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Pleistocene marine fish invasions and paleoenvironmental reconstructions in the eastern Mediterranean

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A B S T R A C T

Marine bioinvasions affect ecosystems in irreversible ways, creating socio-economic problems worldwide. In particular, eastern Mediterranean marine fish faunas today are significantly disturbed due to overfishing, habitat deterioration, the Lessepsian invasion, and climate change. Isolating the impact of each parameter is difficult, because pre-anthropogenic activity data are lacking. In this study, we use the paleontological record to infer the causes and mechanisms behind marine fish invasions, focusing on the Mediterranean basin, which is a restricted basin and a biological hotspot, where the effects of climatic and oceanographic changes are amplified. Therefore, the Mediterranean Sea is an ideal area to study marine biological invasions in relation to abrupt climate changes. Furthermore, we focus on the Pleistocene, which was a period of intense glacial–interglacial changes. Thus, we investigate the effect of climate changes on the fish fauna of an eastern Mediterranean shelf, by identifying the fish otoliths in the Early–Middle Pleistocene marine sediments of Rhodes (Greece). We offer a synthesis of the Mediterranean marine fish from the Tortonian until today and hypothesize on the conditions that drove marine fish distribution range shifts during the Pleistocene. We reconstruct the paleobathymetric evolution of the study areas based on fish otoliths, and we consider taphonomy in our interpretations. The Pleistocene climatic variability induced periodic and gradual replacements of fish taxa. Episodic invasions of cold-water North Atlantic mesopelagic species are correlated with intervals of climatic deterioration, specifically during marine isotope stages 50, 44, 36, 20, and 18.

1. Introduction

Marine ecosystems worldwide are severely disturbed by biological invasions, with direct socio-economic implications for their dependent human populations (Pauly et al., 2005; Byrnes et al., 2007; Early et al., 2016; Dawson et al., 2017; Seebens et al., 2017). This phenomenon is especially intense in the eastern Mediterranean Sea, where alien marine species increasingly invade Mediterranean waters from the Red Sea via the Suez Canal (Lessepsian invasion) and the Atlantic Ocean (Galil et al., 2015; Rilov, 2016; Piroddi et al., 2017).

Marine fish invasions are a major issue with the present-day global warming (Perry et al., 2005; Pörtner and Knust, 2007; Walther et al., 2009; Cheung et al., 2009; Comte and Olden, 2017). Fish are strongly affected by climatic and oceanographic changes (Rose, 2005), through processes (such as distribution shifts, lifestyle adaptations, extinctions, and morphological modifications) that are not well-known and species-specific. In the Mediterranean, in particular, the distribution of pelagic fish in the western, central, and eastern parts of the basin has been linked to different modes of climatic variability (Tsikliras et al., 2018). Moreover, geographic boundaries, such as sills, may restrict the distribution of deep-water demersal species, but not those of pelagic and mesopelagic

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species that could be affected by the chemical and physical parameters of the seawater masses. In order to distinguish between the effects of these processes, we turn to the geological past, as a source of paleodiversity data that is: a) undisturbed by human activity and b) encompasses a much longer record including extreme climatic variations.

What was the imprint of past biological invasions on the fossil record? Paleontological data suggest that distribution range shifts due to environmental changes such as the ones observed today were common in the past (e.g., Enquist et al., 1995; Jablonski et al., 2006, 2013; Peterson and Lieberman, 2012; Palcu et al., 2017). In order to detect past marine biological invasions, in particular Atlantic marine species invading eastern Mediterranean waters, we synthesize and examine the Pleistocene evolution of the marine fish fauna in the area, because intense environmental changes took place during this Epoch due to glacial–interglacial successions, and it is therefore a good candidate for marine species invasions in the Mediterranean Sea. Moreover, we identify the fish otolith assemblages in the early–middle Pleistocene (Gelasian to Ionian) hemipelagic sediments of the island of Rhodes (Greece; Fig. 1). Rhodes is of particular interest, because Pleistocene coastal to deep sea sediments have been uplifted there and are presently well-exposed onshore along the eastern coast of the island. These sediments have been precisely dated (Cornée et al., 2006; Titschack et al., 2013; Quillévéré et al., 2016) and contain abundant fossil fish otoliths that span a long time interval, from the Early to the Middle Pleistocene (Gelasian to Ionian). Fish otoliths are the aragonitic stone-like structure in the inner ear of Teleost fish that facilitate sound and balance perception (Schulz-Mirbach et al., 2018). They are considered an excellent tool for reconstructing past fish faunas due to their generally good preservation and abundance in marine and lake sediments (Nolf, 1985). In this study, we provide evidence for successive marine fish invasions and extripations in the marine fish fauna of the eastern Mediterranean during the Pleistocene. These events are correlated with the marine isotope stages (MIS) record of alternating glacial–interglacial cycles (Lisiecki and Raymo, 2005; Wang et al., 2010).

In the eastern Mediterranean, previous studies of the Pleistocene ichthyofauna have been conducted only in the Ionian Sea (Fig. 1; Girone, 2000; Girone and Varola, 2001; Sorbini and Landini, 2003; Landini and Sorbini, 2005a, 2005b; Girone et al., 2006a,b; Agiadi et al., 2010, 2011). As a result, the eastern Mediterranean fossil fish record remains poor. The examination of the Pleistocene fish otoliths of Rhodes comes to fill this knowledge gap. Furthermore, our synthesis of the marine fish record of the entire Mediterranean Sea, which has been derived from both skeletal and otolith material, from the Tortonian until today, leads to conclusions regarding the general trends in the marine fish faunas and their relation to climate and connectivity changes.

The gradually deteriorating climate and the oligotrophy of the Mediterranean Sea drove the general trends observed in the Pliocene–Pleistocene marine fish fauna. During the Pliocene, the Mediterranean was inhabited by tropical–subtropical fish of Atlantic or circumglobal distribution (Landini and Sorbini, 2005a; Agiadi et al., 2013). Invasions of cold-water Atlantic mesopelagic and bathypelagic fish have been recorded in the western Mediterranean since the Piacenzian and occurred throughout the Early Pleistocene, following the evolution of the Plio-Pleistocene Mediterranean paleoceanographic setting as well as the global climatic deterioration (Landini and Sorbini, 2005a; Girone et al., 2006a,b; Girone, 2007). During the Early and Middle Pleistocene, the climatic variability has been associated with changes in the relative contribution of cold- and warm-water mesopelagic fish species in the Ionian Sea assemblages (Agiadi et al., 2011). Mesopelagic subpolar–temperate species are found in this domain until the Late

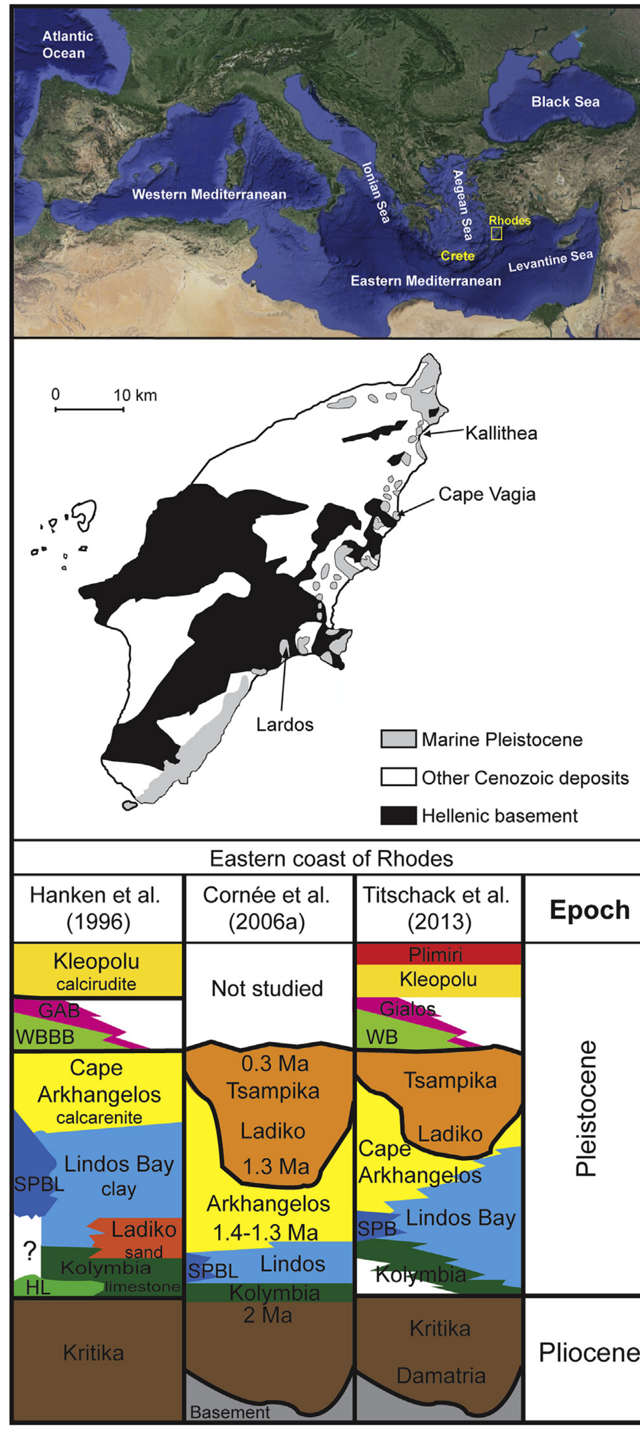

Fig. 1. Map of the Mediterranean Sea with the location of the island of Rhodes (upper panel). Simplified geological map of Rhodes showing the study areas (middle panel; modified from Mutti et al., 1970). Lithostratigraphic schemes for the Plio-Pleistocene deposits of the eastern coast of Rhodes HL: Haraki Limestone, SPBL: Saint Paul's Bay Limestone, WBBB: Windmill Bay Boulder Bed, GAB: Gialos Algal Biolithite, SPB: Saint Paul's Bay, WB: Windmill Bay (lower panel; modified from Quillévéré et al., 2016).

Pleistocene, and their occurrence has been attributed to climatic changes (Girone, 2003; Girone et al., 2006a,b).

The studied deposits of Rhodes correspond to a tectonically controlled transgressive–regressive cycle (Titschack et al., 2013; Quillévéré et al., 2016), which reached maximum paleodepths during the deposition of these otolith-rich clays (Hanken et al.,