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Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna

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Abstract

Tuscany has a rich Pliocene record of marine megafauna (MM), including mysticetes, odontocetes, sirenians and seals among the mammals, and six orders of sharks among the elasmobranchs. This is reviewed with respect to paleogeography and sequence-stratigraphic occurrence in six different basins. Conditions at the ancient seafloor are explored by means of sedimentary facies analysis, taphonomy and multivariate techniques applied to a large quantitative dataset of benthic molluscs. MM is rare or absent in most basins during the Zanclean, except in one basin, and most abundant in Piacenzian deposits in all six basins. MM occurs preferentially in fine-grained shelfal highstand deposits of small-scale depositional sequences, or at condensed horizons of the maximum flooding interval. It is rare in shallow marine paleonvironments and nearly absent in bathyal paleosettings. Paleogeographic and paleoecological evidence and a comparison with modern patterns of marine upwelling suggest that a wedge of nutrient-rich waters sustained in the offshore during the Pliocene a high biomass of primary producers and a community of apex consumers and mesopredators, similarly to the modern Northwestern Mediterranean Sea, with a higher species-richness than the modern. The highest MM diversity coincides with the mid-Piacenzian warm period, suggesting that facies control does not obscure a link between climate and diversity. We underline however that not all marine environments were suitable for marine mammal preservation. Buoyant carcasses were preferentially dismembered and destroyed in high-energy shallow waters, with the possible exception of delta front deposits, where sudden sediment input occasionally buried pristine carcasses. We hypothesise that carcasses sunken on the seafloor below the shelf break underwent destruction through the activity of a whale-fall biota of modern type, specialised in the consumption of decomposing tissues, both soft and mineralised. A taphonomic window was left between storm wave base and the shelf break. Here water pressure is high enough to prevent the formation of decomposing gases and the resurfacing of carcasses, while the lack of a specialised whale-fall biota slows down bone degradation with respect to deeper settings. Sedimentation rate was high enough to cover skeletal material before its complete destruction. An estimate of paleobathymetries based on multivariate techniques suggests that the preferential depth for the inclusion of MM in the fossil record was 30-300 m. The results are compared with major Mesozoic and Cenozoic MM records worldwide. Available evidence suggests that the late Neogene radiation of large whales, true ecosystem engineers, and their size increase, triggered the radiation of a bone-eating fauna that hampered, and hampers, MM preservation in the deep sea. Stratigraphic paleobiology and an ecosystem-level approach deliver useful insights in the nature of the fossil record.

Keywords	Cetacea; Elasmobranchia; whales; dolphins; sharks; Pliocene; Sirenia; sequence stratigraphy; taphonomy; marine megafauna; Mollusca; open marine ecosystem structure; top-down control; shell bed; multivariate analysis; paleodepths; upwelling; Mediterranean; diversity; megabias
Corresponding Author	Stefano Dominici
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Suggested reviewers	Michelangelo Bisconti, Michael Benton, Shanan E. Peters, Steven Holland

Submission Files Included in this PDF

File Name	**[File Type]**
Copy-of-Pliocene NWMS MM cover letter.docx	[Cover Letter]
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Tables 1-6, S1-S4 - Pliocene Tuscany REVISED2.xlsx	[Table]

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Dear editor,

we submit a revised version of the manuscript now entitled “Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna”. We have carefully considered the comments of the first reviewer and your comments and revised the manuscript accordingly.

We look forward hearing from you.

For the authors,

Best regards,

Stefano Dominici

Dear editor,

we submit a revised version of the manuscript now entitled “Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna”. We have carefully considered the comments of the first reviewer and your comments and revised the manuscript accordingly. In particular, we would like to explicit the following answers (in red) to review no. 1 (in blue):

Some suggestions that could improve the manuscript:

1) The ambitious paleoecological considerations intended to link the supposed high diversity/abundance of the marine vertebrate assemblage to the paleobiogeography/food availability of the northwestern Mediterranean are, in my opinion, not supported by solid data. In fact:

A) data about the systematic composition of the vertebrate fossil assemblage are only reported (for the marine mammals) in table 1 and not discussed in the text (note that I disagree with the authors’ statement about "the systematics of Mediterranean Pliocene LMV have been recently reviewed"); data about the sharks are not reported;

B) also admitting that the systematic assignations reported in this list are sufficient for this analysis, no data are reported about, for example, the trophism and, more generally, the ecological behavior of the listed taxa;

C) diversity and abundance are cited for the vertebrates, but not quantified;

D) the link between diversity and primary productivity/food availability must be better analyzed considering the rich and often controversial bibliography on this topic;

E) baleen whales and other vertebrates from the Pliocene of Tuscany are here considered 'apex predator': the authors must define better this ecological term. In my opinion, baleen whales cannot be included among the top predators, as well as other 'large' marine vertebrates as they feed on plancton and small fishes with filtering techniques. Apex or top predators can be considered some (but not all) 'large' sharks as *Carcharodon charcharias* and *Cosmopolitodus hastalis*, and, among cetaceans, *Orcinus citoniensis*.

So, I suggest the authors to review the part focused on the paleoecology of the vertebrate assemblage, improving the data. Alternatively, it could be drastically shortened or totally removed.

1A: We enlarged the marine mammal dataset, from 39 to 64 reports, and carefully controlled existing literature on the systematics.

1B: We have greatly enlarged the literature on the ecology of modern Mediterranean marine mammals and introduced data on the ecology of sharks. Based on these data, we attributed a preferred prey and a feeding mechanism to each taxon of our list.

1C: We calculated minimum number of marine mammal specimens. The systematics were sufficient for a conservative estimate of standing diversity in terms of species richness of both marine mammals and sharks. Marine mammal abundance and richness have been calculated for six consecutive intervals and for the overall epoch and compared to modern values for the north-eastern Mediterranean. A Pliocene-modern comparison is also given for species richness in sharks. We introduced new tables, and two histograms (Fig. 9C-D), for an easy understanding of diversity trends during the Pliocene.

1D: In expanding the reference list, we have highlighted the overwhelming evidence for a relationship between marine megafauna diversity and primary productivity (bottom-up control on marine ecosystems), but also decoupled this from structural factors such as trophic cascade (top-down controls exerted by large predators).

1E: There’s no formal definition of what “marine megafauna” is, but practice adopted also by palaeontologists includes all marine mammals, seabirds, sea turtles, sharks and rays (e.g., Lewison et al., 2004; Pimiento et al., 2017). We clearly stated what we mean by apex predator, using concepts derived from modern ecological literature. In particular we specify that the definitions of apex predators (or top predators) and mesopredators are relative, and to an extent context-dependent (species that in a contact are apex predators, in another are mesopredators). By any means, filter-feeding baleen whales are considered apex-predators of their community. To avoid misunderstanding between ecological and paleoecological usage, we informed on the trophic level of each Pliocene species by comparison with modern values, for both marine mammals and sharks.

2) The authors propose a link between the Pliocene-Pleistocene increase in whale size and in bone-eaters worms diversity: these considerations should be better supported by including more bibliographical data and also by an eventual analysis of the Pliocene Tuscany vertebrate assemblage. Are the marine vertebrates from Pliocene of Tuscany particularly large? If yes, please support this affirmation with data. My preliminary evaluation is that there are some large baleen whales (but not 'giant whales' as today), some medium-small sized baleen whales, and several relatively small marine mammals

(odontocetes, pinnipeds and sirenians). So, why also the 'small' vertebrates are not preserved in the deep sea sediments of the Pliocene of Tuscany?

We have given figures for size differences between Pliocene and modern marine magafauna. We are explicit in stating the complex nature of the comparison between MM at different times, but we are also clear in relating the radiation of bone-eating worms, and the importance of a depth-related taphonomic overprint in the Pliocene fossil record, to the emergence of large whales. That is to say, not all MM were large, but some were. We also see no need to limit this effect to the carcass of true giants, like the modern blue whale. That is to say, we think that large is large enough.

3) The analysis is focused on the 'large' marine vertebrates: in my opinion 'large' is rather vague is it is not well defined by the authors. It seems that the authors consider as 'large vertebrates' all cetaceans (including the smaller odontocetes), all pinnipeds and all sirenians, among the tetrapods (but not the marine turtles and birds), and Carcharhiniformes (note that several carchariformes, as the catsharks, are not longer than 50 cm) and Lamniformes among sharks: it is right?

As stated above, the ecological definition of “marine megafauna” includes smaller animals (sea birds, otters, turtles). We focus on the general structure of the MM association, not on the role of a particular species.

4) in the analysis are also included some 'large' sharks: their fossil record is exclusively based on isolated teeth and most of these are found associated to cetacean skeletons. This should be better outlined, since these remains have a different taphonomic significance that the bones of the other vertebrates

We have expanded the review of the Pliocene shark record of Tuscany in Tables 5-6 and discussed it in the text. Taphonomy has been expanded, also in relationship to evidence of interaction between different MM species.

5) the organization of the manuscript, including the presentation of data, results and discussion is often unclear and could be improved. Some suggestions:

- the numeration of the chapters/paragraphs must be revised (the number 3 is repeated three times)

- all the chapters from 'Distribution of large marine vertebrates', to ‘the Biotic factors’ (lines 950-2012) must be included in the 'Results'
- the paragraph '6.2 Taphonomic control' reports an interesting bibliographical review, but no reference to the material here examined.

We have corrected the organization of the ms as suggested. Tables have been expanded and augmented in number.

6) Table 2 appears as the more important source of this paper, since it condenses all the data about the marine mammals discussed and elaborated in the work. By contrast, the table does not seem to have been carefully prepared. For example, most of the specimens lacks the description, although these data can be easily found in bibliography (e.g.: the Orcinus citoniensis holotype is an articulated partial skeleton) and the few data reported are often wrong (e.g. MOm2-2 and WSi2-1 are not articulated skeleton); moreover it is not easy to identify the specimens reported without the catalogue number of the museum where they are kept. For example it is not possible identify WFi4-3 from Orciano (no data about the systematics and the bones preserved) considering that Lawley (1876) reported several remains from the same locality; similarly, it is reported an articulated skeleton of sirenian from Arcille (MOm2-2) based on Tinelli (2013): but Tinelli (2013) described 4 skeletons from Arcille (3 disarticulated and 1 articulated; see also: Sorbi et al. 2011, Tinelli et al. 2012).

We have expanded Tab. 2 and included much more taphonomic information, making it more homogenous and informative, also with respect to references. We have excluded specimens cited, but no longer traceable (e.g. Lawley 1876).

7) All 'dugongs' in the text must be changed with 'sirenians' ('dugong' is referred only to thWe extant Dugong dugong species)

Done

8) The fossil vertebrates from Tuscany are named in the text using a inhomogeneous approach about their systematic assignation: I suggest to uniform (maybe using the more detailed determination available from the literature for all specimens cited.

Done (see new Tab. 2)

9) It is unclear if the logs of Figure 4 have been measured by the authors or taken from bibliography. In the second case, I suggest to add the references. This is recommended particularly for the ones taken from the PhD thesis of Chiara Tinelli. This thesis is available online, but, since it has not yet been published, it is important to make clear when the authors used these data.

Done, references added in the caption of Fig. 2

10) In the log of Arcille locality (figure 4) the sirenian is placed at the base of the HST. I personally participated to the collection of the 4 skeletons discovered in this locality and all were found inside the TST, under the HST (see also Tinelli et al. 2012; Tinelli, 2013).

Done (we refer to a “maximum flooding interval”, instead of MFS)

Other more punctual corrections and comments are reported in the annotated manuscript.

We corrected the text following comments annotated by the reviewer on the ms

We would also like to answer your comments:

This is an interesting contribution about the fossil record of marine vertebrates and its relationship to depositional environments. Although it is focused on the Pliocene of Tuscany, the topic is wide enough to be of interest to the readership of Earth-Science Reviews.

Both reviewers liked the manuscript. Nevertheless, Reviewer 1 makes many valuable comments and suggestions on how to improve it. For example, he thinks that “The ambitious paleoecological considerations….are…not supported by solid data”, that more data are need to support the relationship between whale size and bone-eating worm diversity, that the definition of “large vertebrates” is quite ambiguous, and that the organisation of the manuscript and the tables need improvement.

Reviewer 2 is satisfied with the manuscript the way it is now. He says that the coordinates of the studied localities should be added, and that the data should be deposited in the Paleobiology Database.

We look forward uploading our data in PBDB

I have looked through the manuscript myself and have to agree with Reviewer 1: there is need for a moderate to major revision to make this basically nice and interesting study ready for publication. Reviewer 1 suggests to either improve or eliminate the palaeoecological analysis. I am strongly in favour of keeping it in (this makes the paper interesting also for a non-specialized scientific community) but in this case complement and improve the data. Consequently, the manuscript should be expanded to accommodate more data and more explanations. Also, please polish the tables (including the supplementary ones) and the general organization of the manuscript.
Additional suggestions from my side: In the legend to Figure 3, say “SCUBA diver” and not “man” for scale. In the legend to Figures 4 and 8, explain the sequence-stratigraphic abbreviations.

We kept the paleoecological analysis, as you suggested, and largely expanded the database and the reference list so as to sustain our point. We corrected Fig. 3 caption as suggested.

We look forward hearing from you.

For the authors,

Best regards,

Stefano Dominici

~~S~~Pliocene stratigraphic paleobiology in ~~the Pliocene of~~ Tuscany and the fossil record of ~~large marine vertebrates~~marine megafauna

Stefano Dominici (Università di Firenze, Museo di Storia Naturale, Firenze, Italy)

Silvia Danise (Plymouth University, School of Geography, Earth and Environmental Sciences, Plymouth, United Kingdom)

Marco Benvenuti (Università di Firenze, Dipartimento di Scienze della Terra, Firenze, Italy)

Abstract

~~Tuscany has a rich Pliocene record of marine megafauna (MM), including mysticetes, odontocetes, sirenians and seals among the mammals, and six orders of sharks among the elasmobranchs. This is reviewed with respect to paleogeography and sequence-stratigraphic occurrence in six different basins. Conditions at the ancient seafloor are explored by means of sedimentary facies analysis, taphonomy and multivariate techniques applied to a large quantitative dataset of benthic molluscs. MM is rare or absent in most basins during the Zanclean, except in one basin, and most abundant in Piacenzian deposits in all six basins. MM occurs preferentially in fine-grained shelfal highstand deposits of small-scale depositional sequences, or at condensed horizons of the maximum flooding interval. It is rare in shallow marine paleonvironments and nearly absent in bathyal paleosettings. Paleogeographic and paleoecologic evidence, and a comparison with modern patterns of marine upwelling suggest that a wedge of nutrient-rich waters sustained in the offshore during the Pliocene a high biomass of primary producers and a community of apex consumers and mesopredators, similarly to the modern Northwestern Mediterranean Sea, with a higher species-richness than the modern. The highest MM diversity coincides with~~

~~the mid-Piacenzian warm period, suggesting a link between climate and diversity. We propose that not all marine environments were suitable for marine mammal preservation. Buoyant carcasses were preferentially dismembered and destroyed in high-energy shallow waters, with the possible exception of delta front deposits, where sudden sediment input occasionally buried pristine carcasses. We hypothesise that carcasses sunken on the seafloor below the shelf break underwent destruction through the activity of a whale-fall biota of modern type, specialised in the consumption of decomposing tissues, both soft and mineralised. A taphonomic window was left between storm wave base and the shelf break. Here water pressure is high enough to prevent the formation of decomposing gases and the resurfacing of carcasses, while the lack of a specialised whale-fall biota slows down bone degradation with respect to deeper settings. Sedimentation rate is high enough to cover skeletal material before its complete destruction. An estimate of paleobathymetries based on multivariate techniques suggests that the preferential depth for the inclusion of MM in the fossil record is 30-300 m. The results are compared with major Mesozoic and Cenozoic MM records worldwide. Available evidence suggests that the Neogene radiation of large whales, true ecosystem engineers, triggered the radiation of a bone-eating fauna that hampered, and hampers, MM preservation in the deep sea.~~Tuscany has a rich Pliocene record of marine megafauna (MM), including mysticetes, odontocetes, sirenians and seals among the mammals, and six orders of sharks among the elasmobranchs. This is reviewed with respect to paleogeography and sequence-stratigraphic occurrence in six different basins. Conditions at the ancient seafloor are explored by means of sedimentary facies analysis, taphonomy and multivariate techniques applied to a large quantitative dataset of benthic molluscs. MM is rare or absent in most basins during the Zanclean, except in one basin, and most abundant in Piacenzian deposits in all six basins. MM occurs preferentially in fine-grained shelfal highstand deposits of small-scale depositional sequences, or at condensed horizons of the maximum flooding interval. It is rare in shallow marine paleonvironments and nearly absent in bathyal paleosettings. Paleogeographic and paleoecological evidence and a comparison with modern patterns of marine upwelling suggest that a wedge of nutrient-rich waters sustained in the offshore during the Pliocene a high biomass of primary producers and a community of apex consumers and mesopredators, similarly to the modern Northwestern Mediterranean Sea, with a higher species-richness than the modern. The highest MM diversity coincides with the mid-Piacenzian warm period, suggesting that facies control does not obscure a link between climate and diversity. We underline however that not all marine environments were suitable for marine mammal preservation. Buoyant carcasses were preferentially dismembered and destroyed in high-energy shallow waters, with the possible exception of delta front deposits, where sudden sediment input occasionally buried pristine carcasses. We hypothesise that carcasses sunken on the seafloor below the shelf break underwent destruction through the activity of a whale-fall biota of modern type, specialised in the consumption of decomposing tissues, both soft and mineralised. A taphonomic window was left between storm wave base and the shelf break. Here water pressure is high enough to prevent the formation of decomposing gases and the resurfacing of carcasses, while the lack of a specialised whale-fall biota slows down bone degradation with respect to deeper settings. Sedimentation rate was high enough to cover skeletal material before its complete destruction. An estimate of paleobathymetries based on multivariate techniques suggests that the preferential depth for the inclusion of MM in the fossil record was 30-300 m. The results are compared with major Mesozoic and Cenozoic MM records worldwide. Available evidence suggests that the late Neogene radiation of large whales, true ecosystem engineers, and their size increase, triggered the radiation of a bone-eating fauna that hampered, and hampers, MM preservation in the deep sea. Stratigraphic paleobiology and an ecosystem-level approach deliver useful insights in the nature of the fossil record.

1. Introduction

~~L~~The modern marine megafauna (MM) includes all marine mammals, seabirds, sea turtles and sharks, apex consumers that influence their associated ecosystems (Lewison et al., 2004), both pelagic and nearshore, through top-down forcing and trophic cascades, and now severely affected by human impact (Estes et al., 1998, 2011, 2016). ~~arge vertebrates have played a key role in structuring marine ecosystems. P~~On a macroevolutionary scale, predation pressure has shaped the evolution of marine preys, with feedbacks on predators, setting the stage for the Mesozoic marine revolution (Vermeji, 1977;~~,~~ Chen ~~&~~and Benton, 2012; ~~,~~Benton et al., 2013). The new ecosystem structure started in the the Early and Middle Triassic with several lineages of Actinopterygian fishes (Chen and Benton, 2012), continuing with marine reptiles possessing feeding styles (Fröbisch et al., 2013;~~,~~ Motani et al., 2015;~~,~~ but see also Motani et al., 2013) and reproductive adaptations (Motani et al., 2014) of modern type. Triassic and Jurassic novelties underwent a prolonged crisis during the Cretaceous, with the gradual extinction of plesiosaurians,~~ and ~~mosasaurs (Benson et al., 2010) and ichthyosaurs (Fischer et al., 2016), and a diversity drop of sharks (Guinot et al., 2012)~~, but marine giants~~. A marine megafauna of comparable size ~~of comparable size~~ returned in the Paleogene, with the new diversification of neoselachian elasmobranchs (Kriwet ~~&~~and Benton, 2004) and the evolution of large marine mammals: Eocene archaeocetes (Uhen, 2008, Gingerich et al., 2009) and Oligocene odontocetes and mysticetes (Gingerich, 2005;~~,~~ Marx ~~&~~and Uhen 2010, Berta, 2012; Marx et al., 2016) empowered by high metabolic rates and new anatomic features (Armfield et al., 2013). Among the largest vertebrates of all times, after a dramatic size increase at the outset of glacial age (Marx et al., 2016; Bisconti et al., 2017; Slater et al., 2017), b~~B~~aleen and sperm whales are among today's ocean's ecosystem engineers (Roman et al., 2014) with which to compare their Mesozoic analogues (Smith et al., 2016)~~.~~ . Notwithstanding ~~an enormous~~a crucial ~~ecological and evolutionary importance~~role in ecology and evolution~~ of these animals~~, the nature and distribution of the MM fossil record ~~of large marine vertebrates (LMVs)~~ has been ~~relatively little~~less explored, compared to that of marine invertebrates and terrestrial vertebrates. Available data suggest a strong correlation between taxic diversity and the number of marine fossiliferous formations, resulting in megabiases in the fossil record (e.g., Cretaceous: Benson et al., 2010). Within its vast history, studies on the geologically recent marine megafauna offer important insights, ~~thanks to a~~considering our better knowledge of: 1) geological setting, in terms of outcrop extent and high-resolution stratigraphy; 2) ecologic role played by individual species, whether extant or extinct, in terms of habitat, trophic role, life histories and population structure, thanks to a comparison with extant descendants, or close relatives; 3) MM taphonomy, based on actuopaleontology. A recent global study revealed that MM extinction peaked in the late Pliocene, between 3.8 and 2.4Ma, ~~linked with the sudden drop in the extension of nearshore environments due to a large sea level regression, confirming that the fossil record offers important insights on the vulnerability of keystone marine species to climate change (Pimiento et al., 2017).~~linked to the sudden drop in the extension of nearshore environments after a large sea level regression (Pimiento et al., 2017), confirming that the fossil record offers important clues on the vulnerability of keystone marine species to climate change. We contribute here to ~~their~~a better understanding of the Pliocene fossil record by reviewing the rich ~~and varied fossil record of Pliocene LMVs~~MM of Tuscany, in Italy. In particular, we consider all reports of Pliocene ~~cetaceans, sharks, sirenians and pinnipeds~~marine mammals and sharks and revise taphonomy and ~~the~~ sedimentary facies associated with all ~~major~~known ~~recent~~ findings, ~~framing~~setting them within a sequence stratigraphic framework. ~~At the same time we expand on We also expand knowledge on paleoenvironmental contextualisation by considering the paleoecology of fossil invertebrates on a regional basis~~We also reconstruct the paleoenvironmental context and review data on a part of the marine ecosystem through the paleoecology of fossil invertebrates on a regional basis, following a stratigraphic paleobiological approach that can be applied to both the recent and the distant geological past (Patzkowsky ~~&~~and Holland,~~,~~ 2012). Published studies that have taken this direction are still a few, examples concerning Jurassic ichthyosaurs, plesiosaurs and pliosaurs (McMullen et al.,~~,~~ 2014), Cretaceous turtles, plesiosaurs, bony fish and sharks (Schemisser McKean ~~&~~and Gillette,~~,~~ 2015), Eocene archaeocetes, ~~dugongs~~sea cows and sharks (Peters et al.~~,~~ 2009), and Neogene ~~whales, pinnipeds~~marine mammals and sharks (Boessenecker et al., 2014). All of these papers record the co-occurrence of shelly faunas, only one undertaking quantitative studies of the distribution of fossil invertebrates~~ associated with sedimentary facies~~ (Jurassic of the Sundance Formation: McMullen et al.,~~,~~ 2014,~~;~~ see also Danise ~~&~~and Holland,~~,~~ 2017). The benefits of an outcrop-scale sequence stratigraphic approach include: (1) an independent record of relative sea-level change to test paleobiological hypotheses (see also Pyenson ~~&~~and Lindberg,~~,~~ 2011;~~;~~ Noakes et al.,~~,~~ 2013); (2) a chronostratigraphic scheme for high-resolution correlations; (3) a means to recognise minor and major breaks of the record; (4) an ecological and sedimentary framework for taphofacies distribution (Patzkowsky ~~&~~and Holland,~~,~~ 2012); and (5) an independent control of onshore-offshore patterns of fossil assemblages (e.g., Tomašových et al.,~~,~~ 2014).

~~From a top-down approach that emphasises the role of large marine vertebrates (LMVs) as apex predators of their trophic web, r~~Researchers that study the geologic history of marine ecosystems have focused on patterns of ecological restructuring based on the taxonomy of selected groups (e.g., Thorne et al.,~~,~~ 2011;~~;~~ Benton et al.,~~,~~ 2013;~~;~~ Scheyer et al.,~~,~~ 2014; Fischer et al., 2016), at the expenses of a more holistic approach that includes functional diversity and embraces as many ecosystem components as possible (Dineen et al., 2014). ~~This attitude should be reversed, similarly to~~By analogy with ecologists ~~working on extant ecosystems ~~who shift focus from models based on single groups (e.g., Steeman et al.,~~,~~ 2009) to an all-embracing vision of marine life (Lawton, 1994; Sergio et al.,~~,~~ 2014), connecting food web ecology with landscape ecology (Polis et al., 1997; Estes et al., 2011), stratigraphic paleobiology can draw from the fossil record and offer multidimensional insights on the complex geological history of modern marine ecosystems~~.~~.

After revising ~~LMVs~~fossil MM hosted in major museums of Tuscany, both isolated and articulated remains, we ~~then ~~focus on all fossil ~~skeletons~~bones that ~~could~~can be stratigraphically (e.g., Bianucci et al., ~~,~~1995, ~~;~~1998,~~;~~ 2001;~~;~~ Tinelli,~~,~~ 2013) and taphonomically framed (e.g., Dominici et al., 2009; ~~,~~Bianucci, 2010;~~,~~ Danise ~~&~~and Dominici, 2014). ~~The systematics of~~MM lists for the Mediterranean Pliocene~~ LMV~~ have been recently ~~reviewed~~updated (~~cetaceans~~marine mammals: Landini et al., 2005; Bianucci et al., 2009a; Sorbi et al., 2012; Bianucci ~~&~~and Vomero, 201~~5~~4; ~~elasmobranchs~~sharks: Marsili, 2006~~; sirenians: Sorbi et al. 2012~~). ~~E~~Species-level ecological data~~,~~ are available ~~from~~on modern ~~Mediterranean studies of ~~apex ~~predators~~consumers and mesocarnivores (Pauly et al., 1998; Cortés, 1999), with detailed information made available for Mediterranean species following conservation concerns ~~-~~(~~e.g., baleen and sperm whales~~marine mammals: Notarbartolo di Sciara~~,~~ et al., ~~2003, 2008,~~2016~~ Pirotta et al. 2011), with species-level data (~~; sharks: Cavanagh ~~&~~and Gibson, 2007), allowing for a ~~significant~~detailed paleoecological evaluation of the Tuscan fossil record. The actualistic approach is also viable for species of benthic molluscs, about half of which are still extant in modern Mediterranean ~~sea floors~~bottoms (55% of extant species of Mediterranean and North Sea bivalves, excluding strictly brackish and bathyal forms, i.e., 202 out of 367 species, survives from the Zanclean: Raffi et al., 1985). The regional quantitative study of molluscan assemblages was the basis for an independent assessment of paleoenvironments, paleoecology and paleobathimetry. A revision~~e~~ of abundance distributions of marine molluscs, the largest contributors to Mediterranean Pliocene shell beds and a key component of Mesozoic and Cenozoic marine ecosystems (Stanley, 1975;~~;~~ Vermeij, 1977), allowed to further explore the structure and composition of ~~the benthic component of ~~Pliocene marine ecosystems, and reconstruct~~ing~~

a paleobathymetric gradient (e.g., Scarponi ~~&~~and Kowaleski, 2004) along which to frame ~~LMV~~MM ~~taphonomy~~occurrence. The present work must necessarily start with a review of the chronostratigraphy and physical stratigraphy of the Tuscan marine Pliocene.

1. Geological setting

The Pliocene succession of Tuscany was deposited in a complex setting characteri~~zed~~sed by continental collision related to the later evolution of the Northern Apennines chain. According to a well-establi~~il~~shed hypothesis, the region, affected by shortening before the Middle-Late Miocene, accommodated by NE-verging thrust and fold systems, underwent crustal extension during the late Neogene and the Quaternary (DeCelles, 2012; Fig. 1). Crustal extension generated differential subsidence in a series of normal-fault controlled hinterland sedimentary basins, filled throughout by continental and shallow marine, mostly clastic successions (Martini ~~&~~and Sagri, 1993;~~,~~ Pascucci et al., 2006;~~,~~ Brogi, 2011). An alternative hypothesis places the late orogenic hinterland basins in a more complex tectonic setting characteri~~zed~~sed by the alternation of compressive, extensional and transcurrent stress fields (Benvenuti et al.,~~,~~ 2014; ~~;~~Bonini et al.,~~,~~ 2014).

The Neogene Tuscan basins considered in this work include, from West to East, and from North to South, the Fine Basin (FB; Bossio et al., 1997), the Volterra-Era Basin (VEB; Bossio et al., 1994), The Elsa Basin (EB; Benvenuti et al., 2014), the Ombrone-Orcia Basin (OOB; Bossio et al., 1991;~~,~~ Nalin et al., 2010), the Siena-Radicofani Basin (SRB; Ghinassi ~~&~~and Lazzarotto, ~~-~~2005;~~,~~ Martini et al., 2011, 2016), and the Chiana Basin (CB; Fig. 1: Pesa Basin not considered here). With one exception (OOB, see below), these basins show a shape conditioned by the structural and physiographic features of the inner portion of the Northern Apennines. Their NW-SE general elongation reflects the trend of the thrust-related anticline ridges developed during earlier collisional stages. These compressive structures have bounded most basins through their infilling, only to be obliterated by younger parallel normal fault systems, leaving an invariant stratigraphic onlap of the Pliocene successions onto the basin margins. Despite a NW-SE distribution of the hinterland basins, the structural setting is responsible for a NE-trending physiographic and paleogeographic gradient, where the FB is closest, and the CB furthest, from offshore settings throughout the late orogenic phase, with important implications for the facies architecture and the distribution of marine vertebrates and shell beds. Differential active uplift of the basin shoulders during the Pliocene, coupled with important erosional phases, resulted in a different preservation of the original stratigraphic architecture. The infill during the Zanclean is generally characteri~~zed~~sed by relatively continuous open marine successions, the correlative fluvial-coastal systems missing due to uplift and erosion of basin margins. On the other hand, the Piacenzian infill is characteri~~zed~~sed by genetically-connected, fluvial, coastal and shallow marine facies tracts, particularly well-preserved in the EB, hinting to reduced uplift of the marginal areas. The modern physiography of OOB, escaping the structurally-controlled geometry of the other basins, mimics instead an original fluvial network developed during the latest Messinian, flooded after the Salinity Crisis (Bossio et al.,~~,~~ 1991;~~;~~ Benvenuti et al.,~~,~~ 2015), filled during the Pliocene, and finally disrupted by post-Pliocene uplift and erosion. This difference in the structural history also justifies the preservation in OOB of Zanclean fluvial and shallow marine facies (Fig. 2).

1.1 Pliocene Stratigraphy

The Neogene succession of Tuscany is up to 2000 m-thick, about half of which belongs to the uppermost Miocene-Pleistocene interval (Bossio et al., 2004; ~~,~~ 1997;~~7,~~ Benvenuti et al., 2014). The Pliocene has been traditionally subdivided into three main informal litostratigraphic units: continental conglomerates and sandstones at the base, overlain by the “Blue Clay Formation” (*Argille Azzurre*: Zanclean-lower Piacenzian), marking the post-Messinian Mediterranean marine transgression and forming the thickest part of the basin infill (e.g., Bossio et al., 1994;~~,~~ 1997; Ghinassi ~~&~~and Lazzarotto, 2005), and the “Upper Sands” (*Sabbie superiori*: Piacenzian-Gelasian) and conglomerates, deposited during the ensuing regression. Several finer litostratigraphic units have been introduced to define the local stratigraphy, resulting in a complex and largely informal litostratigraphic terminology which includes Zanclean lower “Blue Clays” and Zanclean-Piacenzian upper “Blue Clays” (Capezzuoli et al., 2015), the latter eventually further separated by the widespread occurrence of Piacenzian carbonates (Nalin et al., 2016). The lower Zanclean (OOB: Ghinassi, 2007;~~,~~ Nalin et al., 2010; ~~, ~~Dominici et al., 2012) and the Piacenzian, are characterised by the high-frequency alternation of coarse-grained and fine-grained facies, ranging from fluvial to marine shelf settings (Benvenuti et al., 1995;~~,~~ 2007; ~~, ~~2014;~~,~~ Martini et al. 2011, Fig. 2). The dynamics of the Pliocene infilling are better-understood in the EB, where six synthems have been defined, each up to more than 200 m-thick, further subdivided in a number of elementary and composite depositional sequences and chronologically calibrated through marine biostratigraphy and continental vertebrate biochronology (Benvenuti ~~&~~and Del Conte, 2013;~~3,~~ Benvenuti et al., 2014, with references).

2. Materials and methods

Stratigraphic sections were measured and described at several localities (Fig. 1). Siliciclastic and carbonate facies were described, subdivided into groups of facies based on lithology, sedimentary structures and ichnology, and interpreted in terms of process and depositional environment (Tab. 1). Each group represents a set of individual facies forming monogenic associations (in the sense of Mutti et al.,~~,~~1994), i.e., the meter-scale stacking of facies which express the autocyclic behaviour of specific depositional systems within a given accommodation space (Benvenuti ~~&~~and Del Conte,~~;~~ 2013). Sequence stratigraphic concepts have been applied to reconstruct the dynamics of basin infills at a hierarchy of scales, advancing hypotheses on controlling factors. The chronostratigraphic subdivision of Benvenuti et al. (2014), which divides the Pliocene into six synthems, S1-S6 from older to younger, was extended to all six Tuscan basins by referring to available biostratigraphic schemes (Fig. 2). The sequence stratigraphic interpretation of S2 in OOB is based on Tinelli (2013). Other parts of the S1-S3 succession were drawn based on available litostratigraphic literature (see below). Studies integrating sedimentary facies analysis, biostratigraphy and magnetostratigraphy (Nalin et al.,~~;~~ 2016) have helped correlating ~~several discontinuous~~ carbonate bodies typical of S4. The reader is referred to Benvenuti et al. (2007;~~7;~~ 2014) for details on facies analysis and sequence stratigraphic interpretation of synthems S3-S6.

First, data on the geographic distribution of fossil marine mammals, ~~and~~ large sharks and sirenians were ~~collected~~largely based on collections housed at the Natural History museums of the University of Florence (UFMSN), University of Pisa (UPMSN), and Accademia de' Fisiocritici of Siena (AFMSN), the three largest collections of Tuscany, and at the Geological Museum Giovanni Capellini, Bologna University (MGGC). In particular, counts of cetaceans were based on UFMSN collections (Mysticeti and Odontoceti, ~~n~~N = 142), ~~and those of~~ large shark on the sum of UFMSN, UPMSN and AFMSN collections (Carcharhiniformes and Lamniformes, ~~n~~N = 337, data synthesi~~zed~~sed from Marsili, 2006), sirenians from all reports in Tab. 2 (N = 10). Each record is formed either by a single element (e.g., whale bone, shark tooth), by a few elements of the same individual, or by a whole, quasi-articulated skeletons. A large proportion of this dataset lacks precise location, allowing only for some crude stratigraphic attribution (Fig. 3).

On a second step, all fossil Tuscan Pliocene cetaceans ~~and other marine mammals (Sirenia, Carnivora)~~, sirenians and pinnipeds that could be framed within the available high-resolution stratigraphic framework and associated with taphonomic data, were selected. At this step, after excluding ~~isolated and smaller~~unidentified MM remains, a dataset of ~~39 cases~~64 specimens (cetaceans ~~n~~N = ~~32~~50; ~~dugong~~sirenians ~~n~~N = ~~4~~10; pinnipeds ~~n~~N = ~~2~~4) was assembled. ~~Many of them were a~~Associatiation~~ed~~ with shark teeth is frequent (55% of 25 cases according to Danise ~~&~~and Dominici~~,~~ 2014 for the Italian Pliocene; see also Bianucci et al.~~,~~ 2002, 2010). The majority of the ~~39~~64 specimens are ~~part of~~included in the catalogue of UFMSN, UPMSN, ~~and~~ AFMSN and MGGC, whereas a few are stored in smaller collections of the municipalities of Montaione, Scandicci (Florence province), and Certaldo (Pisa province), ~~and~~ one in a private property (Castello di Villa Banfi, near Montalcino, Siena province), and one in the Museum National d'Histoire Naturelle in Paris (France). ~~Each one of the 39 LMVs~~Whenever possible, large marine vertebrates ~~was~~were coded by synthem (N = 60) and depositional environment (N = 54). We analysed abundance distributions among marine mammals, and species richness of marine mammals and sharks. To infer Pliocene paleoecology, fossil taxa recognised in Tuscany were compared with their closest descendants, focusing on the species ~~.~~today living in the North-Western Mediterranean Sea (NWMS).

~~Since a~~All known ~~LMV~~MM-bearing sedimentary facies are associated with a mollusc-dominated benthic fauna. T~~, t~~he third step of the analysis concerned a quantitative study of shell beds, allowing: 1) to interpret the regional evolution from a perspective independent from the sedimentary facies, ~~and~~2) to character~~ize~~ise ~~the~~ MM paleoenvironmental and bathymetric distribution~~ of LMVs. Molluscs are a key component of Pliocene communities,~~, and 3) ~~allowing~~ to explore the structure of the benthic component of marine ecosystems and to identify underlying environmental ~~factors~~controls~~ that underline the paleoenvironmental distribution of LMVs~~. 72 Bulk samples were collected at major shell beds at bed resolution throughout the succession and sieved with 1 mm mesh size. Fossils of bivalves, gastropods and scaphopods were identified to species level. The minimum number of individuals was calculated following standard approaches (see Patzkowsky ~~&~~and Holland, 2012), resulting in a richness of 525 species (S) and a total abundance of 64206 individuals (N). We coded each fossil assemblage by synthem, tract of small-scale depositional sequence, and depositional environment. Most samples belonged to facies types F2-F5 (Tab. 1; see also Tomašových et al.,~~;~~ 2014). Facies F6 usually lacks macrofossils and allowed for the collection of only one sample. No samples were collected in facies F1, lacking marine shells, facies F7, mostly devoid shells, and facies F8, which is richly fossiliferous, but lacks aragonite shells and is associated with specimens hardly extractable from the rock. The resulting quantitative dataset served for statistical analyses on the distribution of species-level abundances on a siliciclastic shelf depositional system, performed with the software Primer 6.0 (Clarke ~~&~~and Gorley, 2006). Analyses included clustering and nMDS ordination techniques on a Bray-Curtis similarity matrix, of standardised, square-root transformed data (72 samples; S = 333 and N = 63518 after the exclusion of singletons). To test statistically whether there is a significant difference between two or more groups of sampling units based on sedimentary facies, we performed an analysis of similarity (ANOSIM). To interpret the outcomes of the quantitative study and the significance of clusters we used species-level autoecologic information available for the most abundant species, based on the distribution of extant forms. This information, retrieved from the Marine Biodiversity and Ecosystem Functioning EU website (MARBEF: www.marbef.org), included the average life depth of 23 modern species that in our dataset had an overall abundance > 0.15%.

3. Results

3.1. Unconformity-bounded units

3.1.1 Synthem S1: the early Zanclean transgression

The Miocene-Pliocene transition, marking the return to marine conditions after the Messinian salinity crisis (Krjigsman et al.,~~,~~ 1999), is recorded in limited exposures of earliest Zanclean, open marine mudstones resting both unconformably or conformably onto latest Messinian non-marine deposits (*Lago-Mare*), an isochronous boundary being dated in the Mediterranean at 5.33 Ma (Roveri et al.,~~,~~ 2014). Differences depend on the specific structurally-controlled distribution of hinterland basins, where an uplifting chain determined the presence of thresholds delaying the early Zanclean marine flooding from inner (EB, OOB: Benvenuti et al.,~~,~~ 2015a) to outer hinterland basins (FB, VEB). In inner basins such as EB, where S1 has been defined, continental deposition continued into the earliest Zanclean, marine flooding occurring within the MPL1 biozone (references in Benvenuti et al., 2015a). A chronostratigraphical equivalent of S1 is represented in FB and VEB (Bossio et al.,~~,~~ 1978) by an open-shelf mudstone, conformably resting on latest Messinian *Lago-Mare* deposits (Roveri et al.,~~,~~ 2014). An apparently analogous situation is documented in OOB, where MPL1 shelfal mudstones of the early Zanclean (normal chron C3n) rest on a Messinian to basal Pliocene paleovalley fill (Benvenuti et al.,~~,~~ 2015a).

3.1.2 Synthem S2: Zanclean differential preservation

Synthem S2, as recogni~~zed~~sed in the EB (Benvenuti et al. 2014), is represented by relatively thin fluvial conglomerates unconformably resting on S1 (biozones MPL1-MPL2), capped by S3 (biozone MPL4a: Bossio et al., 1993; 2001), comprising important stratigraphic gaps at its base and top. On the other hand, in FB (Bossio et al.,~~,~~ 1997), VEB (Bossio et al., 1994) and SRB (Ghinassi ~~&~~and Lazzarotto, 2005), the same chronostratigraphic interval is recorded by monotonous epibathyal mudstones several hundred meters thick, locally intercalated with delta-front hyperpycnal sandstones and conglomerates. In a very broad sense, the concept of S2 is extended to these basins, by assuming that erosional unconformities in EB pass to into correlative conformities in rapidly subsiding adjacent basins, where thick successions could be accomodated. Apart from exceptions, no shells were found in bathyal mudstone or in deltaic sandstone. In OOB, the same time span is marked by a N-S facies gradient characteri~~zed~~sed by a single deepening-upward succession, from fluvio-deltaic sandstone to shelfal mudstone, replaced by a succession made of four distinct regressive-transgressive units in the Orcia valley to the north (Ghinassi, 2005; Benvenuti et al., 2015b). A laterally-continuous shell bed, with sharks remains and skeletons and articulated bones of whales, ~~dugong~~sirenians and large ~~bony~~teleost fishes (Danise, 2010; Sorbi et al., 2012; Tinelli, 2013), marks a major transgressive surface overlain by open shelf mudstones (Sorbi et al., 2012; Tinelli, 2013: biozone MPL2) that is hypothetically traced along a NE-SW profile (Figs. 4, 5).

3.1.3 Synthem S3: Zanclean-Piacenzian transition

Synthem S3 is subdivided in EB into a lower and an upper interval (Benvenuti et al., 2014). The lower division is represented by deepening-upward, coarse-grained delta front system, overlain by an upper mudstone division from an open shelf setting. The upper part is rich with shell beds, and occasional articulated whale skeletons, associated with shark teeth, have been recovered (Danise ~~&~~and Dominici, 2014). Similar shelf mudstones of the MPL4 biozone crop out in VEB and SRB (Bossio et al., 1993; Riforgiato et al., 2005) whereas biostratigraphically equivalent mudstones in FB testify to an upper epibathyal paleoenvironment.

3.1.4 Synthem S4: early Piacenzian warm climate and high sea-level

Synthem S4 (Benvenuti et al., 2014) has been recogni~~zed~~sed in FB and VEB by facies similarities and chronostratigraphic correlation. In EB, S4 comprises a lower interval dominated by richly fossiliferous, massive mudstone or very-fine-grained sandstone (prodelta-inner shelf), overlain by bioclast-rich sandstones recording prograding mixed carbonate-clastic ramp, outcropping in the southeastern part of the Elsa valley. Equivalent deposits, also comprised in biozone MPL4b, are patchily distributed in FB, VEB, SRB, OOB and other basins of southern Tuscany (Ghinassi ~~&~~and Nalin, 2010; Ghinassi, personal communication, 2015). The upper interval of S4 is formed by a succession of delta front sandstones, passing in EB eastern margin to a few tens of m-thick fluvial succession, hinting at an original depositional gradient. S4 is apparently missing due to erosion north of San Gimignano (EB), and around Lajatico (VEB). Biostratigraphic data allow to refer S4 to the upper part of biozone MPL4b and the lower part of MPL5a, thus comprising the mid-lower part of the Piacenzian, globally characteri~~zed~~sed between 3.264-3.025 Ma by warm climate and relatively high sea level (Raymo et al., 2009; Dowsett et al., 2013; Prista et al., 2015).

3.1.5 Synthem S5: mid-Piacenzian high-frequency sea level variation

Synthem S5, recogni~~zed~~sed in EB and VEB, is bounded below by an erosional unconformity that cuts deeply into underlying units, bringing S5 directly on top of S3 (EB: log 15; VEB: logs 5-6 in Fig. 1). S5 is up to about 200 m in EB, where it has been subdivided into a hierarchy of small-scale depositional sequences (Benvenuti et al., 2007; Dominici et al., 2008: see following paragraphs). Each composite depositional sequence forms a tens-of-m-thick asymmetric sedimentary cycle, composed by a deepening-upward part, from fluvial or coastal coarse-grained sediments, to open shelf mudstones, sometimes topped by a regressive shoreface or delta sandstone, other times directly overlain by the next sequence through a sharp contact. Fluvial, ~~lagoonal~~brackish-water, and other intertidal deposits mark the lower part of each composite sequence, usually topped by a laterally-continuous shell bed, from a few cm to a few dm-thick, representing a surface of transgression. Shell beds are particularly well-developed around the middle part of sequences, where they separate shoreface and delta sandstones from overlying open shelf mudstones, marking the time of maximum flooding (MFS). Large marine vertebrates, including articulated whale skeletons and large sharks (Danise ~~&~~and Dominici, 2014), are often recovered both at MFS and overlying mudstone (Fig. 1). Towards the north-eastern margin of EB, cyclothemic fluvial conglomerates, sandstones and mudstones replace coastal and fully marine deposits, testifying to an original facies gradient. In the central part of EB, composite sequences are stacked to form a deepening-upward succession, with a topmost thick and laterally-continuous open shelf mudstone interval, directly onlapping the S4-S5 basal unconformity on the eastern EB (log 15, Fiano: Fig. 1).

3.1.6 Synthem S6: Piacenzian-Gelasian climate change and regression

As S5, synthem S6 is also built through a hierarchy of small-scale depositional sequences, better expressed in EB, but also documented in SRB and CB. In EB, fluvial coarse-grained sandstones fill a deep valley incised in S5 deposits (logs 8-10 in Fig. 1), resting on the basal unconformity of S6. Intertidal or coastal lagoon deposits form the transgressive systems tract of the composite depositional sequence. A laterally-continuous shell bed testifies to the MFS of S6, topped by highstand shoreface and delta front sandstones. The Piacenzian-Gelasian boundary, corresponding to a major climatic transition from warmer-moister to colder-drier conditions (Benvenuti et al., 1995b; 2007), is marked by the Gauss-Matuyama reversal detected at Montopoli (Lindsay et al., 1980). Highstand marine sandstones are characteri~~zed~~sed by the recovery of two mysticete skeletons, at Montopoli (EB, see Capellini, 1905) and Sinalunga (CB, Fig. 7). Fully continental environments were established throughout the Gelasian in all basins here under study (e.g., Benvenuti ~~&~~and Del Conte, 2013; Benvenuti et al., 2014; Bianchi et al., 2015).

3.2 Sedimentary facies and facies associations

Seven groups of siliciclastic facies and one group of carbonate facies, with very different fossil content, have been recogni~~zed~~sed (Tab. 1). Siliciclastic facies form a paleoenvironmental gradient from terrestrial to marine and, in the case of marine facies, from shallowest to deepest (Fig. 8a). Facies types are fluvial conglomerate and sandstone, and alluvial mudstone (F1); intertidal to very shallow subtidal mudstone and muddy sandstone (F2); shallow subtidal coarse- and medium-grained sandstone with sparse conglomerate (F3); deep subtidal muddy fine-grained sandstone (F4); open shelf sandy mudstone (F5); outer shelf to upper bathyal mudstone (F6); outer shelf and bathyal turbidite sandstone and conglomerate (F7). An eighth group is formed by facies deposited subtidally in limited mixed carbonatic-siliciclastic ramps (F8), irrespective of depth (Nalin et al., 2016). Facies F6-F7 are restricted to Zanclean deposits (synthems S1-S3); facies F5 and F8 characterise the upper Zanclean-middle Piacenzian interval (synthems S3-S4); facies F1-F4 characterise the upper Piacenzian (synthems S5-S6). The OOB succession, characterised by facies F1-F4, is an exception within the Zanclean.

3.3 Elementary depositional sequences (EDS)

Both fluvial (Benvenuti ~~&~~and Del Conte, 2013) and marine facies groups (siliciclastics: Benvenuti et al., 2007; 2014; carbonates: Nalin et al., 2016) are stacked to form facies associations which record cyclic variations of depositional and environmental conditions in response to a change in accommodation space. Physical surfaces and the intervening deposits allowed to subdivide depositional sequences in systems tracts (Benvenuti et al., 2007; Dominici et al., 2008). At the simplest scale, these hybrid facies associations form elementary depositional sequences, up to 10-20 m thick, in their turn stacked to form composite sequences (original concepts from Mutti et al., 1994). This hierarchy is particularly evident in synthems S5-S6, formed at a time of pronounced glacio-eustatic oscillations and expressed around coastal settings, where maximum facies contrast allows for the expression of subtle cycle of sea level variation (e.g., Benvenuti ~~&~~and Dominici, 1992; Benvenuti et al., 2007; Dominici et al., 2008). Analogue sharp facies contrast within Zanclean EDS in OBB (Tinelli, 2013), but is otherwise absent in deeper sediments (facies F5-F7). EDSs have different expressions depending on the time interval and the sedimentary basin.

3.3.1 Zanclean EDS (synthems S1-S3)

In most basins, deposition of synthems S1-S2-S3 takes place at outer-shelf or bathyal depths, well below the point on a depositional profile where the rate of relative sea level change is zero (equilibrium point). Here the sediment supply is not sufficient to fill the available accommodation space and an aggradational style of deposition prevails, with the result that in most Zanclean settings smaller cycles of sea level variations are not marked by a facies change. The sharp facies change recorded where the monotonous muddy deposition is interrupted by turbidite sandstone and conglomerate, is connected with synthem boundaries and major tectonic phases of restructuring of the region. ~~LMVs~~MM and shell beds are practically absent. This situation reverses in the Orcia-Ombrone basin, where depths of deposition are shallower and EDS are expressed. At Arcille deltaic sandy conglomerates and sandstones (facies F3) are overlain by a fluvial cross-bedded sandstone (facies F1a), separated by a transgressive surface (TS) from an overlying bioturbated shallow marine sandstone. A *Haustator vermicularis* shell bed (Danise, 2010; Tinelli, 2013) forms the MFS separating the shoreface sandstone from an open marine mudstone with scattered shells (facies F5), marking a sudden and prolonged deepening of the basin (biozone MPL2: Sorbi et al., 2012; Tinelli, 2013). The succession is topped by deposits from shallower depths, expression of the falling-stage (FSST), below the upper SB (Fig. 4). Similar small-scale depositional sequences, expressed through fining-upward cycles no less than 40 m-thick, are also present in synthem S3 at Case al Poggio, near Siena (biozones MPL3-MPL4a: Bianucci et al., 2001) and at Castelfiorentino (biozone MPL4b: Benvenuti et al., 2014).

3.3.2 Piacenzian EDS (synthems S4-S6)

As depth of deposition shallows during the Piacenzian, and cycles of sea level variation widen, the cyclic stacking of EDS becomes the typical depositional theme (Benvenuti et al., 2007, 2014; Dominici et al., 2008). In FB, the northwesternmost basin, depths remain considerable and facies change is more subtle. Pliocene at Orciano Pisano is traditionally assigned to the “Blue Clays” formation (Bossio et al., 1997), but two distinct bodies where evidenced since the late nineteenth century (D’Ancona, 1867). The lower one is formed by grey claystone with very rare shells, the upper one by muddy, very-fine grained gray sandstone richly fossiliferous. The lower part of the latter interval outcrops at the foothill of the small town of Orciano Pisano, around the locality Case Nuove (Bianucci ~~&~~and Landini, 2005; Berta et al., 2015). Here a laterally persistent shell bed is dominated by the turritellid *Archimediella spirata*, overlain by a 25 m-thick monotonous sandstone interval with intercalated shell beds or sparse shells, becoming muddier upward. The *Archimediella* shell bed is interpreted as the TS of an EDS, coinciding with the lower SB of a lower Piacenzian EDS. The overlying muddy fine-grained sandstone is the TST and HST (MPL5a: Dominici et al., 2009; Fig. 6). At shallower settings, in all basins to the East and South of FB, EDS of synthem S4 take the form of an alternation of mudstone and carbonate (facies F5 and F8:

Nalin et al., 2016), or mudstone and sandstone (facies F5 and F3-F4: Benvenuti et al., 2014; biozone MPL5a). Middle and upper Piacenzian EDS form and alternation of coastal mudstone and sandstone (facies F1-F2-F3: Benvenuti ~~&~~and Dominici, 1992; Dominici, 1994), with MFS and HST marked by a shell bed topped by a lower shoreface sandstone, or a shelf mudstone (facies F4-F5: Benvenuti et al., 2007; Dominici et al., 2008).

4~~3~~. Distribution of large marine vertebrates

~~3.~~4.1 Geographic distribution

The MM geographic distribution ~~of all LMVs that could be assigned to a given locality and sedimentary facies~~ is listed in Table 2. All ~~LMVs~~MM that ~~were~~was geographically located, irrespective of stratigraphy, ~~were~~was plotted in Fig. 3. The largest number were recovered in FB in Northwestern Tuscany, with a peak at a few sites around the small town of Orciano Pisano, in the Pisa province. This coincides with the highest number of known species, including mammals, elasmobranchs, turtles, and large bony fishes~~ (see Bianucci & Landini 2005, Marsili 2006)~~. ~~LMV~~MM ~~abundance is also high~~is also abundant in the province of Siena, around Volterra (VEB; Bianucci ~~&~~and Landini 2005), and around San Quirico, particularly rich with elasmobranchs according to the available data (SRB; Marsili, 2006). A fourth basin with a consistent number of findings is OOB, where cetaceans, sharks, ~~dugong~~sirenians and large ~~bony~~teleost fishes have been unearthed.

~~3.~~4.2 ~~S~~MM stratigraphic distribution~~ of LMVs~~

~~3.~~4.2.1 Synthems S1-S2

In the vicinity of Saline di Volterra, ~~provenance of a mandible with teeth of~~one of the sites with remains of ~~-~~*Pliophoca etrusca* (Berta et al.~~,~~ 2015~~5~~) and sperm whale (Tab. 2), S1 is represented by a bathyal mudstone (facies F6, biozone MPL1). Lower-middle Zanclean ~~LMVs~~MM ~~are~~is otherwise absent, with the exception of S2 in OOB, where ~~they~~large marine vertebrates are concentrated ~~along the MFS~~at the maximum flooding interval, outcropping at Poggio alle Mura (Danise, 2010), Camigliano (Sorbi et al.,~~,~~ 2012) and Arcille (Tinelli et al.,~~,~~ 2012;~~;~~ Tinelli,~~,~~ 2013), in biozone MPL2. At Poggio alle Mura a slightly disarticulated ~~balaenopterid~~balaenid whale skeleton (WOm1-1 in Tab. 2) has been excavated in contact with the laterally-persistent *Haustator* shell bed at the maximum flooding interval (Figs. 4, ~~-~~5; Danise, 2010; Tinelli, 2013). At Camigliano and Arcille, tens of km from Poggio alle Mura, the *Haustator* shell bed is associated with other articulated skeletons and isolated ~~LMV~~MM remains, including several specimens of the sirenian *Metaxytherium subapenninum*~~s~~ (MOm2~~1~~-1~~, MOm1-2-~~5), large bony fishes, rays, and sharks *Carcharias taurus*, *Carcharhinus* sp., *Galeocerdo cuvieri*, and *Squatina* sp.~~sharks and rays~~ (Sorbi et al.,~~,~~ 2012; Tinelli et al.,~~,~~ 2012; ~~;~~Tinelli,~~,~~ 2013). A partial skull of the delphinid *Etruridelphis giulii*, with right and left dentaries fractured, but nearly complete and with most teeth still in their alveoli (DSi2-1 in Tab. 2), was recovered southeast of Siena, near Chianciano Terme (SRB) at the top of a mudstone (facies F6) intercalated with turbiditic sandstone beds (Facies F7), topped by a monotonous mudstone interval (upper Zanclean, uppermost part of biozone MPL3: Bianucci et al., 2009b). In the same basin, two undetermined beaked whales and bones of four different specimens attributed to *Metaxytherium subapenninum* were found in the middle of a fining-upward succession, at the boundary between biozones MPL3 and MPL4a (Bianucci et al., 2001; WSi2-1-2 and MSi2-1-4 in Tab. 2), suggesting that findings at the two SRB localities belong to the same MFS, in the upper part of S2. ~~Four~~Three specimens of marine mammals were identified in Synthem S1, ~~13~~seven in Synthem S2.

~~3.~~4.2.2 Synthem S3

~~A partial delphinid skull, with right and left dentaries fractured, but nearly complete and with most teeth still in their alveoli (WSi2-1 in Tab. 2), was recovered southeast of Siena, near Chianciano Terme (SRB) at the top of a mudstone (facies F6) intercalated with turbiditic sandstone beds (Facies F7), topped by a monotonous mudstone interval (upper Zanclean, uppermost part of biozone MPL3: Bianucci et al., 2009). In the same basin, a sirenian skull and mandible were found in the middle of a fining-upward succession, also at the boundary between biozones MPL3 and MPL4a (Bianucci et al., 2001; MSi3-2 in Tab. 2), suggesting that these two findings belong to the same MFS, in the lower part of S3.~~

The upper part of ~~the latter synthem~~S3 yielded ~~several other LMVs, including~~ an articulated and well-preserved balenopterid skeleton found in a 30 m-thick mudstone succession at Castelfiorentino, in the Elsa basin (EB, WEl3-1~~2~~). These strata are richly fossiliferous, with several shell beds with epifaunal cemented taxa, such as vermetid gastropods, oysters and corals (Facies F5), ~~within~~in a normal-polarity magnetostratigraphic interval (Gauss chron: Andrea Albianelli, personal communication, 1999). Based on physical stratigraphic correlation, this can be assigned to a lower Piacenzian HST. ~~Finally, a~~A ~~dolphin~~ skull of *Hemisyntrachelus* sp. (Aldinucci et al., 2011) and ~~an incomplete, almost articulated~~partly articulated vertebrae and costae of a dolphin skeleton (Arbeid et al., 2015) were recently excavated a few hundred meters apart one from the other, along a monotonous mudstone S3 succession intercalated with several *Ostrea* and *Serpulorbis* shell beds, near Certaldo (facies F5, D~~W~~EI3-1-2 in Tab. 2~~4~~). Overall, specimens of marine mammals attributed to Synthem S3 were ~~six~~eleven (some are uncertain and may come from the upper part of S2: Tab. 2).

~~3.~~4.2.3 Synthem S4

Synthem S4 yielded the highest ~~number of the reviewed large marine vertebrates~~abundance and species-richness of the Tuscan MM. In the Fine basin, the locality of Orciano Pisano is represented in Table 2 by ~~nine~~18 records of whales, dolphins (a partial skeleton: Bianucci, 1996; Bianucci et al., 2009), seals (Berta et al., 2015), tens of other ~~cetacean specimens~~unidentified cetacean elements, hundreds of shark teeth and vertebrae (Fig. 3), and sea turtles, large bony fishes, and sea birds hosted in museum collections (Bianucci ~~&~~and Landini, 2005; Marsili, 2007b; Cioppi and Dominici, 2011). In locality Case Nuove, a single middle Piacenzian ~~TS~~transgressive surface ~~is known to have~~has yielded a whole, articulated whale skeleton (Figs. 4, 6), teeth of blue and white sharks and bones of sea birds (Dominici et al., 2009). From the same site comes~~s~~ a ~~n articulated seal~~ skeleton of the monk seal *Pliophoca etrusca* (Berta et al., 2015~~4~~), and possibly many other museum specimens labelled “Orciano Pisano”~~ (e.g., Higgs et al., 2012)~~, suggesting that this ~~surface~~interval ~~is~~forms the most prolific bonebed of the region (Tab. 2). A few cm above the *Archimediella* shell bed, glauconitic and deeply bioeroded whale bones (Danise, 2010), associated with ichnological evidence of the activity of *Osedax* bone-eating worms (see Higgs et al., 2012), lie in a bioturbated muddy, fine-grained sandstone with a complex boxwork of *Ophiomorpha* and *Thalassinoides* trace fossils (Fig. 6), associated with a diverse paleocommunity of molluscs and other benthic invertebrates ~~from several trophic groups~~with complex trophic connections (Dominici et al., 2009; Danise et al., 2010). ~~In the adjacent~~At the boundary between FB and VEB, an incomplete ~~dolphin~~ skull and skeleton of the dolphin *Etruridelphis giulii* was recovered near Lorenzana (Lawley, 1876; Bianucci, 1996; Bianucci et al., 2009b), at a locality associated with a muddy sandstone interval (facies F4) in synthem S4. An incomplete and ~~dis~~articulated mystice~~balenopterid whale~~te was recovered in a sandstone at San Gimignano, associated with pectinid bivalves (Fig. 7; facies F3; Elsa basin, EB: Danise ~~&~~and Dominici, 2014), here tentatively assigned to the uppermost part of the synthem

(WEl4-1 in Tab. 2). Overall, specimens of marine mammals attributed to Synthem S4 were ~~27~~28.

~~3.~~4.2.4 Synthem S5

The next MM richer stratigraphic interval are Piacenzian deposits of synthem S5. An incomplete and disarticulated balaenid skeleton was found in intertidal deposits of the lower part of the synthem, at ~~La Farfalla~~Casenuove (facies F2, EB; Bianucci et al., 1995; Collareta et al., 2016; WEl5-1 in Tab. 2). A large ~~bowhead whale~~balaenid~~ (Balaena)~~ was recovered higher up section, a few meters above a laterally-continuous very thick and complex *Haustator vermicularis* shell bed, up to 2 m-thick (Benvenuti et al., 1995a), traced laterally for 2 km to the east of San Miniato ("*Turritella* strata", De Stefani, 1874), and forming a surface of transgression within the TST of ~~synthem~~ S5 (Benvenuti et al., 2007; 2014; Dominici et al., 2008). The MFS is formed by a *Glycymeris insubricus* shell bed, separating around San Miniato shoreface sandstone (facies F3 or F4) from offshore mudstone (F5; Benvenuti et al., 2007). The ~~*Balaena* s~~balaenid skeleton was almost articulated~~, complete~~ and bioeroded, closely associated with teeth of the great white shark and other scavengers (Borselli ~~&~~and Cozzini, 1992; Bianucci et al., 2002; Danise and Dominici, 2014), in the early HST of synthem S5 (Benvenuti et al., ~~-~~2007; ~~,~~Dominici et al., 2008; WEl5-2 in Tab. 2). The *Glycymeris* shell bed can be traced laterally for several km. In the vicinity of Fiano, it includes bioeroded and encrusted gravels inherited from underlying successions, interpreted as revinement deposits. The interval of maximum flooding~~ and early HST~~ is marked by the stacking of at least three distinct shell beds, all including a high-diversity association with bioeroded and encrusted shells. This situation suggests that balaenid WEl5-2~~, in the middle of EB,~~ lies in correspondence of an interval of low rates of sedimentation. In SRB, near

Castelnuovo Berardenga, shelfal mudstones (facies type F5) have yielded MM remains at a few localities. Delphinid remains were found at the "I Sodi" quarry and at Troiola (DSi5-1-2, in Tab. 2). Bones of a beaked whale and undetermined mysticetes are reported from Guistrigona (Manganelli and Benocci, 2014) and a fragmentary specimen of the monk seal *Pliophoca etrusca* from Castelnuovo Berardenga (Berta et al., 2015). A very rich shark fauna, including sawsharks, thresher, frilled, bluntnose sixgill, bramble, gulper, kitten, sand tiger, shorten mako, basking and requiem sharks, an association suggesting an upper slope paleoenvironment for the surroundings of Castelnuovo Berardenga Scalo (Cigala-Fulgosi et al., 2009; the same mudstone interval at the same locality has been interpreted as a shelfal deposit: Martini et al., 2016). ~~Marine mammals identified in Synthem S5 were eight.~~Judging from historical accounts (Capellini, 1883), the killer whale *Orcinus citonensis* (DCh4-1) was recovered in a sandy unit lying on top of a thick mudstone interval (S3 or S4) and is tentatively assigned to S5. Specimens of marine mammals attributed to Synthem S5 were 10.

~~3.~~4.2.5 Synthem S6

A fairly complete skeleton of a large balaenid whale was recovered in the second half of the 19th Century in the EB near Montopoli Valdarno (Capellini 1905), in open shelf strata attributable to the interval of maximum flooding of ~~Synthem~~ S6 (WEl6-1 in Tab. 2). The MFS of S6, of uppermost Piacenzian age, is marked in EB by a laterally continuous *Pteria phalenacea* shell bed, with a high-diversity association of macroinvertebrates, including a rich decapod paleocommunity (Garassino et al., 2012). In the ~~same locality~~vicinity, near Palaia, a right whale (*Eubalena* sp.) was recovered in 1974 in sandy mudstones, in association with mollusc shells and teeth of the great white shark (*Carcharodon carcharias*: Bisconti, 2002; Sorbini et al., 2014). A tightly articulated balaenopterid skeleton was found at Sinalunga (WCh4-1 in Tab. 2), in deltaic sandstones and conglomerates (Fig. 8). Marine mammal specimens attributed to Synthem S6 ~~with some confidence~~ were three.

4.3 MM facies type distribution

In an ideal deepening-up gradient, multi-element findings of marine mammals are very rare in intertidal and very shallow subtidal paleoenvironments (facies type F2, 1,5%: Fig. 9A), moderately represented in delta or shoreface sandstones (facies type F3, 4,6%), most abundant in sandy mudstone of open shelf settings (facies type F5, ~~87~~70%), rare in outer shelf and bathyal sediments (facies type F6-F7, ~~6,2~~1,5%). The most pristine and complete skeletons are associated with gravelly well-sorted sands from event sedimentation, suggesting a negative relationship between taphonomic loss and sedimentary processes at delta fronts. In the tightly articulated and pristine Sinalunga balaenopterid (WCh4-1 in S4-CB), the cortical surface of the tightly-connected vertebrae is practically intact, and carpal, metacarpal and phalanges of the flipper are in perfect anatomical connection, as if a sudden depositional event buried a fresh carcass (Fig. 8; similar pristine skeleton are found in deep water turbiditic succession: Stinnesbeck et al., 2014). Another pristine and tightly articulated skeleton, belonging to a killer whale (WCh3-1 in CB), was collected at Cetona in the second half of the 19th century, in a locality associated with sandstones, also possibly of deltaic origin. Large vertebrates embedded in fine-grained, muddy matrix (shelf deposit formed below storm wave base) and those associated with laterally-persistent shell beds (condensed deposits) are slightly disarticulated and fairly complete, showing signs of long permanence in a low energy, well-oxygenated seafloor before the final burial. Bioerosion of bones caused by phototrophic cyanobacteria and algae, heterotrophic fungi and bacteria (Orciano balaenopterid WFi4-1 in S4-FB), and eventually by whalebone-eating siboglinid worm of genus *Osedax* (on a ziphiid humerus, WFi4-14: Higgs et al., 2012), occurred at condensed intervals, in association with glauconite (Danise, 2010). In one instance, a condensed shelly interval is traced for a few kilometers, connecting bioturbated shoreface sandstones yielding slightly disarticulated sirenian skeletons (MOm2-1, MOm2-2) and other MM (Tinelli, 2013), with open shelf deposits yielding slightly disarticulated whale remains (WOm2-1 in S2-OOB).

Regarding a sequence stratigraphic interpretation, pristine skeletons from delta front sediments can be part of the FSST (Fig. 4; ~~or~~ in an alternative interpretation it may belong to~~, of~~ the early TST, when incised valleys are filled with coastal deposits). TST deposits account for ~~12~~6,2% of cases (Fig. 9B). Much more frequently, articulated or slightly disarticulated skeletons are associated with the HST of the corresponding depositional sequence, lying above the MFS (~~69~~56,9% of cases), or within the maximum flooding interval~~directly in coincidence with it~~, above a laterally-persistent shell bed (10,8%). Bone bioerosion is less pronounced in the late HST, when sedimentation rate increases (Castelfiorentino whale WEl3-2 in S3-EB).

4.4 MM abundance and species-richness

Some taxa need revision, but a conservative estimate of the different morphologies suggest that at least 17 marine mammal species lived in the NWMS during the Pliocene (possibly more than 20, an estimate for the whole epoch, i.e., 5,332-2,588 Ma), against ~~only 9~~nine presently living in the same area (plus two occasional visitors). Among the cetaceans, six families were present, against only five presently living in the Ligurian Sea (Tab. 3). The most abundant Pliocene species of Tuscany are the sirenian *Metaxytherium subapenninum* (N = 10), the dolphin *Etruridelphis giulii* (N = 7) and the delphinid *Hemisyntrachelus cortesii* (N = 5: Tab. 4). Overall abundance and species richness are not randomly distributed, but are maximum in Piacenzian strata of synthem S4, dated at 3.2-3.0 Ma (Tab. 2, Figs ~~Fig.~~2, 9C-D~~2~~), particularly in the FB and VEB (Tab. 4). A species list of marine mammals summing up ~~findings~~fossils found around Orciano Pisano and at La Rocca, near Volterra, yields a species richness (S) of ~~11-12~~13. This Piacenzian peak in marine mammal diversity is matched by the fossil record of sharks, also maximum near Orciano Pisano (S = 27), with a second peak in S5, around Castelnuovo Berardenga (SRB, S = 16). Differently from the marine mammals, showing a complete turnover from the Pliocene to the recent (Tab. 3), 34% of Pliocene shark species are still extant in the NWMS (Tabs. 5-6). Marine mammal frequency and diversity gradually decreases in S5-S6.

~~3~~5. Paleoenvironment-fauna relations

The paleoecology of Pliocene MM of Tuscany can be reconstructed by comparison with the ecology of their modern relatives. This approach can be applied at the family or genus level for marine mammals (Tab. 3), at the genus or species level for sharks (Tab. 5). With the only exception of the sirenian *Metaxytherium subapenninum*, feeding on seagrasses (Domining, 2001), and small demersal sharks (e.g., catsharks, frilled sharks), all MM studied here are pelagic forms that had no direct connection to conditions at the seafloor (Tabs. 4 and 6). ~~With the exception of the few benthopelagic marine vertebrates (seals, dugongs), many LMVs of the Pliocene of Tuscany were epipelagic (e.g., mysticetes, larger sharks) or mesopelagic (e.g., sperm whales, ziphiids), with no direct connection with the ecological conditions at the seafloor.~~ The paleoecology of benthic habitats informs however on the situation of the overlying water column in terms of ~~ecological~~ factors that matter to the distribution of pelagic~~epipelagic and mesopelagic~~ organisms~~. These factors include~~, such as water depth, salinity and nutrient levels. In the second place, since ~~all LMV~~all MM remains after death ultimately sink to the seafloor, benthic paleoecology is also a means to understand taphonomic controls on ~~LMV~~MM distribution. Cluster analysis based on the distribution of mollusc species in 72 samples resulted in the identification of four main groups of ~~mollusc~~ samples, roughly corresponding to the four main facies types recogni~~zed~~sed based on lithology and sedimentary structures (F2-F5 in Tab. 1). Clusters are formed by samples from outer shelf and upper slope (three samples), open shelf (34 samples), shoreface (23 samples), and transitional settings, such as brackish-water coastal lagoons and tidal flats (12 samples: see Supplement Material, Fig. S1). ANOSIM confirms that sedimentary facies type can broadly predict what benthic assemblage it will yield (Tab. 7~~3~~; general R = 0,632). The difficulty to discriminate between upper and lower shoreface facies, and between shoreface and open shelf facies is confirmed by overlaps in sample distribution in the NMDS ordination diagram (Fig. 10~~9~~A). Samples AG1, MON1 and MON2 allow to re-interpret the associated sandstones, originally included in upper shoreface facies type, as offshore deposits. The presence of gravels and cobbles intensely bioeroded by bivalves and polychaete (ichnofossils include *Gastrochaenolithes*, *Meandripolydora* and *Caulostrepsis*) and encrusted by balanids, oysters, serpulids, and bryozoans, suggests they are part of condensed beds resulting from transgressive pulses (hiatal concentrations). The relationship between facies type and mollusc association is broadly summari~~zed~~sed in the following paragraphs (see online Supplement Information for a list of characteri~~zing~~sing species).

~~3~~5.1 Coastal lagoon, tidal flat and embayment

Intertidal faunas~~-~~ are always associated with facies type F2 and are characterised by low-diversity associations, sometimes with less than 10 taxa and dominated by one or two species, including species today living in brackish waters of the Mediterranean, at intertidal or very shallow subtidal depths (e.g. *Cerastoderma edule*, *Nassarius reticulatus*, *Scrobicularia plana*: Pérès ~~&~~and Picard, 1964). Facies type F2 is also associated with samples having a species richness higher than the preceding and including species typical of seagrass bottoms and known to withstand moderate changes of salinity. In only one instance a ~~LMV~~large vertebrate was associated with intertidal deposits~~. Interestingly, this was~~ (~~not a sirenian, but~~ a balaenid, lying on top of large wood fragments ~~(~~: Bianucci, 1995; Collareta et al., 2016~~; Fig. 9~~8~~A~~).

~~3~~5.2 Upper shoreface

Facies type F3 is associated with a high-diversity assemblage representing a paleocommunity dominated by suspension feeders adapted to shifting sandy bottoms, with bivalves typical of modern shoreface sandy bottoms (e.g., families Glycymeridae, Tellinidae, Donacidae and Veneridae). Among extinct species of this recurring assemblage, some are large-sized or have very thick shells. Some species of this group indicate the presence of vegetated bottoms. Small pyramidellid gastropods are parasitic on echinoderms, also typical of the upper shoreface.

~~3~~5.3 Lower shoreface

Species richness further increases in collections associated with facies type F4 (lower shoreface). Species typical of this recurring assemblage include both suspension-feeding and detritus-feeding bivalves and gastropods. The following gastropod families are usually represented by several species: Trochidae, Rissoidae, Cerithiidae (from vegetated bottoms), Naticidae, Muricidae, Turridae, Conidae, Terebridae, Bullidae, Cylichnidae (carnivores), Pyramidellidae (echinoderm parasites). Many bivalve species occur in both facies types F2 and F3. At three different sites and at different stratigraphic units ~~LMVs~~

~~were~~large marine vertebrates, including mysticetes, sirenians and sharks, were recovered in association with shell beds dominated by the ~~turritellid and~~ gregarious turritellid gastropod *Haustator vermicularis* (Fig. 6C-D).

~~3~~5.4 Offshore and upper slope

Another important set of species recurred in facies type F5 (mudstone deposited in offshore bottoms at shelf depths). Among characteri~~zing~~sing gastropods are the suspension feeders (*Turritella tricarinata*, *Archimediella spirata* and *Petalochoncus intortus*), deposit feeders (*Aporrhais uttingeriana*) and carnivores or scavengers (*Epitonium frondiculoides*, *Nassarius semistriatus*, *Mitrella nassoides*). Also the bivalves occupy many different ecological niches (e.g., infaunal detritus feeders, epifaunal suspension feeders, either free-living, byssate, or cemented). Outer shelf and uppermost bathyal ~~samples~~sediments from F6 mudstones, studied at only one location, are characteri~~zed~~sed by a separate set of carnivorous gastropods and by a few small bivalve species. Ubiquitous molluscs include species found from intertidal to outer shelf depths (e.g., *Corbula gibba*), and those preferential of open marine waters, from lower shoreface to outer shelf. Most multi-element findings of marine mammals are associated with sandy mudstones from open shelf settings, below storm wave base ~~(F5, 75-80% of occurrences; e.g., Orciano whale: Fig. 8A)~~, also in association with an *Archimediella spirata* shell bed (Fig. 6C-D). No molluscs were recovered in facies type F7, with the exception of bathyal mudstone in the lowermost Pliocene of FB, associated with sparse specimens of the gryphaeid epifaunal bivalve *Neopycnodonte navicularis* ~~.~~(not sampled).

~~3~~5.5 Carbonate platform

A recurring benthic assemblage associated with the highly fossiliferous facies type F8, not included in the quantitative analysis, consists of the large pectinid bivalves *Gigantopecten latissima* and *Hinnites crispus* and by a mixture of photozoans (large benthic foraminifera), hard-substrata dwellers (brachiopods, echinoderms), encrusters (red algae, bryozoa) and bioeroders (clionid sponges). All fossil-rich carbonates are associated with synthem S4 , in the mid~~dle part of the ~~-Piacenzian (Fig. 2, see also Nalin et al., 2016).

~~4~~6. Paleodepths

Multivariate techniques ~~can be~~are usefully applied to stratigraphic and paleobiologic analysis (Scarponi ~~&~~and Kowalewski, 2004). We used the results of the ordination analysis to estimate absolute depths of the final resting place of some ~~LMVs~~large vertebrates listed in Tab. 2. Samples in the NMDS ordination plot following a water depth gradient, with shallower samples to the left (low values of NMDS axis 1) and deeper samples to the right (high values of axis 1). Therefore, NMDS values of axis 1 can be used as a proxy for relative water depth. We calculated absolute palaeodepths by fitting a logarithmic regression curve between absolute paleodepth of 23 modern species (data from MARBEF database), common in our dataset, and the values on NMDS axis 1 (Supplement Material: Tabs. S1-S4). The regression analysis, with $R^2 = 0.813$, indicates that scores along the nMDS main axis are a good predictor of the preferred depth for the 23 modern species (Fig. ~~9~~10B, inset), thus supporting the bathymetric interpretation. This allowed to estimate the absolute depth of the 72 ~~mollusc ~~samples, which ranged from 0.4 m to 365 m, i.e., from intertidal to upper slope depths (~~Fig. 109B). These results are, ~~in accordance with a previous estimate of absolute paleodepths~~, carried out~~ in the upper part of the Pliocene ~~succession ~~of EB,~~ and~~ based on counts of foraminifera: ~~(~~Dominici et al., 2007). ~~According to the present estimates,~~ ~~f~~Facies type F2 is deposited at 0-~~10~~5 m depth~~ (mostly 0-5 m)~~, F3 at 3-30 m, F4 at 10-100 m, and F5 at 40-300 m, F5 at around 350 m depth (only one sample: Fig. ~~9~~10B). The position of fossil cetaceans, ~~dugong~~sirenians, pinnipeds and large sharks (respectively W, M, P and S, N = 13) was plotted near the corresponding shell bed in the NMDS ordination. The resulting pattern shows that all ~~large mammals~~MM considered, associated with open shelf settings and with facies types F4-F5, cluster around ~~a depth of about~~ -100 m, spanning -30-300 m~~ (Fig. 9B)~~.

~~5. Interpretation~~

~~Large marine vertebrates are nearly unrecorded in synthem S1-2 (Zanclean, mostly bathyal mudstone and turbiditic sandstone), notwithstanding these successions are the thickest, but they are recovered in S2 in OOB (shoreface and open shelf deposits). LMVs are abundant in synthems S3-5, peaking in synthem S4 (middle part of the Piacenzian), with intermediate abundances in synthem S6 (upper Piacenzian-lowermost Gelasian). In an ideal deepening-up gradient, multi-element findings of marine mammals are very rare in intertidal and very shallow subtidal paleoenvironments (facies type F2: one instance in Bianucci, 1995, out of 39 cases explored), moderately represented in delta or shoreface sandstones (facies type F3), most abundant in sandy mudstone of open shelf settings (facies type F5, 77% of occurrences: Fig. 8A; e.g., Orciano whale: Figs. 4, 6), nearly absent in outer shelf and bathyal sediments (Saline di Volterra seal, PEr1-1 in S1-VB; Lucciolabella dolphin, WSi2-1 in S3-SB). Regarding their taphonomy, the most pristine and complete skeletons are associated with gravelly well-sorted sands from event sedimentation, suggesting a negative relationship between taphonomic loss and sedimentary processes at delta fronts. In the tightly articulated and pristine Sinalunga balaenopterid (WCh4-1 in S4-CB), the cortical surface of the tightly-connected vertebrae is practically intact, and carpal, metacarpal and phalanges of the flipper are in perfect anatomical connection, as if a sudden depositional event buried a fresh carcass (Fig. 7; similar pristine skeleton are found in deep water~~

~~turbiditic succession: Stinnesbeck et al. 2014). Another pristine and tightly articulated skeleton, belonging to a killer whale (WCh3-1 in S4-CB), was collected at Cetona in the second half of the 19th century, in a locality associated with sandstones, also possibly of deltaic origin. LMVs embedded in a fine-grained, muddy matrix (shelf deposit formed below storm wave base) and those associated with laterally-persistent shell beds (condensed deposits) are slightly disarticulated and fairly complete, showing signs of long permanence in a low energy, well-oxygenated seafloor before the final burial. Bioerosion of bones caused by phototrophic cyanobacteria and algae, heterotrophic fungi and bacteria (Orciano balaenopterid WFi4-1 in S4-FB), and eventually by whalebone-eating siboglinid worm of genus *Osedax* (on a ziphiid humerus: Higgs et al. 2012), occurred at condensed intervals, in association with glauconite (Danise 2010). In one instance, a condensed shelly interval is traced for a few kilometers, connecting bioturbated shoreface sandstones yielding slightly disarticulated dugong skeletons (MOm2-1, MOm2-2) and other LMVs (Tinelli, 2013), with open shelf deposits yielding slightly disarticulated whale remains (WOm2-1 in S2-OOB).~~

~~Regarding a sequence stratigraphic interpretation, pristine skeletons from delta front sediments can be part of the FSST (Fig. 4; or in alternative interpretation, of the early TST, when incised valleys are filled with coastal deposits). TST deposits account for 12% of cases. Much more frequently, slightly disarticulated skeletons are associated with the HST of the corresponding depositional sequence, lying above the MFS (69% of cases), or directly in coincidence with it, above a laterally-persistent shell bed (10%). Bone bioerosion is less pronounced in the late HST, when sedimentation rate increases (Castelfiorentino whale WEl3-2 in S3-EB).~~

~~6~~7. ~~Discussion~~Factors of the Pliocene NWMS marine megafauna fossil record

The detailed sequence-stratigraphic framework and the abundant shell beds, offering an independent check on sedimentary facies distribution by benthic paleoecology, allows also to explore factors behind MM geographic and stratigraphic distribution, and to sort out evolutionary, ecological, and taphonomic drivers of this particular fossil record. NWMS Pliocene distribution can be compared with similar studies in different settings and at different times, to draw conclusions on the general quality of MM fossil record.

7.1 Evolutionary control

Available data allow a meaningful comparison of NWMS MM diversity across the Pliocene, particularly detailed for marine mammals (Fig. 9D). Although ~~our~~the study suggests a facies control~~ on MM distribution~~, with ~~large vertebrate~~MM remains being generally ~~connected~~associated with late TST-HST muddy sandstones and mudstones from lower shoreface and offshore shelf paleosettings, the temporal pattern of biodiversity recorded on a regional basis ~~should in part~~likely ~~represent~~reflects also a paleobiologic phanomenon, since lower shoreface and offshore shelf sediments are represented in all synthems. Marine mammals are unrecorded in the thickest part of synthem S1-2 (Zanclean, mostly bathyal mudstone and turbiditic sandstone), but they are present in S2, in OOB (Zanclean shoreface and open shelf deposits) and SRB (Zanclean upper slope deposits). MM ~~is uncommon~~gradually rises in S3, at the upper Zanclean-lower Piacenzian, whereas it suddenly peaks in synthem S4, where species richness of both marine mammals and sharks is highest. S5 reflects a lower diversity of marine mammals, but still a high diversity of sharks, while values of both groups drop to the lowest abundance and species richness in S6, during the upper Piacenzian-lowermost Gelasian (Fig. 9D).

The S4 diversity peak coincides with the middle part (3.264–3.025 Ma) of the Piacenzian, a time interval in which the earth experienced global average temperature 1.84 °C-3.60 °C warmer than the pre-industrial period (Dowsett et al., 2013). Climatic impact is testified by the widespread occurrence of carbonate deposits in S4 (Fig. 2), with sedimentary facies indicative of warm-temperate to subtropical conditions, with summer sea-surface temperature considerably warmer than 20°C and winter temperatures colder than 20°C (Nalin et al., 2016). This suggests a causative link between global climate and biodiversity, S4 diversity peak recording a global phenomenon, possibly an increase of speciation rate connected with global warming. Similarly, we propose that the lower diversities recorded at S5-S6 are the regional expression of an increase in extinction rate related to climatic cooling and global sea-level drop, ultimately leading to the global MM extinction event recorded on a coarser scale at the Pliocene-Pleistocene boundary (Pimiento et al., 2017): the finer stratigraphic resolution adopted here suggests a stepwise extinction event. NWMS data also point to a selective effect, extinction being recorded by marine mammals, with a 100% regional turnover between Pliocene and Recent (Tab. 3), but not as much by the shark fauna, with 34% of the species still living in the Mediterranean, while still others have shrank their distribution to subtropical latitudes. Also the Piacenzian teleost fish fauna (Cigala Fulgosi et al., 2009) and ~~the~~ benthic mollusc~~k~~s (Raffi et al., 1985) show a high percentage of holdovers, suggesting that marine mammals have been particularly prone to climatic change (see also Steeman et al., 2009).

Estimates of body size in Pliocene mysticetes of Tuscany, with several specimens reaching 10 m (Danise and Dominici, 2014: seven specimens in Tab. 1), are comparable to global values derived from the literature for this time interval (Lambert et al., 2010), confirming that NWMS baleen whales were larger than their Miocene analogues, and smaller than modern forms. As with regard to odontocetes, the most common Pliocene delphinid, *Etruridelphis*, was larger than the modern analogue *Stenella* (Bianucci et al., 2009b). The same is true for *Hemisyntrachelus cortesii*, larger than modern *Tursiops* (Bianucci, 1997a). On the other hand, the largest extant delphinid *Orcinus orca*, reaching 9 m, is about twice as long as

Orcinus citonensis (Heyning and Dahlheim, 1988). The high percent of holdover points to a more conservative figure for larger sharks (Tab. 5), but the presence in the Pliocene of the gigantic *Carcharocles megalodon* and some large thermophilic species today restricted to lower latitudes suggests that impoverishment of the fauna is coupled with an average decrease in size (Marsili, 2008). Comparing sizes suggests an overall restructuring of NWMS MM during the last three million years (see also Bisconti, 2009).

~~The geographic and stratigraphic distribution of large marine vertebrates in the fossil record, as that of any other key elements of marine ecosystems, depends on ecological (i.e., the production of organic parts) and taphonomic factors (their preservation). The detailed sequence-stratigraphic framework available for the very thick Pliocene succession of Tuscany, and the abundant shell beds that offer an independent check on sedimentary facies distribution by benthic paleoecology, allow to explore ecological and taphonomic drivers on the distribution of Northwestern Mediterranean LMVs. In its turn, this can be compared with similar studies in different settings and at different times, to draw conclusions on the general quality of LMV fossil record.~~

~~6~~7.2~~1~~ Ecological control

~~Marine~~

The composition of the Pliocene NWMS MM is affected in the first place by the availability of food. At the lowest trophic level, inferring from the ecology of the modern MM (Tabs. 3, 5), we found herbivore sirenians feeding on seagrasses (trophic level, TL = 2,0), all others being carnivores, thus having TL > 3,0 (Fig. ~~12~~11). The lowermost levels among the carnivores were occupied by baleen whales and whale sharks (TL = 3,2-3,4), filter-feeding on pelagic crustaceans and fishes (krill). Roughsharks, catsharks, and houndsharks, with many species living in the modern Mediterranean, have a relatively species-poor Pliocene record, probably due to a preservation bias related to their small size. At TL = 3,7-4,0 were one species of catshark and a monk seal, both feeding near the seafloor on crustaceans, teleost fishes and cephalopods. At TL = 4,1 were sandbar, tiger and blue sharks, feeding on teleost fishes, cephalopods and on marine mammals. At the same level, in slope environments, kitefin sharks mainly fed on other sharks. The majority of MM species were found at TL = 4,2, with smaller odontocetes (three species) and 11 species of sharks, including several requiem sharks, a houndshark and a hammerhead. Larger dephinids, sperm whales, beaked whales, together with mackerel, sand and sand tiger sharks, occupied high trophic levels (TL = 4,3), followed at the top of the global NWMS food web by white shark, megalodon shark, one species of sevengill shark (genus *Notorynchus*), and killer whales, all feeding on marine mammals and smaller sharks (TL = 4,4-4,7). With no exception, all highest levels encountered in modern NWMS offshore pelagic and nearshore communites were occupied during the Pliocene by an analogous MM, often by the same species (large sharks), or by congeneric or con-familial species (marine mammals: Tab. 3, 5). The Pliocene pelagic ecosystem, typified by the mid-Piacenzian S4 association, must have been however trophically more diversified (Fig. 11), including aquatic megaherbivores, several balaenid filter feeders, larger and more diverse dolphins, and sharks species today extinct (e.g., *Carcharocles megalodon*) or restricted to tropical seas (e.g., *Galeocerdo cuvier*). With the exception of TL = 2, all Pliocene NWMS MM were either apex predators of their community, or mesopredators, occupying trophic positions below apex predators. The definitions of apex predators (or top predators) and mesopredators are relative and to an extent context-dependent (species that in a contact are apex predators, in another are mesopredators, e.g., Estes et al., 1998). Since predation is a trophic interaction in which one animal (predator) consumes another (prey) as a source of energy (food), irrespective of the means by which this is accomplished (Lourenço et al., 2013), filter-feeding baleen whales can be considered apex-predators of their community (e.g., Lewiston et al., 2004; Notarbartolo di Sciara et al., 2016). Among sharks, 68% of living Mediterranean elasmobranches are ranked as top predators, with a trophic level of 4 or more (Goffredo and Dubinsky, 2014, including superorder Batoidea, against 22% of teleost fishes), an estimate that can be extended to Pliocene NWMS MM. Relationships between apex predators and mesopredators are complex and hard to define in ecology, involving predation on other predators (intraguild predation, combining competition and predation: Polis et al., 1989), where consumption and competition need to be proved (Lourenço et al., 2013). In the Mediterranean Pliocene, paleontological evidences of carnivores serving as food to MM include killing of prey (Bianucci et al., 2010) and scavenging (Cigala Fulgosi, 1990; Bianucci et al., 2002; Dominici et al., 2009). The occurrence of intraguild predation must have been far more extended than what taphonomy can prove, however, given a Pliocene diversity of NWMS very large raptorial feeders higher than the modern, including the killer whale *Orcinus citonensis*, the large delphinid *Hemisyntrachelus cortesii* (phylogenetically related to the modern killer whale: Murakami et al., 2014), the white shark *Carcharodon carcharias*, the largest shark of all times *Carcharocles magalodon* (Marsili, 2008), and a diverse association of smaller carnivores, including monk seal, delphinids and sharks with 4,0 < TL < 4,2 (Tab. 3, 5), candidate prey for larger raptorial feeders. This interaction likely exerted in its turn a control on community structure at lower trophic levels through processes like “mesopredator release” and trophic cascades (Roemer et al., 2009), eventually linking pelagic and nearshore communities, including benthic animals and plants, like in many modern ecosystems (Estes et al., 2011, 2016), down to slope depths (e.g., Parrish, 2009). Large raptorial feeders could exert a control on the diversity of the filter-feeding MM, like it has been suggested on a global scale since the Miocene (Lambert et al., 2010), and for the Pliocene by Bisconti (2003), when baleen whales were more diversified, both in terms of species richness, size range, and feeding strategies, including both skim- and lunge-filter feeding (respectively balaenid and balaenopterid whales: Berta et al., 2016; Hocking et al., 2017), minimising competition for food and diversifying spatial niches (see also Marx et al., 2017, for the upper Miocene). A further important top-down control on community structure is suggested by modern studies on the role of baleen and sperm whales as nutrient vectors, both in horizontal (during seasonal migration) and vertical direction (during daily feeding migration: Roman and McCarthy, 2010), a process particularly important in oligotrophic seas (Alleger et al., 2017), like large sectors of the Mediterranean. Finally (literally, after death), MM becomes a detrital sources of energy and habitat for deep sea whale-fall communities (Roman et al., 2014; Smith et al., 2015), with paleontological evidence available for the NWMS (Dominici et al., 2009; Higgs et al., 2012; Baldanza et al., 2013).

Much evidence suggests that a bottom-up control on the structure of NWMS MM community was exerted by wind-driven upwelling currents, through enhanced oceanic productivity and concentration of preys. Over geologic time, these factors may have exerted a selection favoring large size, triggering the Plio-Pleistocene emergence of whale gigantism in several lineages (Slater et al., 2017). The largest among marine top predators can travel long distances and cross oceans, but tend to congregate in shallow waters with abundant prey. Baleen whales, abundant in boreal eutrophic waters (Woodley ~~&~~and Gaskin, 1996), with population size under the control of food availability (Croll et al., ~~,~~2005), always require high prey density for efficient bulk filter feeding (Goldbogen et al.,~~;~~ 2011). Six different species of mysticetes currently foraging in the Southern ocean, among which the largest animals that have ever lived in world oceans, exploit the high biomass of Antarctic krill, their main food resource. ~~The g~~Great white sharks ~~is~~are abundant in the offshore of California (Jorgensen et al.,~~;~~ 2010), Australia-New Zealand, South Africa, and ~~formerly~~ in the Mediterranean (~~Compagno, 2001;~~ Bonfil et al.,~~;~~ 2005), clustering in proximity of seal colonies, ~~. Marine mammals are in fact an important food resource in some areas, in addition to fish and cephalopods~~including monk seals. The distribution in the modern Mediterranean is no exception to general rule, only in a smaller scale, with large sharks and marine mammals congregating in productive areas, such as the Strait of Sicily and the Balearic Archipelago

(Tabs. 3, 5), with the second largest animal on earth, the fin whale, showing a movement pattern that parallels seasonal variability in available feeding habitat (Notarbartolo di Sciara, 2016), contributing to the horizontal transfer of nutrients. ~~Large sharks can also prey or scavenge on cetaceans (Compagno, 2002), whereas foraging may also take place in the offshore, diving at 100-200 m on average (Jorgensen et al., 2010). Among the pinnipeds, grey seals live from estuaries to open shelves (Boehme et al. 2012) and elephant seals are abundant in upwelling zones (Biuw et al. 2007). Like whales, also pinnipeds are diverse and abundant in the nutrient-rich Southern Ocean, where they feed on krill, cephalopods, and fish. The diverse association of Pliocene pinnipeds, sharks and whales in Tuscany points therefore to the presence of nutrient-rich waters in the Northwestern sector of the Mediterranean (NWMed). A further and independent paleoecological evidence of a nutrient-rich regime is the association of many LMVs with “*Turritella* beds”, turritelline gastropods showing gregarious habit and high abundance in areas of high nutrient content (Allmon, 1988). The modern Tuscan shoreline faces~~Tuscany faces the Ligurian Sea, ~~the northernmost reach of the Mediterranean,~~ where a deep-water upwelling current coming from Southeast convects nutrients to the water surface, leading to high levels of primary productivity in its western sectors, extending westward to the Provençal and Balearic Seas, with spring algal blooms. These waters host different trophic regimes ~~with respect to other parts of the Mediterranean,~~in an otherwise oligotrophic Mediterranean S~~s~~ea (Lazzari et al., 2012;~~,~~ Melanotte-Rizzoli et al., 2014; Stambler, 2014). Supporting a conspicuous biomass of zooplankton (Cuzin-Roudy 2011), the ~~modern NWMed~~Ligurian Sea sustains large populations of fin whales (*Balaenoptera physalis*) and striped dolphins (*Stenella coeruleoalba*~~), together with other large cetaceans (~~; Notarbartolo di Sciara et al., 2008). Mediterranean-resident fin whales have adapted to exploit localised mesoscale hotspots of productivity that are highly variable in space and time (Notarbartolo di Sciara et al., 2016), feeding behaviors possibly mediated by the depth of prey and species-specific behaviours, allowing to minimise competition with other large filter feeders (see Friedlaender et al., 2014). ~~Among the odontoceti,~~The sperm whale *Physeter macrocephalus* uses habitat across a range of depths and a specialised diet (Rendell and Frantzis, 2016), gather~~s~~ing along ~~NWMed~~NWMS steeper slopes, where water currents allows for higher trophic level biomass (Pirotta et al.,~~,~~ 2011)~~.~~. Beaked whales are particularly abundant in the Ligurian Sea and central Tyrrhenian Sea, preferring submarine canyons at slope depths (Podestà et al., 2016). The largest among common Mediterranean delphinids, *Grampus griseus*, is frequent in the Ligurian and Thyrrenian seas where it forages on cephalopods at depths 300-1500, where upwelling currents are most effective (Azzellino et al., 2016).

The ~~NWMed~~NWMS existed as a Liguro-Provençal back-arc oceanic basin since the upper Miocene, when Sardinia rotated to its present position (Gattacceca et al.,~~,~~ 2007), and in coincidence with the formation of the hinterland basins here under study (Muttoni et al.,~~,~~ 2001), justifying the assumption that the modern ~~NWMed~~NWMS trophic regime is a feature that dates back at least to the upper Miocene. ~~Past eutrophic conditions are testified in Tuscany by d~~Consistently, diatomites deposited in Tuscany during the Messinian, before the salinity crisis (Bossio et al.,~~,~~ 1997;~~;~~ Roveri et al.,~~,~~ 2014), indicate that high productivity was a primitive feature of the Ligurian Sea~~and by t~~. Paleontological evidences include the ~~very~~ high diversity and abundance of Pliocene ~~LMVs~~MM in FB, the closest to modern upwelling areas (Fig. 3), and the association of several MM with “*Turritella* beds”, turritelline gastropods showing gregarious habit and high abundance in areas of high primary productivity (Allmon, 1988). Both a comparison with the modern and paleoecologic data strongly suggest that~~, particularly at times of transgression, maximum flooding and highstand,~~ a wedge of ~~NWMed~~NWMS nutrient-rich waters intersecting the Tuscan shelf ~~would have positively affected the general biomass~~exerted a strong bottom-up control ~~.~~ on community structure through mixing and upwelling of nutrients, stimulation of phytoplankton blooms, followed by zooplankton increase, while nekton and vertebrates tracked plankton concentrations, as is typical of modern upwelling systems throughout the world (Polis et al., 1997). High surface primary productivity in the study area during the Pliocene would have caused a concentration of ~~food~~detritus-falls, supporting a diverse community of deep-sea scavengers.

~~6~~7.3~~2~~ Taphonomic control

Taphonomic data on articulation and completeness of MM specimens are available for large mammals, the shark record being formed mainly by isolated teeth collected through superficial picking during the years (Cigala Fulgosi et al., 2009), with only a few contextualised studies (e.g., Bianucci et al., 2002; Dominici et al., 2009). Our record includes several marine mammals with a high degree of articulation (14%) and completeness (27%), or with at least cranial and post-cranial elements of the same individual (38%). All articulated specimens and the most complete skeletons are associated with shelf mudstones, usually forming the HST of the relative depositional sequence (Tab. 2), with two exceptions, one associated with delta-front, coarse-grained beds (WCh6-1, Fig. 6), another from outer shelf or upper slope sediments (DSi2-1). These data point to a strong environmental control on the quality of the MM fossil record, at least concerning articulation and completeness of skeletons, very shallow and very deep (bathyal) depths being generally unfavourable to the preservation of MM bones (Fig. 9A). To explain these results, hypotheses are based on the available data on carcasses of MM in modern marine environments.

The biostratinomy of lung-breathing marine mammals depends on water depth (Allison et al. 1991; Smith et al., 2005). The vast majority of mammals are negatively buoyant and sink after death, but in shallow waters the low hydrostatic pressure allows putrefaction gases to develop and carcasses to resurface. Skeletons are scavenged (Dicken, 2008) and disintegrate while floating, leading to the preferential deposition of isolated bones. At deeper settings, where high hydrostatic pressure allows the carcass to lay relatively undisturbed on the seafloor, the skeleton becomes only slightly disarticulated after soft tissue removal (Reisdorf et al., 2012). The subsequent fate of deep-water, disarticulated skeletons depends on the nature of the scavenging fauna and other elements of the whale-fall community, and on the time of exposure on the seafloor (Boessenecker et al. 2014). At depths deeper than the slope breaks, where sedimentation rate is very low, carcasses are exposed for a long time and the skeleton is rapidly disintegrated. Time-series analyses carried out at modern whale-fall communities at slope depths (range 382-2893 m: Lundsen et al., 2010) suggests that carcasses up to 17 m are rapidly degraded, with the deepest whale carcasses disappearing after only seven years of exposure on the sea floor. Larger skeletons may persist on deeper settings for decades, but if not buried, they also ultimately undergo complete destruction. Although environmental forcing triggered by higher temperatures, active currents and sediment transport, clearly plays a role, a speciali~~zed~~sed whale-fall fauna rapidly consumes both soft and minerali~~zed~~sed tissues. This fauna is characteri~~zed~~sed by low diversity and high abundance of microorganisms, most likely as a result of both specialis~~z~~ation to nutrient enrichment and high growth rates. Whale-fall habitats likely undergo a temporal microbial succession from primarily heterotrophic to more heterotrophic/chemosynthetic metabolisms until the whale biomass is completely exploited (Smith et al., 2015). Of all the speciali~~zed~~sed taxa, bone-eating polychaetes of genus *Osedax*, with their soft root-like tissues that erode the bones to access nutrients (Tresguerres et al., 2013;~~,~~ Minamoto et al., 2017), are the primary cause of bone disintegration, particularly of denser bones (Higgs et al., 2011). Found also at shelf depths, but invariably in low abundance (Huusgaard et al., 2012;~~,~~ Higgs et al., 2014b), bone-eating worms occur in high numbers in the deep sea (Smith et al., 2015) where they act as biodiversity regulators (Alfaro-Lucas et al., 2017). The general paucity of novel taxa on shallow-water whale falls suggests that species-rich, speciali~~zed~~sed whale-fall communities develop only in the food-poor deep sea. Accordingly, among new animal species described in the recent literature from whale falls, only about 10% have been found on whale remains at depths of less than 260 m (12 out of 129 new species: Smith et al., 2015). Of all ~~large marine vertebrates~~MM investigated so far, only whales are known to host a whale-fall community, but also carcasses of large elasmobranchs undergo rapid destruction ~~on the deep sea~~at bathyal depths, teeth being all that eventually remains (Higgs et al., 2014a; teeth are also lost by sharks during feeding: Pokines and Symes, 2013). As a consequence, over geological time no large marine vertebrate is expected to be recovered at depths greater than the shelf break. On the opposite side, the lack of a biota speciali~~zed~~sed in exploiting large organic falls, coupled with higher rates of deposition in proximity of sediment sources, make it more probable that ~~articulated, or only partially disarticulated~~the most articulated and complete whale skeletons become part of the fossil record of shelf settings below storm wave base.

~~7~~8. Comparison with other studies

The study of sedimentary facies uncovers some environmental factors that directly control the taphonomy of large marine vertebrates. Such abiotic drivers include water pressure, wave energy and sedimentation rate — three factors summari~~zed~~sed by water depth, and upwelling, bringing to the surface deep sea nutrients and concentrating preys. The taphonomic pathway of large marine carcasses is also driven by biotic factors that change in geological time in response to coevolution between bacteria, scavengers and their substrates. We now explore the multifaceted nature of ~~LMV~~MM taphonomy by reviewing Mesozoic and Cenozoic studies ~~comparable to ours~~where sufficient data for stratigraphic paleobiology are available.

~~7.~~8.1 Abiotic factors

According to one of the few previous studies on the sequence stratigraphic distribution of ~~large marine vertebrates~~MM, Jurassic ichthyosaurs, plesiosaurs, and pliosaurs of the Sundance Seaway, in North America, display facies control and are found primarily in offshore mudstone and at condensed intervals at the maximum flooding surface, rather than shoreface and estuarine sandstone (McMullen et al.,~~,~~ 2014~~, in a study that included isolated LMV remains~~). Taphonomic data on Upper Cretaceous marine reptiles and large fishes suggest that partially articulated and disarticulated skeletons are associated with little biological activity and relatively rapid burial by muddy sediments, deposited in the North American seaway during an interval of maximum flooding (Schemisser McKean ~~&~~and Gillette,~~,~~ 2015). Upper Cretaceous mosasaur remains are particularly concentrated in fine-grained shelf deposits in Europe (Jagt ~~&~~and Jagt-Yazykova, 2016). Complete, partially articulated whale skeletons of archaeocetes, together with bones and teeth of ~~dugong~~sirenians and sharks, are abundant in offshore marine flooding surfaces (MFS) in the Priabonian late TST of Egypt. In a further parallelism with the Pliocene of Tuscany, Late Eocene well-articulated whales are associated with rapidly accumulating shoreface sediments of the FSST, comprising “*Turritella* shell beds” (Peters et al.,~~,~~ 2009). During the Oligocene, eomysticete whale bones were deposited at shelf depth below storm wave base. The occurrence of sparse traces attributed to *Osedax* and the association with a glauconitic limestone testify to the exposure of bones on the seafloor without undergoing complete destruction (Boessenecker ~~&~~and Fordyce,~~,~~ 2014), in a manner similar to ~~LMVs~~MM at Orciano (see Danise et al.,~~,~~ 2010;~~;~~ Higgs et al.,~~,~~ 2012). Burdigalian/Langhian MM recovered in the Antwerpen Sands, in Belgium (including isolated remains of a baleen whale, several odontocetes and a pinniped) are fragmented, worn and associated with clayey sandstone rich in glauconite, suggesting long exposure on the sea-floor (Louwye et al., 2010). Bones are concentrated at the base of a coarsening-upward succession, on top of shallow marine, coarse-grained sandstone, suggesting this is a surface of maximum flooding. An association of ~~LMVs~~MM taxonomically comparable to ~~those~~that here under study is encountered in the Mio-Pliocene of the Purisima Formation, in Central California. Taphofacies differ in some aspects. The Pliocene of California yields laterally persistent bonebeds with polished and phosphatised bones, and abundant phosphate nodules that are absent in Tuscany, indicating times of higher sediment starvation during transgressive pulses, in an area of much stronger nutrient content (the California Current system is a northern-hemisphere analogue of the Peruvian upwelling system, associated with the economically most important fish stocks in the world: Mann ~~&~~and Lazier,~~,~~ 2006). Shoreface deposits indicate stronger wave energy, and the preferential absence of molluscs in bonebeds indicates chemical destruction of carbonate shells (Boessenecker et al.,~~,~~ 2014, in a quantitative MM taphonomic study~~ that includes isolated LMV fragments~~). Episodic sedimentation, however, causes the preferential preservation of articulated remains in the Californian offshore as in the Pliocene of ~~NWMed~~NWMS. The late Miocene Pisco Formation in Perù offers another, more extreme example of ~~LMV~~MM taphonomy in a eutrophic setting. Here almost two hundred cetaceans, pinnipeds, and sharks were described in an exceptional state of preservation (Bianucci et al., 2015), within a monotonous succession of finely laminated white diatomites (Di Celma et al., 2015), suggesting very high primary productivity in an area of intense upwelling and volcanic activity. Algal blooms sustained high biomass of apex predators (see Marx ~~&~~and Uhen, 2010), triggering at the same time anoxic conditions at the seafloor where ~~LMV~~MM carcasses remained intact (Brand et al., 2004;~~;~~ see also Gioncada et al., 2016; Marx et al., 2017, also in offshore paleosettings). Finally, the stratigraphic distribution of Pliocene cetaceans in western Emilia (Italy) shows an uneven distribution of findings (N = 24, dolphins and baleen whales) and a strong positive correlation with offshore mudstones (no findings in shoreface sandstones, rare occurrences in epibathyal mudstones: Freschi and Cau, 2016), paralleling the distribution of Tuscan Pliocene MM.

~~7~~8.2 Biotic factors

Many reviews of Triassic (Camp, 1980;~~,~~ Hogler, 1992; Motani et al., 2008; Hu et al., 2011; Liu et al., 2014) and Early Jurassic marine reptiles (Benton ~~&~~and Taylor, 1984) report mostly good preservation and a high degree of completeness and articulation of skeletal material. This record might be partially controlled by prevailing anoxic or dysoxic conditions in the bottom waters of many Mesozoic fossiliferous deposits (e.g., Middle Triassic Besano and Guangling Formations, Lower Jurassic Blue Lias and Posidonia Shale Formations), which precluded organism activity within the sediment, and prevented predation or scavenging of the carcasses on the sea bottom (Beardmore ~~&~~and Furrer, 2016). Evidence of advanced levels of disarticulation or bone degradation (Martill, 1985; sauropterygians, crocodilians, ichthyosaurs and fishes from the Middle Jurassic Oxford Clay Formation), is mostly attributed to physical factors (e.g., weathering on the sea floor). Up to the early-Late Cretaceous, biological activity is testified by circumstantial evidence of scavenging (*Hybodus* teeth associated with marine reptile skeletons, Martill et al., 1994), and by the more common occurrence of microbial mats, grazers and encrusters (Martill, 1987;~~,~~ Meyer, 2011;~~,~~ Danise et al., 2014;~~,~~ Reolid et al., 2015), but lack traces of bone-eating worms and sulphophilic fauna typical of modern whale falls. The siboglinid *Osedax* is an evolutionary novelty in possessing a root system that hosts heterotrophic mutualists and secretes bone-dissolving acids (Tresguerres et al., 2013;~~,~~ Miyamoto et al., 2017), and an ecosystem engineer (Alfaro-Lucas et al., 2017). Genus *Osedax* is today associated with whale falls worldwide (Taboada et al., 2015), but its impact on ~~LMV~~MM has changed in time. The oldest trace fossils attributable to a bone-eating fauna is found on early-Late Cretaceous plesiosaur and sea turtle bones (about 100 Ma: Danise ~~&~~and Higgs, 2015). Time estimates suggest that *Osedax* diverged from other siboglinids in the Middle Cretaceous (around 108 Ma: Taboada et al., 2015). However, if the bone-eating worm lives also on the bones of birds and terrestrial mammals (Rouse et al., 2011), its global nature and high species diversity in modern oceans suggest that whale falls, as complex and species-rich habitats, have been the most important biodiversity generators (Higgs et al., 2014b; Smith et al., 2015). And although the first appearance of *Osedax* is concomitant with the occurrence of large marine reptiles and teleost fishes in the oceans, long before whale evolution, and although their distribution is not limited to large carcasses (Pyenson and Haas, 2007), the radiation of ocean-going mysticetes at the Oligocene onset of the Antarctic Circumpolar Current (Fordyce, 2003) clearly increased available substrata worldwide. The steady increase of cetacean size during the Neogene, with a dramatic pulse in the last five million years, when Neoceti surpassed 10 m length and reached 30 m in the Pleistocene (Lambert et al., 2010; Slater et al., 2017), would have thus triggered a second and more massive radiation of bone-eating worms (Kiel and Goedert, 2006). Consistently with this hypothesis, the preferential distribution of modern *Osedax* in high latitude settings worldwide (Taboada et al., 2015) suggests that biodiversity hotspots coincide with the feeding grounds of larger cetaceans. Other bone-eaters of modern deep water whale-fall ecosystem belong to the group of abyssochrysoid snails, with fossils found on Late Cretaceous plesiosaur ~~bones~~ (Kaim et al. 2008) and sea turtle bones (within a chemosynthesis-based association: Jenkins et al., 2017). Modern abyssochrysoid whalebone-eaters of genus *Rubyspira*, hosting a specific and exclusive microbiome (Aronson et al., 2017), split during the upper Eocene/lower Oligocene (Johnson et al., 2010). ~~Like for *Osedax*, s~~Species of *Rubyspira* ~~likely~~ benefited too from the radiation of ocean-going whales. Although scanty, available evidence on the geological history of bone-eaters thus makes the ephemeral nature of large carcasses in modern deep seas — and their absence in bathyal deposits of the Pliocene of ~~NWMed~~NWMS — a larger-than-life model for the Mesozoic and the early Paleogene.

~~C~~9. Conclusions

1) Sedimentary facies in the Pliocene of Tuscany are vertically stacked to form small-scale depositional sequences particularly in the upper half, Piacenzian part of the succession, with laterally-continuous shell beds marking transgressive surfaces and ~~the surface~~intervals of maximum flooding. Small-scale sedimentary sequences are stacked to form six major, unconformity-bounded stratigraphic units (synthems) of regional extension, forming a high-resolution framework to study the chronostratigraphic distribution of marine megafauna (MM).

~~2) Sedimentary facies~~Benthic biotopes, identified through a quantitative study of a large ~~mollusk~~mollusc dataset, can be arranged to form an ideal onshore-offshore, bathymetric gradient, connecting terrestrial environments with deep sea epibathyal bottoms, consistently with the distribution of sedimentary facies. ~~Bones~~MM remains ~~of large marine vertebrates~~ and shell beds are present in all marine paleoenvironments, but their distribution is uneven.

2) The fossil record of large vertebrates, including marine mammals (abundance data) and ~~larger~~ sharks (presence-absence data), is particularly rich in sediments deposited between storm wave base and ~~the~~ shelf break, moderately rich in shoreface sediments, very poor in epibathyal sediments. Paleobathymetric estimates suggest that a peak of abundance of better preserved skeletons occurs around 100 m depth, within the 30-300 m range.

3) Species-richenns of MM and abundance of marine mammal remains steadily increase during the Zanclean, reaching a peak in synthem 4, possibly as a response to the mid-

Piacenzian warm period, and gradually decrease until reaching a minimum in proximity of the Plio-Pleistocene boaundary.

4) Comparison with ecological data on a global scale, paleogeographic and topographic considerations on the North-Western Mediterranean Sea (NWMS)~~Mediterranean paleogeography~~, and the ~~frequent~~occasional association of Pliocene ~~large marine vertebrates~~MM with *Turritella* beds, suggest that upwelling and high-nutrient conditions in the Northwestern Mediterranean offshore sustained during the Pliocene a rich community of apex predators and mesopredators. Higher taxonomic MM diversity in the NWMS during the Pliocene, suggests higher niche-partitioning~~.~~ with respect to the modern NWMS and a top-down control on community structure.

5) A comparison with studies on the biota exploiting tissues of large food particles sunken on the seafloor, both modern and ancient, suggests that the poor epibathyal record of Pliocene larger vertebrates of Tuscany may be caused by the destructive action of bone-eating invertebrates. This biotic driver of the marine vertebrate fossil record was less efficient before the radiation of ocean-going whales in the late Eocene-lower Oligocene. On the other hand, bone-eaters played a major taphonomic role on a global scale after the Pliocene-Pleistocene increase in whale size.

6) Due to resurfacing of carcasses in shallow waters, the ~~taphonomy of large marine vertebrates~~MM fossil record through the Mesozoic-Cenozoic ~~is~~reviewed through stratigraphic paleobiology shows a strong facies control, being more continuous ~~comparable through the Mesozoic-Cenozoic~~ in rocks ~~formed~~deposited below storm wave base and above the shelf-slope break during sea-level transgressions and highstands.

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Figure and table captions:

Fig. 1 - Location of sedimentary logs within the largest Pliocene basins of Tuscany. Fine Basin (FB): Pagliana (1), Pieve Vecchia (2) and Orciano Pisano (3). Volterra-Era Basin (VEB): Parlascio (4), Lajatico (5), Fabbrica (6) and Volterra (7). Era Basin (EB): San Lorenzo (8), La Serra (9), Poggio al lupo (10), San Maiano (11), Canneto (12), Casenuove (13), Castelfiorentino (14), Fiano (15) and San Gimignano (16). Orcia-Ombrone Basin: Arcille (17) and Poggio alle Mura (18). Siena-Radicofani Basin (SRB): Siena (19), Monteaperto (20), Castelnuovo Berardenga (21~~0~~), ~~and~~ Radicofani (~~21~~22) and Fastelli (23). Chiana Basin (CB): Sinalunga (24~~2~~), Cetona (25~~3~~) and Allerona (26~~4~~).

Fig. 2 - Pliocene stratigraphy of Tuscany, see Fig. 1 for the location of numbered sections. All logs measured and described by the authors, except Volterra (log 7: Bianucci et al. 1998), Arcille (log 17: Tinelli et al., 2012; Tinelli, 2013), Siena (log 19: Bianucci et al., 2001), Monteaperto (log 20: Martini et al., 2011), Castelnuovo Berardenga (log 21: Martini et al.,

2016) and Radicofani (log 22: Ghinassi and Lazzarotto, 2005)~~(chronostratigraphy based on biostratigraphic data from several sources, see main text). See Fig. 1 for the location of numbered logs~~. ~~(~~(Chronostratigraphy of localities 25 (Poltriciano, Cetona: Capellini, 1883) and 26 (Allerona: Danise, 2010) are unknown~~logs 21-23 not shown)~~. Correlation between sections is also shown as boundaries of planktonic foraminifera biozones (dashed lines), following the scheme of Sprovieri (1992), based on available biostratigraphic studies for each basin (see main text for relevant references).

Fig. 3 - ~~Number~~Abundance of fossil ~~large marine vertebrate~~MM records in major museums of Tuscany~~ catalogues~~, distributed by locality of provenance. Each record ranges from a single fragment or ~~single ~~tooth, to ~~a quasi-~~articulated, nearly complete skeleton. A: ~~whales and dolphins~~masticates and odontocetes; B: large sharks; C: ~~dugong~~sirenians — ~~man~~scuba diver for scale in each figure. Symbols for basins as in Fig. 1.

Fig. 4 - Detailed sedimentary logs measured at three localities, representing three different stratigraphic contexts for the large marine vertebrate fossil record of the Tuscan Pliocene. The succession at Orciano Pisano is included in synthems S3-S4 of FB, at Arcille-Poggio alle Mura-Camigliano in synthem S2 of OOB, at Sinalunga in synthem S6 of CB. See Figs.1-2 for the location of the numbered localities and references in the main text for facies analysis and sequence stratigraphy of synthem S5. Arcille log from Tinelli et al., 2012, and Tinelli, 2013.

Fig. 5 - Taphonomy of large marine vertebrates at Poggio alle Mura (Figs. 5A-5D) and Arcille (Fig. 5E, see Fig. 4 for the sequence stratigraphic and sedimentary context; plan view of the sirenian skeleton is modified from Tinelli et al., 2012), synthem S2. A: Plan view of the Poggio alle Mura undetermined balaenopterid. Parts of the skeleton are quasi-articulated,

others are scattered, but not far from the original position. B: Quasi-articulated vertebrae of the same specimen, lying on top of a *Haustator* shell bed. C: Side view of a vertebra on top of the densely-packed shell bed. D. Detail of the shell bed, in top view. The turritelline gastropod *Haustator vermicularis* is visible in the upper left, a large fragment of wood in the lower right, with the inchnofossil *Teredolithes* produced by wood-dwelling teredinid bivalves, in the centre of the photograph. E: Plan view of one of the Arcille ~~dugong~~sirenian specimens~~,~~ ~~belonging to the species~~ of *Metaxitherium appenninicum*. Same scale as in 5A, the arrows points to the North.

Fig. 6 - Taphonomy of a 10m-long, undetermined balaenopterid at Orciano Pisano (see Fig. 4 for the sequence stratigraphic and sedimentary context), synthem 4. A: Planimetry of the quasi-articulated and nearly complete skeleton. B: Detail of the central part of the skeleton in the field. The cortex layer of vertebrae and flipper bones is badly consumed, whereas some of the costae are still pristine. C: Lateral view of a turritellid shell bed, below, and the surface where the whale skeleton lied (dashed line), about 15 cm above the shell bed. The sediment is a very fine-grained silty sand, completely bioturbated (large vertical burrows are visible). D: Top view detail of the turritellid shell bed. At the center a valve of *Yoldia nitida*, surrounded by a few specimens of the turritellid *Archimediella spirata*.

Fig. 7 - Taphonomy of an incomplete, undetermined mystecete at Castel San Gimignano, synthem 4, comprising articulated torso elements. A: Planimetry of the articulated elements. B: Detail of one of the limbs in the field (trowel for scale = 22 cm): humerus, radius and ulna are in anatomical relationship; the cortex layer is well preserved, suggesting quick burial of the carcass. C: Bones of the chest region; on the background the massive sandstone associated with the fossil whale. Articulated shoreface pectinid bivalves (*Pecten flabelliformis*) were interspersed in the sandstone (photographs by Fabio Cozzini, 1985).

Fig. 8~~7~~ - Taphonomy of a 5m-long, undetermined balaenopterid at Sinalunga (see Fig. 4 for a tentative sequence stratigraphic interpretation), synthem 6. A: Oblique view of the fully articulated skeleton lying in a gravelly sandstone, stratified in the lower part, massive in the upper. Vertebrae are tightly connected as if in life. B: Plan view of the flipper, with carpals, metacarpals and phalanges in perfect anatomical connection. C: The gravelly sandstone lies above a bioturbated muddy sandstone, with vertical burrows (*Ophiomorpha*). D: The lower part of the unit with the whale skeleton if formed by three fining-upward beds. Each bed grades from gravel to medium-grained sand. Articulated and empty shoreface bivalves (e.g., *Callista chione*), not in life position, are interspersed with the coarse gravel.

Fig. 9~~8~~ - Quantitative analysis of the facies type and sequence stratigraphic distribution of large marine vertebrates, Pliocene of Tuscany (N = 39, see Tab. 2). A: The vast majority of cases (77%) are associated with fine-grained muddy sediments of the shelf, a few are found in deltaic coarse-grained strata. B: Most ~~LMVs~~MM (69%) ~~are~~is found in highstand deposits, a few in proximity of the maximum flooding interval, or in transgressive deposits.

Fig. 10~~9~~ - NMDS ordination of bulk samples (N = 72, see Fig. 2 for their stratigraphic position), based on the distribution of standardised abundances of 329 mollusc species (further explanation on multivariate techniques in the main text). A: Samples are subdivided based on the associated sedimentary facies types (F2-F5 in Tab. 1). The main axis ordinates samples along a paleodepth gradient, from shallowest to deepest, moving from the left to the right side of the bivariate plot. B: Same ordination, with an estimate of absolute paleodepth of each sample based on score along the main axis and calibrated through the average modern depth distribution of 23 extant species characterising the Pliocene dataset (abundance > 0.15%, see text; regression logarithmic curve in the inset). Vertebrates recovered in proximity of some of the samples (N = 13) are plotted on the diagram, confirming that, on average, the ~~LMV~~MM fossil record is concentrated on the open shelf at an estimated depth of 30-300 m (M =~~dugongs~~ sirenians; S = sharks; P = pinnipeds; W = whales).

Fig. 11 - Occupancy of trophic levels by Pliocene marine mammals and sharks in the north-western Mediterranean, expressed by number of species per trophic level (see Tabs 3, 5 for explanation and references). This figure, summing up data for the whole epoch, spanning circa 2,8 My, closely matches the association found in one single synthem S4, of much shorter duration (mid-Piacenzian, 3-4 hundred thousand years).

Tab. 1 - Sedimentary facies types.

Tab. 2 - Stratigraphic, taphonomic and paleoenvironmental framework for Pliocene ~~large marine vertebrates~~marine mammals recovered ~~of~~in Tuscany, with abundance data (N = ~~39~~64). A: ~~Highly a~~Articulated and quasi-articulated skeleton; C: ~~Highly c~~Complete and quasi-complete skeleton; C+PC: Cranial and post-cranial ~~bones~~remains.

Tab. 3 - Paleoecology of Pliocene large mammals ~~compared to~~and ecology of modern NWMS analogues.

Tab. 4 - Geographic distribution of Pliocene large mammals in Tuscany.

Tab. 5 . Paleoecology of Pliocene sharks ~~compared to~~and ecology of modern NWMS analogues.

Tab. 6 - Geographic distribution of Pliocene sharks in Tuscany.

Supplement Material

Fig. S1 - Dendrogram resulting from cluster analysis of a dataset of 336 species distributed in 72 samples (standardised abundance, square-root transformed, Bray-Curtis similarity).

Tab. S1 - Ranked total average of standardised abundance of Pliocene molluscs.

Tab. S2 - Score on main axis of NMDS ordination (NMDS1) of Pliocene mollusc species (N=329).

Tab. S3 - Average depth of extant mollusc species with >1,5% abundance in the Pliocene dataset (N=23).

Tab. S4 - Estimated depth of Pliocene samples (N=72) based on NMDS1.

Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna

Abstract

Tuscany has a rich Pliocene record of marine megafauna (MM), including mysticetes, odontocetes, sirenians and seals among the mammals, and six orders of sharks among the elasmobranchs. This is reviewed with respect to paleogeography and sequence-stratigraphic occurrence in six different basins. Conditions at the ancient seafloor are explored by means of sedimentary facies analysis, taphonomy and multivariate techniques applied to a large quantitative dataset of benthic molluscs. MM is rare or absent in most basins during the Zanclean, except in one basin, and most abundant in Piacenzian deposits in all six basins. MM occurs preferentially in fine-grained shelfal highstand deposits of small-scale depositional sequences, or at condensed horizons of the maximum flooding interval. It is rare in shallow marine paleonvironments and nearly absent in bathyal paleosettings. Paleogeographic and paleoecological evidence and a comparison with modern patterns of marine upwelling suggest that a wedge of nutrient-rich waters sustained in the offshore during the Pliocene a high biomass of primary producers and a community of apex consumers and mesopredators, similarly to the modern Northwestern Mediterranean Sea, with a higher species-richness than the modern. The highest MM diversity coincides with the mid-Piacenzian warm period, suggesting that facies control does not obscure a link between climate and diversity. We underline however that not all marine environments were suitable for marine mammal preservation. Buoyant carcasses were preferentially dismembered and destroyed in high-energy shallow waters, with the possible exception of delta front deposits, where sudden sediment input occasionally buried pristine carcasses. We hypothesise that carcasses sunken on the seafloor below the shelf break underwent destruction through the activity of a whale-fall biota of modern type, specialised in the consumption of decomposing tissues, both soft and mineralised. A taphonomic window was left between storm wave base and the shelf break. Here water pressure is high enough to prevent the formation of decomposing gases and the resurfacing of carcasses, while the lack of a specialised whale-fall biota slows down bone degradation with respect to deeper settings. Sedimentation rate was high enough to cover skeletal material before its complete destruction. An estimate of paleobathymetries based on multivariate techniques suggests that the preferential depth for the inclusion of MM in the fossil record was 30-300 m. The results are compared with major Mesozoic and Cenozoic MM records worldwide. Available evidence suggests that the late Neogene radiation of large whales, true ecosystem engineers, and their size increase, triggered the radiation of a bone-eating fauna that hampered, and hampers, MM preservation in the deep sea. Stratigraphic paleobiology and an ecosystem-level approach deliver useful insights in the nature of the fossil record.

Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna

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Abstract

Tuscany has a rich Pliocene record of marine megafauna (MM), including mysticetes, odontocetes, sirenians and seals among the mammals, and six orders of sharks among the elasmobranchs. This is reviewed with respect to paleogeography and sequence-stratigraphic occurrence in six different basins. Conditions at the ancient seafloor are explored by means of sedimentary facies analysis, taphonomy and multivariate techniques applied to a large quantitative dataset of benthic molluscs. MM is rare or absent in most basins during the Zanclean, except in one basin, and most abundant in Piacenzian deposits in all six basins. MM occurs preferentially in fine-grained shelfal highstand deposits of small-scale depositional sequences, or at condensed horizons of the maximum flooding interval. It is rare in shallow marine paleonvironments and nearly absent in bathyal paleosettings. Paleogeographic and paleoecological evidence and a comparison with modern patterns of marine upwelling suggest that a wedge of nutrient-rich waters sustained in the offshore during the Pliocene a high biomass of primary producers and a community of apex consumers and mesopredators, similarly to the modern Northwestern Mediterranean Sea, with a higher species-richness than the modern. The highest MM diversity coincides with the mid-Piacenzian warm period, suggesting that facies control does not obscure a link between climate and diversity. We underline however that not all marine environments were suitable for marine mammal preservation. Buoyant carcasses were preferentially dismembered and destroyed in high-energy shallow waters, with the possible exception of delta front deposits, where sudden sediment input occasionally buried pristine carcasses. We hypothesise that carcasses sunken on the seafloor below the shelf break underwent destruction through the activity of a whale-fall biota of modern type, specialised in the consumption of decomposing tissues, both soft and mineralised. A taphonomic window was left between storm wave base and the shelf break. Here water pressure is high enough to prevent the formation of decomposing gases and the resurfacing of carcasses, while the lack of a specialised whale-fall biota slows down bone degradation with respect to deeper settings. Sedimentation rate was high enough to cover skeletal material before its complete destruction. An estimate of paleobathymetries based on multivariate techniques suggests that the preferential depth for the inclusion of MM in the fossil record was 30-300 m. The results are compared with major Mesozoic and Cenozoic MM records worldwide. Available evidence suggests that the late Neogene radiation of large whales, true ecosystem engineers, and their size increase, triggered the radiation of a bone-eating fauna that hampered, and hampers, MM preservation in the deep sea. Stratigraphic paleobiology and an ecosystem-level approach deliver useful insights in the nature of the fossil record.

1. Introduction

The modern marine megafauna (MM) includes all marine mammals, seabirds, sea turtles and sharks, apex consumers that influence their associated ecosystems (Lewison et al., 2004), both pelagic and nearshore, through top-down forcing and trophic cascades, and now severely affected by human impact (Estes et al., 1998, 2011, 2016). On a macroevolutionary scale, predation pressure has shaped the evolution of marine preys, with feedbacks on predators, setting the stage for the Mesozoic marine revolution (Vermeji, 1977; Chen and Benton, 2012; Benton et al., 2013). The new ecosystem structure started in the the Early and Middle Triassic with several lineages of Actinopterygian fishes (Chen and Benton, 2012), continuing with marine reptiles possessing feeding styles (Fröbisch et al., 2013; Motani et al., 2015; but see also Motani et al., 2013) and reproductive adaptations (Motani et al., 2014) of modern type. Triassic and Jurassic novelties underwent a prolonged crisis during the Cretaceous, with the gradual extinction of plesiosaurians,mosasaurs (Benson et al., 2010) and ichthyosaurs (Fischer et al., 2016), and a diversity drop of sharks (Guinot et al., 2012). A marine megafauna of comparable size returned in the Paleogene, with the new diversification of neoselachian elasmobranchs (Kriwet and Benton, 2004) and the evolution of large marine mammals: Eocene archaeocetes (Uhen, 2008, Gingerich et al., 2009) and Oligocene odontocetes and mysticetes (Gingerich, 2005; Marx and Uhen 2010, Berta, 2012; Marx et al., 2016) empowered by high metabolic rates and new anatomic features (Armfield et al., 2013). Among the largest vertebrates of all times, after a dramatic size increase at the outset of glacial age (Marx et al., 2016; Bisconti et al., 2017; Slater et al., 2017), baleen and sperm whales are among today's ocean's ecosystem engineers (Roman et al., 2014) with which to compare their Mesozoic analogues (Smith et al., 2016). Notwithstanding a crucial role in ecology and evolution, the nature and distribution of the MM fossil record has been less explored, compared to that of marine invertebrates and terrestrial vertebrates. Available data suggest a strong correlation between taxic diversity and the number of marine fossiliferous formations, resulting in megabiases in the fossil record (e.g., Cretaceous: Benson et al., 2010). Within its vast history, studies on the geologically recent marine megafauna offer important insights, considering our better knowledge of: 1) geological setting, in terms of outcrop extent and high-resolution stratigraphy; 2) ecologic role played by individual species, whether extant or extinct, in terms of habitat, trophic role, life histories and population structure, thanks to a comparison with extant descendants, or close relatives; 3) MM taphonomy, based on actuopaleontology. A recent global study revealed that MM extinction peaked in the late Pliocene, between 3.8 and 2.4Ma, linked to the sudden drop in the extension of nearshore environments after a large sea level regression (Pimiento et al., 2017), confirming that the fossil record offers important clues on the vulnerability of keystone marine species to climate change. We contribute here to a better understanding of the Pliocene fossil record by reviewing the rich MM of Tuscany, in Italy. In particular, we consider all reports of Pliocene marine mammals and sharks and revise taphonomy and sedimentary facies associated with all known findings, setting them within a sequence stratigraphic framework. We also reconstruct the paleoenvironmental context and review data on a part of the marine ecosystem through the paleoecology of fossil invertebrates on a regional basis, following a stratigraphic paleobiological approach that can be applied to both the recent and the distant geological past (Patzkowsky and Holland, 2012). Published studies that have taken this direction are still a few, examples concerning Jurassic ichthyosaurs, plesiosaurs and pliosaurs (McMullen et al., 2014), Cretaceous turtles, plesiosaurs, bony fish and sharks (Schemisser McKean and Gillette, 2015), Eocene archaeocetes, sea cows and sharks (Peters et al. 2009), and Neogene marine mammals and sharks (Boessenecker et al., 2014). All of these papers record the co-occurrence of shelly faunas, only one undertaking quantitative studies of the distribution of fossil invertebrates (Jurassic of the Sundance Formation: McMullen et al., 2014, see also Danise and Holland, 2017). The benefits of an outcrop-scale sequence stratigraphic approach include: (1) an independent record of relative sea-level change to test paleobiological hypotheses (see also Pyenson and Lindberg, 2011; Noakes et al., 2013); (2) a chronostratigraphic scheme for high-resolution correlations; (3) a means to recognise minor and major breaks of the record; (4) an ecological and sedimentary framework for taphofacies distribution (Patzkowsky and Holland, 2012); and (5) an independent control of onshore-offshore patterns of fossil assemblages (e.g., Tomašových et al., 2014).

Researchers that study the geologic history of marine ecosystems have focused on patterns of ecological restructuring based on the taxonomy of selected groups (e.g., Thorne et al., 2011; Benton et al., 2013; Scheyer et al., 2014; Fischer et al., 2016), at the expenses of a more holistic approach that includes functional diversity and embraces as many ecosystem components as possible (Dineen et al., 2014). By analogy with ecologists who shift focus from models based on single groups (e.g., Steeman et al., 2009) to an all-embracing vision of marine life (Lawton, 1994; Sergio et al., 2014), connecting food web ecology with landscape ecology (Polis et al., 1997; Estes et al., 2011), stratigraphic paleobiology can draw from the fossil record and offer multidimensional insights on the complex geological history of modern marine ecosystems.

After revising fossil MM hosted in major museums of Tuscany, both isolated and articulated remains, we focus on all fossil bones that can be stratigraphically (e.g., Bianucci et al., 1995, 1998, 2001; Tinelli, 2013) and taphonomically framed (e.g., Dominici et al., 2009; Bianucci, 2010; Danise and Dominici, 2014). MM lists for the Mediterranean Pliocene have been recently updated (marine mammals: Landini et al., 2005; Bianucci et al., 2009a; Sorbi et al., 2012; Bianucci and Vomero, 2014; sharks: Marsili, 2006). Species-level ecological data are available on modern apex consumers and mesocarnivores (Pauly et al., 1998; Cortés, 1999), with detailed information made available for Mediterranean species following conservation concerns (marine mammals: Notarbartolo di Sciara et al., 2016; sharks: Cavanagh and Gibson, 2007), allowing for a detailed paleoecological evaluation of the Tuscan fossil record. The actualistic approach is also viable for species of benthic molluscs, about half of which are still extant in modern Mediterranean bottoms (55% of extant species of Mediterranean and North Sea bivalves, excluding strictly brackish and bathyal forms, i.e., 202 out of 367 species, survives from the Zanclean: Raffi et al., 1985). The regional quantitative study of molluscan assemblages was the basis for an independent assessment of paleoenvironments, paleoecology and paleobathimetry. A revision of abundance distributions of marine molluscs, the largest contributors to Mediterranean Pliocene shell beds and a key component of Mesozoic and Cenozoic marine ecosystems (Stanley, 1975; Vermeij, 1977), allowed to further explore the structure and composition of Pliocene marine ecosystems, and reconstruct a paleobathymetric gradient (e.g., Scarponi and Kowaleski, 2004) along which to frame MM occurrence. The present work must necessarily start with a review of the chronostratigraphy and physical stratigraphy of the Tuscan marine Pliocene.

1. Geological setting

The Pliocene succession of Tuscany was deposited in a complex setting characterised by continental collision related to the later evolution of the Northern Apennines chain. According to a well-established hypothesis, the region, affected by shortening before the Middle-Late Miocene, accommodated by NE-verging thrust and fold systems, underwent crustal extension during the late Neogene and the Quaternary (DeCelles, 2012; Fig. 1). Crustal extension generated differential subsidence in a series of normal-fault controlled hinterland sedimentary basins, filled throughout by continental and shallow marine, mostly clastic successions (Martini and Sagri, 1993; Pascucci et al., 2006; Brogi, 2011). An alternative hypothesis places the late orogenic hinterland basins in a more complex tectonic setting characterised by the alternation of compressive, extensional and transcurrent stress fields (Benvenuti et al., 2014; Bonini et al., 2014).

The Neogene Tuscan basins considered in this work include, from West to East, and from North to South, the Fine Basin (FB; Bossio et al., 1997), the Volterra-Era Basin (VEB; Bossio et al., 1994), The Elsa Basin (EB; Benvenuti et al., 2014), the Ombrone-Orcia Basin (OOB; Bossio et al., 1991; Nalin et al., 2010), the Siena-Radicofani Basin (SRB; Ghinassi and

Lazzarotto, 2005; Martini et al., 2011, 2016), and the Chiana Basin (CB; Fig. 1: Pesa Basin not considered here). With one exception (OOB, see below), these basins show a shape conditioned by the structural and physiographic features of the inner portion of the Northern Apennines. Their NW-SE general elongation reflects the trend of the thrust-related anticline ridges developed during earlier collisional stages. These compressive structures have bounded most basins through their infilling, only to be obliterated by younger parallel normal fault systems, leaving an invariant stratigraphic onlap of the Pliocene successions onto the basin margins. Despite a NW-SE distribution of the hinterland basins, the structural setting is responsible for a NE-trending physiographic and paleogeographic gradient, where the FB is closest, and the CB furthest, from offshore settings throughout the late orogenic phase, with important implications for the facies architecture and the distribution of marine vertebrates and shell beds. Differential active uplift of the basin shoulders during the Pliocene, coupled with important erosional phases, resulted in a different preservation of the original stratigraphic architecture. The infill during the Zanclean is generally characterised by relatively continuous open marine successions, the correlative fluvial-coastal systems missing due to uplift and erosion of basin margins. On the other hand, the Piacenzian infill is characterised by genetically-connected, fluvial, coastal and shallow marine facies tracts, particularly well-preserved in the EB, hinting to reduced uplift of the marginal areas. The modern physiography of OOB, escaping the structurally-controlled geometry of the other basins, mimics instead an original fluvial network developed during the latest Messinian, flooded after the Salinity Crisis (Bossio et al., 1991; Benvenuti et al., 2015), filled during the Pliocene, and finally disrupted by post-Pliocene uplift and erosion. This difference in the structural history also justifies the preservation in OOB of Zanclean fluvial and shallow marine facies (Fig. 2).

1.1 Pliocene Stratigraphy

The Neogene succession of Tuscany is up to 2000 m-thick, about half of which belongs to the uppermost Miocene-Pleistocene interval (Bossio et al., 2004; 1997; Benvenuti et al., 2014). The Pliocene has been traditionally subdivided into three main informal litostratigraphic units: continental conglomerates and sandstones at the base, overlain by the “Blue Clay Formation” (*Argille Azzurre*: Zanclean-lower Piacenzian), marking the post-Messinian Mediterranean marine transgression and forming the thickest part of the basin infill (e.g., Bossio et al., 1994; 1997; Ghinassi and Lazzarotto, 2005), and the “Upper Sands” (*Sabbie superiori*: Piacenzian-Gelasian) and conglomerates, deposited during the ensuing regression. Several finer litostratigraphic units have been introduced to define the local stratigraphy, resulting in a complex and largely informal litostratigraphic terminology which includes Zanclean lower “Blue Clays” and Zanclean-Piacenzian upper “Blue Clays” (Capezzuoli et al., 2015), the latter eventually further separated by the widespread occurrence of Piacenzian carbonates (Nalin et al., 2016). The lower Zanclean (OOB: Ghinassi, 2007; Nalin et al., 2010; Dominici et al., 2012) and the Piacenzian, are characterised by the high-frequency alternation of coarse-grained and fine-grained facies, ranging from fluvial to marine shelf settings (Benvenuti et al., 1995; 2007; 2014; Martini et al. 2011, Fig. 2). The dynamics of the Pliocene infilling are better-understood in the EB, where six synthems have been defined, each up to more than 200 m-thick, further subdivided in a number of elementary and composite depositional sequences and chronologically calibrated through marine biostratigraphy and continental vertebrate biochronology (Benvenuti and Del Conte, 2013; Benvenuti et al., 2014, with references).

2. Materials and methods

Stratigraphic sections were measured and described at several localities (Fig. 1). Siliciclastic and carbonate facies were described, subdivided into groups of facies based on lithology, sedimentary structures and ichnology, and interpreted in terms of process and depositional environment (Tab. 1). Each group represents a set of individual facies forming monogenic associations (in the sense of Mutti et al.,1994), i.e., the meter-scale stacking of facies which express the autocyclic behaviour of specific depositional systems within a given accommodation space (Benvenuti and Del Conte, 2013). Sequence stratigraphic concepts have been applied to reconstruct the dynamics of basin infills at a hierarchy of scales, advancing hypotheses on controlling factors. The chronostratigraphic subdivision of Benvenuti et al. (2014), which divides the Pliocene into six synthems, S1-S6 from older to younger, was extended to all six Tuscan basins by referring to available biostratigraphic schemes (Fig. 2). The sequence stratigraphic interpretation of S2 in OOB is based on Tinelli (2013). Other parts of the S1-S3 succession were drawn based on available litostratigraphic literature (see below). Studies integrating sedimentary facies analysis, biostratigraphy and magnetostratigraphy (Nalin et al., 2016) have helped correlating carbonate bodies typical of S4. The reader is referred to Benvenuti et al. (2007; 2014) for details on facies analysis and sequence stratigraphic interpretation of synthems S3-S6.

First, data on the geographic distribution of fossil marine mammals, large sharks and sirenians were largely based on collections housed at the Natural History museums of the University of Florence (UFMSN), University of Pisa (UPMSN), and Accademia de’ Fisiocritici of Siena (AFMSN), the three largest collections of Tuscany, and at the Geological Museum Giovanni Capellini, Bologna University (MGGC). In particular, counts of cetaceans were based on UFMSN collections (Mysticeti and Odontoceti, N = 142), large shark on the sum of UFMSN, UPMSN and AFMSN collections (Carcharhiniformes and Lamniformes, N = 337, data synthesised from Marsili, 2006), sirenians from all reports in Tab. 2 (N = 10). Each record is formed either by a single element (e.g., whale bone, shark tooth), by a few elements of the same individual, or by a whole, quasi-articulated skeletons. A large proportion of this dataset lacks precise location, allowing only for some crude stratigraphic attribution (Fig. 3).

On a second step, all fossil Tuscan Pliocene cetaceans, sirenians and pinnipeds that could be framed within the available high-resolution stratigraphic framework and associated with taphonomic data, were selected. At this step, after excluding unidentified MM remains, a dataset of 64 specimens (cetaceans N = 50; sirenians N = 10; pinnipeds N = 4) was assembled. Associatiation with shark teeth is frequent (55% of 25 cases according to Danise and Dominici 2014 for the Italian Pliocene; see also Bianucci et al. 2002, 2010). The majority of the 64 specimens are included in the catalogue of UFMSN, UPMSN, AFMSN and MGGC, whereas a few are stored in smaller collections of the municipalities of Montaione, Scandicci (Florence province), and Certaldo (Pisa province), one in a private property (Castello di Villa Banfi, near Montalcino, Siena province), and one in the Museum National d'Histoire Naturelle in Paris (France). Whenever possible, large marine vertebrates were coded by synthem (N = 60) and depositional environment (N = 54). We analysed abundance distributions among marine mammals, and species richness of marine mammals and sharks. To infer Pliocene paleoecology, fossil taxa recognised in Tuscany were compared with their closest descendants, focusing on the species today living in the North-Western Mediterranean Sea (NWMS).

All known MM-bearing sedimentary facies are associated with a mollusc-dominated benthic fauna. The third step of the analysis concerned a quantitative study of shell beds, allowing: 1) to interpret the regional evolution from a perspective independent from the sedimentary facies, 2) to characterise MM paleoenvironmental and bathymetric distribution, and 3) to explore the structure of the benthic component of marine ecosystems and to identify underlying environmental controls. 72 Bulk samples were collected at major shell beds at bed resolution throughout the succession and sieved with 1 mm mesh size. Fossils of bivalves, gastropods and scaphopods were identified to species level. The minimum number of individuals was calculated following standard approaches (see Patzkowsky and Holland, 2012), resulting in a richness of 525 species (S) and a total abundance of 64206 individuals (N). We coded each fossil assemblage by synthem, tract of small-scale depositional sequence, and depositional environment. Most samples belonged to facies types F2-F5 (Tab. 1; see also Tomašových et al., 2014). Facies F6 usually lacks macrofossils and allowed for the collection of only one sample. No samples were collected in facies F1, lacking marine shells, facies F7, mostly devoid shells, and facies F8, which is richly fossiliferous, but lacks aragonite shells and is associated with specimens hardly extractable from the rock. The resulting quantitative dataset served for statistical analyses on the distribution of species-level abundances on a siliciclastic shelf depositional system, performed with the software Primer 6.0 (Clarke and Gorley, 2006). Analyses included clustering and nMDS ordination techniques on a Bray-Curtis similarity matrix, of standardised, square-root transformed data (72 samples; S = 333 and N = 63518 after the exclusion of singletons). To test statistically whether there is a significant difference between two or more groups of sampling units based on sedimentary facies, we performed an analysis of similarity (ANOSIM). To interpret the outcomes of the quantitative study and the significance of clusters we used species-level autoecologic information available for the most abundant species, based on the distribution of extant forms. This information, retrieved from the Marine Biodiversity and Ecosystem Functioning EU website (MARBEF: www.marbef.org), included the average life depth of 23 modern species that in our dataset had an overall abundance > 0.15%.

3. Results

3.1. Unconformity-bounded units

3.1.1 Synthem S1: the early Zanclean transgression

The Miocene-Pliocene transition, marking the return to marine conditions after the Messinian salinity crisis (Krjigsman et al., 1999), is recorded in limited exposures of earliest Zanclean, open marine mudstones resting both unconformably or conformably onto latest Messinian non-marine deposits (*Lago-Mare*), an isochronous boundary being dated in the Mediterranean at 5.33 Ma (Roveri et al., 2014). Differences depend on the specific structurally-controlled distribution of hinterland basins, where an uplifting chain determined the presence of thresholds delaying the early Zanclean marine flooding from inner (EB, OOB: Benvenuti et al., 2015a) to outer hinterland basins (FB, VEB). In inner basins such as EB, where S1 has been defined, continental deposition continued into the earliest Zanclean, marine flooding occurring within the MPL1 biozone (references in Benvenuti et al., 2015a). A chronostratigraphical equivalent of S1 is represented in FB and VEB (Bossio et al., 1978) by an open-shelf mudstone, conformably resting on latest Messinian *Lago-Mare* deposits (Roveri et al., 2014). An apparently analogous situation is documented in OOB, where MPL1 shelfal mudstones of the early Zanclean (normal chron C3n) rest on a Messinian to basal Pliocene paleovalley fill (Benvenuti et al., 2015a).

3.1.2 Synthem S2: Zanclean differential preservation

Synthem S2, as recognised in the EB (Benvenuti et al. 2014), is represented by relatively thin fluvial conglomerates unconformably resting on S1 (biozones MPL1-MPL2), capped by S3 (biozone MPL4a: Bossio et al., 1993; 2001), comprising important stratigraphic gaps at its base and top. On the other hand, in FB (Bossio et al., 1997), VEB (Bossio et al., 1994) and SRB (Ghinassi and Lazzarotto, 2005), the same chronostratigraphic interval is recorded by monotonous epibathyal mudstones several hundred meters thick, locally intercalated with delta-front hyperpycnal sandstones and conglomerates. In a very broad sense, the concept of S2 is extended to these basins, by assuming that erosional unconformities in EB pass to into correlative conformities in rapidly subsiding adjacent basins, where thick successions could be accomodated. Apart from exceptions, no shells were found in bathyal mudstone or in deltaic sandstone. In OOB, the same time span is marked by a N-S facies gradient characterised by a single deepening-upward succession, from fluvio-deltaic sandstone to shelfal mudstone, replaced by a succession made of four distinct regressive-transgressive units in the Orcia valley to the north (Ghinassi, 2005; Benvenuti et al., 2015b). A laterally-continuous shell bed, with sharks remains and skeletons and articulated bones of whales, sirenians and large teleost fishes (Danise, 2010; Sorbi et al., 2012; Tinelli, 2013), marks a major transgressive surface overlain by open shelf mudstones (Sorbi et al., 2012; Tinelli, 2013: biozone MPL2) that is hypothetically traced along a NE-SW profile (Figs. 4, 5).

3.1.3 Synthem S3: Zanclean-Piacenzian transition

Synthem S3 is subdivided in EB into a lower and an upper interval (Benvenuti et al., 2014). The lower division is represented by deepening-upward, coarse-grained delta front system, overlain by an upper mudstone division from an open shelf setting. The upper part is rich with shell beds, and occasional articulated whale skeletons, associated with shark teeth, have been recovered (Danise and Dominici, 2014). Similar shelf mudstones of the MPL4 biozone crop out in VEB and SRB (Bossio et al., 1993; Riforgiato et al., 2005) whereas biostratigraphically equivalent mudstones in FB testify to an upper epibathyal paleoenvironment.

3.1.4 Synthem S4: early Piacenzian warm climate and high sea-level

Synthem S4 (Benvenuti et al., 2014) has been recognised in FB and VEB by facies similarities and chronostratigraphic correlation. In EB, S4 comprises a lower interval dominated by richly fossiliferous, massive mudstone or very-fine-grained sandstone (prodelta-inner shelf), overlain by bioclast-rich sandstones recording prograding mixed carbonate-clastic ramp, outcropping in the southeastern part of the Elsa valley. Equivalent deposits, also comprised in biozone MPL4b, are patchily distributed in FB, VEB, SRB, OOB and other basins of southern Tuscany (Ghinassi and Nalin, 2010; Ghinassi, personal communication, 2015). The upper interval of S4 is formed by a succession of delta front sandstones, passing in EB eastern margin to a few tens of m-thick fluvial succession, hinting at an original depositional gradient. S4 is apparently missing due to erosion north of San Gimignano (EB), and around Lajatico (VEB). Biostratigraphic data allow to refer S4 to the upper part of biozone MPL4b and the lower part of MPL5a, thus comprising the mid-lower part of the Piacenzian, globally characterised between 3.264-3.025 Ma by warm climate and relatively high sea level (Raymo et al., 2009; Dowsett et al., 2013; Prista et al., 2015).

3.1.5 Synthem S5: mid-Piacenzian high-frequency sea level variation

Synthem S5, recognised in EB and VEB, is bounded below by an erosional unconformity that cuts deeply into underlying units, bringing S5 directly on top of S3 (EB: log 15; VEB: logs 5-6 in Fig. 1). S5 is up to about 200 m in EB, where it has been subdivided into a hierarchy of small-scale depositional sequences (Benvenuti et al., 2007; Dominici et al., 2008: see following paragraphs). Each composite depositional sequence forms a tens-of-m-thick asymmetric sedimentary cycle, composed by a deepening-upward part, from fluvial or coastal coarse-grained sediments, to open shelf mudstones, sometimes topped by a regressive shoreface or delta sandstone, other times directly overlain by the next sequence through a sharp contact. Fluvial, brackish-water, and other intertidal deposits mark the lower part of each composite sequence, usually topped by a laterally-continuous shell bed, from a few cm to a few dm-thick, representing a surface of transgression. Shell beds are particularly well-developed around the middle part of sequences, where they separate shoreface and delta sandstones from overlying open shelf mudstones, marking the time of maximum flooding (MFS). Large marine vertebrates, including articulated whale skeletons and large sharks (Danise and Dominici, 2014), are often recovered both at MFS and overlying mudstone (Fig. 1). Towards the north-eastern margin of EB, cyclothemic fluvial conglomerates, sandstones and mudstones replace coastal and fully marine deposits, testifying to an original facies gradient. In the central part of EB, composite sequences are stacked to form a deepening-upward succession, with a topmost thick and laterally-continuous open shelf mudstone interval, directly onlapping the S4-S5 basal unconformity on the eastern EB (log 15, Fiano: Fig. 1).

3.1.6 Synthem S6: Piacenzian-Gelasian climate change and regression

As S5, synthem S6 is also built through a hierarchy of small-scale depositional sequences, better expressed in EB, but also documented in SRB and CB. In EB, fluvial coarse-grained sandstones fill a deep valley incised in S5 deposits (logs 8-10 in Fig. 1), resting on the basal unconformity of S6. Intertidal or coastal lagoon deposits form the transgressive systems tract of the composite depositional sequence. A laterally-continuous shell bed testifies to the MFS of S6, topped by highstand shoreface and delta front sandstones. The Piacenzian-Gelasian boundary, corresponding to a major climatic transition from warmer-moister to colder-drier conditions (Benvenuti et al., 1995b; 2007), is marked by the Gauss-Matuyama reversal detected at Montopoli (Lindsay et al., 1980). Highstand marine sandstones are characterised by the recovery of two mysticete skeletons, at Montopoli (EB, see Capellini, 1905) and Sinalunga (CB, Fig. 7). Fully continental environments were established throughout the Gelasian in all basins here under study (e.g., Benvenuti and Del Conte, 2013; Benvenuti et al., 2014; Bianchi et al., 2015).

3.2 Sedimentary facies and facies associations

Seven groups of siliciclastic facies and one group of carbonate facies, with very different fossil content, have been recognised (Tab. 1). Siliciclastic facies form a paleoenvironmental gradient from terrestrial to marine and, in the case of marine facies, from shallowest to deepest (Fig. 8a). Facies types are fluvial conglomerate and sandstone, and alluvial mudstone (F1); intertidal to very shallow subtidal mudstone and muddy sandstone (F2); shallow subtidal coarse- and medium-grained sandstone with sparse conglomerate (F3); deep subtidal muddy fine-grained sandstone (F4); open shelf sandy mudstone (F5); outer shelf to upper bathyal mudstone (F6); outer shelf and bathyal turbidite sandstone and conglomerate (F7). An eighth group is formed by facies deposited subtidally in limited mixed carbonatic-siliciclastic ramps (F8), irrespective of depth (Nalin et al., 2016). Facies F6-F7 are restricted to Zanclean deposits (synthems S1-S3); facies F5 and F8 characterise the upper Zanclean-middle Piacenzian interval (synthems S3-S4); facies F1-F4 characterise the upper Piacenzian (synthems S5-S6). The OOB succession, characterised by facies F1-F4, is an exception within the Zanclean.

3.3 Elementary depositional sequences (EDS)

Both fluvial (Benvenuti and Del Conte, 2013) and marine facies groups (siliciclastics: Benvenuti et al., 2007; 2014; carbonates: Nalin et al., 2016) are stacked to form facies associations which record cyclic variations of depositional and environmental conditions in response to a change in accommodation space. Physical surfaces and the intervening deposits allowed to subdivide depositional sequences in systems tracts (Benvenuti et al., 2007; Dominici et al., 2008). At the simplest scale, these hybrid facies associations form elementary depositional sequences, up to 10-20 m thick, in their turn stacked to form composite sequences (original concepts from Mutti et al., 1994). This hierarchy is particularly evident in synthems S5-S6, formed at a time of pronounced glacio-eustatic oscillations and expressed around coastal settings, where maximum facies contrast allows for the expression of subtle cycle of sea level variation (e.g., Benvenuti and Dominici, 1992; Benvenuti et al., 2007; Dominici et al., 2008). Analogue sharp facies contrast within Zanclean EDS in OBB (Tinelli, 2013), but is otherwise absent in deeper sediments (facies F5-F7). EDSs have different expressions depending on the time interval and the sedimentary basin.

3.3.1 Zanclean EDS (synthems S1-S3)

In most basins, deposition of synthems S1-S2-S3 takes place at outer-shelf or bathyal depths, well below the point on a depositional profile where the rate of relative sea level change is zero (equilibrium point). Here the sediment supply is not sufficient to fill the available accommodation space and an aggradational style of deposition prevails, with the result that in most Zanclean settings smaller cycles of sea level variations are not marked by a facies change. The sharp facies change recorded where the monotonous muddy deposition is interrupted by turbidite sandstone and conglomerate, is connected with synthem boundaries and major tectonic phases of restructuring of the region. MM and shell beds are practically absent. This situation reverses in the Orcia-Ombrone basin, where depths of deposition are shallower and EDS are expressed. At Arcille deltaic sandy conglomerates and sandstones (facies F3) are overlain by a fluvial cross-bedded sandstone (facies F1a), separated by a transgressive surface (TS) from an overlying bioturbated shallow marine sandstone. A *Haustator vermicularis* shell bed (Danise, 2010; Tinelli, 2013) forms the MFS separating the shoreface sandstone from an open marine mudstone with scattered shells (facies F5), marking a sudden and prolonged deepening of the basin (biozone MPL2: Sorbi et al., 2012; Tinelli, 2013). The succession is topped by deposits from shallower depths, expression of the falling-stage (FSST), below the upper SB (Fig. 4). Similar small-scale depositional sequences, expressed through fining-upward cycles no less than 40 m-thick, are also present in synthem S3 at Case al Poggio, near Siena (biozones MPL3-MPL4a: Bianucci et al., 2001) and at Castelfiorentino (biozone MPL4b: Benvenuti et al., 2014).

3.3.2 Piacenzian EDS (synthems S4-S6)

As depth of deposition shallows during the Piacenzian, and cycles of sea level variation widen, the cyclic stacking of EDS becomes the typical depositional theme (Benvenuti et al., 2007, 2014; Dominici et al., 2008). In FB, the northwesternmost basin, depths remain considerable and facies change is more subtle. Pliocene at Orciano Pisano is traditionally assigned to the “Blue Clays” formation (Bossio et al., 1997), but two distinct bodies where evidenced since the late nineteenth century (D’Ancona, 1867). The lower one is formed by grey claystone with very rare shells, the upper one by muddy, very-fine grained gray sandstone richly fossiliferous. The lower part of the latter interval outcrops at the foothill of the small town of Orciano Pisano, around the locality Case Nuove (Bianucci and Landini, 2005; Berta et al., 2015). Here a laterally persistent shell bed is dominated by the turritellid *Archimediella spirata*, overlain by a 25 m-thick monotonous sandstone interval with intercalated shell beds or sparse shells, becoming muddier upward. The *Archimediella* shell bed is interpreted as the TS of an EDS, coinciding with the lower SB of a lower Piacenzian EDS. The overlying muddy fine-grained sandstone is the TST and HST (MPL5a: Dominici et al., 2009; Fig. 6). At shallower settings, in all basins to the East and South of FB, EDS of synthem S4 take the form of an alternation of mudstone and carbonate (facies F5 and F8: Nalin et al., 2016), or mudstone and sandstone (facies F5 and F3-F4: Benvenuti et al., 2014; biozone MPL5a). Middle and upper Piacenzian EDS form and alternation of coastal mudstone and sandstone (facies F1-F2-F3: Benvenuti and Dominici, 1992; Dominici, 1994), with MFS and HST marked by a shell bed topped by a lower shoreface sandstone, or a shelf mudstone (facies F4-F5: Benvenuti et al., 2007; Dominici et al., 2008).

4. Distribution of large marine vertebrates

4.1 Geographic distribution

The MM geographic distribution is listed in Table 2. All MM that was geographically located, irrespective of stratigraphy, was plotted in Fig. 3. The largest number were recovered in FB in Northwestern Tuscany, with a peak at a few sites around the small town of Orciano Pisano, in the Pisa province. This coincides with the highest number of known species, including mammals, elasmobranchs, turtles, and large bony fishes. MM is also abundant in the province of Siena, around Volterra (VEB; Bianucci and Landini 2005), and around San Quirico, particularly rich with elasmobranchs according to the available data (SRB; Marsili, 2006). A fourth basin with a consistent number of findings is OOB, where cetaceans, sharks, sirenians and large teleost fishes have been unearthed.

4.2 MM stratigraphic distribution

4.2.1 Synthems S1-S2

In the vicinity of Saline di Volterra, one of the sites with remains of *Pliophoca etrusca* (Berta et al. 2015) and sperm whale (Tab. 2), S1 is represented by a bathyal mudstone (facies F6, biozone MPL1). Lower-middle Zanclean MM is otherwise absent, with the exception of S2 in OOB, where large marine vertebrates are concentrated at the maximum flooding interval, outcropping at Poggio alle Mura (Danise, 2010), Camigliano (Sorbi et al., 2012) and Arcille (Tinelli et al., 2012; Tinelli, 2013), in biozone MPL2. At Poggio alle Mura a slightly disarticulated balaenid whale skeleton (WOm1-1 in Tab. 2) has been excavated in contact with the laterally-persistent *Haustator* shell bed at the maximum flooding interval (Figs. 4, 5; Danise, 2010; Tinelli, 2013). At Camigliano and Arcille, tens of km from Poggio alle Mura, the *Haustator* shell bed is associated with other articulated skeletons and isolated MM remains, including several specimens of the sirenian *Metaxytherium subapenninum* (MOm2-1-5), large bony fishes, rays, and sharks *Carcharias taurus*, *Carcharhinus* sp., *Galeocerdo cuvieri*, and *Squatina* sp. (Sorbi et al., 2012; Tinelli et al., 2012; Tinelli, 2013). A partial skull of the delphinid *Etruridelphis giulii*, with right and left dentaries fractured, but nearly complete and with most teeth still in their alveoli (DSi2-1 in Tab. 2), was recovered southeast of Siena, near Chianciano Terme (SRB) at the top of a mudstone (facies F6) intercalated with turbiditic sandstone beds (Facies F7), topped by a monotonous mudstone interval (upper Zanclean, uppermost part of biozone MPL3: Bianucci et al., 2009b). In the same basin, two undetermined beaked whales and bones of four different specimens attributed to *Metaxytherium subapenninum* were found in the middle of a fining-upward succession, at the boundary between biozones MPL3 and MPL4a (Bianucci et al., 2001; WSi2-1-2 and MSi2-1-4 in Tab. 2), suggesting that findings at the two SRB localities belong to the same MFS, in the upper part of S2. Three specimens of marine mammals were identified in Synthem S1, seven in Synthem S2.

4.2.2 Synthem S3

The upper part of S3 yielded an articulated and well-preserved balenopterid skeleton found in a 30 m-thick mudstone succession at Castelfiorentino, in the Elsa basin (EB, WEl3-1). These strata are richly fossiliferous, with several shell beds with epifaunal cemented taxa, such as vermetid gastropods, oysters and corals (Facies F5), in a normal-polarity magnetostratigraphic interval (Gauss chron: Andrea Albianelli, personal communication, 1999). Based on physical stratigraphic correlation, this can be assigned to a lower Piacenzian HST. A skull of *Hemisyntrachelus* sp. (Aldinucci et al., 2011) and partly articulated vertebrae and costae of a dolphin skeleton (Arbeid et al., 2015) were recently excavated a few hundred meters apart one from the other, along a monotonous mudstone S3 succession intercalated with several *Ostrea* and *Serpulorbis* shell beds, near Certaldo (facies F5, DEl3-1-2 in Tab. 2). Overall, specimens of marine mammals attributed to Synthem S3 were eleven (some are uncertain and may come from the upper part of S2: Tab. 2).

4.2.3 Synthem S4

Synthem S4 yielded the highest abundance and species-richness of the Tuscan MM. In the Fine basin, the locality of Orciano Pisano is represented in Table 2 by 18 records of whales, dolphins (a partial skeleton: Bianucci, 1996; Bianucci et al., 2009), seals (Berta et al., 2015), tens of other unidentified cetacean elements, hundreds of shark teeth and vertebrae (Fig. 3), and sea turtles, large bony fishes, and sea birds hosted in museum collections (Bianucci and Landini, 2005; Marsili, 2007b; Cioppi and Dominici, 2011). In locality Case Nuove, a single middle Piacenzian transgressive surface has yielded a whole, articulated whale skeleton (Figs. 4, 6), teeth of blue and white sharks and bones of sea birds (Dominici et al., 2009). From the same site comes a skeleton of the monk seal *Pliophoca etrusca* (Berta et al., 2015), and possibly many other museum specimens labelled “Orciano Pisano”, suggesting that this interval forms the most prolific bonebed of the region (Tab. 2). A few cm above the *Archimediella* shell bed, glauconitic and deeply bioeroded whale bones (Danise, 2010), associated with ichnological evidence of the activity of *Osedax* bone-eating worms (see Higgs et al., 2012), lie in a bioturbated muddy, fine-grained sandstone with a complex boxwork of *Ophiomorpha* and *Thalassinoides* trace fossils (Fig. 6), associated with a diverse paleocommunity of molluscs and other benthic invertebrates with complex trophic connections (Dominici et al., 2009; Danise et al., 2010). At the boundary between FB and VEB, an incomplete skull and skeleton of the dolphin *Etruridelphis giulii* was recovered near Lorenzana (Lawley, 1876; Bianucci, 1996; Bianucci et al., 2009b), at a locality associated with a muddy sandstone interval (facies F4) in synthem S4. An incomplete and articulated mysticete was recovered in a sandstone at San Gimignano, associated with pectinid bivalves (Fig. 7; facies F3; Elsa basin, EB: Danise and Dominici, 2014), here tentatively assigned to the uppermost part of the synthem (WEl4-1 in Tab. 2). Overall, specimens of marine mammals attributed to Synthem S4 were 28.

4.2.4 Synthem S5

The next MM richer stratigraphic interval are Piacenzian deposits of synthem S5. An incomplete and disarticulated balaenid skeleton was found in intertidal deposits of the lower part of the synthem, at Casenuove (facies F2, EB; Bianucci et al., 1995; Collareta et al., 2016; WEl5-1 in Tab. 2). A large balaenid was recovered higher up section, a few meters above a laterally-continuous very thick and complex *Haustator vermicularis* shell bed, up to 2 m-thick (Benvenuti et al., 1995a), traced laterally for 2 km to the east of San Miniato (“*Turritella* strata”, De Stefani, 1874), and forming a surface of transgression within the TST of S5 (Benvenuti et al., 2007; 2014; Dominici et al., 2008). The MFS is formed by a

Glycymeris insubricus shell bed, separating around San Miniato shoreface sandstone (facies F3 or F4) from offshore mudstone (F5; Benvenuti et al., 2007). The balaenid skeleton was almost articulated and bioeroded, closely associated with teeth of the great white shark and other scavengers (Borselli and Cozzini, 1992; Bianucci et al., 2002; Danise and Dominici, 2014), in the early HST of synthem S5 (Benvenuti et al., 2007; Dominici et al., 2008; WEl5-2 in Tab. 2). The *Glycymeris* shell bed can be traced laterally for several km. In the vicinity of Fiano, it includes bioeroded and encrusted gravels inherited from underlying successions, interpreted as revinement deposits. The interval of maximum flooding is marked by the stacking of at least three distinct shell beds, all including a high-diversity association with bioeroded and encrusted shells. This situation suggests that balaenid WEl5-2 lies in correspondence of an interval of low rates of sedimentation. In SRB, near Castelnuovo Berardenga, shelfal mudstones (facies type F5) have yielded MM remains at a few localities. Delphinid remains were found at the “I Sodi” quarry and at Troiola (DSi5-1-2, in Tab. 2). Bones of a beaked whale and undetermined mysticetes are reported from Guistrigona (Manganelli and Benocci, 2014) and a fragmentary specimen of the monk seal *Pliophoca etrusca* from Castelnuovo Berardenga (Berta et al., 2015). A very rich shark fauna, including sawsharks, thresher, frilled, bluntnose sixgill, bramble, gulper, kitten, sand tiger, shorten mako, basking and requiem sharks, an association suggesting an upper slope paleoenvironment for the surroundings of Castelnuovo Berardenga Scalo (Cigala-Fulgosi et al., 2009; the same mudstone interval at the same locality has been interpreted as a shelfal deposit: Martini et al., 2016). Judging from historical accounts (Capellini, 1883), the killer whale *Orcinus citonensis* (DCh4-1) was recovered in a sandy unit lying on top of a thick mudstone interval (S3 or S4) and is tentatively assigned to S5. Specimens of marine mammals attributed to Synthem S5 were 10.

4.2.5 Synthem S6

A fairly complete skeleton of a large balaenid whale was recovered in the second half of the 19th Century in the EB near Montopoli Valdarno (Capellini 1905), in open shelf strata attributable to the interval of maximum flooding of S6 (WEl6-1 in Tab. 2). The MFS of S6, of uppermost Piacenzian age, is marked in EB by a laterally continuous *Pteria phalenacea* shell bed, with a high-diversity association of macroinvertebrates, including a rich decapod paleocommunity (Garassino et al., 2012). In the vicinity, near Palaia, a right whale (*Eubalena* sp.) was recovered in 1974 in sandy mudstones, in association with mollusc shells and teeth of the great white shark (*Carcharodon carcharias*: Bisconti, 2002; Sorbini et al., 2014). A tightly articulated balaenopterid skeleton was found at Sinalunga (WCh4-1 in Tab. 2), in deltaic sandstones and conglomerates (Fig. 8). Marine mammal specimens attributed to Synthem S6 were three.

4.3 MM facies type distribution

In an ideal deepening-up gradient, multi-element findings of marine mammals are very rare in intertidal and very shallow subtidal paleoenvironments (facies type F2, 1,5%: Fig. 9A), moderately represented in delta or shoreface sandstones (facies type F3, 4,6%), most abundant in sandy mudstone of open shelf settings (facies type F5, 70%), rare in outer shelf and bathyal sediments (facies type F6-F7, 1,5%). The most pristine and complete skeletons are associated with gravelly well-sorted sands from event sedimentation, suggesting a negative relationship between taphonomic loss and sedimentary processes at delta fronts. In the tightly articulated and pristine Sinalunga balaenopterid (WCh4-1 in S4-CB), the cortical surface of the tightly-connected vertebrae is practically intact, and carpal, metacarpal and phalanges of the flipper are in perfect anatomical connection, as if a sudden depositional event buried a fresh carcass (Fig. 8; similar pristine skeleton are found in deep water turbiditic succession: Stinnesbeck et al., 2014). Another pristine and tightly articulated skeleton, belonging to a killer whale (WCh3-1 in CB), was collected at Cetona in the second half of the 19th century, in a locality associated with sandstones, also possibly of deltaic origin. Large vertebrates embedded in fine-grained, muddy matrix (shelf deposit formed below storm wave base) and those associated with laterally-persistent shell beds (condensed deposits) are slightly disarticulated and fairly complete, showing signs of long permanence in a low energy, well-oxygenated seafloor before the final burial. Bioerosion of bones caused by phototrophic cyanobacteria and algae, heterotrophic fungi and bacteria (Orciano balaenopterid WFi4-1 in S4-FB), and eventually by whalebone-eating siboglinid worm of genus *Osedax* (on a ziphiid humerus, WFi4-14: Higgs et al., 2012), occurred at condensed intervals, in association with glauconite (Danise, 2010). In one instance, a condensed shelly interval is traced for a few kilometers, connecting bioturbated shoreface sandstones yielding slightly disarticulated sirenian skeletons (MOm2-1, MOm2-2) and other MM (Tinelli, 2013), with open shelf deposits yielding slightly disarticulated whale remains (WOm2-1 in S2-OOB).

Regarding a sequence stratigraphic interpretation, pristine skeletons from delta front sediments can be part of the FSST (Fig. 4; in an alternative interpretation it may belong to the early TST, when incised valleys are filled with coastal deposits). TST deposits account for 6,2% of cases (Fig. 9B). Much more frequently, articulated or slightly disarticulated skeletons are associated with the HST of the corresponding depositional sequence, lying above the MFS (56,9% of cases), or within the maximum flooding interval, above a laterally-persistent shell bed (10,8%). Bone bioerosion is less pronounced in the late HST, when sedimentation rate increases (Castelfiorentino whale WEl3-2 in S3-EB).

4.4 MM abundance and species-richness

Some taxa need revision, but a conservative estimate of the different morphologies suggest that at least 17 marine mammal species lived in the NWMS during the Pliocene (possibly more than 20, an estimate for the whole epoch, i.e., 5,332-2,588 Ma), against nine presently living in the same area (plus two occasional visitors). Among the cetaceans, six families were present, against only five presently living in the Ligurian Sea (Tab. 3). The most abundant Pliocene species of Tuscany are the sirenian *Metaxytherium subapenninum* (N = 10), the dolphin *Etruridelphis giulii* (N = 7) and the delphinid *Hemisyntrachelus cortesii* (N = 5: Tab. 4). Overall abundance and species richness are not randomly distributed, but are maximum in Piacenzian strata of synthem S4, dated at 3.2-3.0 Ma (Tab. 2, Figs 2, 9C-D), particularly in the FB and VEB (Tab. 4). A species list of marine mammals summing up fossils found around Orciano Pisano and at La Rocca, near Volterra, yields a species richness (S) of 13. This Piacenzian peak in marine mammal diversity is matched by the fossil record of sharks, also maximum near Orciano Pisano (S = 27), with a second peak in S5, around Castelnuovo Berardenga (SRB, S = 16). Differently from the marine mammals, showing a complete turnover from the Pliocene to the recent (Tab. 3), 34% of Pliocene shark species are still extant in the NWMS (Tabs. 5-6). Marine mammal frequency and diversity gradually decreases in S5-S6.

5. Paleoenvironment-fauna relations

The paleoecology of Pliocene MM of Tuscany can be reconstructed by comparison with the ecology of their modern relatives. This approach can be applied at the family or genus level for marine mammals (Tab. 3), at the genus or species level for sharks (Tab. 5). With the only exception of the sirenian *Metaxytherium subapenninum*, feeding on seagrasses (Domining, 2001), and small demersal sharks (e.g., catsharks, frilled sharks), all MM studied here are pelagic forms that had no direct connection to conditions at the seafloor (Tabs. 4

and 6). The paleoecology of benthic habitats informs however on the situation of the overlying water column in terms of factors that matter to the distribution of pelagic organisms, such as water depth, salinity and nutrient levels. In the second place, since all MM remains after death ultimately sink to the seafloor, benthic paleoecology is also a means to understand taphonomic controls on MM distribution. Cluster analysis based on the distribution of mollusc species in 72 samples resulted in the identification of four main groups of samples, roughly corresponding to the four main facies types recognised based on lithology and sedimentary structures (F2-F5 in Tab. 1). Clusters are formed by samples from outer shelf and upper slope (three samples), open shelf (34 samples), shoreface (23 samples), and transitional settings, such as brackish-water coastal lagoons and tidal flats (12 samples: see Supplement Material, Fig. S1). ANOSIM confirms that sedimentary facies type can broadly predict what benthic assemblage it will yield (Tab. 7; general R = 0,632). The difficulty to discriminate between upper and lower shoreface facies, and between shoreface and open shelf facies is confirmed by overlaps in sample distribution in the NMDS ordination diagram (Fig. 10A). Samples AG1, MON1 and MON2 allow to re-interpret the associated sandstones, originally included in upper shoreface facies type, as offshore deposits. The presence of gravels and cobbles intensely bioeroded by bivalves and polychaete (ichnofossils include *Gastrochaenolithes*, *Meandripolydora* and *Caulostrepsis*) and encrusted by balanids, oysters, serpulids, and bryozoans, suggests they are part of condensed beds resulting from transgressive pulses (hiatal concentrations). The relationship between facies type and mollusc association is broadly summarised in the following paragraphs (see online Supplement Information for a list of characterising species).

5.1 Coastal lagoon, tidal flat and embayment

Intertidal faunas are always associated with facies type F2 and are characterised by low-diversity associations, sometimes with less than 10 taxa and dominated by one or two species, including species today living in brackish waters of the Mediterranean, at intertidal or very shallow subtidal depths (e.g. *Cerastoderma edule*, *Nassarius reticulatus*, *Scrobicularia plana*: Pérés and Picard, 1964). Facies type F2 is also associated with samples having a species richness higher than the preceding and including species typical of seagrass bottoms and known to withstand moderate changes of salinity. In only one instance a large vertebrate was associated with intertidal deposits (a balaenid, lying on top of large wood fragments: Bianucci, 1995; Collareta et al., 2016).

5.2 Upper shoreface

Facies type F3 is associated with a high-diversity assemblage representing a paleocommunity dominated by suspension feeders adapted to shifting sandy bottoms, with bivalves typical of modern shoreface sandy bottoms (e.g., families Glycymeridae, Tellinidae, Donacidae and Veneridae). Among extinct species of this recurring assemblage, some are large-sized or have very thick shells. Some species of this group indicate the presence of vegetated bottoms. Small pyramidellid gastropods are parasitic on echinoderms, also typical of the upper shoreface.

5.3 Lower shoreface

Species richness further increases in collections associated with facies type F4 (lower shoreface). Species typical of this recurring assemblage include both suspension-feeding and detritus-feeding bivalves and gastropods. The following gastropod families are usually represented by several species: Trochidae, Rissoidae, Cerithiidae (from vegetated bottoms), Naticidae, Muricidae, Turridae, Conidae, Terebridae, Bullidae, Cylichnidae (carnivores), Pyramidellidae (echinoderm parasites). Many bivalve species occur in both facies types F2 and F3. At three different sites and at different stratigraphic units large marine vertebrates, including mysticetes, sirenians and sharks, were recovered in association with shell beds dominated by the gregarious turritellid gastropod *Haustator vermicularis* (Fig. 6C-D).

5.4 Offshore and upper slope

Another important set of species recurred in facies type F5 (mudstone deposited in offshore bottoms at shelf depths). Among characterising gastropods are the suspension feeders (*Turritella tricarinata*, *Archimediella spirata* and *Petalochoncus intortus*), deposit feeders (*Aporrhais uttingeriana*) and carnivores or scavengers (*Epitonium frondiculoides*, *Nassarius semistriatus*, *Mitrella nassoides*). Also the bivalves occupy many different ecological niches (e.g., infaunal detritus feeders, epifaunal suspension feeders, either free-living, byssate, or cemented). Outer shelf and uppermost bathyal sediments from F6 mudstones, studied at only one location, are characterised by a separate set of carnivorous gastropods and by a few small bivalve species. Ubiquitous molluscs include species found from intertidal to outer shelf depths (e.g., *Corbula gibba*), and those preferential of open marine waters, from lower shoreface to outer shelf. Most multi-element findings of marine mammals are associated with sandy mudstones from open shelf settings, below storm wave base, also in association with an *Archimediella spirata* shell bed (Fig. 6C-D). No molluscs were recovered in facies type F7, with the exception of bathyal mudstone in the lowermost Pliocene of FB, associated with sparse specimens of the gryphaeid epifaunal bivalve *Neopycnodonte navicularis* (not sampled).

5.5 Carbonate platform

A recurring benthic assemblage associated with the highly fossiliferous facies type F8, not included in the quantitative analysis, consists of the large pectinid bivalves *Gigantopecten latissima* and *Hinnites crispus* and by a mixture of photozoans (large benthic foraminifera), hard-substrata dwellers (brachiopods, echinoderms), encrusters (red algae, bryozoa) and bioeroders (clionid sponges). All fossil-rich carbonates are associated with synthem S4 , in the mid-Piacenzian (Fig. 2, see also Nalin et al., 2016).

6. Paleodepths

Multivariate techniques are usefully applied to stratigraphic and paleobiologic analysis (Scarponi and Kowalewski, 2004). We used the results of the ordination analysis to estimate absolute depths of the final resting place of some large vertebrates listed in Tab. 2. Samples in the NMDS ordination plot following a water depth gradient, with shallower samples to the left (low values of NMDS axis 1) and deeper samples to the right (high values of axis 1). Therefore, NMDS values of axis 1 can be used as a proxy for relative water depth. We calculated absolute palaeodepths by fitting a logarithmic regression curve between absolute paleodepth of 23 modern species (data from MARBEF database), common in our dataset, and the values on NMDS axis 1 (Supplement Material: Tabs. S1-S4). The regression analysis, with $R^2 = 0.813$, indicates that scores along the nMDS main axis are a good predictor of the preferred depth for the 23 modern species (Fig. 10B, inset), thus supporting the bathymetric interpretation. This allowed to estimate the absolute depth of the 72 samples, which ranged from 0.4 m to 365 m, i.e., from intertidal to upper slope depths (in accordance with a previous estimate of absolute paleodepths in the upper part of the Pliocene of EB, based on counts of foraminifera: Dominici et al., 2007). Facies type F2 is deposited at 0-5 m depth, F3 at 3-30 m, F4 at 10-100 m, and F5 at 40-300 m, F5 at around 350 m depth (only one sample: Fig. 10B). The position of fossil cetaceans, sirenians, pinnipeds and large sharks (respectively W, M, P and S, N = 13) was plotted near the corresponding shell bed in the NMDS ordination. The resulting pattern shows that all MM considered, associated with open shelf settings and with facies types F4-F5, cluster around -100 m, spanning -30-300 m.

7. Factors of the Pliocene NWMS marine megafauna fossil record

The detailed sequence-stratigraphic framework and the abundant shell beds, offering an independent check on sedimentary facies distribution by benthic paleoecology, allows also to explore factors behind MM geographic and stratigraphic distribution, and to sort out evolutionary, ecological, and taphonomic drivers of this particular fossil record. NWMS Pliocene distribution can be compared with similar studies in different settings and at different times, to draw conclusions on the general quality of MM fossil record.

7.1 Evolutionary control

Available data allow a meaningful comparison of NWMS MM diversity across the Pliocene, particularly detailed for marine mammals (Fig. 9D). Although the study suggests a facies control, with MM remains being generally associated with late TST-HST muddy sandstones and mudstones from lower shoreface and offshore shelf paleosettings, the temporal pattern of biodiversity recorded on a regional basis likely reflects also a paleobiologic phanomenon, since lower shoreface and offshore shelf sediments are represented in all synthems. Marine mammals are unrecorded in the thickest part of synthem S1-2 (Zanclean, mostly bathyal mudstone and turbiditic sandstone), but they are present in S2, in OOB (Zanclean shoreface and open shelf deposits) and SRB (Zanclean upper slope deposits). MM gradually rises in S3, at the upper Zanclean-lower Piacenzian, whereas it suddenly peaks in synthem S4, where species richness of both marine mammals and sharks is highest. S5 reflects a lower diversity of marine mammals, but still a high diversity of sharks, while values of both groups drop to the lowest abundance and species richness in S6, during the upper Piacenzian-lowermost Gelasian (Fig. 9D).

The S4 diversity peak coincides with the middle part (3.264–3.025 Ma) of the Piacenzian, a time interval in which the earth experienced global average temperature 1.84 °C-3.60 °C warmer than the pre-industrial period (Dowsett et al., 2013). Climatic impact is testified by the widespread occurrence of carbonate deposits in S4 (Fig. 2), with sedimentary facies indicative of warm-temperate to subtropical conditions, with summer sea-surface temperature considerably warmer than 20°C and winter temperatures colder than 20°C (Nalin et al., 2016). This suggests a causative link between global climate and biodiversity, S4 diversity peak recording a global phenomenon, possibly an increase of speciation rate connected with global warming. Similarly, we propose that the lower diversities recorded at S5-S6 are the regional expression of an increase in extinction rate related to climatic cooling and global sea-level drop, ultimately leading to the global MM extinction event recorded on a coarser scale at the Pliocene-Pleistocene boundary (Pimiento et al., 2017): the finer stratigraphic resolution adopted here suggests a stepwise extinction event. NWMS data also point to a selective effect, extinction being recorded by marine mammals, with a 100% regional turnover between Pliocene and Recent (Tab. 3), but not as much by the shark fauna, with 34% of the species still living in the Mediterranean, while still others have shrank their distribution to subtropical latitudes. Also the Piacenzian teleost fish fauna (Cigala Fulgosi et al., 2009) and benthic molluscs (Raffi et al., 1985) show a high percentage of holdovers, suggesting that marine mammals have been particularly prone to climatic change (see also Steeman et al., 2009).

Estimates of body size in Pliocene mysticetes of Tuscany, with several specimens reaching 10 m (Danise and Dominici, 2014: seven specimens in Tab. 1), are comparable to global values derived from the literature for this time interval (Lambert et al., 2010), confirming that NWMS baleen whales were larger than their Miocene analogues, and smaller than modern forms. As with regard to odontocetes, the most common Pliocene delphinid, *Etruridelphis*, was larger than the modern analogue *Stenella* (Bianucci et al., 2009b). The same is true for *Hemisyntrachelus cortesii*, larger than modern *Tursiops* (Bianucci, 1997a). On the other hand, the largest extant delphinid *Orcinus orca*, reaching 9 m, is about twice as long as *Orcinus citonensis* (Heyning and Dahlheim, 1988). The high percent of holdover points to a more conservative figure for larger sharks (Tab. 5), but the presence in the Pliocene of the gigantic *Carcharocles megalodon* and some large thermophilic species today restricted to lower latitudes suggests that impoverishment of the fauna is coupled with an average decrease in size (Marsili, 2008). Comparing sizes suggests an overall restructuring of NWMS MM during the last three million years (see also Bisconti, 2009).

7.2 Ecological control

The composition of the Pliocene NWMS MM is affected in the first place by the availability of food. At the lowest trophic level, inferring from the ecology of the modern MM (Tabs. 3, 5), we found herbivore sirenians feeding on seagrasses (trophic level, TL = 2,0), all others being carnivores, thus having TL > 3,0 (Fig. 11). The lowermost levels among the carnivores were occupied by baleen whales and whale sharks (TL = 3,2-3,4), filter-feeding on pelagic crustaceans and fishes (krill). Roughsharks, catsharks, and houndsharks, with many species living in the modern Mediterranean, have a relatively species-poor Pliocene record, probably due to a preservation bias related to their small size. At TL = 3,7-4,0 were one species of catshark and a monk seal, both feeding near the seafloor on crustaceans, teleost fishes and cephalopods. At TL = 4,1 were sandbar, tiger and blue sharks, feeding on teleost fishes, cephalopods and on marine mammals. At the same level, in slope environments, kitefin sharks mainly fed on other sharks. The majority of MM species were found at TL = 4,2, with smaller odontocetes (three species) and 11 species of sharks, including several requiem sharks, a houndshark and a hammerhead. Larger dephinids, sperm whales, beaked whales, together with mackerel, sand and sand tiger sharks, occupied high trophic levels (TL = 4,3), followed at the top of the global NWMS food web by white shark, megalodon shark, one species of sevengill shark (genus *Notorynchus*), and killer whales, all feeding on marine mammals and smaller sharks (TL = 4,4-4,7). With no exception, all highest levels encountered in modern NWMS offshore pelagic and nearshore communites were occupied during the Pliocene by an analogous MM, often by the same species (large sharks), or by congeneric or con-familial species (marine mammals: Tab. 3, 5). The Pliocene pelagic ecosystem, typified by the mid-Piacenzian S4 association, must have been however trophically more diversified (Fig. 11), including aquatic megaherbivores, several balaenid filter feeders, larger and more diverse dolphins, and sharks species today extinct (e.g., *Carcharocles megalodon*) or restricted to tropical seas (e.g., *Galeocerdo cuvier*). With the exception of TL = 2, all Pliocene NWMS MM were either apex predators of their community, or mesopredators, occupying trophic positions below apex predators. The definitions of apex predators (or top predators) and mesopredators are relative and to an extent context-dependent (species that in a contact are apex predators, in another are mesopredators, e.g., Estes et al., 1998). Since predation is a trophic interaction in which one animal (predator) consumes another (prey) as a source of energy (food), irrespective of the means by which this is accomplished (Lourenço et al., 2013), filter-feeding baleen whales can be considered apex-predators of their community (e.g., Lewiston et al., 2004; Notarbartolo di Sciara et al., 2016). Among sharks, 68% of living Mediterranean elasmobranches are ranked as top predators, with a trophic level of 4 or more (Goffredo and Dubinsky, 2014, including superorder Batoidea, against 22% of teleost fishes), an estimate that can be extended to Pliocene NWMS MM. Relationships between apex predators and mesopredators are complex and hard to define in ecology, involving predation on other predators (intraguild predation, combining competition and predation: Polis et al., 1989), where consumption and competition need to be proved (Lourenço et al., 2013). In the Mediterranean Pliocene, paleontological evidences of carnivores serving as food to MM include killing of prey (Bianucci et al., 2010) and scavenging (Cigala Fulgosi, 1990; Bianucci et al., 2002; Dominici et al., 2009). The occurrence of intraguild predation must have been far more extended than what taphonomy can prove, however, given a Pliocene diversity of NWMS very large raptorial feeders higher than the modern, including the killer whale *Orcinus citonensis*, the large delphinid *Hemisyntrachelus cortesii* (phylogenetically related to the modern killer whale: Murakami et al., 2014), the white shark *Carcharodon carcharias*, the largest shark of all times *Carcharocles magalodon* (Marsili, 2008), and a diverse association of smaller carnivores, including monk seal, delphinids and sharks with 4,0 < TL < 4,2 (Tab. 3, 5), candidate prey for larger raptorial feeders. This interaction likely exerted in its turn a control on community structure at lower trophic levels through processes like “mesopredator release” and trophic cascades (Roemer et al., 2009), eventually linking pelagic and nearshore communities, including benthic animals and plants, like in many modern ecosystems (Estes et al., 2011, 2016), down to slope depths (e.g., Parrish, 2009). Large raptorial feeders could exert a control on the diversity of the filter-feeding MM, like it has been suggested on a global scale since the Miocene (Lambert et al., 2010), and for the Pliocene by Bisconti (2003), when baleen whales were more diversified, both in terms of species richness, size range, and feeding strategies, including both skim- and lunge-filter feeding (respectively balaenid and balaenopterid whales: Berta et al., 2016; Hocking et al., 2017), minimising competition for food and diversifying spatial niches (see also Marx et al., 2017, for the upper Miocene). A further important top-down control on community structure is suggested by modern studies on the role of baleen and sperm whales as nutrient vectors, both in horizontal (during seasonal migration) and vertical direction (during daily feeding migration: Roman and McCarthy, 2010), a process particularly important in oligotrophic seas (Alleger et al., 2017), like large sectors of the Mediterranean. Finally (literally, after death), MM becomes a detrital sources of energy and habitat for deep sea whale-fall communities (Roman et al., 2014; Smith et al., 2015), with paleontological evidence available for the NWMS (Dominici et al., 2009; Higgs et al., 2012; Baldanza et al., 2013).

Much evidence suggests that a bottom-up control on the structure of NWMS MM community was exerted by wind-driven upwelling currents, through enhanced oceanic productivity and concentration of preys. Over geologic time, these factors may have exerted a selection favoring large size, triggering the Plio-Pleistocene emergence of whale gigantism in several lineages (Slater et al., 2017). The largest among marine top predators can travel long distances and cross oceans, but tend to congregate in shallow waters with abundant prey. Baleen whales, abundant in boreal eutrophic waters (Woodley and Gaskin, 1996), with population size under the control of food availability (Croll et al., 2005), always require high prey density for efficient bulk filter feeding (Goldbogen et al., 2011). Six different species of mysticetes currently foraging in the Southern ocean, among which the largest animals that have ever lived in world oceans, exploit the high biomass of Antarctic krill, their main food resource. Great white sharks are abundant in the offshore of California (Jorgensen et al., 2010), Australia-New Zealand, South Africa, and in the Mediterranean (Bonfil et al., 2005), clustering in proximity of seal colonies, including monk seals. The distribution in the modern Mediterranean is no exception to general rule, only in a smaller scale, with large sharks and marine mammals congregating in productive areas, such as the Strait of Sicily and the Balearic Archipelago (Tabs. 3, 5), with the second largest animal on earth, the fin whale, showing a movement pattern that parallels seasonal variability in available feeding habitat (Notarbartolo di Sciara, 2016), contributing to the horizontal transfer of nutrients. Tuscany faces the Ligurian Sea, where a deep-water upwelling current coming from Southeast convects nutrients to the water surface, leading to high levels of primary productivity in its western sectors, extending westward to the Provençal and Balearic Seas, with spring algal blooms. These waters host different trophic regimes in an otherwise oligotrophic Mediterranean Sea (Lazzari et al., 2012; Melanotte-Rizzoli et al., 2014; Stambler, 2014). Supporting a conspicuous biomass of zooplankton (Cuzin-Roudy 2011), the Ligurian Sea sustains large populations of fin whales (*Balaenoptera physalis*) and striped dolphins (*Stenella coeruleoalba*: Notarbartolo di Sciara et al., 2008). Mediterranean-resident fin whales have adapted to exploit localised mesoscale hotspots of productivity that are highly variable in space and time (Notarbartolo di Sciara et al., 2016), feeding behaviors possibly mediated by the depth of prey and species-specific behaviours, allowing to minimise competition with other large filter feeders (see Friedlaender et al., 2014). The sperm whale *Physeter macrocephalus* uses habitat across a range of depths and a specialised diet (Rendell and Frantzis, 2016), gathering along NWMS steeper slopes, where water currents allows for higher trophic level biomass (Pirotta et al., 2011). Beaked whales are particularly abundant in the Ligurian Sea and central Tyrrhenian Sea, preferring submarine canyons at slope depths (Podestà et al., 2016). The largest among common Mediterranean delphinids, *Grampus griseus*, is frequent in the Ligurian and Thyrrenian seas where it forages on cephalopods at depths 300-1500, where upwelling currents are most effective (Azzellino et al., 2016).

The NWMS existed as a Liguro-Provençal back-arc oceanic basin since the upper Miocene, when Sardinia rotated to its present position (Gattacceca et al., 2007), and in coincidence with the formation of the hinterland basins here under study (Muttoni et al., 2001), justifying the assumption that the modern NWMS trophic regime is a feature that dates back at least to the upper Miocene. Consistenly, diatomites deposited in Tuscany during the Messinian, before the salinity crisis (Bossio et al., 1997; Roveri et al., 2014), indicate that high productivity was a primitive feature of the Ligurian Sea. Paleontological evidences include the high diversity and abundance of Pliocene MM in FB, the closest to modern upwelling areas (Fig. 3), and the association of several MM with "*Turritella* beds", turritelline gastropods showing gregarious habit and high abundance in areas of high primary productivity (Allmon, 1988). Both a comparison with the modern and paleoecologic data strongly suggest that a wedge of NWMS nutrient-rich waters intersecting the Tuscan shelf exerted a strong bottom-up control on community structure through mixing and upwelling of nutrients, stimulation of phytoplankton blooms, followed by zooplankton increase, while nekton and vertebrates tracked plankton concentrations, as is typical of modern upwelling systems throughout the world (Polis et al., 1997). High surface primary productivity in the study area during the Pliocene would have caused a concentration of detritus-falls, supporting a diverse community of deep-sea scavengers.

7.3 Taphonomic control

Taphonomic data on articulation and completeness of MM specimens are available for large mammals, the shark record being formed mainly by isolated teeth collected through superficial picking during the years (Cigala Fulgosi et al., 2009), with only a few contextualised studies (e.g., Bianucci et al., 2002; Dominici et al., 2009). Our record includes several marine mammals with a high degree of articulation (14%) and completeness (27%), or with at least cranial and post-cranial elements of the same individual (38%). All articulated specimens and the most complete skeletons are associated with shelf mudstones, usually forming the HST of the relative depositional sequence (Tab. 2), with two exceptions, one associated with delta-front, coarse-grained beds (WCh6-1, Fig. 6), another from outer shelf or upper slope sediments (DSi2-1). These data point to a strong environmental control on the quality of the MM fossil record, at least concerning articulation and completeness of skeletons, very shallow and very deep (bathyal) depths being generally unfavourable to the preservation of MM bones (Fig. 9A). To explain these results, hypotheses are based on the available data on carcasses of MM in modern marine environments.

The biostratinomy of lung-breathing marine mammals depends on water depth (Allison et al. 1991; Smith et al., 2005). The vast majority of mammals are negatively buoyant and sink after death, but in shallow waters the low hydrostatic pressure allows putrefaction gases to develop and carcasses to resurface. Skeletons are scavenged (Dicken, 2008) and disintegrate while floating, leading to the preferential deposition of isolated bones. At deeper settings, where high hydrostatic pressure allows the carcass to lay relatively undisturbed on the seafloor, the skeleton becomes only slightly disarticulated after soft tissue removal (Reisdorf et al., 2012). The subsequent fate of deep-water, disarticulated skeletons depends on the nature of the scavenging fauna and other elements of the whale-fall community, and on the time of exposure on the seafloor (Boessenecker et al. 2014). At depths deeper than the slope breaks, where sedimentation rate is very low, carcasses are exposed for a long time and the skeleton is rapidly disintegrated. Time-series analyses carried out at modern whale-fall communities at slope depths (range 382-2893 m: Lundsen et al., 2010) suggests that carcasses up to 17 m are rapidly degraded, with the deepest whale carcasses disappearing after only seven years of exposure on the sea floor. Larger skeletons may persist on deeper settings for decades, but if not buried, they also ultimately undergo complete destruction. Although environmental forcing triggered by higher temperatures, active currents and sediment transport, clearly plays a role, a specialised whale-fall fauna rapidly consumes both soft and mineralised tissues. This fauna is characterised by low diversity and high abundance of microorganisms, most likely as a result of both specialisation to nutrient enrichment and high growth rates. Whale-fall habitats likely undergo a temporal microbial succession from primarily heterotrophic to more heterotrophic/chemosynthetic metabolisms until the whale biomass is completely exploited (Smith et al., 2015). Of all the specialised taxa, bone-eating polychaetes of genus *Osedax*, with their soft root-like tissues that erode the bones to access nutrients (Tresguerres et al., 2013; Minamoto et al., 2017), are the primary cause of bone disintegration, particularly of denser bones (Higgs et al., 2011). Found also at shelf depths, but invariably in low abundance (Huusgaard et al., 2012; Higgs et al., 2014b), bone-eating worms occur in high numbers in the deep sea (Smith et al., 2015) where they act as biodiversity regulators (Alfaro-Lucas et al., 2017). The general paucity of novel taxa on shallow-water whale falls suggests that species-rich, specialised whale-fall communities develop only in the food-poor deep sea. Accordingly, among new animal species described in the recent literature from whale falls, only about 10% have been found on whale remains at depths of less than 260 m (12 out of 129 new species: Smith et al., 2015). Of all MM investigated so far, only whales are known to host a whale-fall community, but also carcasses of large elasmobranchs undergo rapid destruction at bathyal depths, teeth being all that eventually remains (Higgs et al., 2014a; teeth are also lost by sharks during feeding: Pokines and Symes, 2013). As a consequence, over geological time no large marine vertebrate is expected to be recovered at depths greater than the shelf break. On the opposite side, the lack of a biota specialised in exploiting large organic falls, coupled with higher rates of deposition in proximity of sediment sources, make it more probable that the most articulated and complete whale skeletons become part of the fossil record of shelf settings below storm wave base.

8. Comparison with other studies

The study of sedimentary facies uncovers some environmental factors that directly control the taphonomy of large marine vertebrates. Such abiotic drivers include water pressure, wave energy and sedimentation rate — three factors summarised by water depth, and upwelling, bringing to the surface deep sea nutrients and concentrating preys. The taphonomic pathway of large marine carcasses is also driven by biotic factors that change in geological time in response to coevolution between bacteria, scavengers and their substrates. We now explore the multifaceted nature of MM taphonomy by reviewing Mesozoic and Cenozoic studies where sufficient data for stratigraphic paleobiology are available.

8.1 Abiotic factors

According to one of the few previous studies on the sequence stratigraphic distribution of MM, Jurassic ichthyosaurs, plesiosaurs, and pliosaurs of the Sundance Seaway, in North America, display facies control and are found primarily in offshore mudstone and at condensed intervals at the maximum flooding surface, rather than shoreface and estuarine sandstone (McMullen et al., 2014). Taphonomic data on Upper Cretaceous marine reptiles and large fishes suggest that partially articulated and disarticulated skeletons are associated with little biological activity and relatively rapid burial by muddy sediments, deposited in the North American seaway during an interval of maximum flooding (Schemisser McKean and Gillette, 2015). Upper Cretaceous mosasaur remains are particularly concentrated in fine-grained shelf deposits in Europe (Jagt and Jagt-Yazykova, 2016). Complete, partially articulated whale skeletons of archaeocetes, together with bones and teeth of sirenians and sharks, are abundant in offshore marine flooding surfaces (MFS) in the Priabonian late TST of Egypt. In a further parallelism with the Pliocene of Tuscany, Late Eocene well-articulated whales are associated with rapidly accumulating shoreface sediments of the FSST, comprising “*Turritella* shell beds” (Peters et al., 2009). During the Oligocene, eomysticete whale bones were deposited at shelf depth below storm wave base. The occurrence of sparse traces attributed to *Osedax* and the association with a glauconitic limestone testify to the exposure of bones on the seafloor without undergoing complete destruction (Boessenecker and Fordyce, 2014), in a manner similar to MM at Orciano (see Danise et al., 2010; Higgs et al., 2012). Burdigalian/Langhian MM recovered in the Antwerpen Sands, in Belgium (including isolated remains of a baleen whale, several odontocetes and a pinniped) are fragmented, worn and associated with clayey sandstone rich in glauconite, suggesting long exposure on the sea-floor (Louwye et al., 2010). Bones are concentrated at the base of a coarsening-upward succession, on top of shallow marine, coarse-grained sandstone, suggesting this is a surface of maximum flooding. An association of MM taxonomically comparable to that here under study is encountered in the Mio-Pliocene of the Purisima Formation, in Central California. Taphofacies differ in some aspects. The Pliocene of California yields laterally persistent bonebeds with polished and phosphatised bones, and abundant phosphate nodules that are absent in Tuscany, indicating times of higher sediment starvation during transgressive pulses, in an area of much stronger nutrient content (the California Current system is a northern-hemisphere analogue of the Peruvian upwelling system, associated with the economically most important fish stocks in the world: Mann and Lazier, 2006). Shoreface deposits indicate stronger wave energy, and the preferential absence of molluscs in bonebeds indicates chemical destruction of carbonate shells (Boessenecker et al., 2014, in a quantitative MM taphonomic study). Episodic sedimentation, however, causes the preferential preservation of articulated remains in the Californian offshore as in the Pliocene of NWMS. The late Miocene Pisco Formation in Perù offers another, more extreme example of MM taphonomy in a eutrophic setting. Here almost two hundred cetaceans, pinnipeds, and sharks were described in an exceptional state of preservation (Bianucci et al., 2015), within a monotonous succession of finely laminated white diatomites (Di Celma et al., 2015), suggesting very high primary productivity in an area of intense upwelling and volcanic activity. Algal blooms sustained high biomass of apex predators (see Marx and Uhen, 2010), triggering at the same time anoxic conditions at the seafloor where MM carcasses remained intact (Brand et al., 2004; see also Gioncada et al., 2016; Marx et al., 2017, also in offshore paleosettings). Finally, the stratigraphic distribution of Pliocene cetaceans in western Emilia (Italy) shows an uneven distribution of findings (N = 24, dolphins and baleen whales) and a strong positive correlation with offshore mudstones (no findings in shoreface sandstones, rare occurrences in epibathyal mudstones: Freschi and Cau, 2016), paralleling the distribution of Tuscan Pliocene MM.

8.2 Biotic factors

Many reviews of Triassic (Camp, 1980; Hogler, 1992; Motani et al., 2008; Hu et al., 2011; Liu et al., 2014) and Early Jurassic marine reptiles (Benton and Taylor, 1984) report mostly good preservation and a high degree of completeness and articulation of skeletal material. This record might be partially controlled by prevailing anoxic or dysoxic conditions in the bottom waters of many Mesozoic fossiliferous deposits (e.g., Middle Triassic Besano and Guangling Formations, Lower Jurassic Blue Lias and Posidonia Shale Formations), which precluded organism activity within the sediment, and prevented predation or scavenging of the carcasses on the sea bottom (Beardmore and Furrer, 2016). Evidence of advanced levels of disarticulation or bone degradation (Martill, 1985; sauropterygians, crocodilians, ichthyosaurs and fishes from the Middle Jurassic Oxford Clay Formation), is mostly attributed to physical factors (e.g., weathering on the sea floor). Up to the early-Late Cretaceous, biological activity is testified by circumstantial evidence of scavenging (*Hybodus* teeth associated with marine reptile skeletons, Martill et al., 1994), and by the more common occurrence of microbial mats, grazers and encrusters (Martill, 1987; Meyer, 2011; Danise et al., 2014; Reolid et al., 2015), but lack traces of bone-eating worms and sulphophilic fauna typical of modern whale falls. The siboglinid *Osedax* is an evolutionary novelty in possessing a root system that hosts heterotrophic mutualists and secretes bone-dissolving acids (Tresguerres et al., 2013; Miyamoto et al., 2017), and an ecosystem engineer (Alfaro-Lucas et al., 2017). Genus *Osedax* is today associated with whale falls worldwide (Taboada et al., 2015), but its impact on MM has changed in time. The oldest trace fossils attributable to a bone-eating fauna is found on early-Late Cretaceous plesiosaur and sea turtle bones (about 100 Ma: Danise and Higgs, 2015). Time estimates suggest that *Osedax* diverged from other siboglinids in the Middle Cretaceous (around 108 Ma: Taboada et al., 2015). However, if the bone-eating worm lives also on the bones of birds and terrestrial mammals (Rouse et al., 2011), its global nature and high species diversity in modern oceans suggest that whale falls, as complex and species-rich habitats, have been the most important biodiversity generators (Higgs et al., 2014b; Smith et al., 2015). And although the first appearance of *Osedax* is concomitant with the occurrence of large marine reptiles and teleost fishes in the oceans, long before whale evolution, and although their distribution is not limited to large carcasses (Pyenson and Haas, 2007), the radiation of ocean-going mysticetes at the Oligocene onset of the Antarctic Circumpolar Current (Fordyce, 2003) clearly increased available substrata worldwide. The steady increase of cetacean size during the Neogene, with a dramatic pulse in the last five million years, when Neoceti surpassed 10 m length and reached 30 m in the Pleistocene (Lambert et al., 2010; Slater et al., 2017), would have thus triggered a second and more massive radiation of bone-eating worms (Kiel and Goedert, 2006). Consistently with this hypothesis, the preferential distribution of modern *Osedax* in high latitude settings worldwide (Taboada et al., 2015) suggests that biodiversity hotspots coincide with the feeding grounds of larger cetaceans. Other bone-eaters of modern deep water whale-fall ecosystem belong to the group of abyssochrysoid snails, with fossils found on Late Cretaceous plesiosaur (Kaim et al. 2008) and sea turtle bones (within a chemosynthesis-based association: Jenkins et al., 2017). Modern abyssochrysoid whalebone-eaters of genus *Rubyspira*, hosting a specific and exclusive microbiome (Aronson et al., 2017), split during the upper Eocene/lower Oligocene (Johnson et al., 2010). Species of *Rubyspira* benefited too from the radiation of ocean-going whales. Although scanty, available evidence on the geological history of bone-eaters thus makes the ephemeral nature of large carcasses in modern deep seas — and their absence in bathyal deposits of the Pliocene of NWMS — a larger-than-life model for the Mesozoic and the early Paleogene.

9. Conclusions

1) Sedimentary facies in the Pliocene of Tuscany are vertically stacked to form small-scale depositional sequences particularly in the upper half, Piacenzian part of the succession, with laterally-continuous shell beds marking transgressive surfaces and intervals of maximum flooding. Small-scale sedimentary sequences are stacked to form six major, unconformity-bounded stratigraphic units (synthems) of regional extension, forming a high-resolution framework to study the chronostratigraphic distribution of marine megafauna (MM).
2) Benthic biotopes, identified through a quantitative study of a large mollusc dataset, can be arranged to form an ideal onshore-offshore, bathymetric gradient, connecting terrestrial environments with deep sea epibathyal bottoms, consistently with the distribution of sedimentary facies. MM remains and shell beds are present in all marine paleoenvironments, but their distribution is uneven. The fossil record of large vertebrates, including marine mammals (abundance data) and sharks (presence-absence data), is particularly rich in sediments deposited between storm wave base and shelf break, moderately rich in shoreface sediments, very poor in epibathyal sediments. Paleobathymetric estimates suggest that a peak of abundance of better preserved skeletons occurs around 100 m depth, within the 30-300 m range.

3) Species-richenns of MM and abundance of marine mammal remains steadily increase during the Zanclean, reaching a peak in synthem 4, possibly as a response to the mid-Piacenzian warm period, and gradually decrease until reaching a minimum in proximity of the Plio-Pleistocene boaundary.
4) Comparison with ecological data on a global scale, paleogeographic and topographic considerations on the North-Western Mediterranean Sea (NWMS), and the occasional association of Pliocene MM with *Turritella* beds, suggest that upwelling and high-nutrient conditions in the Northwestern Mediterranean offshore sustained during the Pliocene a rich community of apex predators and mesopredators. Higher taxonomic MM diversity in the NWMS during the Pliocene, suggests higher niche-partitioning with respect to the modern NWMS and a top-down control on community structure.
5) A comparison with studies on the biota exploiting tissues of large food particles sunken on the seafloor, both modern and ancient, suggests that the poor epibathyal record of Pliocene larger vertebrates of Tuscany may be caused by the destructive action of bone-eating invertebrates. This biotic driver of the marine vertebrate fossil record was less efficient before the radiation of ocean-going whales in the late Eocene-lower Oligocene. On the other hand, bone-eaters played a major taphonomic role on a global scale after the Pliocene-Pleistocene increase in whale size.
6) Due to resurfacing of carcasses in shallow waters, the MM fossil record through the Mesozoic-Cenozoic reviewed through stratigraphic paleobiology shows a strong facies control, being more continuous in rocks deposited below storm wave base and above the shelf-slope break during sea-level transgressions and highstands.

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Figure and table captions:

Fig. 1 - Location of sedimentary logs within the largest Pliocene basins of Tuscany. Fine Basin (FB): Pagliana (1), Pieve Vecchia (2) and Orciano Pisano (3). Volterra-Era Basin (VEB): Parlascio (4), Lajatico (5), Fabbrica (6) and Volterra (7). Era Basin (EB): San Lorenzo (8), La Serra (9), Poggio al lupo (10), San Maiano (11), Canneto (12), Casenuove (13),

Castelfiorentino (14), Fiano (15) and San Gimignano (16). Orcia-Ombrone Basin: Arcille (17) and Poggio alle Mura (18). Siena-Radicofani Basin (SRB): Siena (19), Monteaperto (20), Castelnuovo Berardenga (21), Radicofani (22) and Fastelli (23). Chiana Basin (CB): Sinalunga (24), Cetona (25) and Allerona (26).

Fig. 2 - Pliocene stratigraphy of Tuscany, see Fig. 1 for the location of numbered sections. All logs measured and described by the authors, except Volterra (log 7: Bianucci et al. 1998), Arcille (log 17: Tinelli et al., 2012; Tinelli, 2013), Siena (log 19: Bianucci et al., 2001), Monteaperto (log 20: Martini et al., 2011), Castelnuovo Berardenga (log 21: Martini et al., 2016) and Radicofani (log 22: Ghinassi and Lazzarotto, 2005). Chronostratigraphy of localities 25 (Poltriciano, Cetona: Capellini, 1883) and 26 (Allerona: Danise, 2010) are unknown. Correlation between sections is also shown as boundaries of planktonic foraminifera biozones (dashed lines), following the scheme of Sprovieri (1992), based on available biostratigraphic studies for each basin (see main text for relevant references).

Fig. 3 - Abundance of fossil MM records in major museums of Tuscany, distributed by locality of provenance. Each record ranges from a single fragment or tooth, to articulated, nearly complete skeleton. A: masticates and odontocetes; B: large sharks; C: sirenians — scuba diver for scale in each figure. Symbols for basins as in Fig. 1.

Fig. 4 - Detailed sedimentary logs measured at three localities, representing three different stratigraphic contexts for the large marine vertebrate fossil record of the Tuscan Pliocene. The succession at Orciano Pisano is included in synthems S3-S4 of FB, at Arcille-Poggio alle Mura-Camigliano in synthem S2 of OOB, at Sinalunga in synthem S6 of CB. See Figs.1-2 for the location of the numbered localities and references in the main text for facies

analysis and sequence stratigraphy of synthem S5. Arcille log from Tinelli et al., 2012, and Tinelli, 2013.

Fig. 5 - Taphonomy of large marine vertebrates at Poggio alle Mura (Figs. 5A-5D) and Arcille (Fig. 5E, see Fig. 4 for the sequence stratigraphic and sedimentary context; plan view of the sirenian skeleton is modified from Tinelli et al., 2012), synthem S2. A: Plan view of the Poggio alle Mura undetermined balaenopterid. Parts of the skeleton are quasi-articulated, others are scattered, but not far from the original position. B: Quasi-articulated vertebrae of the same specimen, lying on top of a *Haustator* shell bed. C: Side view of a vertebra on top of the densely-packed shell bed. D. Detail of the shell bed, in top view. The turritelline gastropod *Haustator vermicularis* is visible in the upper left, a large fragment of wood in the lower right, with the inchnofossil *Teredolithes* produced by wood-dwelling teredinid bivalves, in the centre of the photograph. E: Plan view of one of the Arcille sirenian specimens of *Metaxitherium appenninicum*. Same scale as in 5A, the arrows points to the North.

Fig. 6 - Taphonomy of a 10m-long, undetermined balaenopterid at Orciano Pisano (see Fig. 4 for the sequence stratigraphic and sedimentary context), synthem 4. A: Planimetry of the quasi-articulated and nearly complete skeleton. B: Detail of the central part of the skeleton in the field. The cortex layer of vertebrae and flipper bones is badly consumed, whereas some of the costae are still pristine. C: Lateral view of a turritellid shell bed, below, and the surface where the whale skeleton lied (dashed line), about 15 cm above the shell bed. The sediment is a very fine-grained silty sand, completely bioturbated (large vertical burrows are visible). D: Top view detail of the turritellid shell bed. At the center a valve of *Yoldia nitida*, surrounded by a few specimens of the turritellid *Archimediella spirata*.

Fig. 7 - Taphonomy of an incomplete, undetermined mystecete at Castel San Gimignano, synthem 4, comprising articulated torso elements. A: Planimetry of the articulated elements. B: Detail of one of the limbs in the field (trowel for scale = 22 cm): humerus, radius and ulna are in anatomical relationship; the cortex layer is well preserved, suggesting quick burial of the carcass. C: Bones of the chest region; on the background the massive sandstone associated with the fossil whale. Articulated shoreface pectinid bivalves (*Pecten flabelliformis*) were interspersed in the sandstone (photographs by Fabio Cozzini, 1985).

Fig. 8 - Taphonomy of a 5m-long, undetermined balaenopterid at Sinalunga (see Fig. 4 for a tentative sequence stratigraphic interpretation), synthem 6. A: Oblique view of the fully articulated skeleton lying in a gravelly sandstone, stratified in the lower part, massive in the upper. Vertebrae are tightly connected as if in life. B: Plan view of the flipper, with carpals, metacarpals and phalanges in perfect anatomical connection. C: The gravelly sandstone lies above a bioturbated muddy sandstone, with vertical burrows (*Ophiomorpha*). D: The lower part of the unit with the whale skeleton if formed by three fining-upward beds. Each bed grades from gravel to medium-grained sand. Articulated and empty shoreface bivalves (e.g., *Callista chione*), not in life position, are interspersed with the coarse gravel.

Fig. 9 - Quantitative analysis of the facies type and sequence stratigraphic distribution of large marine vertebrates, Pliocene of Tuscany (N = 39, see Tab. 2). A: The vast majority of cases (77%) are associated with fine-grained muddy sediments of the shelf, a few are found in deltaic coarse-grained strata. B: Most MM (69%) is found in highstand deposits, a few in proximity of the maximum flooding interval, or in transgressive deposits.

Fig. 10 - NMDS ordination of bulk samples (N = 72, see Fig. 2 for their stratigraphic position), based on the distribution of standardised abundances of 329 mollusc species (further

explanation on multivariate techniques in the main text). A: Samples are subdivided based on the associated sedimentary facies types (F2-F5 in Tab. 1). The main axis ordinates samples along a paleodepth gradient, from shallowest to deepest, moving from the left to the right side of the bivariate plot. B: Same ordination, with an estimate of absolute paleodepth of each sample based on score along the main axis and calibrated through the average modern depth distribution of 23 extant species characterising the Pliocene dataset (abundance > 0.15%, see text; regression logarithmic curve in the inset). Vertebrates recovered in proximity of some of the samples (N = 13) are plotted on the diagram, confirming that, on average, the MM fossil record is concentrated on the open shelf at an estimated depth of 30-300 m (M = sirenians; S = sharks; P = pinnipeds; W = whales).

Fig. 11 - Occupancy of trophic levels by Pliocene marine mammals and sharks in the north-western Mediterranean, expressed by number of species per trophic level (see Tabs 3, 5 for explanation and references). This figure, summing up data for the whole epoch, spanning circa 2,8 My, closely matches the association found in one single synthem S4, of much shorter duration (mid-Piacenzian, 3-4 hundred thousand years).

Tab. 1 - Sedimentary facies types.

Tab. 2 - Stratigraphic, taphonomic and paleoenvironmental framework for Pliocene marine mammals recovered in Tuscany, with abundance data (N = 64). A: Articulated and quasi-articulated skeleton; C: Complete and quasi-complete skeleton; C+PC: Cranial and post-cranial remains.

Tab. 3 - Paleoecology of Pliocene large mammals and ecology of modern NWMS analogues.

Tab. 4 - Geographic distribution of Pliocene large mammals in Tuscany.

Tab. 5 . Paleoecology of Pliocene sharks and ecology of modern NWMS analogues.

Tab. 6 - Geographic distribution of Pliocene sharks in Tuscany.

Supplement Material

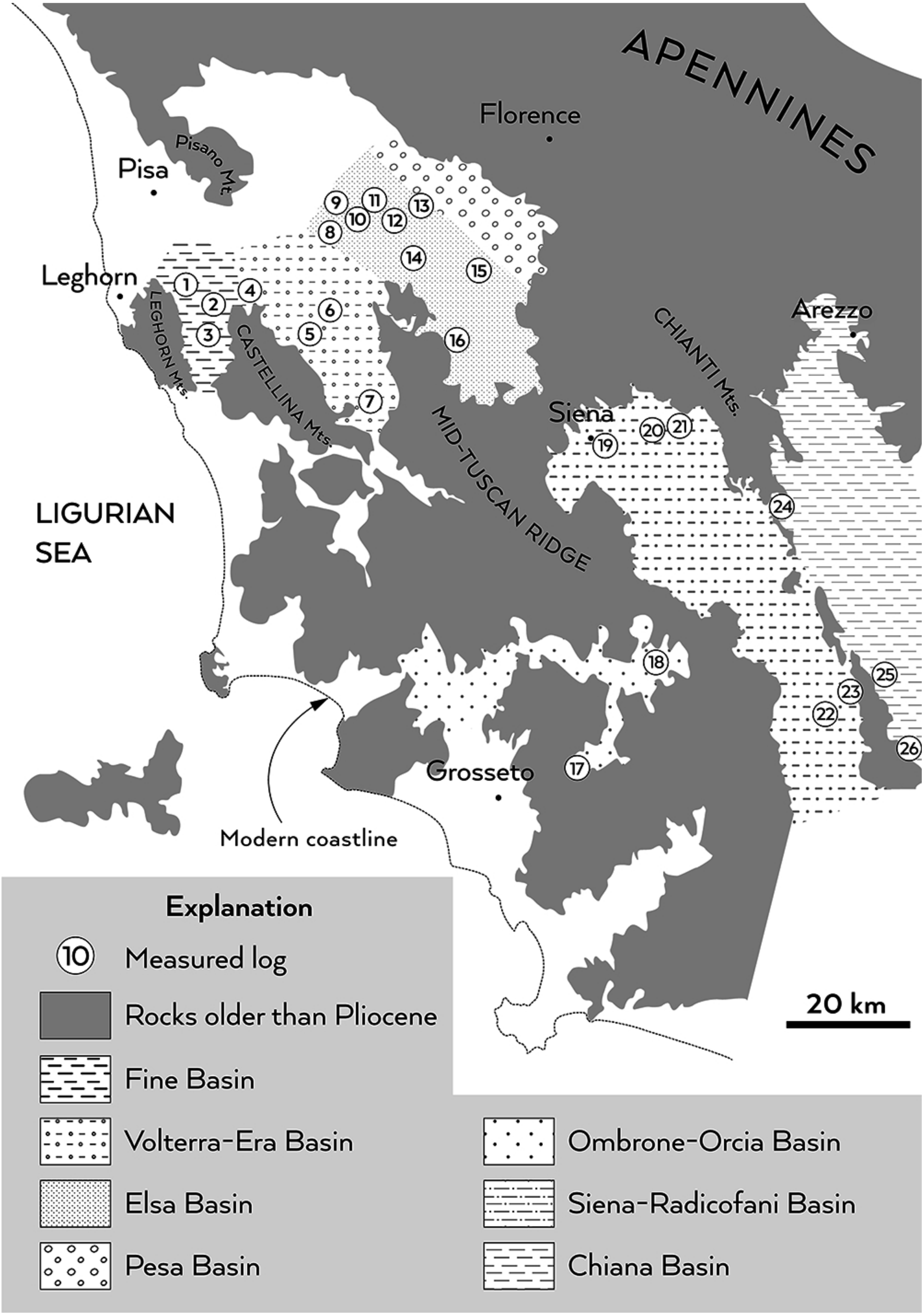
Fig. S1 - Dendrogram resulting from cluster analysis of a dataset of 336 species distributed in 72 samples (standardised abundance, square-root transformed, Bray-Curtis similarity).

Tab. S1 - Ranked total average of standardised abundance of Pliocene molluscs.

Tab. S2 - Score on main axis of NMDS ordination (NMDS1) of Pliocene mollusc species (N=329).

Tab. S3 - Average depth of extant mollusc species with >1,5% abundance in the Pliocene dataset (N=23).

Tab. S4 - Estimated depth of Pliocene samples (N=72) based on NMDS1.


APENNINES
Florence
Pisano Mt.
Pisa
Leghorn
LEGHORN Mts.
CASTELLINA Mts.
MID-TUSCAN RIDGE
CHIANTI Mts.
Arezzo
Siena
LIGURIAN SEA
Grosseto
Modern coastline
20 km
1
2
3
4
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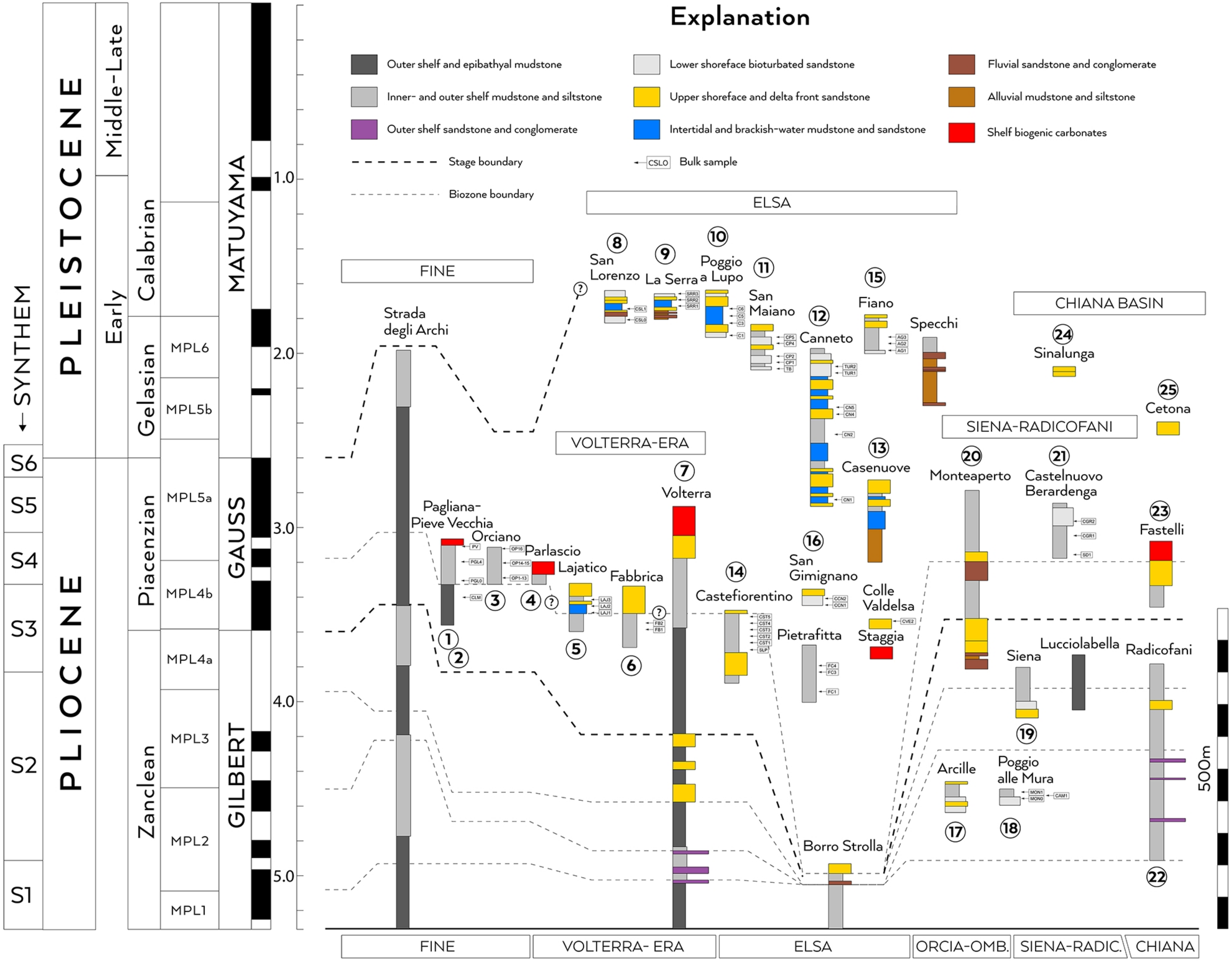
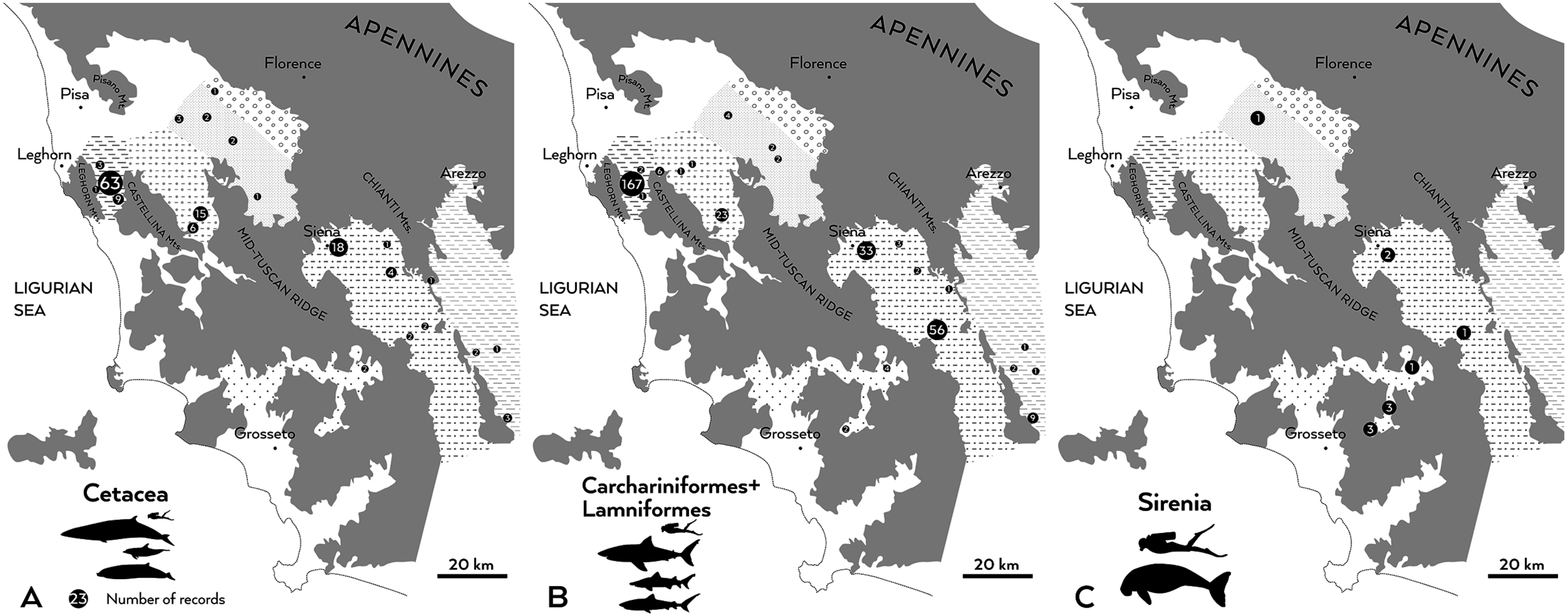
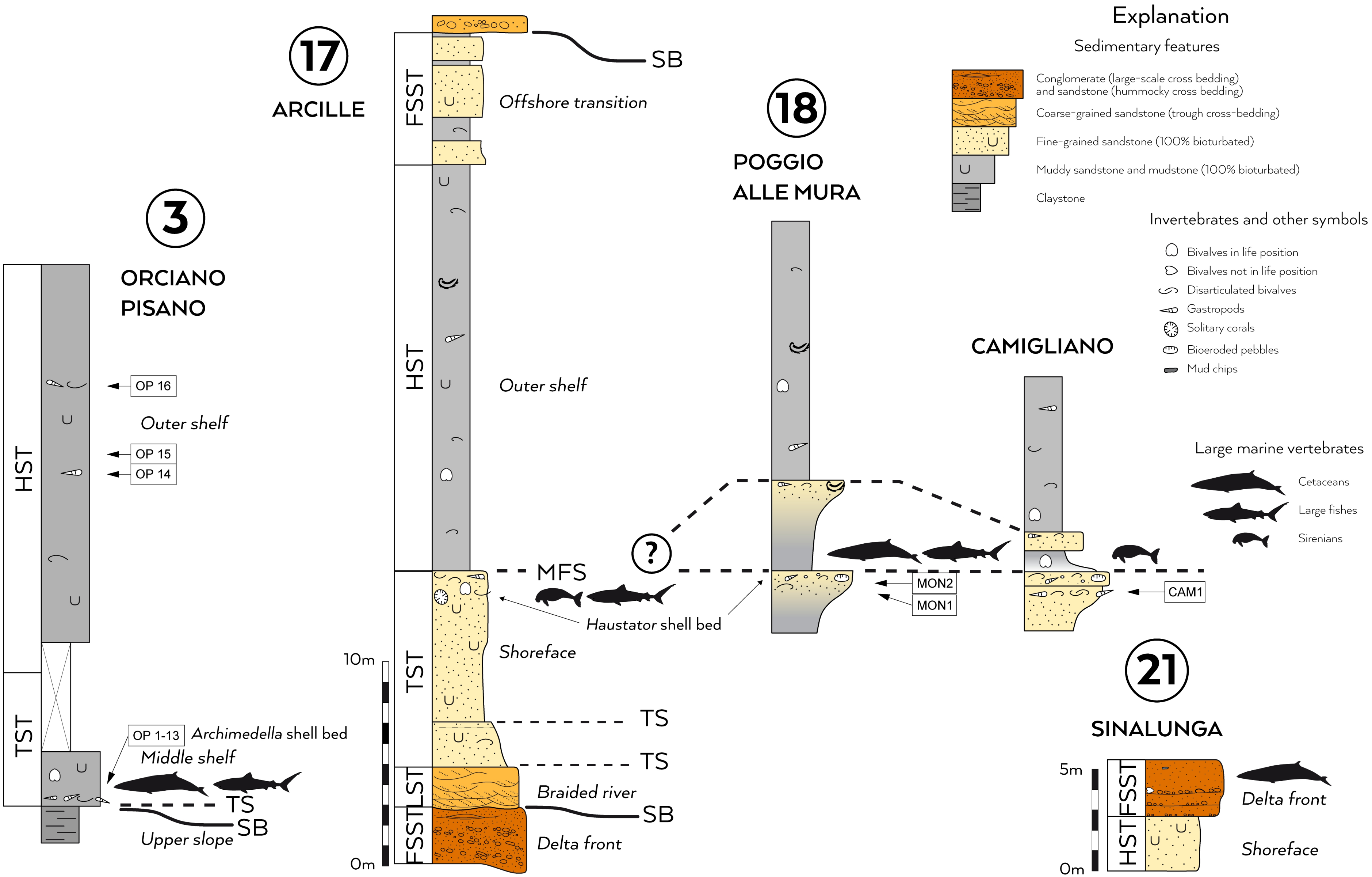
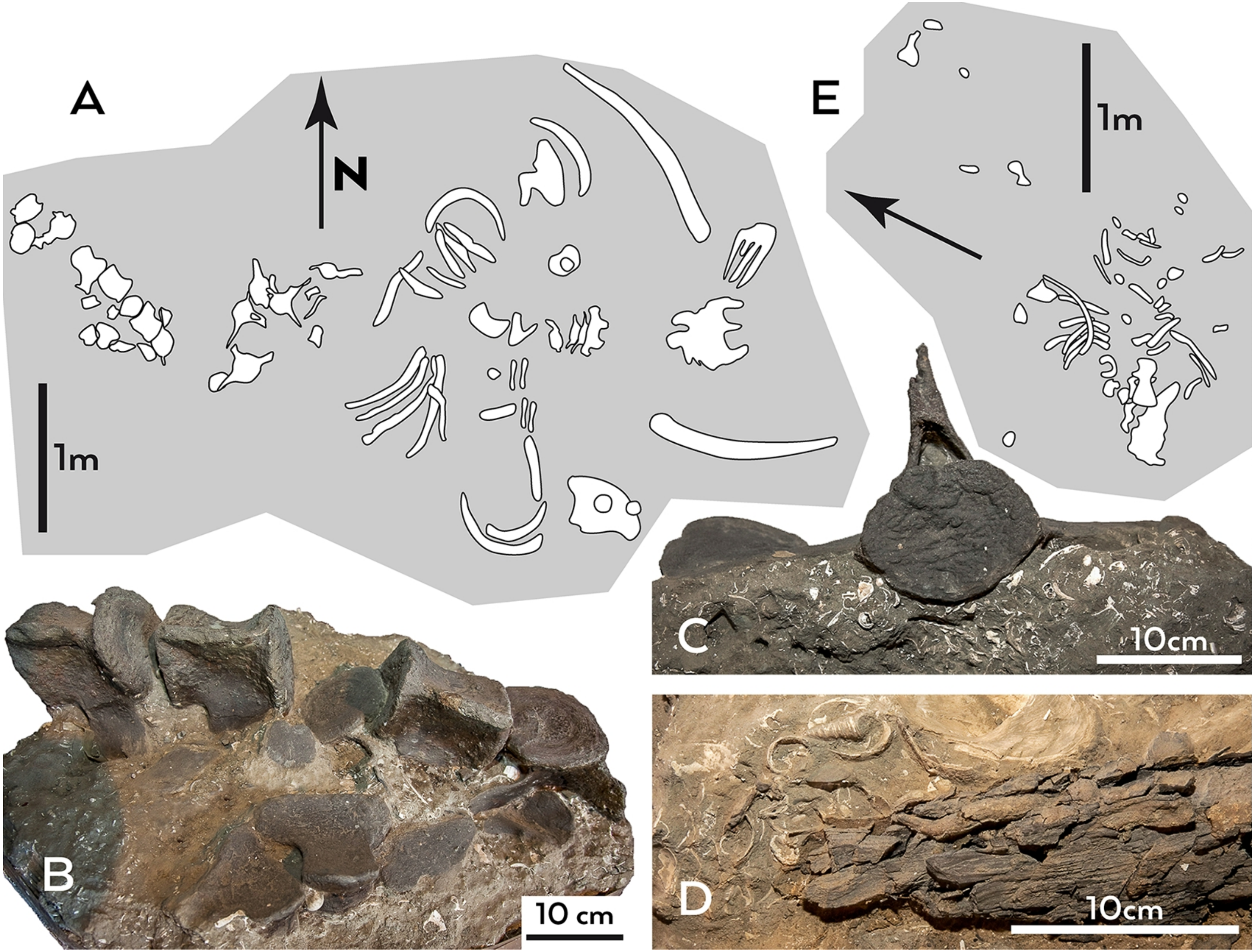
Explanation
10 Measured log
Rocks older than Pliocene
Fine Basin
Volterra-Era Basin
Elsa Basin
Pesa Basin
Ombrone-Orcia Basin
Siena-Radicofani Basin
Chiana Basin

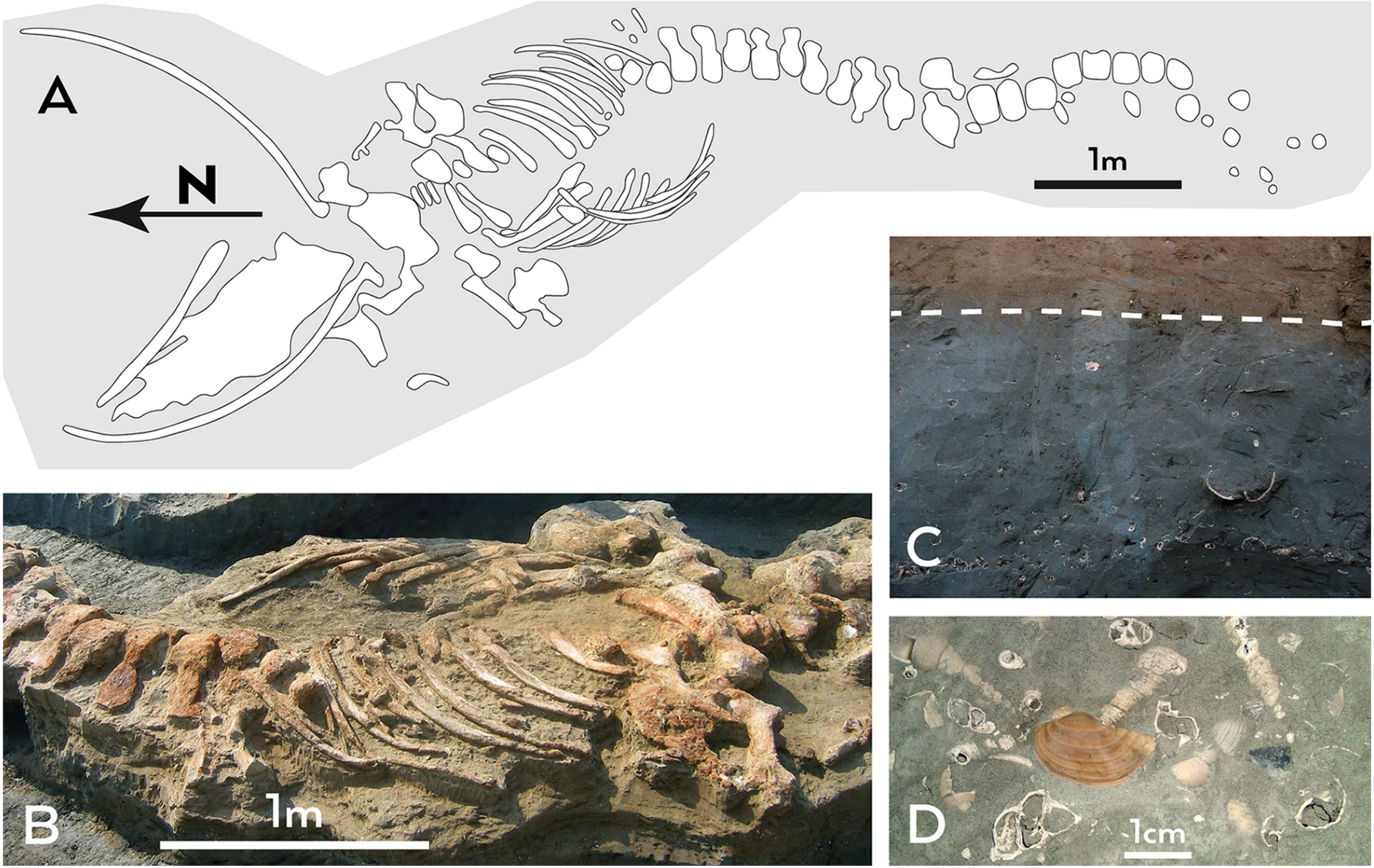


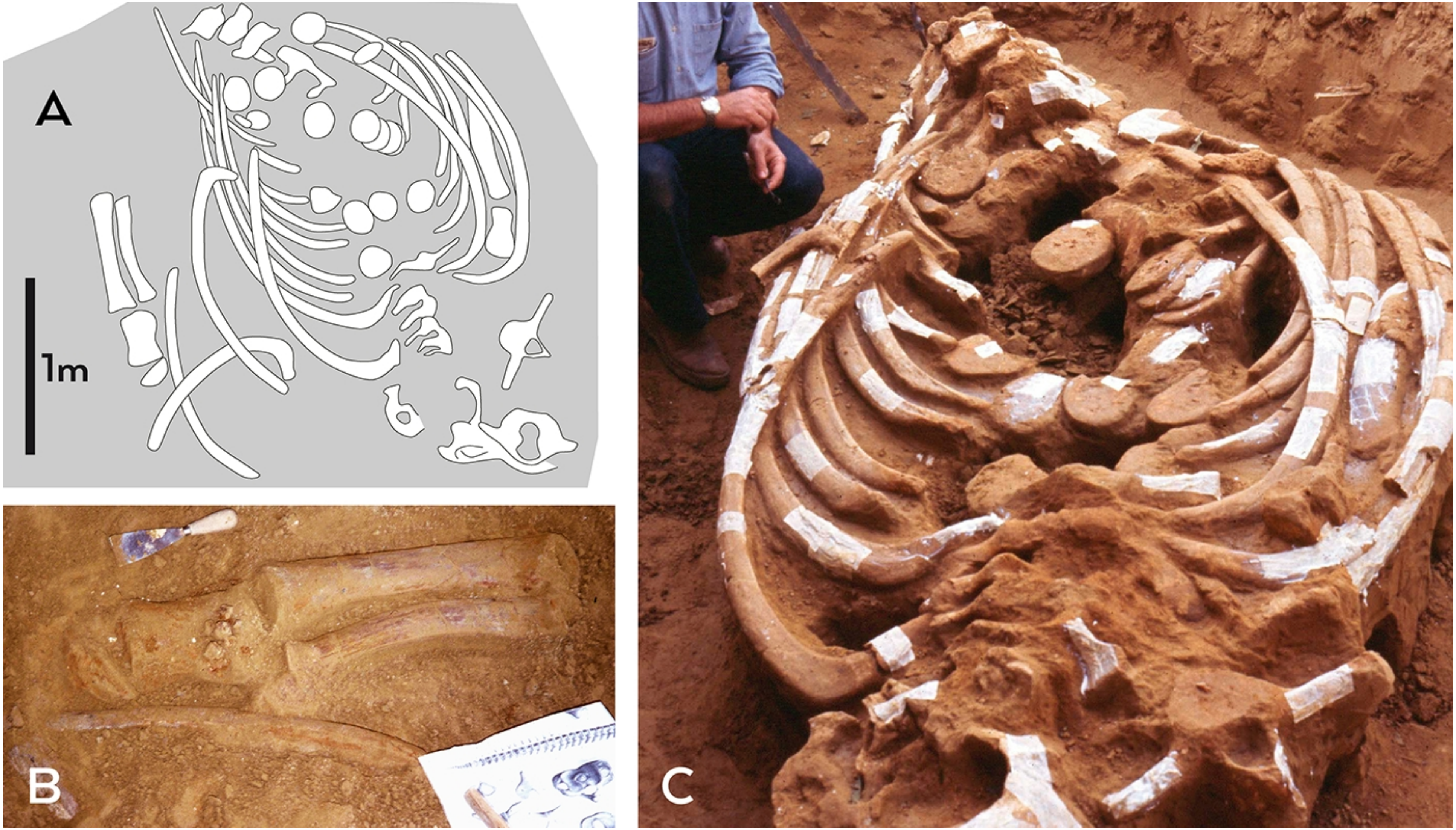
Explanation
Outer shelf and epibathyal mudstone
Inner- and outer shelf mudstone and siltstone
Outer shelf sandstone and conglomerate
Stage boundary
Biozone boundary
Lower shoreface bioturbated sandstone
Upper shoreface and delta front sandstone
Intertidal and brackish-water mudstone and sandstone
CSLO
Bulk sample
Fluvial sandstone and conglomerate
Alluvial mudstone and siltstone
Shelf biogenic carbonates
SYNTHEM
S6
S5
S4
S3
S2
S1
PLEISTOCENE
PLIOCENE
Middle-Late
Early
Calabrian
Gelasian
Piacenzian
Zanclean
MPL6
MPL5b
MPL5a
MPL4b
MPL4a
MPL3
MPL2
MPL1
MATUYAMA
GAUSS
GILBERT
1.0
2.0
3.0
4.0
5.0
FINE
VOLTERRA-ERA
ELSA
CHIANA BASIN
SIENA-RADICOFANI
Strada degli Archi
Pagliana-Pieve Vecchia
Orciano
Parlascio
Lajatico
Fabbrica
Volterra
San Lorenzo
La Serra
Poggio a Lupo
San Maiano
Canneto
Fiano
Specchi
Sinalunga
Cetona
Casenuove
Castefiorentino
San Gimignano
Colle Valdelsa
Staggia
Pietrafitta
Borro Strolla
Monteaperto
Castelnuovo Berardenga
Fastelli
Siena
Lucciolabella
Radicofani
Arcille
Poggio alle Mura
①
②
③
④
⑤
⑥
⑦
⑧
⑨
⑩
⑪
⑫
⑬
⑭
⑮
⑯
⑰
⑱
⑲
⑳
㉑
㉒
㉓
㉔
㉕
?
PV
PGL4
PGL0
CLM
OP16
OP14-15
OP1-13
LAJ3
LAJ2
LAJ1
FB2
FB1
CSL1
CSL0
SRR3
SRR2
SRR1
C6
C5
C3
C1
CP5
CP4
CP2
CP1
TB
TUR2
TUR1
CN5
CN4
CN2
CN1
AG3
AG2
AG1
CST5
CST4
CST3
CST2
CST1
SLP
CCN2
CCN1
CVE2
FC4
FC3
FC1
CGR2
CGR1
SD1
MON1
MON0
CAM1
500m
FINE
VOLTERRA- ERA
ELSA
ORCIA-OMB.
SIENA-RADIC.
CHIANA


APENNINES
Florence
Pisa
Pisano Mt.
Leghorn
Arezzo
LEGHORN Mts.
CASTELLINA Mts.
CHIANTI Mts.
MID-TUSCAN RIDGE
Siena
LIGURIAN SEA
Grosseto
20 km
Cetacea
A
23 Number of records
63
18
15
9
6
B
Carchariniformes+ Lamniformes
167
56
33
23
C
Sirenia

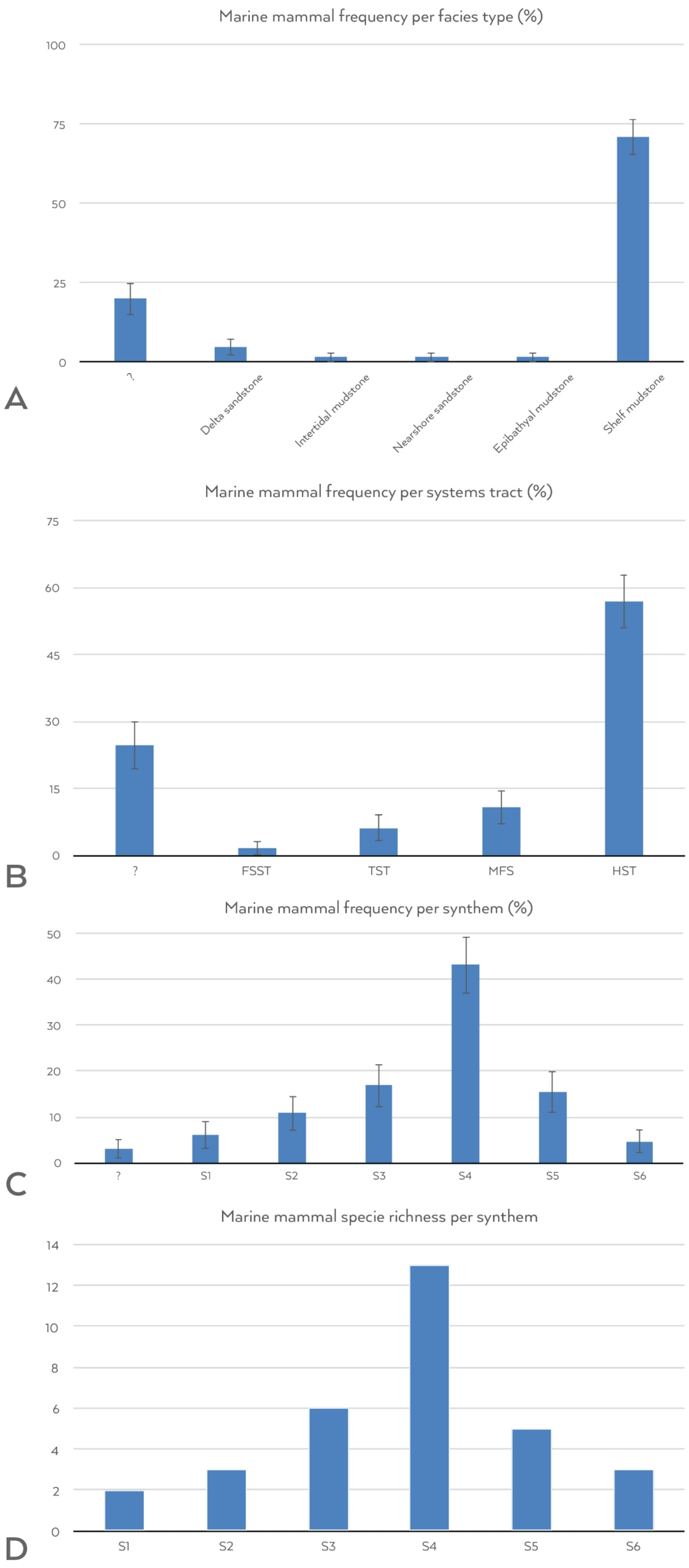

3
ORCIANO PISANO
HST
TST
OP 16
Outer shelf
OP 15
OP 14
OP 1-13
Archimedella shell bed
Middle shelf
TS
SB
Upper slope
17
ARCILLE
FSST
HST
TST
LST
FSST
SB
Offshore transition
Outer shelf
MFS
Haustator shell bed
Shoreface
TS
TS
Braided river
SB
Delta front
10m
0m
18
POGGIO ALLE MURA
?
MON2
MON1
CAMIGLIANO
CAM1
21
SINALUNGA
5m
0m
FSST
HST
Delta front
Shoreface
Explanation
Sedimentary features
Conglomerate (large-scale cross bedding) and sandstone (hummocky cross bedding)
Coarse-grained sandstone (trough cross-bedding)
Fine-grained sandstone (100% bioturbated)
Muddy sandstone and mudstone (100% bioturbated)
Claystone
Invertebrates and other symbols
Bivalves in life position
Bivalves not in life position
Disarticulated bivalves
Gastropods
Solitary corals
Bioeroded pebbles
Mud chips
Large marine vertebrates
Cetaceans
Large fishes
Sirenians

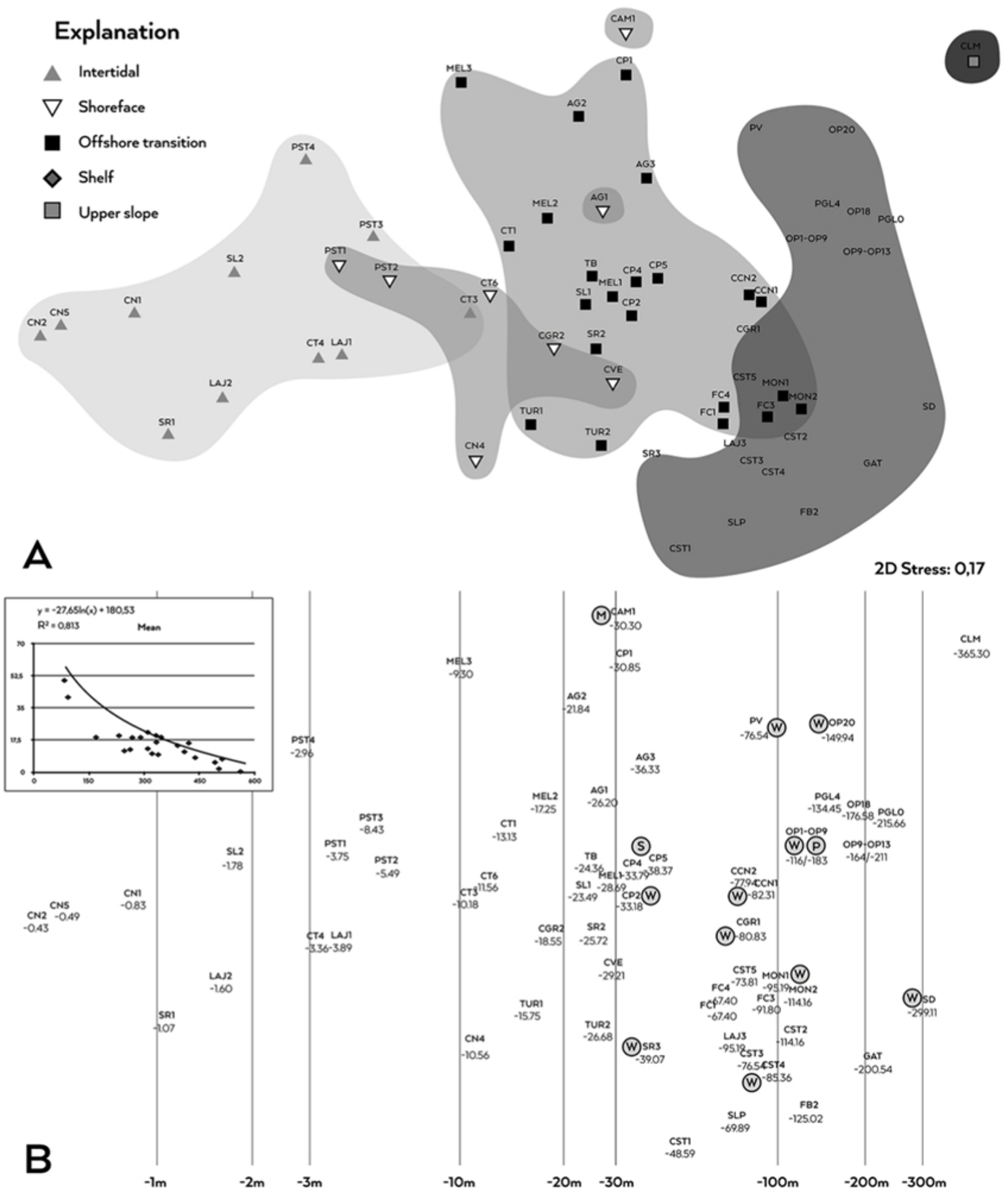

A
N
1m
E
1m
B
10 cm
C
10cm
D
10cm

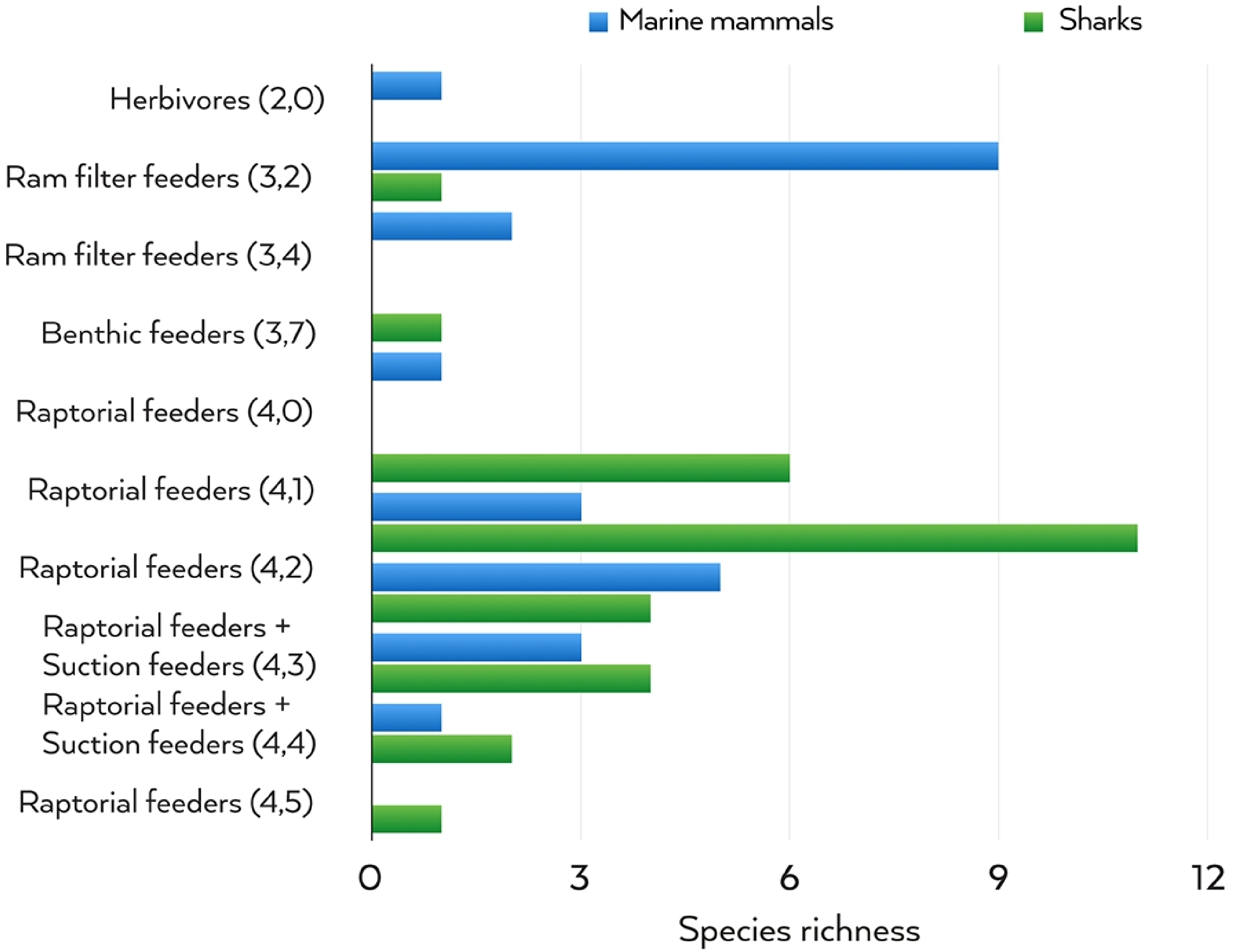

A
N
1m
B
1m
C
D
1cm

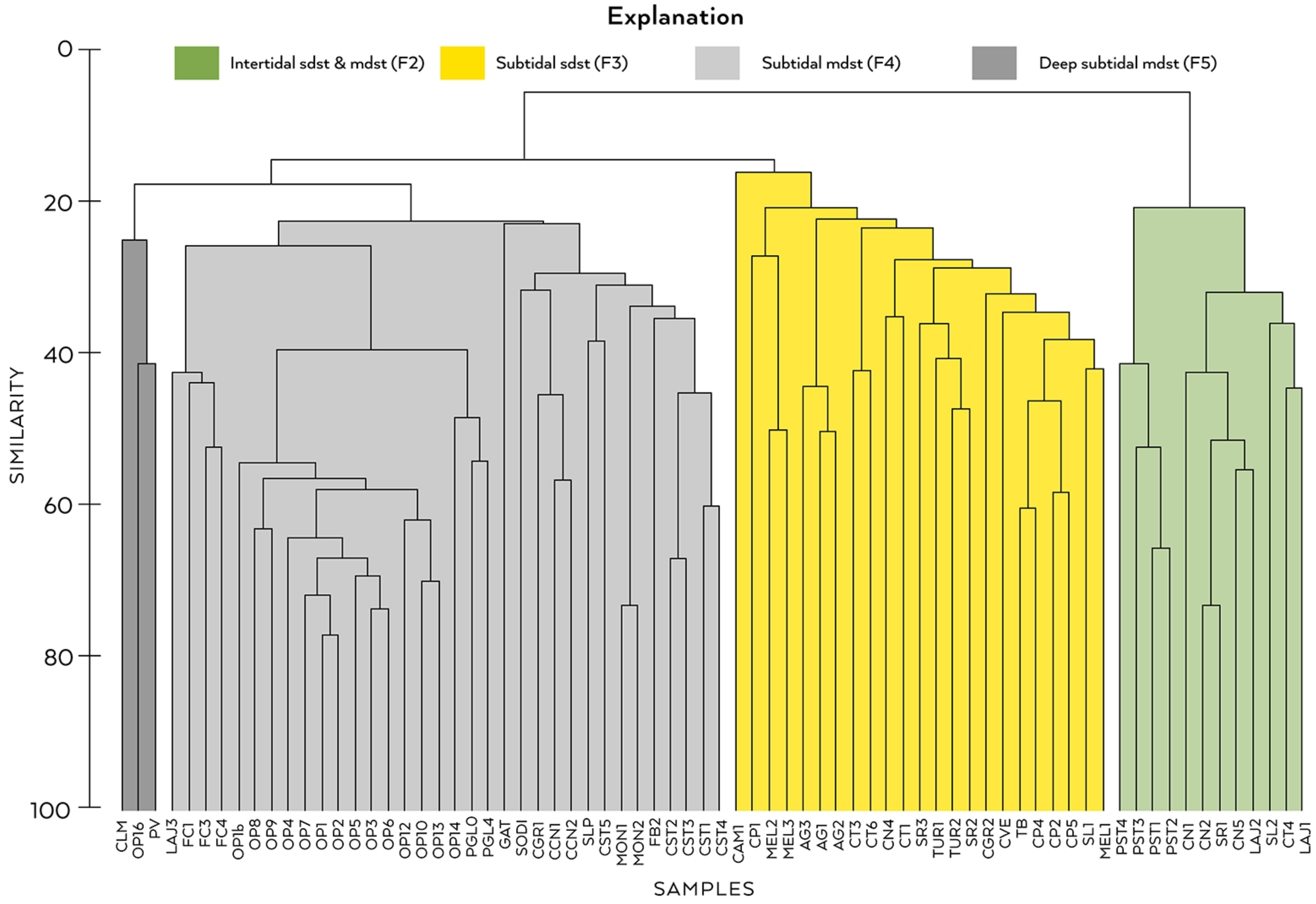

A
1m
B
C


A
Bed 4
Bed 3
Bed 2
Bed 1
B
Bed 2
Bed 1
10cm
C
Bed 4
Bed 3
Bed 2
Bed 1
25cm
9cm
10cm
D


Marine mammal frequency per facies type (%)
100
75
50
25
0
?
Delta sandstone
Intertidal mudstone
Nearshore sandstone
Epibathyal mudstone
Shelf mudstone
A
Marine mammal frequency per systems tract (%)
75
60
45
30
15
0
?
FSST
TST
MFS
HST
B
Marine mammal frequency per synthem (%)
50
40
30
20
10
0
?
S1
S2
S3
S4
S5
S6
C
Marine mammal specie richness per synthem
14
12
10
8
6
4
2
0
S1
S2
S3
S4
S5
S6
D


Explanation
▲ Intertidal
▽ Shoreface
■ Offshore transition
◆ Shelf
▨ Upper slope
CAM1
CLM
MEL3
CP1
AG2
AG3
PV
OP20
PST4
AG1
MEL2
PGL4
OP18
PGL0
PST3
CT1
OP1-OP9
OP9-OP13
PST1
SL2
PST2
TB
CP4
CP5
CT6
MEL1
CCN2
CCN1
CN1
CT3
SL1
CP2
CN5
CN2
CGR2
SR2
CGR1
CT4
LAJ1
CVE
CST5
MON1
LAJ2
FC4
MON2
FC3
SD
FC1
SR1
TUR1
TUR2
LAJ3
CST2
SR3
CN4
CST3
CST4
GAT
FB2
SLP
CST1
A
2D Stress: 0,17
y = -27,65ln(x) + 180,53
R² = 0,813
Mean
70
52,5
35
17,5
0
0
150
300
450
600
M CAM1 -30.30
CP1 -30.85
CLM -365.30
MEL3 -9.30
AG2 -21.84
PV -76.54 W
W OP20 -149.94
PST4 -2.96
AG3 -36.33
MEL2 -17.25
AG1 -26.20
PGL4 -134.45
OP18 -176.58
PGL0 -215.66
PST3 -8.43
CT1 -13.13
S
OP1-OP9 W P -116/-183
OP9-OP13 -164/-211
PST1 -3.75
SL2 -1.78
PST2 -5.49
TB -24.36
CP4
CP5 -38.37
MEL1 -33.79
CT6 -11.56
CCN2 -77.94
CCN1 W -82.31
CN1 -0.83
CT3 -10.18
SL1 -23.49
MEL -28.69
CP2 W -33.18
CN5 -0.49
CN2 -0.43
CGR2 -18.55
SR2 -25.72
CGR1 W -80.83
CT4 -3.36
LAJ1 -3.89
CVE -29.21
CST5 -73.81
MON1 -95.19 W
LAJ2 -1.60
FC4 -67.40
MON2 -114.16
FC3 -91.80
W SD -299.11
FC1 -67.40
SR1 -1.07
TUR1 -15.75
TUR2 -26.68
LAJ3 -95.12
CST2 -114.16
CN4 -10.56
W SR3 -39.07
CST3 -76.54
CST4 -85.36
W
GAT -200.54
SLP -69.89
FB2 -125.02
CST1 -48.59
B
-1m
-2m
-3m
-10m
-20m
-30m
-100m
-200m
-300m


Marine mammals
Sharks
Herbivores (2,0)
Ram filter feeders (3,2)
Ram filter feeders (3,4)
Benthic feeders (3,7)
Raptorial feeders (4,0)
Raptorial feeders (4,1)
Raptorial feeders (4,2)
Raptorial feeders + Suction feeders (4,3)
Raptorial feeders + Suction feeders (4,4)
Raptorial feeders (4,5)
0
3
6
9
12
Species richness


Explanation
Intertidal sdst & mdst (F2)
Subtidal sdst (F3)
Subtidal mdst (F4)
Deep subtidal mdst (F5)
SIMILARITY
0
20
40
60
80
100
SAMPLES
CLM
OP16
PV
LAJ3
FC1
FC3
FC4
OP1b
OP8
OP9
OP4
OP7
OP1
OP2
OP5
OP3
OP6
OP12
OP10
OP13
OP14
PGL0
PGL4
GAT
SOD1
CGR1
CCN1
CCN2
SLP
CST5
MON1
MON2
FB2
CST2
CST3
CST1
CST4
CAM1
CP1
MEL2
MEL3
AG3
AG1
AG2
CT3
CT6
CN4
CT1
SR3
TUR1
TUR2
SR2
CGR2
CVE
TB
CP4
CP2
CP5
SL1
MEL1
PST4
PST3
PST1
PST2
CN1
CN2
SR1
CN5
LAJ2
SL2
CT4
LAJ1