



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	<ul style="list-style-type: none"> – Ocean temperature – Sea-level – Ice cover – Seawater salinity – Ocean pH 	<ul style="list-style-type: none"> – Changes population connectivity as species distributions shift due to: <ul style="list-style-type: none"> 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) 	<ul style="list-style-type: none"> – 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	<ul style="list-style-type: none"> – Marine gateways size – Coast and shelf areas sizes and physical connectivity 	<ul style="list-style-type: none"> – Population connectivity changes – Migration routes closed with the restriction of marine gateways – Changes dispersal pathways 	<ul style="list-style-type: none"> – 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	<ul style="list-style-type: none"> – Water-column stratification – (De)oxygenation 	<ul style="list-style-type: none"> – 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) 	<ul style="list-style-type: none"> – 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	<ul style="list-style-type: none"> – C, N, S, P, and O availability and distribution in the oceans 	<ul style="list-style-type: none"> – Changes in migration routes driven by nutrient availability – Vertical migration patterns controlled by changing productivity at surface 	<ul style="list-style-type: none"> – Change in nutrient supply during the Early Oligocene drove lanternfishes to deeper waters, potentially initiating their diel vertical migration (Schwarzjans and Carnevale 2022).
Evolution		<ul style="list-style-type: none"> – Organismal traits associated with MFC (e.g. larval dispersal capacity) may be favoured or not by the evolutionary process 	<ul style="list-style-type: none"> – 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 de-

scribing 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

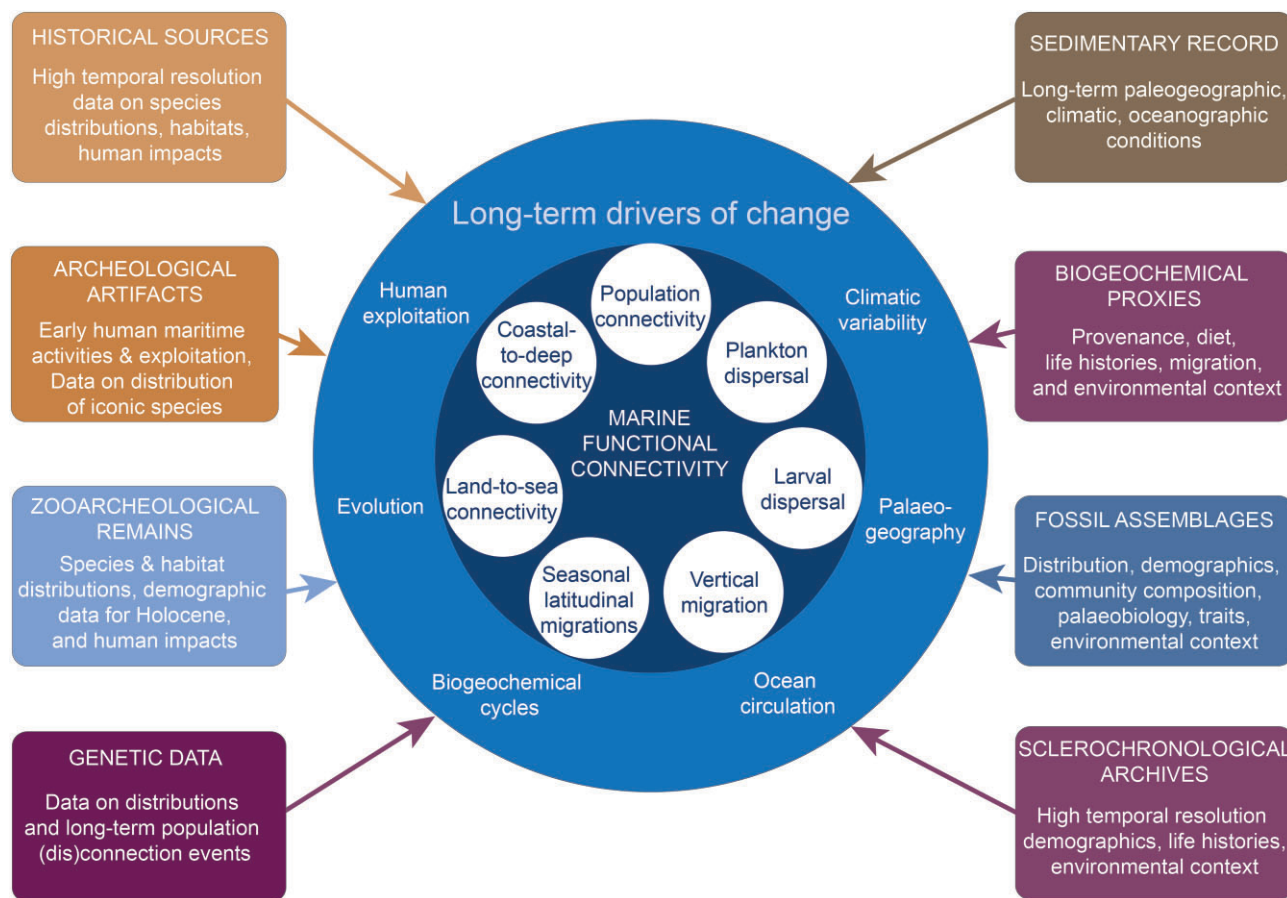


Figure 1. Overview of MFC processes, their long-term drivers, and how geohistorical data can help unravel their changes over time. The boxes reflect the methods and materials used: human sources and archaeological artifacts are remains from human activities; zooarchaeological remains and fossil assemblages 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 salmon, 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 barna-

cles 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 Montagnioni 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, Schwarzshans 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 Muñoz 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	<ul style="list-style-type: none"> –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 	<ul style="list-style-type: none"> –Disconnects populations/communities –Isolates habitat-forming species and organisms that inhabit them 	<ul style="list-style-type: none"> –The spawning 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 <i>et al.</i> 2011, Sturrock <i>et al.</i> 2019, Lenders <i>et al.</i> 2016, Mattocks <i>et al.</i> 2017)
Anthropogenic transport (hitchhikers on hulls or within ballast tanks, aquarium trade, and aquaculture)		<ul style="list-style-type: none"> –Connects or disconnects populations/communities –Makes novel connections between species and populations (natural and genetically modified) –Introduces diseases 	<ul style="list-style-type: none"> – Marine non-native species have been transported since at least 1200 (Crosby 2004, Lotze <i>et al.</i> 2014, Hoffmann 2023).
Historical biomass removal	<ul style="list-style-type: none"> –Destroys, damages, or fragments seafloor habitats, including biogenic coral, bryozoans, and oyster reefs 	<ul style="list-style-type: none"> –Connects or disconnects populations/communities –Deteriorations in population demographics 	<ul style="list-style-type: none"> –Substantial historical removal of fish and shellfish biomass impacted population size and demographics (Clements <i>et al.</i> 2017), and caused extirpations (Caribbean monk seal (Baker 2008, Brito and Vieira 2016, Vieira and Brito 2017, Vieira <i>et al.</i> 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), its limitations, and references for examples from the literature. Taphonomy includes all the processes involved in fossilization.

Resource	Type of observational data provided	Derived information for studying MFC?	Limitations and biases	Example references
<p>A. Sedimentary record Timescales covered: 10–10⁹ <i>Sediments and once lithified sedimentary rocks</i></p>	<ul style="list-style-type: none"> • 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) • Species presence and abundance • Body size • Morphological characteristics related to modes of movement • Soft tissue for extraction of aDNA • Living conditions, burial conditions 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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 	<p>Adame et al. (2012), López-Merino et al. (2015), Bernhardt et al. (2017), Butiseacă et al. (2022)</p>
<p>B. Frozen remains Timescales covered: 10²–10⁴ <i>Ice cores and frozen animal remains*</i> *aDNA and approaches for other fossils may be used</p>	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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 	<p>McMahon et al. (2006), Meiners et al. (2012), Kohlbach et al. (2016)</p>	
<p>C. Fish bones, scales, or denticles Timescales covered: 10²–10⁸</p>	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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 	<p>Dillon et al. (2017), Salvatelli et al. (2022)</p>	
<p>D. Fish otoliths Timescales covered: 10²–10⁸</p>	<ul style="list-style-type: none"> • Species presence and abundance • Body size • Age and growth rates (sclerochronology) • Oxygen and strontium isotopes • Morphological characteristics associated with modes of movement 	<ul style="list-style-type: none"> • 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 sclerochronology 	<ul style="list-style-type: none"> • Taphonomic bias • Time-averaged • Availability declines with time • Preservation may be incomplete • Material may be transported • Environmental and geological context important for interpretations 	<p>Morrongiello et al. (2019), Tanner et al. (2019), Denechaud et al. (2020), Agiadi et al. (2011, 2018, 2023)</p>

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	<ul style="list-style-type: none"> Species presence (and abundance under conditions) Body size Oxygen and strontium isotopes Age and growth rates (sclerochronology) 	<ul style="list-style-type: none"> Past species distribution (population connectivity) Identify refugia Isotopic evidence of latitudinal migrations Body size as a proxy of migration capacity 	<ul style="list-style-type: none"> 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. <i>Polychaeta [aus]</i>).	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> 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. <i>sponge spicules</i>	<ul style="list-style-type: none"> Species presence (and abundance under conditions) Assemblage composition is used to reconstruct palaeoenvironmental conditions 	<ul style="list-style-type: none"> Past species distribution (population connectivity) Identify refugia Environmental context that is necessary for interpreting most geohistorical archives 	<ul style="list-style-type: none"> 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 <i>Coccolithophores, dinoflagellates, diatoms, foraminifera, and radiolarians</i>	<ul style="list-style-type: none"> Species presence and abundance Body size Assemblage composition, elemental and isotopic biogeochemical proxies are used to reconstruct palaeoenvironmental conditions 	<ul style="list-style-type: none"> Past species distribution (population connectivity) Body size as a proxy of dispersal capacity Environmental context that is necessary for interpreting most geohistorical archives 	<ul style="list-style-type: none"> 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 <i>aDNA from recent fossilized + nonfossilized organic residues and sediments (sedaDNA)</i>	<ul style="list-style-type: none"> Species presence and abundance Evolutionary relationships 	<ul style="list-style-type: none"> Past species distribution (population connectivity) Identify refugia Evolutionary patterns provide evidence of the persistence (and resilience) of MFC patterns and traits over long timescales 	<ul style="list-style-type: none"> 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 <i>Shell middens, bones, teeth, shells, scales, skin, hair, and feathers*</i> *aDNA approaches can be used on many of these materials	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> 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 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 	<ul style="list-style-type: none"> 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), Çakırlar (2014), Bernal-Casasola et al. (2016), Butler et al. (2019)
K. Archaeological remains Timescales covered: 10 ² –10 ⁵ <i>Tools, clothing, adornments, dwellings, and vehicles</i>	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> Cultural context that is necessary for interpreting most geohistorical records Trade may be linked to human transport of nonindigenous species 	<ul style="list-style-type: none"> 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 <i>Cave paintings, mosaics, sculpture, and ornaments</i>	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> Past species distribution (population connectivity) Body size as a proxy of migration capacity Cultural context that is necessary for interpreting most geohistorical records 	<ul style="list-style-type: none"> 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 <i>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 philology treatises</i>	<ul style="list-style-type: none"> • 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 biollogging • 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 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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	<ul style="list-style-type: none"> • Biogenic habitat extent • Species presence • Trade links and human infrastructure 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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 <i>Accounts from present-day fishers, the families of deceased fishers, or recorded accounts (oral histories)</i>	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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 <i>Paintings, book illustrations, sculpture, tapestries, photographs, stamps, shipwright plans, images of gear, and architectural plans</i>	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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 	<ul style="list-style-type: none"> • 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
<p>Q. Historical collections of animal remains Timescales covered: 10^2–10^3</p>	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> 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 sclerochronology 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 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 	<ul style="list-style-type: none"> Location data may be coarse Biased to iconic, charismatic, or exploited species Availability declines with time 	Gallmetzer et al. (2017)
<p>R. Historical collections of human artefacts Timescales covered: 10^2–10^3 <i>Tools, vehicles, clothing, engravings, and ornaments (scrimshaw)</i></p>	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> Location data may be coarse Qualitative Biased to exploited species Cultural and historical context important for interpretations 	Barrett (2019)
<p>S. Trace fossils (ichnology) Timescales covered: 10^2–10^4</p>	<ul style="list-style-type: none"> Ichnospecies presence Body size Palaeoenvironment can be reconstructed based on the presence of particular ichnofossil types 	<ul style="list-style-type: none"> 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 	<ul style="list-style-type: none"> Taphonomic bias Time-averaged Species identification uncertain (or even some times impossible), because the tchnofossil confirms only the presence of a behaviour Availability declines with time 	Caswell and Herringshaw (2023)
<p>T. Remains of terrestrial / freshwater organisms Timescales covered: 10^2–10^8 <i>e.g. pollen</i></p>	<ul style="list-style-type: none"> Pollen, plant remains, dendrochronology, and other palaeoclimate proxies Palaeoenvironment can be reconstructed based on the species presences and abundance 	<ul style="list-style-type: none"> Evidence of land-to-sea connectivity pathways (e.g. rivers, deltas) Environmental context that is necessary for interpreting most geohistorical records 	<ul style="list-style-type: none"> Taphonomic bias Time-averaged Geological context important for interpretations 	Ye and Peters (2023)
<p>U. Phylogenetics Timescales covered: 10^3–10^8</p>	<ul style="list-style-type: none"> Evolutionary relationships and events derived from analysis of DNA in modern tissue or morphology 	<ul style="list-style-type: none"> Inferred gene flow between populations 	<ul style="list-style-type: none"> 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 recon-

struct 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 (Egins 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 $^{87}\text{Sr}/^{86}\text{Sr}$ 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. Andreotto et al. 2021, Hoyle et al. 2021). The $^{15}\text{N}/^{14}\text{N}$ 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 $^{13}\text{C}/^{12}\text{C}$ and $^{18}\text{O}/^{16}\text{O}$ 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. Salvatelli 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, Çakırlar 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 (*sedaDNA*) 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 popula-

tions 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 tempo-

rally 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 cen-

turies 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

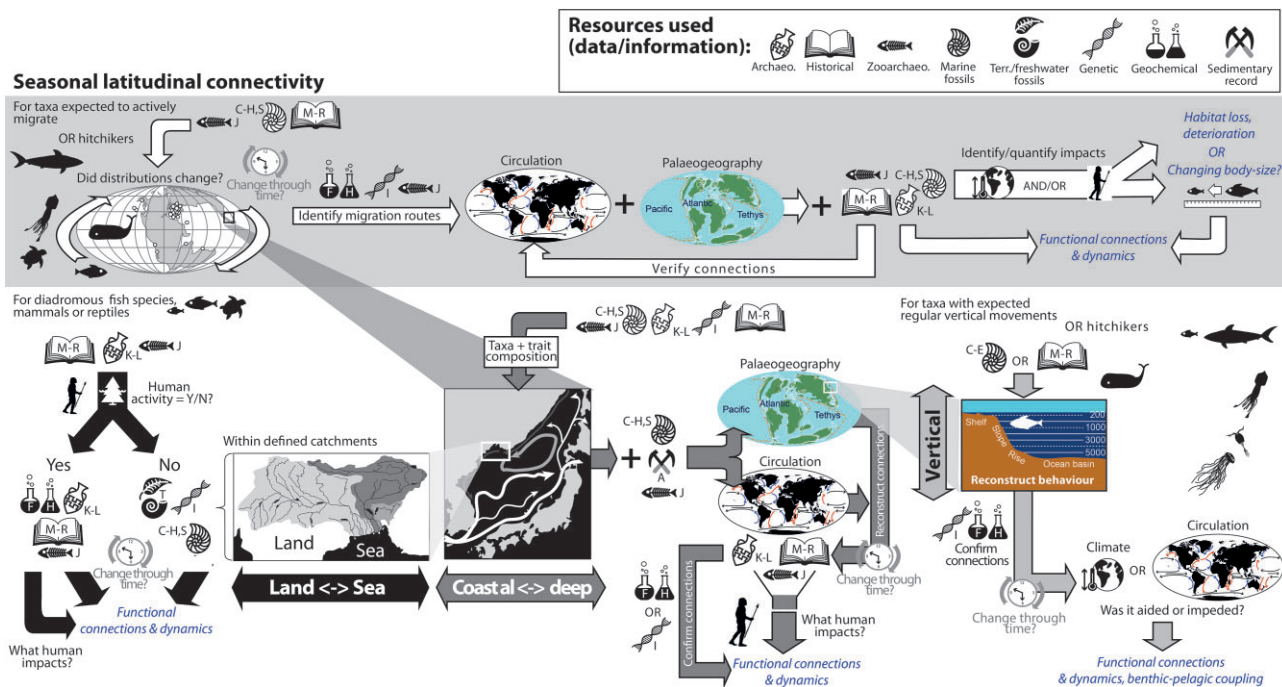


Figure 3. Roadmap for studying MFC using geohistorical resources, including key linkages, steps, and intermediate questions. A range of resources can be used to answer questions about seasonal latitudinal, coastal-to-deep, land-to-sea, and vertical connectivity and their dynamics. The contexts and contributions 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 to 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-

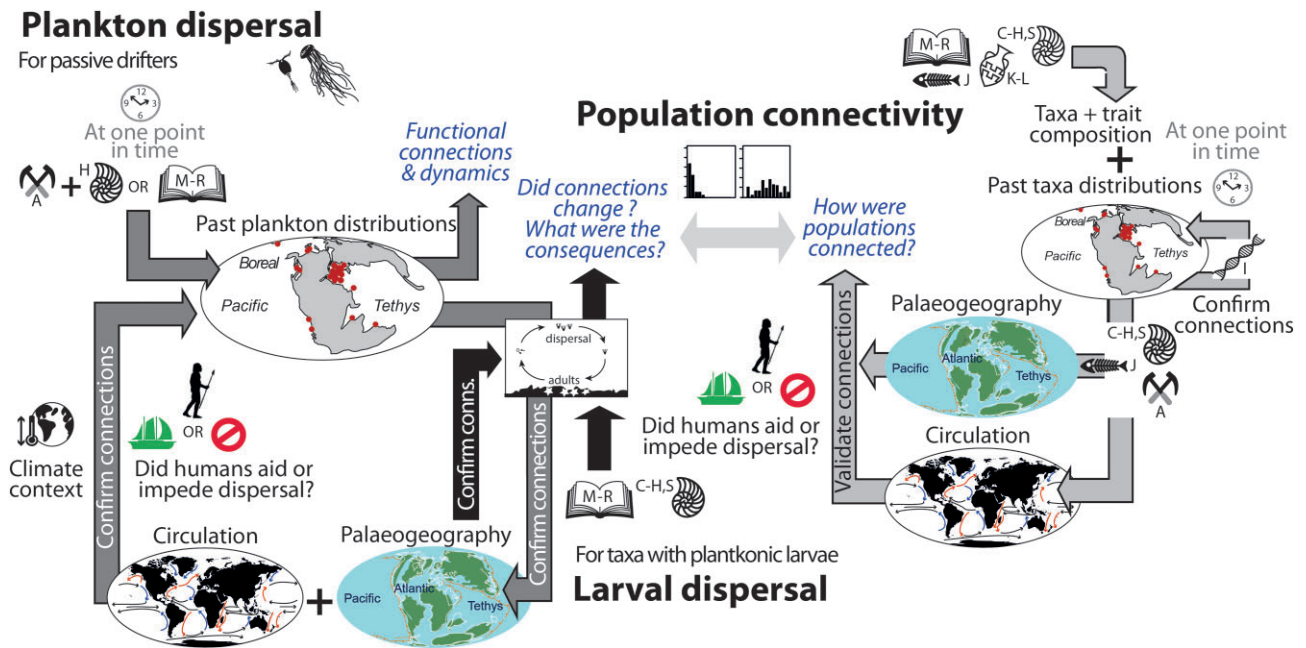


Figure 4. Roadmap for studying MFC using geohistorical resources, including key linkages, steps, and intermediate questions. A range of resources can be used to answer questions about plankton dispersal, larval dispersal, and population connectivity and their dynamics. The contexts and contributions 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.

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