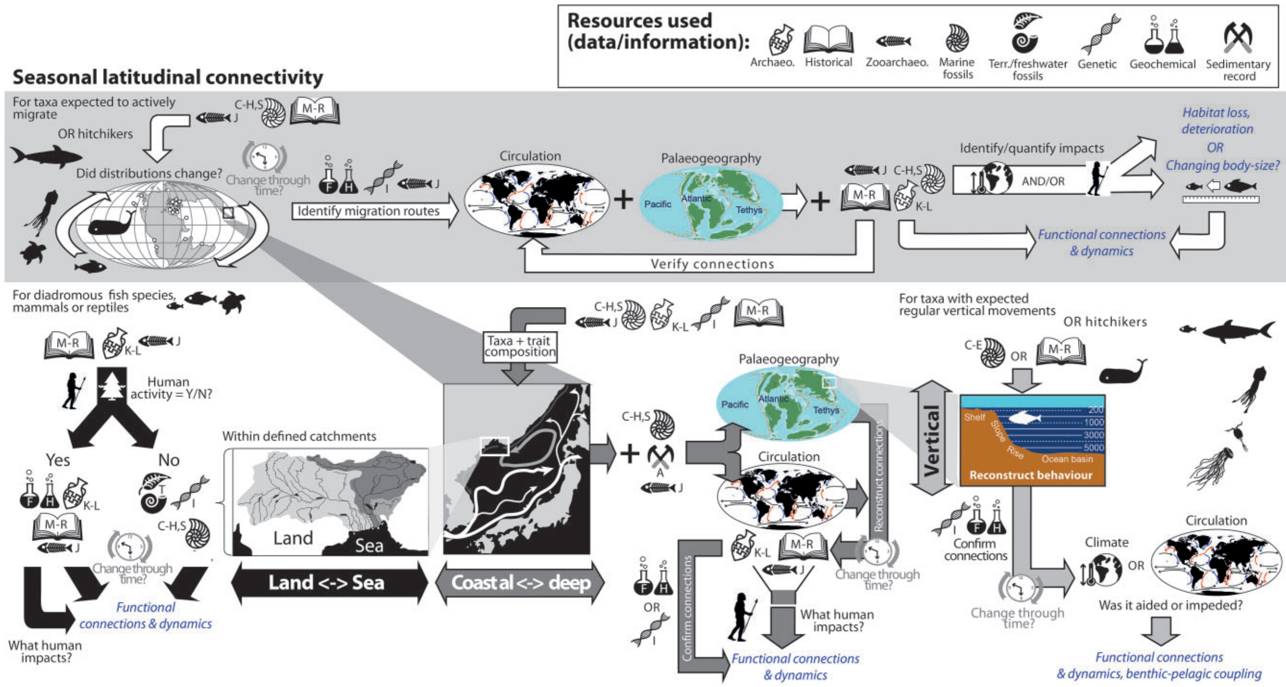

Figure 3. Roadmap for studying MFC using geohistorical resources, including key linkages, steps, and intermediate questions. A range of resources can be used to answer questions about seasonal latitudinal, coastal-to-deep, land-to-sea, and vertical connectivity and their dynamics. The contexts and contributions from humans are incorporated, where relevant. Eight broad categories of geohistorical resource are considered, each subtype is designated by a letter, which refers to Table 3. Approaches apply to any taxa for which there are records or remains, unless otherwise specified, e.g. in the case of vertical connections only those with vertical movements will convey information on vertical connectivity. 'Archaeo.' = archaeological, 'Zooarchaeo.' = zooarchaeological, and 'terre.' = terrestrial.

(Johnson et al. 2008, Jackson and O'Dea 2023). Both corals and lucinids rely on MFC not only to disperse their larvae, but also to horizontally acquire symbiotic microbes (dinoflagellates and sulphur-oxidizing bacteria, respectively) critical to nutrient acquisition in oligotrophic waters.

This case study highlights how geohistorical records can provide information on changes to oceanic, energetic, and genetic connectivity and quantify the resulting cascading effects, especially when combined with an understanding of the functional roles and life histories of the organisms and communities. This must therefore also be true if we wish to predict how species and communities will respond to future changes in connectivity. For example, connectivity between the nutrient-poor upper and nutrient-rich lower ocean layers is consistently predicted to decline in the tropics as oceans warm and stratify (Moore et al. 2018). As the Isthmus of Panama case study shows, such a reduction in vertical connectivity of energy will likely manifest at multiple different biological levels, and perhaps with extended and unpredictable time lags.

In general, this is an especially important topic for tropical systems where many taxa have already reached their environmental limits. The ability of tropical species, and their symbiotic microbes (Leray et al. 2021), to adapt, expand, or shift their biogeographic range to occupy more favourable regions will be critical to their future resilience in the face of climate change. This may not be the case at higher latitude systems where ocean warming is predicted, in contrast, to increase productivity and connectivity to new habitats (see Mediterranean case study). More tropical geohistorical records are therefore essential to provide low-latitude-specific predictions and recommendations for the most biodiverse and yet threatened ecosystems in the world.

Roadmap

MFC refers to all the flows of matter, genes, and energy that are caused by the passive and active movements of marine life (Darnaude et al. 2022; Fig. 1). Here, we propose workflows for studying long-term MFC (decadal to millions of years) and scientific questions that we believe should be prioritized by future research.

How to analyse and interpret geohistorical data in the study of MFC

The application of geohistorical resources to understanding of long-term changes in MFC varies with the process of interest (Figs 3 and 4). Geographic distributions of the species suspected to have performed seasonal latitudinal migrations can be acquired from fossils, historical, and archaeological materials. Biogeochemical markers and sclerochronology from the fossil hard parts of the target species or any hitchhikers can be used to establish if migration was occurring and if so via what routes, paleogeography, and ocean circulation can be used confirm whether those routes were possible or not. Coastal-to-deep connections can be interpreted from the taxonomic composition and the traits of the species present from a range of archives (Fig. 3). Fossils and sedimentary records additionally provide evidence for water flows and paleogeographic changes that may be used to reconstruct structural and functional connections onshore–offshore (and through time). The effects of large-scale oceanic circulation patterns on changes in coastal-to-deep connectivity can be constrained with biogeochemical proxies from fossil materials. The possible roles of human activities in facilitating or impeding seasonal latitudinal migration or coastal-to-deep connections can be estab-

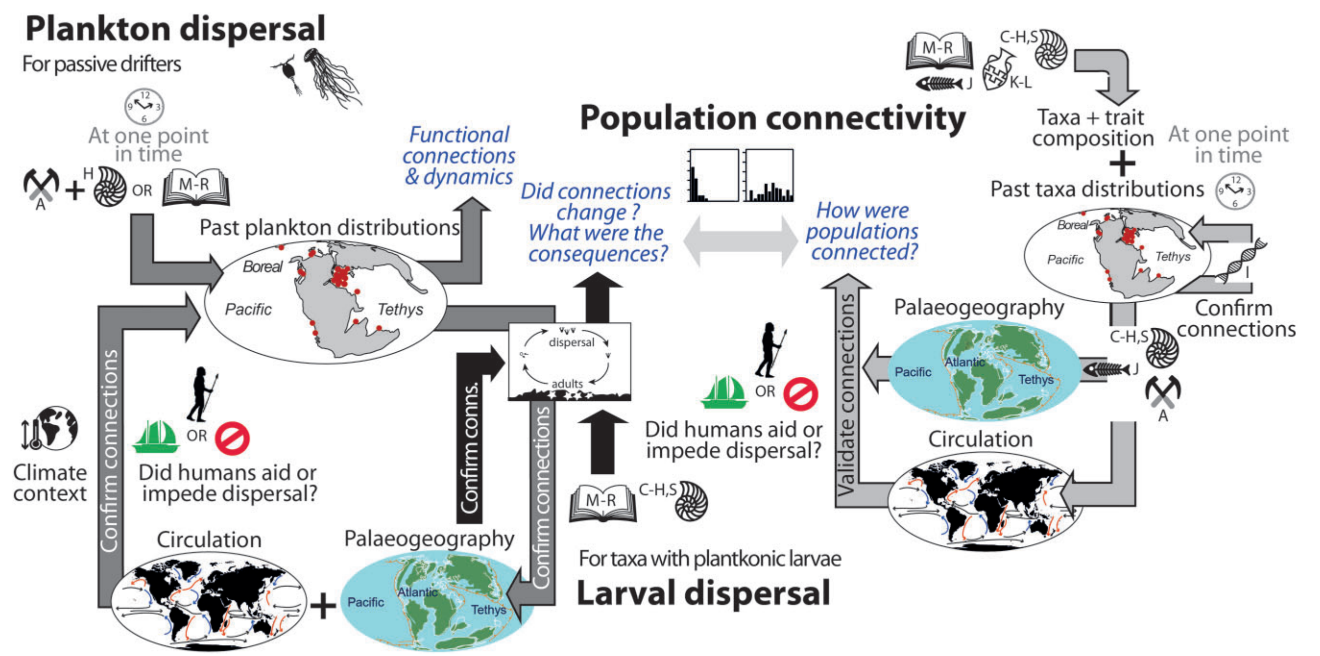

Figure 4. Roadmap for studying MFC using geohistorical resources, including key linkages, steps, and intermediate questions. A range of resources can be used to answer questions about plankton dispersal, larval dispersal, and population connectivity and their dynamics. The contexts and contributions from humans are incorporated, where relevant. Eight broad categories of geohistorical resource are considered, each subtype is designated by a letter, which refers to Table 3. Approaches apply to any taxa for which there are records or remains, unless otherwise specified. 'Archaeo.' = archaeological, 'Zooarchaeo.' = zooarchaeological, and 'terre.' = terrestrial.

lished from historical and archaeological records (Fig. 3). Fossils can provide information on the presence of taxa suspected to perform vertical migration, historical materials may also provide this information, but include taxa that do not leave fossil remains (e.g. jellyfishes, copepods, and so on; Hartman et al. 2018, Fox et al. 2020; Fig. 3). Biogeochemical signals and sclerochronology can confirm vertical migrations.

Within a defined drainage basin, human presence may be determined from historical and archaeological evidence, and this can be combined with biogeochemical data to quantify and interpret the impacts of human activities on land-to-sea connectivity (Fig. 3). If human activities were absent or insignificant (in relation to the timescale of the study), the fossil record can be used together with genetic, sclerochronological, and biogeochemical data to explore functional connections from land-to-sea. The composition of microfossil assemblages in laterally time-equivalent rock formations and sediments and historical records can provide information on plankton distributions and dispersal of plankton (Fig. 3). Historical archives can provide specimens and direct measurements of fish eggs or plankton/larvae, images e.g. plankton atlases and early drawings or measurements. Pelagic larval dispersal can also be inferred from the composition of microfossil assemblages, particularly the presence of fossil larval forms (e.g. for molluscs). Population connectivity can be assessed through examination of laterally time-equivalent fossil assemblages, archaeological remains, or historical records for information on taxonomic composition and the traits of species, especially reproductive mode and larval development (Fig. 4). Suspected connectivity of plankton, pelagic larvae, and populations can be confirmed using genetics, with palaeogeography and climate contexts indicating whether the necessary physical connections existed. The role of humans in preventing or facilitating transport of adults and larvae between populations can then be established from historical or archaeological materials (Fig. 4).

Directions for future research on long-term MFC

Based on the state-of-the-art presented in this paper, we propose a number of research questions that we believe are a priority for future research on MFC and should be addressed using geohistorical resources.

Geohistorical data can provide ecological baselines that extend beyond the onset of modern, ecological monitoring programs (c. 1950s), that should be used as a basis for assessing recent ecosystem changes due to anthropogenic activities, including how they impact MFC. Although many datasets now exist that might be used to establish preindustrial ecological baselines (e.g. Thurstan 2022), these should be expanded to explicitly include MFC processes, for instance by reconstructing the biogeographic ranges and routes of seasonal migrations of whales or large pelagic fishes during key periods of palaeoenvironmental change, such as the last interglacial. Moreover, preindustrial MFC as determined from historical and archaeological records could be used to determine the long-term (decadal–millennial) impacts of human activities (such as changing the physical connections e.g. between basins or between the land and the sea) on MFC, as well as quantifying the scale of those impacts and rates of change.

As the ocean is unambiguously intertwined with the climate system, palaeoclimatic variability has had a considerable influence on the biological, chemical, and physical ocean processes, with knock-on impacts on past MFC. Past climate analogues (Yin and Berger 2015, Burke et al. 2018) offer insights into the possible future ecosystem states and MFC under different climate change scenarios. Understanding long-term (centennial–millions of years) MFC dynamics under natural climate variability, that includes the extreme changes associated with major climate transitions, can reveal tipping points for MFC. Specifically, geohistorical data can help to infer how climate change will impact MFC in marginal and semienclosed seas, such as the Mediterranean Sea, that are experiencing accelerated rates of environmental change (e.g. Albano et al. 2021, Scarponi et al. 2022, 2024). At the same time, these past analogues may help predict potential future MFC patterns due to the formation of new connections, e.g. the opening of polar corridors as the Earth continues to warm (e.g. Vermeij and Roopnarine 2008).

The two-way connections between MFC and biogeochemical cycles must have evolved since the first appearance of life on Earth (Falkowski et al. 1998, Ridgwell and Zeebe 2005, Ziveri et al. 2023) and yet remains largely unexplored beyond the level of hypotheses. For example, assumptions are often made regarding the efficiency of the biological carbon pump during past hyperthermals that imply MFC changes (Li et al. 2023), but these are not validated with evidence for changing MFC.

Continental configurations have ranged from periods where there was one large supercontinent (Pangaea; e.g. Cavin et al. 2008, Torsvik et al. 2021, Li et al. 2021) and the remainder of the Earth's surface was open ocean, to periods when there were extensive areas of shallow epicontinental seas (e.g. in the Cretaceous; Lagomarcino and Miller 2012). Geohistorical resources can be leveraged to ask: What are the effects of the large-scale changes in MFC that are created by palaeogeographic reconfigurations? Restriction and disconnection of oceanic basins severed the functional connections transferring critical energy and genetic materials between basins or between the land and sea. Although some research addresses this theme (e.g. O'Dea et al. 2016, Agiadi et al. 2024), there are also many periods that could be studied further such as the impacts of the opening of the Atlantic Ocean or the entire evolution of the Paratethys.

Some deep-time ecosystems were structured very differently from modern marine ecosystems and their study within an MFC framework could demonstrate the broad range of MFC possible. For instance, changes in MFC across major periods of ecological reorganization, such as the Cambrian substrate revolution wherein the seafloor first became colonized by infauna (Bottjer 2010, Mángano and Buatois 2017, Herringshaw et al. 2017), or in the aftermath of mass extinctions such as at the end of the Permian (Wignall and Bond 2023). The communities and ecosystems produced by changes in MFC may have functioned very differently than those prior.

We might ask: What were the impacts of deep-time changes in oceanic circulation on larval and plankton dispersal? This topic has been only partially addressed for phyto- and zooplankton (Sexton and Norris 2008, Henderiks et al. 2020, Boscolo-Galazzo et al. 2022) and not at all for higher trophic-levels.

Geohistorical resources can show how the ecological and evolutionary interdependence of populations over long timescales has been affected by changes in MFC. Species' ability to disperse through the seascape and connect with other populations is linked with various biological traits (Burgess et al. 2016). For instance, species larval dispersal capacity, which is determined by the duration of larval development, buoyancy, and behaviour, determines how far the species can passively disperse via ocean currents (e.g. Shanks 2009, Leis 2020). Greater functional connectivity enhances the resilience of ecosystems, allowing populations to survive environmental changes and persist over time (Magris et al. 2014). However, evolution does not always lead to the selection of characteristics that favour dispersal and connectivity (Magris et al. 2014).

How does the magnitude of MFC relate to the observed genetic diversity and population or ecosystem resilience? Examples from geohistorical records may indicate whether there is a minimum (or optimal) level of MFC required for healthy, stable, and resilient marine ecosystems? The changes in the palaeobiogeography of marine species associated with basin restrictions (e.g. during the Messinian Salinity Crisis in the Mediterranean; Agiadi et al. 2024), combined with paleoceanographic data from within the restricted basin and outside it, can be used to elucidate such thresholds. This information can be used to inform models of MFC patterns and help to understand MFC at community and ecosystem levels, which is critical for inferring future ecosystem health and managing marine resources (Darnaude et al. 2022).

At what point does MFC become a disadvantage? If diverse ecosystems are more resilient to change because they have greater potential for adaptation and evolution in the face of environmental change, then will functionally very well-connected and therefore genetically more homogeneous systems transfer the impacts of perturbations through ecosystems faster and farther?

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Author contributions

Conceptualization: KA, BAC, AD; Data curation: BAC; Funding acquisition: KA, BAC, AD; Investigation: all authors; Project administration: KA, BAC, AD; Supervision; KA, BAC; Visualization: KA, BAC, AB, LLL; Writing—original draft: all authors; Writing—review and editing: all authors. KA and BAC contributed equally and shared first and corresponding authorship. AD is listed as senior author due to her key role in the overall conceptualization of this article and the organization of the international exchanges that led to its production. The remaining authors contributed equally and are listed alphabetically.

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Data availability

All data produced for this work have been made available within the main manuscript or in the supplementary material.

References

Adame MF, Wright SF, Grinham A *et al.* Terrestrial–marine connectivity: patterns of terrestrial soil carbon deposition in coastal sediments determined by analysis of glomalin related soil protein. *Limnol Oceanogr* 2012;**57**:1492–502. https://doi.org/10.4319/lo.2012.57.5.1492

Agiadi K, Antonarakou A, Kontakiotis G *et al.* Connectivity controls on the Late Miocene eastern Mediterranean fish fauna. *Int J Earth Sci* 2017;**106**:1147–59. https://doi.org/10.1007/s00531-016-1355-7

Agiadi K, Azzarone M, Hua Q *et al.* The taphonomic clock in fish otoliths. *Paleobiology* 2022;**48**:154–70. https://doi.org/10.1017/pab.2021.30

Agiadi K, Girone A, Koskeridou E *et al.* Pleistocene marine fish invasions and paleoenvironmental reconstructions in the eastern Mediterranean. *Quat Sci Rev* 2018;**196**:80–99. https://doi.org/10.1016/j.quascirev.2018.07.037

Agiadi K, Hohmann N, Gliozzi E *et al.* The marine biodiversity impact of the Late Miocene Mediterranean salinity crisis. *Science* 2024;**385**:986–91. https://doi.org/10.1126/science.adp3703

Agiadi K, Koskeridou E, Thivaiou D. At the crossroads: early miocene marine fishes of the proto-Mediterranean Sea. *Fossil Record* 2021;**24**:233–46. https://doi.org/10.5194/fr-24-233-2021

Agiadi K, Quillévéré F, Nawrot R *et al.* Palaeontological evidence for community-level decrease in mesopelagic fish size during pleistocene climate warming in the eastern Mediterranean. *Proc R Soc B Biol Sci* 2023;**290**:20221994. https://doi.org/10.1098/rspb.2022.1994

Agiadi K, Triantaphyllou M, Girone A *et al.* The early quaternary palaeobiogeography of the eastern Ionian deep-sea teleost fauna: a novel palaeocirculation approach. *Palaeogeogr Palaeoclimatol Palaeoecol* 2011;**306**:228–42. https://doi.org/10.1016/j.palaeo.2011.04.029

Albano PG, Gallmetzer I, Haselmair A *et al.* Historical ecology of a biological invasion: the interplay of eutrophication and pollution determines time lags in establishment and detection. *Biol Invasions* 2018;**20**:1417–30. https://doi.org/10.1007/s10530-017-1634-7

Albano PG, Hua Q, Kaufman DS *et al.* Radiocarbon dating supports bivalve-fish age coupling along a bathymetric gradient in high-resolution paleoenvironmental studies. *Geology* 2020;**48**:589–93. https://doi.org/10.1130/G47210.1

Albano PG, Schultz L, Wessely J *et al.* The dawn of the tropical Atlantic invasion into the Mediterranean Sea. *Proc Natl Acad Sci* 2024;**121**:e2320687121. https://doi.org/10.1073/pnas.2320687121

Albano PG, Steger J, Bošnjak M *et al.* Native biodiversity collapse in the eastern Mediterranean. *Proc R Soc B Biol Sci* 2021;**288**:20202469. https://doi.org/10.1098/rspb.2020.2469

Alheit J, Licandro P, Coombs S *et al.* Atlantic multidecadal oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic. *J Mar Syst* 2014;**131**:21–35. https://doi.org/10.1016/j.jmarsys.2013.11.002

Allen MS, Ladefoged TN, Wall JJ. Traditional Rotuman fishing in temporal and regional context. *Int J Osteoarchaeol* 2001;**11**:56–71. https://doi.org/10.1002/oa.546

Alleway HK, Connell SD. Loss of an ecological baseline through the eradication of oyster reefs from coastal ecosystems and human memory. *Conserv Biol* 2015;**29**:795–804. https://doi.org/10.1111/cobi.12452

Amekawa S, Kubota K, Miyairi Y *et al.* Fossil otoliths, from the Gulf of Kutch, Western India, as a paleo-archive for the mid- to late-holocene environment. *Quat Int* 2016;**397**:281–8. https://doi.org/10.1016/j.quaint.2015.07.006

Andreetto F, Aloisi G, Raad F *et al.* Freshening of the Mediterranean Salt Giant: controversies and certainties around the terminal (Upper Gypsum and Lago-Mare) phases of the Messinian salinity crisis. *Earth Sci Rev* 2021;**216**:103577. https://doi.org/10.1016/j.earscirev.2021.103577

Arz HW, Pätzold J, Müller PJ *et al.* Influence of Northern Hemisphere climate and global sea level rise on the restricted Red Sea marine environment during termination I. *Paleoceanography* 2003;**18**:1053. https://doi.org/10.1029/2002PA000864

Auffret AG, Plue J, Cousins SAO. The spatial and temporal components of functional connectivity in fragmented landscapes. *Ambio* 2015;**44**:51–9. https://doi.org/10.1007/s13280-014-0588-6

Avery G, Underhill LG. Seasonal exploitation of seabirds by late holocene coastal foragers: analysis of modern and archaeological data from the Western Cape, South Africa. *J Archaeolog Sci* 1986;**13**:339–60. https://doi.org/10.1016/0305-4403(86)90053-1

Babila TL, Penman DE, Hönisch B *et al.* Capturing the global signature of surface ocean acidification during the palaeocene–eocene thermal maximum. *Philos Trans R Soc A* 2018;**376**:20170072. https://doi.org/10.1098/rsta.2017.0072

Baglinière JL, Castanet J, Conand F *et al. Tissus Durs et Age Individuel des Vertébrés. Colloque National, Bondy*. (FRA) 4-6/3/1991. ORSTOM. Paris: INRA, 1992.

Baker K. So many seals, so little time: the rapid extinction of the Caribbean monk seal. *Monachus Sci* 2008;**11**.

Ballester B. El Médano rock art style: izcuña paintings and the marine hunter-gatherers of the Atacama Desert. *Antiquity* 2018;**92**:132–48. https://doi.org/10.15184/aqy.2017.185

Barrenechea-Angeles IB, Romero-Martínez ML, Cavaliere M *et al.* Encapsulated in sediments: eDNA deciphers the ecosystem history of one of the most polluted European marine sites. *Environ Int* 2023;**172**:107738. https://doi.org/10.1016/j.envint.2023.107738

Barrett JH, Orton D, Johnstone C *et al.* Interpreting the expansion of sea fishing in medieval Europe using stable isotope analysis of archaeological cod bones. *J Archaeolog Sci* 2011;**38**:1516–24. https://doi.org/10.1016/j.jas.2011.02.017

Barrett JH. An environmental (pre)history of European fishing: past and future archaeological contributions to sustainable fisheries. *J Fish Biol* 2019;**94**:1033–44. https://doi.org/10.1111/jfb.13929

Béarez P, Fuentes-Mucherl F, Rebolledo S *et al.* Billfish foraging along the northern coast of Chile during the Middle Holocene (7400–5900 cal BP). *J Anthropol Archaeol* 2016;**41**:185–95. https://doi.org/10.1016/j.jaa.2016.01.002

Béarez P, Gay P, Lunniss R. Sea fishing at Salango (Manabí Province, Ecuador) during the middle formative Machalilla phase. *Latin Am Antiquity* 2012;**23**:195–214. https://doi.org/10.7183/1045-6635.23.2.195

Bekker-Nielsen T. The technology and productivity of ancient sea fishing. In: T Bekker-Nielsen (ed.), *Ancient Fishing and Fish Processing in the Black Sea region*. Vol. **2**. Black Sea Studies. Aarhus: Aarhus University Press, 83–95, 2005.

Beller EE, McClenachan L, Zavaleta ES *et al.* Past forward: recommendations from historical ecology for ecosystem management. *Global Ecol Conser* 2020;**21**:e00836. https://doi.org/10.1016/j.gecco.2019.e00836

Benkwitt CE, Carr P, Wilson SK *et al.* Seabird diversity and biomass enhance cross-ecosystem nutrient subsidies. *Proc R Soc B Biol Sci* 2022;**289**:20220195. https://doi.org/10.1098/rspb.2022.0195

Bernal-Casasola D, Gardeisen A, Morgenstern P *et al.* Ancient whale exploitation in the Mediterranean: the archaeological record. *Antiquity* 2016;**90**:914–27. https://doi.org/10.15184/aqy.2016.116

Bernhardt A, Schwanghart W, Hebbeln D *et al.* Immediate propagation of deglacial environmental change to deep-marine turbidite systems along the Chile convergent margin. *Earth Planet Sci Lett* 2017;**473**:190–204. https://doi.org/10.1016/j.epsl.2017.05.017

Betts MW, Noël S, Tourigny E *et al.* Zooarchaeology of the historic cod fishery in Newfoundland and Labrador, Canada. *J North Atlantic* 2014;**2014**:1–21.

Beu AG, Griffin M, Maxwell PA. Opening of Drake Passage gateway and late miocene to pleistocene cooling reflected in Southern Ocean molluscan dispersal: evidence from New Zealand and Argentina. *Tectonophysics* 1997;**281**:83–97. https://doi.org/10.1016/S0040-1951(97)00160-1

Beu AG. Gradual miocene to pleistocene uplift of the Central American isthmus: evidence from tropical American tonnoidean gastropods. *J Paleontol* 2001;**75**:706–20. https://doi.org/10.1666/0022-3360(2001)075%3c0706:GMTPUO%3e2.0.CO;2

Bianucci G, Landini W, Buckeridge J. Whale barnacles and Neogene cetacean migration routes. *NZ J Geol Geophys* 2006;**49**:115–20. https://doi.org/10.1080/00288306.2006.9515152

Boethius A, Kjällquist M, Kielman-Schmitt M *et al.* Early Holocene Scandinavian foragers on a journey to affluence: mesolithic fish exploitation, seasonal abundance and storage investigated through strontium isotope ratios by laser ablation (LA-MC-ICP-MS). *PLoS One* 2021;**16**:e0245222. https://doi.org/10.1371/journal.pone.0245222

Borge T, Bachmann L, Bjornstad G *et al.* Genetic variation in Holocene bowhead whales from Svalbard. *Mol Ecol* 2007;**16**:2223–35, https://doi.org/10.1111/j.1365-294X.2007.03287.x

Boscolo-Galazzo F, Jones A, Dunkley Jones T *et al.* Late Neogene evolution of modern deep-dwelling plankton. *Biogeosciences* 2022;**19**:743–62. https://doi.org/10.5194/bg-19-743-2022

Bottjer DJ. The cambrian substrate revolution and early evolution of the phyla. *J Earth Sci* 2010;**21**:21–4. https://doi.org/10.1007/s12583-010-0160-7

Brito C, Vieira N. A sea-change in the sea? Perceptions and practices towards sea turtles and Manatees in Portugal's Atlantic Ocean legacy. In: K Schwerdtner Máñez, B Poulsen (eds), *Perspectives on Oceans Past*. Dordrecht: Springer, 2016, 175–91.

Brito C. *Humans and Aquatic Animals in Early Modern America and Africa*. Amsterdam: Amsterdam University Press, 2023.

Bryan-Brown D, Brown C, Hughes J *et al.* Patterns and trends in marine population connectivity research. *Mar Ecol Progr Ser* 2017;**585**:243–56. https://doi.org/10.3354/meps12418

Buchholz H-G, Jöhrens J. Jagd und fischfang. In: *Archaeologia Homerica J*. Göttingen: Vandenhoeck & Ruprecht Gmbh & Co, 1973.

Bulian F, Kouwenhoven TJ, Andersen N *et al.* Reflooding and repopulation of the Mediterranean Sea after the Messinian salinity crisis: benthic foraminifer assemblages and stable isotopes of Spanish basins. *Mar Micropaleontol*:2022a;**176**, 102160. https://doi.org/10.1016/j.marmicro.2022.102160

Bulian F, Kouwenhoven TJ, Jiménez-Espejo FJ *et al.* Impact of the Mediterranean-Atlantic connectivity and the late miocene carbon shift on deep-sea communities in the Western Alboran Basin. *Palaeogeogr Palaeoclimatol Palaeoecol* 2022b;**589**:110841. https://doi.org/10.1016/j.palaeo.2022.110841

Burgess SC, Baskett ML, Grosberg RK *et al.* When is dispersal for dispersal? Unifying marine and terrestrial perspectives. *Biol Rev* 2016;**91**:867–82. https://doi.org/10.1111/brv.12198

Burke KD, Williams JW, Chandler MA. *et al.* Pliocene and eocene provide best analogs for near-future climates. *Proc Natl Acad Sci* 2018;**115**:201809600.

Butiseacă GA, van der Meer MTJ, Kontakiotis G *et al.* Multiple crises preceded the Mediterranean salinity crisis: aridification and vegetation changes revealed by biomarkers and stable isotopes. *Global Planet Change* 2022;**217**:103951. https://doi.org/10.1016/j.gloplacha.2022.103951

Butler PG, Freitas PS, Burchell M. *et al.* Archaeology and sclerochronology of marine bivalves. In: AC Smaal, JG Ferreira, J Grant, JK Petersen, Ø Strand (eds), *Goods and Services of Marine Bivalves*. New York: Springer International Publishing, 2019, 413–44.

Çakirlar C. Molluscs (invertebrates) : analyses in environmental archaeology. In: C Smith (ed.), *Encyclopedia of Global Archaeology*. Berlin: Springer, 2014, 5005–10.

Campana SE, Thorrold SR. Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations?. *Can J Fish Aquat Sci* 2001;**58**:30–8. https://doi.org/10.1139/f00-177

Canonico G, Buttigieg PL, Montes E *et al.* Global observational needs and resources for marine biodiversity. *Front Mar Sci* 2019;**6**:367. https://www.frontiersin.org/articles/10.3389/fmars.2019.00367

Carolin N, Bajpai S, Maurya AS. *et al.* New perspectives on late Tethyan Neogene biodiversity development of fishes based on miocene (∼ 17 Ma) otoliths from southwestern India. *Paläontologische Zeitschrift* 2023;**97**:43–80. https://doi.org/10.1007/s12542-022-00623-9

Caswell BA, Coe AL. Primary productivity controls on opportunistic bivalves during early Jurassic oceanic deoxygenation. *Geology* 2013;**41**:1163–6. https://doi.org/10.1130/G34819.1

Caswell BA, Frid CLJ. Learning from the past: functional ecology of marine benthos during eight million years of aperiodic hypoxia, lessons from the Late Jurassic. *Oikos* 2013;**122**:1687–99. https://doi.org/10.1111/j.1600-0706.2013.00380.x

Caswell BA, Herringshaw L. Marine bioturbation collapse during Early Jurassic deoxygenation: implications for post-extinction marine ecosystem functioning. In: *Conservation Palaeobiology of Marine Ecosystems*. Vol. **529**. Special Publications. London: Geological Society, 2023, 311–44. https://doi.org/10.1144/SP529-2022-226.

Cavin L, Longbottom A, Richter M. Fishes and the break-up of Pangaea: an introduction. Vol. **295**. Special Publications. London: Geological Society, 2008, 7–8. https://doi.org/10.1144/SP295.2

Claassen C. Shells. In: *Cambridge Manuals in Archaeology*. Cambridge: Cambridge University Press, 1998.

Clapham PJ, Aguilar A, Hatch LT. Determining spatial and temporal scales for management: lessons from whaling. *Mar Mammal Sci* 2008;**24**:183–201. https://doi.org/10.1111/j.1748-7692.2007.00175.x

Clements CF, Blanchard JL, Nash KL *et al.* Body size shifts and early warning signals precede the historic collapse of whale stocks. *Nat Ecol Evol* 2017;**1**:1–6.

Clementz MT, Fordyce RE, Peek SL *et al.* Ancient marine isoscapes and isotopic evidence of bulk-feeding by oligocene cetaceans. *Palaeogeogr Palaeoclimatol Palaeoecol* 2014;**400**:28–40. https://doi.org/10.1016/j.palaeo.2012.09.009

Cleyet-Merle J-J, Madelaine S. Inland evidence of human sea coast exploitation in Palaeolithic Europe. In: A. Fischer (ed.), *Man and Sea* *in the Mesolithic. Coastal Settlement Above and Below Present Sea Level*. Oxford: Oxbow Books, 1995, 303–8

Cleyet-Merle J-J. La préhistoire de la pêche. In: *Collections Les Hespérides*. Paris: Errance, 1991.

Colley SM. Fishing for facts. Can we reconstruct fishing methods from archaeological evidence?. *Austr Archaeol* 1987;**24**:16–26. http://www.jstor.org/stable/40286850

Cooke JG. *Eubalaena glacialis* (errata version published in 2020). In: *The IUCN Red List of Threatened Species: e.T41712A178589687*. Gland: IUCN, 2020.https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T41712A178589687.en.

Cooper JA, Griffin JN, Kindlimann R *et al.* Are shark teeth proxies for functional traits? A framework to infer ecology from the fossil record. *J Fish Biol* 2023;**103**:798–814. https://doi.org/10.1111/jfb.15326

Cortés Sánchez M, Morales Muñiz A, Simón Vallejo MD *et al.* Palaeoenvironmental and cultural dynamics of the coast of Málaga (Andalusia, Spain) during the upper Pleistocene and early Holocene. *Quat Sci Rev* 2008;**27**:2176–93. https://doi.org/10.1016/j.quascirev.2008.03.010

Cowen RK, Sponaugle S. Larval dispersal and marine population connectivity. *Ann Rev Mar Sci* 2009;**1**:443–66. https://doi.org/10.1146/annurev.marine.010908.163757

Crosby AW. Ecological imperialism: the biological expansion of Europe, 900–1900. In: *Studies in Environment and History*. Cambridge: Cambridge University Press, 2004.

Cunningham JA, Jeffery Abt CH. Coordinated shifts to non-planktotrophic development in spatangoid echinoids during the Late Cretaceous. *Biol Lett* 2009;**5**:647–50. https://doi.org/10.1098/rsbl.2009.0302

D'Amore DV, Bonzey NS, Berkowitz J *et al.* Holocene soil-geomorphic surfaces influence the role of salmon-derived nutrients in the coastal temperate rainforest of Southeast Alaska. *Geomorphology* 2011;**126**:377–86. https://doi.org/10.1016/j.geomorph.2010.04.014

Damm CB, Skandfer M, Jordan PD. Peopling prehistoric coastlines: identifying mid-holocene forager settlement strategies in Northern Norway. *J Maritime Archaeol* 2022;**17**:131–60. https://doi.org/10.1007/s11457-021-09316-x

Darnaude A, Arnaud-Haond S, Hunter E *et al.* Unifying approaches to functional marine connectivity for improved marine resource management: the European Sea-UNICORN COST Action. *Res Ideas Outcomes* 2022;**8**:e80223. https://doi.org/10.3897/rio.8.e80223

Davidson JM, Leach BF. Fishing on Nukuoro Atoll: ethnographic and archaeological viewpoints. In: M Julien, M Orliac, C Orliac (eds), *Mémoire de pierre, mémoire D'homme: Tradition et archéologie en Océanie. Hommage à José Garanger*. Paris: Publications de la Sorbonne, 1996, 184–202.

De Schepper S, Ray JL, Skaar KS *et al.* The potential of sedimentary ancient DNA for reconstructing past sea ice evolution. *ISME J* 2019;**13**:2566–77. https://doi.org/10.1038/s41396-019-0457-1

Delorme J, Roux C. *Guide illustré de la faune aquatique dans l'art grec*. Juan Les Pins: A.P.D.C.A., 1987.

Denechaud C, Smoliński S, Geffen AJ *et al.* A century of fish growth in relation to climate change, population dynamics and exploitation. *Global Change Biol* 2020;**26**:5661–78. https://doi.org/10.1111/gcb.15298

Der Sarkissian C, Möller P, Hofman CA *et al.* Unveiling the ecological applications of ancient DNA from mollusk shells. *Front Ecol Evol* 2020;**8**:37. https://doi.org/10.3389/fevo.2020.00037

Der Sarkissian C, Pichereau V, Dupont C *et al.* Ancient DNA analysis identifies marine mollusc shells as new metagenomic archives of the past. *Mol Ecol Resour* 2017;**17**:835–53. https://doi.org/10.1111/1755-0998.12679

Desse J, Desse-Berset N. Age et saison de mort des poissons : applications à l'archéologie. In: J-L Baglinière, J Castanet, F Conard, FJ Meunier, J Desse, N Desse-Berset (eds), *Tissus durs et âge individuel des vertébrés : Colloque national, Bondy, 4-6/3/1991*. Paris: ORSTOM, INRA, 1992, 341–53.

Desse J, Desse-Berset N. Le cortège de Neptune: les poissons de la Méditerranée durant l'Holocène. In: A Gardeisen (ed.), *Mouvements ou déplacements de populations animales en Méditerranée au cours de l'Holocène. Séminaire de recherche du thème 15. Archéologie de l'Animal (UMR 154–CNRS). Lattes-Montpellier (France), 29 Septembre 2000, (pp. 83–96). BAR International Series, 1017*. Oxford: BAR Publishing, 2002.

Desse J, Desse-Berset N. Préhistoire du Mérou. *Mar Life* 1999;**9**:19–30.

Dickson AJ, Cohen AS, Coe AL. Seawater oxygenation during the paleocene-eocene thermal maximum. *Geology* 2012;**40**:639–42. https://doi.org/10.1130/g32977.1

Dietl GP, Flessa KW. Conservation paleobiology: putting the dead to work. *Trends Ecol Evol* 2011;**26**:30–7.

Dillon EM, Norris RD, O'Dea A. Dermal denticles as a tool to reconstruct shark communities. *Mar Ecol Progr Ser* 2017;**566**:117–34. https://doi.org/10.3354/meps12018

Disspain MC, Wilson CJ, Gillanders BM. Morphological and chemical analysis of archaeological fish otoliths from the Lower Murray River, South Australia. *Archaeol Ocean* 2012;**47**:141–50. https://doi.org/10.1002/j.1834-4453.2012.tb00126.x

Dunne JA, Labandeira CC, Williams RJ. Highly resolved early Eocene food webs show development of modern trophic structure after the end-cretaceous extinction. *Proc R Soc B Biol Sci* 2014;**281**:20133280. https://doi.org/10.1098/rspb.2013.3280

Dynesius M, Jansson R. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc Natl Acad Sci* 2000;**97**:9115–20. https://doi.org/10.1073/pnas.97.16.9115

Eggins S, De Deckker P, Marshall J. Mg/Ca variation in planktonic foraminifera tests: implications for reconstructing palaeo-seawater temperature and habitat migration. *Earth Planet Sci Lett* 2003;**212**:291–306. https://doi.org/10.1016/S0012-821X(03)00283-8

Engelhard GH, Thurstan RH, MacKenzie BR *et al.* ICES meets marine historical ecology: placing the history of fish and fisheries in current policy context. *ICES J Mar Sci* 2016;**73**:1386–403. https://doi.org/10.1093/icesjms/fsv219

Engelhaupt D, Rus Hoelzel A, Nicholson C *et al.* Female philopatry in coastal basins and male dispersion across the North Atlantic in a highly mobile marine species, the sperm whale (*Physeter macrocephalus*). *Mol Ecol* 2009;**18**:4193–205. https://doi.org/10.1111/j.1365-294X.2009.04355.x

Erlandson J, Rick T. Archaeology, marine ecology, and human impacts marine ecosystems. In: T Rick, J Erlandson (eds), *Human Impacts on Ancient Marine Ecosystems. A Global Perspective*. Berkeley: University of California Press, 2008, 1–18.

Erlandson JM, Graham MH, Bourque BJ *et al.* The Kelp Highway hypothesis: marine ecology, the Coastal Migration theory, and the peopling of the Americas. *J Island Coast Archaeol* 2007;**2**:161–74. https://doi.org/10.1080/15564890701628612

Falkowski PG, Barber RT, Smetacek V. Biogeochemical controls and feedbacks on ocean primary production. *Science* 1998;**281**:200–6. https://doi.org/10.1126/science.281.5374.200

Fariña JM, Salazar S, Wallem KP *et al.* Nutrient exchanges between marine and terrestrial ecosystems: the case of the Galapagos Sea lion Zalophus wollebaecki. *J Anim Ecol* 2003;**72**:873–87. https://doi.org/10.1046/j.1365-2656.2003.00760.x

Farris DW, Jaramillo C, Bayona G *et al.* Fracturing of the Panamanian isthmus during initial collision with South America. *Geology* 2011;**39**:1007–10. https://doi.org/10.1130/G32237.1

Fenton IS, Aze T, Farnsworth A *et al.* Origination of the modern-style diversity gradient 15 million years ago. *Nature* 2023;**614**:1–5.

Fenton M, Geiselhart S, Rohling EJ *et al.* Aplanktonic zones in the Red Sea. *Mar Micropaleontol* 2000;**40**:277–94. https://doi.org/10.1016/S0377-8398(00)00042-6

Fox L, Stukins S, Hill T *et al.* Quantifying the effect of anthropogenic climate change on calcifying plankton. *Sci Rep* 2020;**10**:1620. https://doi.org/10.1038/s41598-020-58501-w

Fraass AJ, Leckie RM, Lowery CM *et al.* Precision in biostratigraphy: evidence for a temporary flow reversal in the Central American seaway during or after the oligocene-miocene transition. *J Foraminiferal Res* 2019;**49**:357–66. https://doi.org/10.2113/gsjfr.49.4.357

Friedman M, Carnevale G. The Bolca Lagerstätten: shallow marine life in the Eocene. *J Geological Soc* 2018;**175**:569–79. https://doi.org/10.1144/jgs2017-164

Fuksi T, Tomašových A, Gallmetzer I *et al.* 20th century increase in body size of a hypoxia-tolerant bivalve documented by sediment cores from the northern Adriatic Sea (Gulf of Trieste). *Mar Pollut Bull* 2018;**135**:361–75. https://doi.org/10.1016/j.marpolbul.2018.07.004

Gallmetzer I, Haselmair A, Tomašových A *et al.* Responses of molluscan communities to centuries of human impact in the northern Adriatic Sea. *PLoS One* 2017;**12**:e0180820. https://doi.org/10.1371/journal.pone.0180820

Geffen AJ, Høie H, Folkvord A *et al.* High-latitude climate variability and its effect on fisheries resources as revealed by fossil cod otoliths. *ICES J Mar Sci* 2011;**68**:1081–9. https://doi.org/10.1093/icesjms/fsr017

Gerber LR, Mancha-Cisneros MDM, O'Connor MI *et al.* Climate change impacts on connectivity in the ocean: implications for conservation. *Ecosphere* 2014;**5**:1. https://doi.org/10.1890/ES13-00336.1

Girone A, De Astis A, Sierro FJ *et al.* Planktonic foraminifera response to orbital and millennial-scale climate variability at the southern Iberian Margin (IODP Site U1385) during Marine Isotope stages 20 and 19. *Palaeogeogr Palaeoclimatol Palaeoecol* 2023;**615**:111450. https://doi.org/10.1016/j.palaeo.2023.111450

Girone A, Nolf D, Cappetta H. Pleistocene fish otoliths from the Mediterranean Basin: a synthesis. *Geobios* 2006;**39**:651–71. https://doi.org/10.1016/j.geobios.2005.05.004

Glykou A, Eriksson G, Storå J *et al.* Intra- and inter-tooth variation in strontium isotope ratios from prehistoric seals by laser ablation multi-collector inductively coupled plasma mass spectrometry. *Rapid Commun Mass Spectrom* 2018;**32**:1215–24. https://doi.org/10.1002/rcm.8158

Gómez-Cabrera MDC, Young J, Roff G *et al.* Broadening the taxonomic scope of coral reef paleoecological studies using ancient DNA. *Mol Ecol* 2019;**28**:2636–52. https://doi.org/10.1111/mec.15038

Gorlova EN, Krylovich OA, Savinetsky AB. *et al.* Ecology of the ringed seal (*Pusa hispida*) from the Bering Strait in the late Holocene. *Biol Bull* 2012;**39**:464–71. https://doi.org/10.1134/S1062359012050056

Grossman EL, Robbins JA, Rachello-Dolmen PG. *et al.* Freshwater input, upwelling, and the evolution of Caribbean coastal ecosystems during formation of the Isthmus of Panama. *Geology* 2019;**47**:857–61. https://doi.org/10.1130/G46357.1

Harnik PG, Torstenson ML, Williams MA. Assessing the effects of anthropogenic eutrophication on marine bivalve life history in the northern gulf of Mexico. *Palaios* 2017;**32**:678–88. https://doi.org/10.2110/palo.2017.033

Hartman JD, Bijl PK, Sangiorgi F. A review of the ecological affinities of marine organic microfossils from a holocene record offshore of Adélie Land (East Antarctica). *J Micropalaeontol* 2018;**37**:445–97. https://doi.org/10.5194/jm-37-445-2018

Harzhauser M, Kroh A, Mandic O. *et al.* Biogeographic responses to geodynamics: a key study all around the Oligo–Miocene Tethyan seaway. *Zoologischer Anzeiger—A J Compar Zool* 2007;**246**:241–56. https://doi.org/10.1016/j.jcz.2007.05.001

Hays J, Imbrie J, Shackleton N. Variations in the Earth's orbit: pacemaker of the ice ages. *Science* 1976;**194**:1121–32. https://doi.org/10.1126/science.194.4270.1121

Henderiks J, Bartol M, Pige N. *et al.* Shifts in phytoplankton composition and stepwise climate change during the middle miocene. *Paleoceanogr Paleoclimatol* 2020;**35**:e2020PA003915. https://doi.org/10.1029/2020PA003915

Henry L-A, Frank N, Hebbeln D *et al.* Global ocean conveyor lowers extinction risk in the deep sea. *Deep Sea Res Part I* 2014;**88**:8–16. https://doi.org/10.1016/j.dsr.2014.03.004

Hentati-Sundberg J, Raymond C, Sköld M. *et al.* Fueling of a marine-terrestrial ecosystem by a major seabird colony. *Sci Rep*, 2020;**10**:15455. https://doi.org/10.1038/s41598-020-72238-6

Herringshaw LG, Callow RHT, McIlroy D. *Engineering the Cambrian Explosion: The Earliest Bioturbators as Ecosystem Engineers*. Vol. **448**. Special Publications. London: Geological Society, 2017, 369–82.

Hesslein RH, Capel MJ, Fox DE. *et al.* Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie river basin. *Can J Fish Aquat Sci* 1991;**48**:2258–65. https://doi.org/10.1139/f91-265

Hillman JR, Lundquist CJ, Thrush SF. The challenges associated with connectivity in ecosystem processes. *Front Mar Sci* 2018;**5**:365. https://doi.org/10.3389/fmars.2018.00364

Hodell F, Grespan R, de Rafélis M *et al.* Drake Passage gateway opening and Antarctic Circumpolar Current onset 31 ma ago: the message of foraminifera and reconsideration of the neodymium isotope record. *Chem Geol* 2021;**570**:120171. https://doi.org/10.1016/j.chemgeo.2021.120171

Hoffmann RC. The catch: an environmental history of medieval European fisheries. In: *Studies in Environment and History*. Cambridge: Cambridge University Press, 2023. https://doi.org/10.1017/9781108955898

Holm P, Ludlow F, Scherer C *et al. The North Atlantic Fish Revolution (ca. AD 1500)*. Vol. **108**. Quaternary Research. Cambridge: Cambridge University Press, 2022a, 92–106. https://doi.org/10.1017/qua.2018.153

Holm P, Nicholls J, Hayes PW. *et al.* Accelerated extractions of North Atlantic cod and herring, 1520–1790. *Fish Fish* 2022b;**23**:54–72. https://doi.org/10.1111/faf.12598

Hongo C, Montaggioni LF. Biogeography of holocene coral species in the western Indian Ocean. *Palaeogeogr Palaeoclimatol Palaeoecol* 2015;**438**:51–69. https://doi.org/10.1016/j.palaeo.2015.07.044

Hoyle TM, Bista D, Flecker R. *et al.* Climate-driven connectivity changes of the Black Sea since 430 ka: testing a dual palynological and geochemical approach. *Palaeogeogr Palaeoclimatol Palaeoecol* 2021;**561**:110069. https://doi.org/10.1016/j.palaeo.2020.110069

Huang H-HM, Yasuhara M, Iwatani H. *et al.* Benthic biotic response to climate changes over the last 700,000 years in a deep marginal sea: impacts of deoxygenation and the mid-brunhes event. *Paleoceanogr Paleoclimatol* 2018;**33**:766–77. https://doi.org/10.1029/2018PA003343

Hunt CO, Reynolds TG, El-Rishi HA. *et al.* Resource pressure and environmental change on the North African littoral: epipalaeolithic to roman gastropods from Cyrenaica. *Quat Int* 2011;**244**:15–26. https://doi.org/10.1016/j.quaint.2011.04.045

Iba Y, Mutterlose J, Tanabe K. *et al.* Belemnite extinction and the origin of modern cephalopods 35 m.y. prior to the cretaceous−paleogene event. *Geology* 2011;**39**:483–6. https://doi.org/10.1130/G31724.1

Immenhauser A, Schöne BR, Hoffmann R. *et al.* Mollusc and brachiopod skeletal hard parts: intricate archives of their marine environment. *Sedimentology* 2016;**63**:1–59. https://doi.org/10.1111/sed.12231

IUCN SSC Cetacean Specialist Group; regional assessment by European Mammal Assessment team. *Eschrichtius robustus* (Europe assessment). In: *The IUCN Red List of Threatened Species*. Gland: IUCN, 2007, e.T8097A12885185.

Jackson JBC, O'Dea A. Evolution and environment of Caribbean coastal ecosystems. *Proc Natl Acad Sci* 2023;**120**:e2307520120. https://doi.org/10.1073/pnas.2307520120

Jacobsen ALL. The reliability of fishing statistics as a source for catches and fish stocks in antiquity. In: T Bekker-Nielsen (ed.), *Ancient Fishing and Fish Processing in the Black Sea Region*. Vol. **2**. Black Sea Studies. Aarhus: Aarhus University Press, 2005, 97–104.

Jakobsson M, Backman J, Rudels B *et al.* The early Miocene onset of a ventilated circulation regime in the Arctic Ocean. *Nature* 2007;**447**:986–90. https://doi.org/10.1038/nature05924
Johnson KG, Jackson JBC, Budd AF. Caribbean reef development was independent of coral diversity over 28 million years. *Science* 2008;**319**:1521–3. https://doi.org/10.1126/science.1152197
Johnsson L. Vertebrate fauna during the Mesolithic on the Swedish west coast. In: A Fischer (ed.), *Man and Sea in the Mesolithic. Coastal Settlement Above and Below Present Sea Level*. Oxford: Oxbow, 1995, 147–60.
Kankeleit A. Fisch und fischer. *AntikeWelt* 2003;**3**:273–8.
Kidwell SM, Tomašových A. Implications of time-averaged death assemblages for ecology and conservation biology. *Annu Rev Ecol Evol Syst* 2013;**44**:539–63. https://doi.org/10.1146/annurev-ecolsys-110512-135838
Kidwell SM. Biology in the Anthropocene: challenges and insights from young fossil records. *Proc Natl Acad Sci* 2015;**112**:4922–9. https://doi.org/10.1073/pnas.1403660112
Kidwell SM. Evaluating human modification of shallow marine ecosystems: mismatch in composition of molluscan living and time-averaged death assemblages. In: GP Dietl, KW Flessa (eds), *Conservation Paleobiology: Using the Past to Manage for the Future*. Vol. **15**. The Paleontological Society Papers. 2009, 113–39.
Kidwell SM. Preservation of species abundance in marine death assemblages. *Science* 2001;**294**:1091–4. https://doi.org/10.1126/science.1064539
Kidwell SM. Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 1997;**30**:977–95. https://doi.org/10.1016/S0016-6995(97)80219-7
Kiessling W, Simpson C, Beck B. *et al.* Equatorial decline of reef corals during the last pleistocene interglacial. *Proc Natl Acad Sci* 2012;**109**:21378–83. https://doi.org/10.1073/pnas.1214037110
Kjær KH, Winther Pedersen M, De Sanctis B *et al.* A 2-million-year-old ecosystem in Greenland uncovered by environmental DNA. *Nature* 2022;**612**:283–91. https://doi.org/10.1038/s41586-022-05453-y
Koch PL, Halliday AN, Walter LM. *et al.* Sr isotopic composition of hydroxyapatite from recent and fossil salmon: the record of lifetime migration and diagenesis. *Earth Planet Sci Lett* 1992;**108**:277–87. https://doi.org/10.1016/0012-821X(92)90028-T
Kocsis L, Vennemann TW, Fontignie D. Migration of sharks into freshwater systems during the Miocene and implications for Alpine paleoelevation. *Geology* 2007;**35**:451–4. https://doi.org/10.1130/G23404A.1
Kohlbach D, Graeve M, Lange A *et al.* The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: food web relationships revealed by lipid and stable isotope analyses. *Limnol Oceanogr* 2016;**61**:2027–44. https://doi.org/10.1002/lno.10351
Kokkini P. Scènes de pêche sur les mosaïques de la péninsule balkanique : tradition romaine et iconographie paléochrétienne. *SAS* 2016;**3**:89–124.
Kowalewski M, Casebolt S, Hua Q. *et al.* One fossil record, multiple time resolutions: disparate time-averaging of echinoids and mollusks on a holocene carbonate platform. *Geology* 2018;**46**:51–4. https://doi.org/10.1130/G39789.1
Krijgsman W, Hilgen FJ, Raffi I. *et al.* Chronology, causes and progression of the Messinian salinity crisis. *Nature* 1999;**400**:652–5. https://doi.org/10.1038/23231
Kroh A, Nebelsick JH. Echinoid assemblages as a tool for palaeoenvironmental reconstruction—an example from the early Miocene of Egypt. *Palaeogeogr Palaeoclimatol Palaeoecol* 2003;**201**:157–77. https://doi.org/10.1016/S0031-0182(03)00610-2
Lagomarcino AJ, Miller AI. The relationship between genus richness and geographic area in late cretaceous marine biotas: epicontinental sea versus open-ocean-facing settings. *PLoS One* 2012;**7**:e40472. https://doi.org/10.1371/journal.pone.0040472
Lamberti GA, Chaloner DT, Hershey AE. Linkages among aquatic ecosystems. *J North Am Benthol Soc* 2010;**29**:245–63. https://doi.org/10.1899/08-166.1
Landau B, Marques Da Silva C, Vermeij G. Pacific elements in the Caribbean Neogene gastropod fauna: the source-sink model, larval development, disappearance, and faunal units. *Bulletin de la Société Géologique de France* 2009;**180**:343–52. https://doi.org/10.2113/gssgfbull.180.4.343
Leach F, Davidson J. The use of size-frequency diagrams to characterize prehistoric fish catches and to assess human impact on inshore fisheries. *Int J Osteoarchaeol* 2001;**11**:150–62. https://doi.org/10.1002/oa.553
Leach F. Fishing in Pre-European New Zealand. *Archaeufauna* 2006;**15**:1–266.
Leigh EG, O'Dea A, Vermeij GJ. Historical biogeography of the Isthmus of Panama. *Biol Rev* 2014;**89**:148–72. https://doi.org/10.1111/brv.12048
Leis JM. Perspectives on larval behaviour in biophysical modelling of larval dispersal in marine, demersal fishes. *Oceans* 2020;**2**:1–25. https://doi.org/10.3390/oceans201000
Lenders HJR, Chamuleau TPM, Hendriks AJ. *et al.* Historical rise of waterpower initiated the collapse of salmon stocks. *Sci Rep* 2016;**6**:29269. https://doi.org/10.1038/srep29269
Leprieur F, Descombes P, Gaboriau T *et al.* Plate tectonics drive tropical reef biodiversity dynamics. *Nat Commun* 2016;**7**:11461. https://doi.org/10.1038/ncomms11461
Leray M, Wilkins LGE, Apprill A *et al.* Natural experiments and long-term monitoring are critical to understand and predict marine host–microbe ecology and evolution. *PLoS Biol* 2021;**19**:e3001322. https://doi.org/10.1371/journal.pbio.3001322
Lessios HA. The great American schism: divergence of marine organisms after the rise of the Central American isthmus. *Annu Rev Ecol Evol Syst* 2008;**39**:63–91. https://doi.org/10.1146/annurev.ecolsys.38.091206.095815
Letessier TB, Mannocci L, Goodwin B. *et al.* Contrasting ecological information content in whaling archives with modern cetacean surveys for conservation planning and identification of historical distribution changes. *Conserv Biol* 2023;**37**:e14043. https://doi.org/10.1111/cobi.14043
Li C, Olave M, Hou Y *et al.* Genome sequences reveal global dispersal routes and suggest convergent genetic adaptations in seahorse evolution. *Nat Commun* 2021;**12**:1094. https://doi.org/10.1038/s41467-021-21379-x
Li Z, Zhang YG, Torres M. *et al.* Neogene burial of organic carbon in the global ocean. *Nature* 2023;**613**:90–5. https://doi.org/10.1038/s41586-022-05413-6
Limburg KE, Walther Y, Hong B. *et al.* Prehistoric versus modern Baltic Sea cod fisheries: selectivity across the millennia. *Proc R Soc B Biol Sci* 2008;**275**:2659–65. https://doi.org/10.1098/rspb.2008.0711
Lin C-H, Taviani M, Angeletti L. *et al.* Fish otoliths in superficial sediments of the Mediterranean Sea. *Palaeogeogr Palaeoclimatol Palaeoecol* 2017;**471**:134–43. https://doi.org/10.1016/j.palaeo.2016.12.050
Lin C-H, Wei C-L, Ho SL. *et al.* Ocean temperature drove changes in the mesopelagic fish community at the edge of the Pacific Warm Pool over the past 460,000 years. *Sci Adv* 2023;**9**:eadf0656. https://doi.org/10.1126/sciadv.adf0656
Lo EY, Duke NC, Sun M. Phylogeographic pattern of Rhizophora (Rhizophoraceae) reveals the importance of both vicariance and long-distance oceanic dispersal to modern mangrove distribution. *BMC Evol Biol* 2014;**14**:83. https://doi.org/10.1186/1471-2148-14-83
López-Merino L, Serrano O, Adame MF., *et al.* Glomalin accumulated in seagrass sediments reveals past alterations in soil quality due to land-use change. *Global Planet Change* 2015;**133**:87–95. https://doi.org/10.1016/j.gloplacha.2015.08.004
Lotze H, Hoffmann R, Erlandson J. Lessons from historical ecology and management. In: *The Sea: Marine Ecosystem-Based Management*. Vol. **16**. Cambridge: Harvard University Press, 2014, 17–55.
Lough RG, Broughton EA, Kristiansen T. Changes in spatial and temporal variability of prey affect functional connectivity of larval and

juvenile cod. *ICES J Mar Sci* 2017;**74**:1826–37. https://doi.org/10.1093/icesjms/fsx080
Ludt WB, Rocha LA. Shifting seas: the impacts of pleistocene sea-level fluctuations on the evolution of tropical marine taxa. *J Biogeogr* 2015;**42**:25–38. https://doi.org/10.1111/jbi.12416
Lukeneder A, Harzhauser M, Müllegger S. *et al.* Ontogeny and habitat change in mesozoic cephalopods revealed by stable isotopes (δ18O, δ13C). *Earth Planet Sci Lett* 2010;**296**:103–14. https://doi.org/10.1016/j.epsl.2010.04.053
Łukowiak M. Utilizing sponge spicules in taxonomic, ecological and environmental reconstructions: a review. *PeerJ* 2020;**8**:e10601. https://doi.org/10.7717/peerj.10601
Magris RA, Pressey RL, Weeks R. *et al.* Integrating connectivity and climate change into marine conservation planning. *Biol Conserv* 2014;**170**:207–21. https://doi.org/10.1016/j.biocon.2013.12.032
Mancini AM, Grelaud M, Ziveri P. *et al.* Calcareous nannofossil size and abundance response to the Messinian salinity crisis onset and paleoenvironmental dynamics. *Paleoceanogr Paleoclimatol* 2021;**36**:e2020PA004155. https://doi.org/10.1029/2020PA004155
Mancosu A, Nebelsick JH, Kroh A. *et al.* The origin of echinoid shell beds in siliciclastic shelf environments: three examples from the Miocene of Sardinia. *Lethaia* 2015;**48**:83–99. https://doi.org/10.1111/let.12090
Máñez KS, Holm P, Blight L *et al.* The future of the oceans past: towards a global marine historical research initiative. *PLoS One* 2014;**9**:e101466. https://doi.org/10.1371/journal.pone.0101466
Mángano MG, Buatois LA. The Cambrian revolutions: trace-fossil record, timing, links and geobiological impact. *Earth Sci Rev* 2017;**173**:96–108. https://doi.org/10.1016/j.earscirev.2017.08.009
Marcos C, Díaz D, Fietz K *et al.* Reviewing the ecosystem services, societal goods, and benefits of marine protected areas. *Front Mar Sci* 2021;**8**. https://www.frontiersin.org/articles/10.3389/fmars.2021.613819
Marcott SA, Bauska TK, Buizert C *et al.* Centennial-scale changes in the global carbon cycle during the last deglaciation. *Nature* 2014;**514**:616–9. https://doi.org/10.1038/nature13799
Marino M, Girone A, Maiorano P. *et al.* Calcareous plankton and the mid-Brunhes climate variability in the Alboran Sea (ODP Site 977). *Palaeogeogr Palaeoclimatol Palaeoecol*.2018;**508**:91–106, http://www.sciencedirect.com/science/article/pii/S0031018218304024
Martínez-García L, Ferrari G, Hufthammer AK. *et al.* Ancient DNA reveals a southern presence of the Northeast Arctic cod during the holocene. *Biol Lett* 2022;**18**:20220021. https://doi.org/10.1098/rsbl.2022.0021
Maschner HDG, Betts MW, Reedy-Maschner KL. *et al. Fish Bull* 2008;**106**:386–94.
Mattocks S, Hall CJ, Jordaan A. *et al.* Lost connectivity, and the historical role of anadromous fish in freshwater ecosystem dynamics. *Bioscience* 2017;**67**:713–28. https://doi.org/10.1093/biosci/bix069
McCauley DJ, Pinsky ML, Palumbi SR. *et al.* Marine defaunation: animal loss in the global ocean. *Science* 2015;**347**:1255641. https://doi.org/10.1126/science.1255641
McClymont EL, Ho SL, Ford HL *et al.* Climate evolution through the onset and intensification of Northern Hemisphere glaciation. *Rev Geophys* 2023;**61**:e2022RG000793. https://doi.org/10.1029/2022RG000793
McInturf AG, Pollack L, Yang LH. *et al.* Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors?. *Biol Rev* 2019;**94**:1761–73. https://doi.org/10.1111/brv.12525
McMahon KW, Jr WGA, Johnson BJ. *et al.* Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. *Mar Ecol Progr Ser* 2006;**310**:1–14. https://doi.org/10.3354/meps310001
Meiners KM, Vancoppenolle M, Thanassekos S *et al.* Chlorophyll *a* in Antarctic sea ice from historical ice core data. *Geophys Res Lett* 2012;**39**:L21602.
Melo CS, Martín-González E, da Silva CM *et al.* Range expansion of tropical shallow-water marine molluscs in the NE Atlantic during the last interglacial (MIS 5e): causes, consequences and utility of ecostratigraphic indicators for the Macaronesian archipelagos. *Quat Sci Rev* 2022;**278**:107377. https://doi.org/10.1016/j.quascirev.2022.107377
Menegotto A, Rangel TF. Mapping knowledge gaps in marine diversity reveals a latitudinal gradient of missing species richness. *Nat Commun* 2018;**9**:4713. https://doi.org/10.1038/s41467-018-07217-7
Michael MM. Fishing activity in Cyprus through time: an archaeologically neglected aspect in Cypriot society. *J Archaeol Sci Rep* 2023;**49**:103949. https://doi.org/10.1016/j.jasrep.2023.103949
Mitsui S, Lin C-H, Taru H. *et al.* Fish otolith record reveals possible tropical-subtropical fish community in temperate Japan during the exceptionally warm last interglacial period. *Historical Biol* 2023;**0**:1–21.
Miura O, Torchin ME, Bermingham E. *et al.* Flying shells: historical dispersal of marine snails across Central America. *Proc R Soc B Biol Sci* 2012;**279**:1061–7. https://doi.org/10.1098/rspb.2011.1599
Monk CT, Bekkevold D, Klefoth T. *et al.* The battle between harvest and natural selection creates small and shy fish. *Proc Natl Acad Sci* 2021;**118**:e2009451118. https://doi.org/10.1073/pnas.2009451118
Moore JK, Fu W, Primeau F *et al.* Sustained climate warming drives declining marine biological productivity. *Science* 2018;**359**:1139–43. https://doi.org/10.1126/science.aao6379
Morales Muñiz A, Roselló Izquierdo E. Twenty thousand years of fishing in the Strait: archaeological fish and shellfish assemblages from Southern Iberia. In: TC Rick, JM Erlandson (eds), *Human Impacts on Ancient Marine Ecosystems: A Global Perspective*. Berkeley: University of California Press, 2008, 243–77.
Morrongiello JR, Sweetman PC, Thresher RE. Fishing constrains phenotypic responses of marine fish to climate variability. *J Anim Ecol* 2019;**88**:1645–56. https://doi.org/10.1111/1365-2656.12999
Munday PL, Leis JM, Lough JM. *et al.* Climate change and coral reef connectivity. *Coral Reefs* 2009;**28**:379–95. https://doi.org/10.1007/s00338-008-0461-9
Nanninga G, Manica A. Larval swimming capacities affect genetic differentiation and range size in demersal marine fishes. *Mar Ecol Progr Ser* 2018;**589**:1–12. https://doi.org/10.3354/meps12515
Nawrot R, Zuschin M, Tomašových A. *et al.* Ideas and perspectives: human impacts alter the marine fossil record. *Biogeosciences* 2024;**21**:2177–88. https://doi.org/10.5194/bg-21-2177-2024
Nee S, May RM. Dynamics of metapopulations: habitat destruction and competitive coexistence. *J Anim Ecol* 1992;**61**:37–40. https://doi.org/10.2307/5506
Nguyen N-L, Devendra D, Szyman´ska N *et al.* Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Proc Natl Acad Sci* 2021;**118**:932–5.https://doi.org/10.1073/pnas.2009451118
NOAA. Voices: oral history archives. 2023. https://voices.nmfs.noaa.gov.
Nützel A. Larval ecology and morphology in fossil gastropods. *Palaeontology* 2014;**57**:479–503. https://doi.org/10.1111/pala.12104
O'Dea A, Jackson JBC. Bryozoan growth mirrors contrasting seasonal regimes across the Isthmus of Panama. *Palaeogeogr Palaeoclimatol Palaeoecol* 2002;**185**:77–94. https://doi.org/10.1016/S0031-0182(02)00278-X
O'Dea A, Lessios HA, Coates AG *et al.* Formation of the isthmus of Panama. *Sci Adv* 2016;**2**:e1600883. https://doi.org/10.1126/sciadv.1600883
Orton D, Morris J, Locker A. *et al.* Fish for the city: meta-analysis of archaeological cod remains and the growth of London's northern trade. *Antiquity* 2014;**88**:516–30. https://doi.org/10.1017/S0003598×00101152
Orton D. Archaeology as a tool for understanding past marine resource use and its impact. In: K Schwerdtner Mánez, B Poulsen (eds), *Perspectives on Oceans Past*. Dordrecht: Springer, 2016, 47–70.
Oschmann W. Sclerochronology: editorial. *Int J Earth Sci* 2009;**98**:1–2. https://doi.org/10.1007/s00531-008-0403-3

Owen JF, Merrick JR. Analysis of coastal middens in South-Eastern Australia: sizing of fish remains in holocene deposits. *J Archaeolog Sci* 1994;**21**:3–10. https://doi.org/10.1006/jasc.1994.1002

Palcu DV, Golovina LA, Vernyhorova YV. *et al.* Middle Miocene paleoenvironmental crises in Central Eurasia caused by changes in marine gateway configuration. *Global Planet Change* 2017;**158**:57–71. https://doi.org/10.1016/j.gloplacha.2017.09.013

Panfili J, de Pontual H, Troadec H. *et al. Manual of Fish Sclerochronology*. Ifremer-IRD co-edn. Plouzané: Ifremer, 2002, 464.

Pawlik AF. Technology, adaptation, and mobility in maritime environments in the Philippines from the late pleistocene to early/Mid-holocene. *Quat Int* 2021;**596**:109–23. https://doi.org/10.1016/j.quaint.2020.11.007

Pedersen L. 7000 years of fishing: stationary fishing structures in the Mesolithic and afterwards. In: A Fischer (ed.), *Man and Sea in the Mesolithic. Coastal Settlement Above and Below Present Sea Level*. Oxford: Oxbow, 1995, 75–86.

Pellissier L, Leprieur F, Parravicini V. *et al.* Quaternary coral reef refugia preserved fish diversity. *Science* 2014;**344**:1016–9. https://doi.org/10.1126/science.1249853

Penman DE, Hönisch B, Zeebe RE. *et al.* Rapid and sustained surface ocean acidification during the Paleocene-Eocene thermal maximum. *Paleoceanography* 2014;**29**:357–69. https://doi.org/10.1002/2014PA002621

Pickard C, Bonsall C. Deep-sea fishing in the European Mesolithic: fact or fantasy?. *Eur J Archaeol* 2004;**7**:273–90. https://doi.org/10.1177/1461957104056504

Por FD. One hundred years of Suez Canal—a century of Lessepsian migration: retrospect and viewpoints. *Syst Biol* 1971;**20**:138–59.

Praetorius SK, Mix AC, Walczak MH. *et al.* North Pacific deglacial hypoxic events linked to abrupt ocean warming. *Nature* 2015;**527**:362–6. https://doi.org/10.1038/nature15753

Prieto R, Pham CK, Brito C. *et al.* Biomass removal from shore-based whaling in the Azores. *Fish Res* 2013;**143**:98–101. https://doi.org/10.1016/j.fishres.2013.02.001

Pyenson ND, Lindberg DR. What happened to Gray whales during the pleistocene? The ecological impact of sea-level change on benthic feeding areas in the North Pacific Ocean. *PLoS One* 2011;**6**:e21295. https://doi.org/10.1371/journal.pone.0021295

Quillévéré F, Nouailhat N, Joannin S *et al.* An onshore bathyal record of tectonics and climate cycles at the onset of the Early-Middle Pleistocene transition in the eastern Mediterranean. *Quat Sci Rev* 2019;**209**:23–39. https://doi.org/10.1016/j.quascirev.2019.02.012

Rahiminejad AH, Yazdi M, Ashouri AR. Reconstruction of the last marine connectivity of the Zagros basin, based on fossil evidences of the clastic-dominated Bakhtiari Formation. *Historical Biol* 2011;**23**:155–67. https://doi.org/10.1080/08912963.2010.502368

Rankin KJ, Holm P. Cartographical perspectives on the evolution of fisheries in Newfoundland's Grand Banks area and adjacent North Atlantic waters in the sixteenth and seventeenth centuries. *Terrae Incognitae* 2019;**51**:190–218. https://doi.org/10.1080/00822884.2019.1679487

READMAP. Range Extension Database & Mapping project. 2023. https://www.redmap.org.au/.

Reddin CJ, Kocsis ÁT, Kiessling W. Marine invertebrate migrations trace climate change over 450 million years. *Global Ecol Biogeogr* 2018;**27**:704–13. https://doi.org/10.1111/geb.12732

Reitz EJ. Fishing in Peru between 10 000 and 3750 BP. *Int J Osteoarchaeol* 2001;**11**:163–71. https://doi.org/10.1002/oa.554

Ridgwell A, Zeebe RE. The role of the global carbonate cycle in the regulation and evolution of the Earth system. *Earth Planet Sci Lett* 2005;**234**:299–315. https://doi.org/10.1016/j.epsl.2005.03.006

Rita P, Nätscher P, Duarte LV. *et al.* Mechanisms and drivers of belemnite body-size dynamics across the Pliensbachian–Toarcian crisis. *R Soc Open Sci* 2019;**6**:190494. https://doi.org/10.1098/rsos.190494

Ritter MN, Erthal F, Kosnik MA. *et al.* Onshore-offshore trends in the temporal resolution of molluscan death assemblages: how age-frequency distributions reveal quaternary sea-level history. *Palaios* 2023;**38**:148–57. https://doi.org/10.2110/palo.2021.041

Rocha RC, Clapham PJ, Ivashchenko Y. Emptying the oceans: a summary of industrial whaling catches in the 20th century. *Mar Fish Rev* 2014;**76**:37–48. https://doi.org/10.7755/mfr.76.4.3

Rödder D, Lawing AM, Flecks M *et al.* Evaluating the significance of paleophylogeographic species distribution models in reconstructing quaternary range-shifts of Nearctic chelonians. *PLoS One* 2013;**8**:e72855. https://doi.org/10.1371/journal.pone.0072855

Rodrigo García MJ. Remains of *Melanogrammus Aglefinus* (Linnaeus, 1758) in the Pleistocene-Holocene passage of the Cave of Nerja (Malaga, Spain). In: *Archaeo-Ichthyological Studies. Proceedings of the 6th Meeting of the ICAZ Fish Remains Working Group, Ossa*. Vol. **51**. Special Issue. 1994, 348–51.

Rodrigues ASL, Horwitz LK, Monsarrat S. *et al.* Ancient whale exploitation in the Mediterranean: species matters *Antiquity* 2016;**90**:928–38. https://doi.org/10.15184/aqy.2016.109

Rodrigues ASL, Monsarrat S, Charpentier A *et al.* Unshifting the baseline: a framework for documenting historical population changes and assessing long-term anthropogenic impacts. *Philos Trans R Soc B Biol Sci* 2019;**374**:20190220. https://doi.org/10.1098/rstb.2019.0220

Rohling EJ, Marino G, Grant KM. Mediterranean climate and oceanography, and the periodic development of anoxic events (sapropels). *Earth Sci Rev* 2015;**143**:62–97. https://doi.org/10.1016/j.earscirev.2015.01.008

Rossi V, Azzarone M, Capraro L. *et al.* Dynamics of benthic marine communities across the early-Middle Pleistocene boundary in the Mediterranean region (Valle di Manche, Southern Italy): biotic and stratigraphic implications. *Palaeogeogr Palaeoclimatol Palaeoecol* 2018;**495**:127–38. https://doi.org/10.1016/j.palaeo.2017.12.042

Rossi VM, Longhitano SG, Olariu C. *et al.* Straits and seaways: end members within the continuous spectrum of the dynamic connection between basins. *Geological Soc Lond* 2023; **523**:85–109. https://doi.org/10.1144/SP523-2022-159

Sabelli B, Taviani M. The making of the Mediterranean molluscan biodiversity. In: S Goffredo, Z Dubinsky (eds), *The Mediterranean Sea: Its history and Present Challenges*. Dordrecht: Springer, 2014, 285–306. https://doi.org/10.1007/978-94-007-6704-1_16

Salvatteci R, Schneider RR, Galbraith E *et al.* Smaller fish species in a warm and oxygen-poor Humboldt current system. *Science* 2022;**375**:101–4. https://doi.org/10.1126/science.abj0270

Scarponi D, Kaufman D, Amorosi A. *et al.* Sequence stratigraphy and the resolution of the fossil record. *Geology* 2013;**41**:239–42. https://doi.org/10.1130/G33849.1

Scarponi D, Nawrot R, Azzarone M. *et al.* Resilient biotic response to long-term climate change in the Adriatic Sea. *Global Change Biol* 2022;**28**:4041–53. https://doi.org/10.1111/gcb.16168

Schöne BR. *Arctica islandica* (Bivalvia): a unique paleoenvironmental archive of the northern North Atlantic Ocean. *Global Planet Change* 2013;**111**:199–225. https://doi.org/10.1016/j.gloplacha.2013.09.013

Schwarzhans W, Agiadi K, Carnevale G. Late Miocene–Early Pliocene evolution of Mediterranean gobies and their environmental and biogeographic significance. *Rivista Italiana di Paleontologia e Stratigrafia* 2020;**126**:657–724.

Schwarzhans W, Carnevale G. The rise to dominance of lanternfishes (Teleostei: myctophidae) in the oceanic ecosystems: a paleontological perspective. *Paleobiology* 2021;**47**:446–63. https://doi.org/10.1017/pab.2021.2

Sexton PF, Norris RD. Dispersal and biogeography of marine plankton: long-distance dispersal of the foraminifer truncorotalia truncatulinoides. *Geology* 2008;**36**:899–902. https://doi.org/10.1130/G25232A.1

Shanks AL. Pelagic larval duration and dispersal distance revisited. *Biol Bull* 2009;**216**:373–85. https://doi.org/10.1086/BBLv216n3p373

Shaw J, Weyrich L, Hallegraeff G. *et al.* Retrospective eDNA assessment of harmful algae in historical ship ballast tank and marine port sediments. *Mol Ecol* 2019;**28**:2476–85. https://doi.org/10.1111/mec.15055

Siqueira AC, Bellwood DR, Cowman PF. The evolution of traits and functions in herbivorous coral reef fishes through space and time. *Proc R Soc B* 2019;**286**:2018672.

Smith J, Rillo MC, Kocsis ÁT *et al.* BioDeepTime: a database of biodiversity time series for modern and fossil assemblages. *Global Ecol Biogeogr* 2023;**32**:1680–9. https://doi.org/10.1111/geb.13735

Springer AM. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling?. *Proc Natl Acad Sci* 2003;**100**:12223–8. https://doi.org/10.1073/pnas.1635156100

Sremba AL, Martin AR, Wilson P *et al.* Diversity of mitochondrial DNA in 3 species of great whales before and after modern whaling. *J Hered* 2023;**114**:587–97. https://doi.org/10.1093/jhered/esad048

Stevens K, Mutterlose J, Wiedenroth K. Stable isotope data (δ18O, δ13C) of the ammonite genus Simbirskites—implications for habitat reconstructions of extinct cephalopods. *Palaeogeogr Palaeoclimatol Palaeoecol* 2015;**417**:164–75. https://doi.org/10.1016/j.palaeo.2014.10.031

Strugnell JM, Rogers AD, Prodöhl PA. *et al.* The thermohaline expressway: the Southern Ocean as a centre of origin for deep-sea octopuses. *Cladistics* 2008;**24**:853–60. https://doi.org/10.1111/j.1096-0031.2008.00234.x

Sturrock AM, Satterthwaite WH, Cervantes-Yoshida KM. *et al.* Eight decades of hatchery salmon releases in the California Central Valley: factors influencing straying and resilience. *Fisheries* 2019;**44**:433–44. https://doi.org/10.1002/fsh.10267

Tanner SE, Vieira AR, Vasconcelos RP. *et al.* Regional climate, primary productivity and fish biomass drive growth variation and population resilience in a small pelagic fish. *Ecol Indic* 2019;**103**:530–41. https://doi.org/10.1016/j.ecolind.2019.04.056

Taylor LD, O'Dea A, Bralower TJ. *et al.* Isotopes from fossil coronulid barnacle shells record evidence of migration in multiple pleistocene whale populations. *Proc Natl Acad Sci* 2019;**116**:7377–81. https://doi.org/10.1073/pnas.1808759116

Taylor LT, Totten RL, Suarez CA *et al.* Oxygen isotopes from the teeth of cretaceous marine lizards reveal their migration and consumption of freshwater in the Western Interior Seaway, North America. *Palaeogeogr Palaeoclimatol Palaeoecol* 2021;**573**:110406. https://doi.org/10.1016/j.palaeo.2021.110406

Teixeira A, Venâncio R, Brito C. Archaeological remains accounting for the presence and exploitation of the North Atlantic right whale *Eubalaena glacialis* on the Portuguese Coast (Peniche, West Iberia), 16th to 17th century. *PLoS One* 2014;**9**:e85971. https://doi.org/10.1371/journal.pone.0085971

Terry RC, Novak M. Where does the time go? Mixing and the depth-dependent distribution of fossil ages. *Geology* 2015;**43**:487–90. https://doi.org/10.1130/G36483.1

Teske PR, Hamilton H, Matthee CA. *et al.* Signatures of seaway closures and founder dispersal in the phylogeny of a circumglobally distributed seahorse lineage. *BMC Evol Biol* 2007;**7**:138. https://doi.org/10.1186/1471-2148-7-138

Theodoropoulou T. Preservation and sampling of fish, shell and other invertebrate remains. In: E Margaritis, A Oikonomou, E Nikita, T Rehren (eds), *Field Sampling for Laboratory Analysis in Archaeology*. Nicosia: The Cyprus Institute, 2023, 43–52.

Thibon F, Goedert J, Séon N *et al.* The ecology of modern and fossil vertebrates revisited by lithium isotopes. *Earth Planet Sci Lett* 2022;**599**:117840. https://doi.org/10.1016/j.epsl.2022.117840

Thomka JR, Mosher D, Lewis RD. *et al.* The utility of isolated crinoid ossicles and fragmentary crinoid remains in taphonomic and paleoenvironmental analysis: an example from the Upper Pennsylvanian of Oklahoma, United States. *Palaios* 2012;**27**:465–80. https://doi.org/10.2110/palo.2011.p11-125r

Thurstan RH. The potential of historical ecology to aid understanding of human–ocean interactions throughout the Anthropocene. *J Fish Biol* 2022;**101**:351–64. https://doi.org/10.1111/jfb.15000

Tilman D, May RM, Lehman CL. *et al.* Habitat destruction and the extinction debt. *Nature* 1994;**371**:65–6. https://doi.org/10.1038/371065a0

Tischendorf L, Fahrig L. On the usage and measurement of landscape connectivity. *Oikos* 2000;**90**:7–19. https://doi.org/10.1034/j.1600-0706.2000.900102.x

Tomašových A, Berensmeier M, Gallmetzer I. *et al.* Pyrite-lined shells as indicators of inefficient bioirrigation in the holocene–anthropocene stratigraphic record. *Biogeosciences* 2021;**18**:5929–65. https://doi.org/10.5194/bg-18-5929-2021

Tomašových A, Kidwell SM, Barber RF. Inferring skeletal production from time-averaged assemblages: skeletal loss pulls the timing of production pulses towards the modern period. *Paleobiology* 2016;**42**:54–76. https://doi.org/10.1017/pab.2015.30

Torsvik TH, Domeier M, Cocks LRM. Chapter 18–phanerozoic paleogeography and pangea. In: LJ Pesonen, J Salminen, S-Å Elming, DAD Evans, T Veikkolainen (eds), *Ancient Supercontinents and the Paleogeography of Earth*. Amsterdam: Elsevier, 2021, 577–603.

Townsend M, Davies K, Hanley N. *et al.* The challenge of implementing the marine ecosystem service concept. *Front Mar Sci* 2018;**5**. https://doi.org/10.3389/fmars.2018.00359

Tribot A-S, Faget D, Villesseche H. *et al.* Multi-secular and regional trends of aquatic biodiversity in European Early Modern paintings: toward an ecological and historical significance. *Ecol Soc* 2021;**26**. https://doi.org/10.5751/ES-12740-260426

Trofimova T, Alexandroff SJ, Mette MJ *et al.* Fundamental questions and applications of sclerochronology: community-defined research priorities. *Estuar Coast Shelf Sci* 2020;**245**:106977. https://doi.org/10.1016/j.ecss.2020.106977

Trueman CN, Chung M-T, Shores D. Ecogeochemistry potential in deep time biodiversity illustrated using a modern deep-water case study. *Philos Trans R Soc B Biol Sci* 2016;**371**:20150223. https://doi.org/10.1098/rstb.2015.0223

Tsikliras AC, Licandro P, Pardalou A. *et al.* Synchronization of Mediterranean pelagic fish populations with the North Atlantic climate variability. *Deep Sea Res Part II* 2019;**159**:143–51. https://doi.org/10.1016/j.dsr2.2018.07.005

Tyler C, Kowalewski M. The quality of the fossil record across higher taxa: compositional fidelity of phyla and classes in benthic marine associations. *PeerJ* 2023;**11**:e15574 https://doi.org/10.7717/peerj.15574

van den Hurk Y, Rielly K, Buckley M. Cetacean exploitation in Roman and medieval London: reconstructing whaling activities by applying zooarchaeological, historical, and biomolecular analysis. *J Archaeol Sci Rep* 2021;**36**, 102795. https://doi.org/10.1016/j.jasrep.2021.102795

van den Hurk Y, Sikstrom F, Amkreutz L *et al.* The prelude to industrial whaling: identifying the targets of ancient European whaling using zooarchaeology and collagen mass-peptide fingerprinting. *R Soc Open Sci* 2023;**10**:230741. https://doi.org/10.1098/rsos.230741

Van Neer W, Lõugas L, Rijnsdorp AD. Reconstructing age distribution, season of capture and growth rate of fish from archaeological sites based on otoliths and vertebrae. *Int J Osteoarchaeol* 1999;**9**:116–30. https://doi.org/10.1002/(SICI)1099-1212(199903/04)9:2%3c116::AID-OA465%3e3.0.CO;2-H

Vermeij GJ, Roopnarine PD. The coming Arctic Invasion. *Science* 2008;**321**:780–1. https://doi.org/10.1126/science.1160852

Vermeij GJ. When biotas meet: understanding biotic interchange. *Science* 1991;**253**:1099–104. https://doi.org/10.1126/science.253.5024.1099

Vieira N, Brito C. Brazilian manatees (re)discovered: early modern accounts reflecting the overexploitation of aquatic resources and the emergence of conservation concerns. *Int J Maritime Hist* 2017;**29**:513–28. https://doi.org/10.1177/0843871417713683

Vieira N, Patrick H, Matthews A. Facing changes, changing targets: sperm whale hunting in the 18th century Brazil. Environment & Society Portal, Arcadia. München: Rachel Carson Center for Environment and Society, 2019. https://doi.org/10.5282/rcc/8798

Vieira N. Whales lost and found: rescuing a history of biodiversity loss in early modern Brazil. *Exchanges Interdisc Res J* 2023;**10**:106–30. https://doi.org/10.31273/eirj.v10i2.976

Wagner MA, Reynolds JD. Salmon increase forest bird abundance and diversity. *PLoS One* 2019;**14**:e0210031. https://doi.org/10.1371/journal.pone.0210031
Welker MH, Quintana Morales EM. The North Atlantic cod trade: a meta-analysis of the North American and European archaeological records. *J Island Coast Archaeol* 2024;**19**:269–91, https://doi.org/10.1080/15564894.2022.2035856
Weslawski J, Hacquebord L, Stempniewicz L. *et al.* Greenland whales and walruses in the Svalbard food web before and after exploitation. *Oceanologia* 2000;**42**:37–56.
Wheeler A, Jones AKG. Fishes. In:*Cambridge Manuals in Archaeology*. Cambridge: Cambridge University Press, 1989.
Whitfield AK, Weerts SP, Weyl OLF. A review of the influence of biogeography, riverine linkages, and marine connectivity on fish assemblages in evolving lagoons and lakes of coastal southern. *Ecol Evol* 2017;**7**:7382–98. https://doi.org/10.1002/ece3.3266
Wignall PB, Bond DPG. The great catastrophe: causes of the Permo-Triassic marine mass extinction. *Natl Sci Rev* 2023;**11**: nwad273.
Wood SLR, Martins KT, Dumais-Lalonde V *et al.* Missing interactions: the current State of multispecies connectivity analysis. *Front Ecol Evol* 2022;**10**:830822.
Yasuhara M, Huang H-HM, Reuter M *et al.* Hotspots of cenozoic tropical marine biodiversity. In: SJ Hawkins, AJ Lemasson, AI Allcock et al. (eds), *Oceanography and Marine Biology: An Annual Review*. Vol. **60**. 2022, 243–300.
Yasuhara M, Hunt G, Cronin TM. *et al.* Climatic forcing of quaternary deep-sea benthic communities in the North Pacific Ocean. *Paleobiology* 2012;**38**:162–79. https://doi.org/10.1666/10068.1
Yasuhara M, Okahashi H. Late quaternary deep-sea ostracod taxonomy of the eastern North Atlantic Ocean. *J Micropalaeontol* 2015;**34**:21–49. https://doi.org/10.1144/jmpaleo2013-022
Yasuhara M, Rabalais NN, Conley DJ *et al.* Palaeo-records of histories of deoxygenation and its ecosystem impact. In: D Laffoley, JM Baxter (eds), *Ocean Deoxygenation: Everyone's Problem*. Gland: IUCN, 2019, 213–24.
Ye S, Peters SE. Bedrock geological map predictions for phanerozoic fossil occurrences. *Paleobiology* 2023;**49**:394–413. https://doi.org/10.1017/pab.2022.46
Yin Q, Berger A. Interglacial analogues of the Holocene and its natural near future. *Quat Sci Rev* 2015;**120**:28–46. https://doi.org/10.1016/j.quascirev.2015.04.008
Zachos JC, Röhl U, Schellenberg SA. *et al.* Rapid acidification of the ocean during the paleocene-eocene thermal maximum. *Science* 2005;**308**:1611–5. https://doi.org/10.1126/science.1109004
Zaffos A, Finnegan S, Peters SE. Plate tectonic regulation of global marine animal diversity. *Proc Natl Acad Sci* 2017;**114**:5653–8. https://doi.org/10.1073/pnas.1702297114
Zazzo A, Smith GR, Patterson WP. *et al.* Life history reconstruction of modern and fossil sockeye salmon (*Oncorhynchus nerka*) by oxygen isotopic analysis of otoliths, vertebrae, and teeth: implication for paleoenvironmental reconstructions. *Earth Planet Sci Lett* 2006;**249**:200–15. https://doi.org/10.1016/j.epsl.2006.07.003
Zilhão J, Angelucci DE, Igreja MA *et al.* Last interglacial iberian neandertals as fisher-hunter-gatherers. *Science* 2020;**367**:367. https://doi.org/10.1126/science.aaz7943
Ziveri P, Gray WR, Anglada-Ortiz G *et al.* Pelagic calcium carbonate production and shallow dissolution in the North Pacific Ocean. *Nat Commun* 2023;**14**:805. https://doi.org/10.1038/s41467-023-36177-w
Zu Ermgassen PSE, Spalding MD, Blake B *et al.* Historical ecology with real numbers: past and present extent and biomass of an imperilled estuarine habitat. *Proc R Soc B Biol Sci* 2012;**279**:3393–400. https://doi.org/10.1098/rspb.2012.0313

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