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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 paleoenvironments 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

Order of Authors Stefano Dominici, Silvia Danise, Marco Benvenuti

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]

Pliocene NWMS MM cover letter.docx [Response to Reviewers]

Pliocene NWMS MM Submitted_September.docx [Revised Manuscript with Changes Marked]

Pliocene NWMS MM Revised Abstract.docx [Abstract]

Pliocene NWMS MM Submitted_September_untracked.docx [Manuscript File]

Fig. 1.tif [Figure]

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Fig. S1.tif [Figure]

Submission Files Not Included in this PDF

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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

1
2 Dear editor,
3
4

5 we submit a revised version of the manuscript now entitled "Pliocene stratigraphic
6 paleobiology in Tuscany and the fossil record of marine megafauna". We have carefully
7 considered the comments of the first reviewer and your comments and revised the
8 manuscript accordingly. In particular, we would like to explicit the following answers (in
9 red) to review no. 1 (in blue):
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15 Some suggestions that could improve the manuscript:
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18 1) The ambitious paleoecological considerations intended to link the supposed high
19 diversity/abundance of the marine vertebrate assemblage to the paleobiogeography/food
20 availability of the northwestern Mediterranean are, in my opinion, not supported by solid
21 data. In fact:
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23
24 A) data about the systematic composition of the vertebrate fossil assemblage are only
25 reported (for the marine mammals) in table 1 and not discussed in the text (note that I
26 disagree with the authors' statement about "the systematics of Mediterranean Pliocene
27 LMV have been recently reviewed"); data about the sharks are not reported;
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30 B) also admitting that the systematic assignments reported in this list are sufficient for this
31 analysis, no data are reported about, for example, the trophism and, more generally, the
32 ecological behavior of the listed taxa;
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35 C) diversity and abundance are cited for the vertebrates, but not quantified;
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38 D) the link between diversity and primary productivity/food availability must be better
39 analyzed considering the rich and often controversial bibliography on this topic;
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41
42 E) baleen whales and other vertebrates from the Pliocene of Tuscany are here considered
43 'apex predator': the authors must define better this ecological term. In my opinion, baleen
44 whales cannot be included among the top predators, as well as other 'large' marine
45 vertebrates as they feed on plancton and small fishes with filtering techniques. Apex or top
46 predators can be considered some (but not all) 'large' sharks as *Carcharodon carcharias*
47 and *Cosmopolitodus hastalis*, and, among cetaceans, *Orcinus citoniensis*.
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50 So, I suggest the authors to review the part focused on the paleoecology of the vertebrate
51 assemblage, improving the data. Alternatively, it could be drastically shortened or totally
52 removed.
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63 1A: We enlarged the marine mammal dataset, from 39 to 64 reports, and carefully
64 controlled existing literature on the systematics.

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66 1B: We have greatly enlarged the literature on the ecology of modern Mediterranean
67 marine mammals and introduced data on the ecology of sharks. Based on these data, we
68 attributed a preferred prey and a feeding mechanism to each taxon of our list.
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71 1C: We calculated minimum number of marine mammal specimens. The systematics were
72 sufficient for a conservative estimate of standing diversity in terms of species richness of
73 both marine mammals and sharks. Marine mammal abundance and richness have been
74 calculated for six consecutive intervals and for the overall epoch and compared to modern
75 values for the north-eastern Mediterranean. A Pliocene-modern comparison is also given
76 for species richness in sharks. We introduced new tables, and two histograms (Fig. 9C-D),
77 for an easy understanding of diversity trends during the Pliocene.
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80 1D: In expanding the reference list, we have highlighted the overwhelming evidence for a
81 relationship between marine megafauna diversity and primary productivity (bottom-up
82 control on marine ecosystems), but also decoupled this from structural factors such as
83 trophic cascade (top-down controls exerted by large predators).
84

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86 1E: There's no formal definition of what "marine megafauna" is, but practice adopted also
87 by palaeontologists includes all marine mammals, seabirds, sea turtles, sharks and rays
88 (e.g., Lewison et al., 2004; Pimiento et al., 2017). We clearly stated what we mean by
89 apex predator, using concepts derived from modern ecological literature. In particular we
90 specify that the definitions of apex predators (or top predators) and mesopredators are
91 relative, and to an extent context-dependent (species that in a contact are apex predators,
92 in another are mesopredators). By any means, filter-feeding baleen whales are considered
93 apex-predators of their community. To avoid misunderstanding between ecological and
94 paleoecological usage, we informed on the trophic level of each Pliocene species by
95 comparison with modern values, for both marine mammals and sharks.
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106 2) The authors propose a link between the Pliocene-Pleistocene increase in whale size
107 and in bone-eaters worms diversity: these considerations should be better supported by
108 including more bibliographical data and also by an eventual analysis of the Pliocene
109 Tuscany vertebrate assemblage. Are the marine vertebrates from Pliocene of Tuscany
110 particularly large? If yes, please support this affirmation with data. My preliminary
111 evaluation is that there are some large baleen whales (but not 'giant whales' as today),
112 some medium-small sized baleen whales, and several relatively small marine mammals
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120 (odontocetes, pinnipeds and sirenians). So, why also the 'small' vertebrates are not
121 preserved in the deep sea sediments of the Pliocene of Tuscany?
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125 We have given figures for size differences between Pliocene and modern marine
126 megafauna. We are explicit in stating the complex nature of the comparison between MM
127 at different times, but we are also clear in relating the radiation of bone-eating worms, and
128 the importance of a depth-related taphonomic overprint in the Pliocene fossil record, to the
129 emergence of large whales. That is to say, not all MM were large, but some were. We also
130 see no need to limit this effect to the carcass of true giants, like the modern blue whale.
131 That is to say, we think that large is large enough.
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138 3) The analysis is focused on the 'large' marine vertebrates: in my opinion 'large' is rather
139 vague is it is not well defined by the authors. It seems that the authors consider as 'large
140 vertebrates' all cetaceans (including the smaller odontocetes), all pinnipeds and all
141 sirenians, among the tetrapods (but not the marine turtles and birds), and
142 Carcharhiniformes (note that several carchariformes, as the catsharks, are not longer than
143 50 cm) and Lamniformes among sharks: it is right?
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149 As stated above, the ecological definition of "marine megafauna" includes smaller animals
150 (sea birds, otters, turtles). We focus on the general structure of the MM association, not on
151 the role of a particular species.
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155 4) in the analysis are also included some 'large' sharks: their fossil record is exclusively
156 based on isolated teeth and most of these are found associated to cetacean skeletons.
157 This should be better outlined, since these remains have a different taphonomic
158 significance that the bones of the other vertebrates
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163 We have expanded the review of the Pliocene shark record of Tuscany in Tables 5-6 and
164 discussed it in the text. Taphonomy has been expanded, also in relationship to evidence of
165 interaction between different MM species.
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169 5) the organization of the manuscript, including the presentation of data, results and
170 discussion is often unclear and could be improved. Some suggestions:
171 - the numeration of the chapters/paragraphs must be revised (the number 3 is repeated
172 three times)
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- 178
179 - all the chapters from 'Distribution of large marine vertebrates', to 'the Biotic factors' (lines
180 950-2012) must be included in the 'Results'
181
182 - the paragraph '6.2 Taphonomic control' reports an interesting bibliographical review, but
183 no reference to the material here examined.
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187 We have corrected the organization of the ms as suggested. Tables have been expanded
188 and augmented in number.
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192 6) Table 2 appears as the more important source of this paper, since it condenses all the
193 data about the marine mammals discussed and elaborated in the work. By contrast, the
194 table does not seem to have been carefully prepared. For example, most of the specimens
195 lacks the description, although these data can be easily found in bibliography (e.g.: the
196 *Orcinus citoniensis* holotype is an articulated partial skeleton) and the few data reported
197 are often wrong (e.g. MOm2-2 and WSi2-1 are not articulated skeleton); moreover it is not
198 easy to identify the specimens reported without the catalogue number of the museum
199 where they are kept. For example it is not possible identify WFi4-3 from Orciano (no data
200 about the systematics and the bones preserved) considering that Lawley (1876) reported
201 several remains from the same locality; similarly, it is reported an articulated skeleton of
202 sirenian from Arcille (MOm2-2) based on Tinelli (2013): but Tinelli (2013) described 4
203 skeletons from Arcille (3 disarticulated and 1 articulated; see also: Sorbi et al. 2011, Tinelli
204 et al. 2012).
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214 We have expanded Tab. 2 and included much more taphonomic information, making it
215 more homogenous and informative, also with respect to references. We have excluded
216 specimens cited, but no longer traceable (e.g. Lawley 1876).
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221 7) All 'dugongs' in the text must be changed with 'sirenians' ('dugong' is referred only to
222 the extant *Dugong dugong* species)
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225 Done
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228 8) The fossil vertebrates from Tuscany are named in the text using a inhomogeneous
229 approach about their systematic assignation: I suggest to uniform (maybe using the more
230 detailed determination available from the literature for all specimens cited.
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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.

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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

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3 **SPliocene stratigraphic paleobiology in the Pliocene of**
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6 **Tuscany and the fossil record of large marine**
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9 **vertebratesmarine megafauna**
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13 Stefano Dominici (Università di Firenze, Museo di Storia Naturale, Firenze, Italy)

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

16
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18 Marco Benvenuti (Università di Firenze, Dipartimento di Scienze della Terra, Firenze, Italy)

19
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23 **Abstract**
24

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26
27 Tuscany has a rich Pliocene record of marine megafauna (MM), including mysticetes,
28 odontocetes, sirenians and seals among the mammals, and six orders of sharks among the
29 elasmobranchs. This is reviewed with respect to paleogeography and sequence-
30 stratigraphic occurrence in six different basins. Conditions at the ancient seafloor are
31 explored by means of sedimentary facies analysis, taphonomy and multivariate techniques
32 applied to a large quantitative dataset of benthic molluscs. MM is rare or absent in most
33 basins during the Zanclean, except in one basin, and most abundant in Piacenzian deposits
34 in all six basins. MM occurs preferentially in fine-grained shelfal highstand deposits of small-
35 scale depositional sequences, or at condensed horizons of the maximum flooding interval.
36 It is rare in shallow marine paleoenvironments and nearly absent in bathyal paleosettings.
37 Paleogeographic and paleoecologic evidence, and a comparison with modern patterns of
38 marine upwelling suggest that a wedge of nutrient-rich waters sustained in the offshore
39 during the Pliocene a high biomass of primary producers and a community of apex
40 consumers and mesopredators, similarly to the modern Northwestern Mediterranean Sea,
41 with a higher species richness than the modern. The highest MM diversity coincides with
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62 the mid-Piacenzian warm period, suggesting a link between climate and diversity. We
63 propose that not all marine environments were suitable for marine mammal preservation.
64 Buoyant carcasses were preferentially dismembered and destroyed in high-energy shallow
65 waters, with the possible exception of delta front deposits, where sudden sediment input
66 occasionally buried pristine carcasses. We hypothesise that carcasses sunken on the
67 seafloor below the shelf break underwent destruction through the activity of a whale-fall biota
68 of modern type, specialised in the consumption of decomposing tissues, both soft and
69 mineralised. A taphonomic window was left between storm-wave base and the shelf break.
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71 resurfacing of carcasses, while the lack of a specialised whale-fall biota slows down bone
72 degradation with respect to deeper settings. Sedimentation rate is high enough to cover
73 skeletal material before its complete destruction. An estimate of paleobathymetries based
74 on multivariate techniques suggests that the preferential depth for the inclusion of MM in the
75 fossil record is 30-300 m. The results are compared with major Mesozoic and Cenozoic MM
76 records worldwide. Available evidence suggests that the Neogene radiation of large whales,
77 true ecosystem engineers, triggered the radiation of a bone-eating fauna that hampered,
78 and hampers, MM preservation in the deep sea.
79 Tuscany has a rich Pliocene record of
80 marine megafauna (MM), including mysticetes, odontocetes, sirenians and seals among the
81 mammals, and six orders of sharks among the elasmobranchs. This is reviewed with respect
82 to paleogeography and sequence-stratigraphic occurrence in six different basins. Conditions
83 at the ancient seafloor are explored by means of sedimentary facies analysis, taphonomy
84 and multivariate techniques applied to a large quantitative dataset of benthic molluscs. MM
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86 abundant in Piacenzian deposits in all six basins. MM occurs preferentially in fine-grained
87 shelfal highstand deposits of small-scale depositional sequences, or at condensed horizons
88 of the maximum flooding interval. It is rare in shallow marine paleoenvironments and nearly
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123 comparison with modern patterns of marine upwelling suggest that a wedge of nutrient-rich
124 waters sustained in the offshore during the Pliocene a high biomass of primary producers
125 and a community of apex consumers and mesopredators, similarly to the modern
126 Northwestern Mediterranean Sea, with a higher species-richness than the modern. The
127 highest MM diversity coincides with the mid-Piacenzian warm period, suggesting that facies
128 control does not obscure a link between climate and diversity. We underline however that
129 not all marine environments were suitable for marine mammal preservation. Buoyant
130 carcasses were preferentially dismembered and destroyed in high-energy shallow waters,
131 with the possible exception of delta front deposits, where sudden sediment input
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133 seafloor below the shelf break underwent destruction through the activity of a whale-fall biota
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135 mineralised. A taphonomic window was left between storm wave base and the shelf break.
136 Here water pressure is high enough to prevent the formation of decomposing gases and the
137 resurfacing of carcasses, while the lack of a specialised whale-fall biota slows down bone
138 degradation with respect to deeper settings. Sedimentation rate was high enough to cover
139 skeletal material before its complete destruction. An estimate of paleobathymetries based
140 on multivariate techniques suggests that the preferential depth for the inclusion of MM in the
141 fossil record was 30-300 m. The results are compared with major Mesozoic and Cenozoic
142 MM records worldwide. Available evidence suggests that the late Neogene radiation of large
143 whales, true ecosystem engineers, and their size increase, triggered the radiation of a bone-
144 eating fauna that hampered, and hampers, MM preservation in the deep sea. Stratigraphic
145 paleobiology and an ecosystem-level approach deliver useful insights in the nature of the
146 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). Large vertebrates have played a key role in structuring marine ecosystems. 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 (Vermeij, 1977; Chen & 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 plesiosaurs, 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 & 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 & 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 an enormous

241
242 ~~crucial ecological and evolutionary importance~~role in ecology and evolution of these
243 ~~animals~~, the nature ~~and distribution~~ of the ~~MM~~ fossil record ~~of large marine vertebrates~~
244 ~~(LMVs)~~ has been ~~relatively little~~less explored, compared to that of marine invertebrates and
245 terrestrial vertebrates. ~~Available data suggest a strong correlation between taxic diversity~~
246 ~~and the number of marine fossiliferous formations, resulting in megabiases in the fossil~~
247 ~~record (e.g., Cretaceous: Benson et al., 2010). Within its vast history, studies on the~~
248 ~~geologically recent marine megafauna offer important insights, thanks to a~~considering our
249 ~~better knowledge of: 1) geological setting, in terms of outcrop extent and high-resolution~~
250 ~~stratigraphy; 2) ecologic role played by individual species, whether extant or extinct, in terms~~
251 ~~of habitat, trophic role, life histories and population structure, thanks to a comparison with~~
252 ~~extant descendants, or close relatives; 3) MM taphonomy, based on actuopaleontology. A~~
253 ~~recent global study revealed that MM extinction peaked in the late Pliocene, between 3.8~~
254 ~~and 2.4Ma, linked with the sudden drop in the extension of nearshore environments due to~~
255 ~~a large sea level regression, confirming that the fossil record offers important insights on the~~
256 ~~vulnerability of keystone marine species to climate change (Pimiento et al., 2017).~~linked to
257 ~~the sudden drop in the extension of nearshore environments after a large sea level~~
258 ~~regression (Pimiento et al., 2017), confirming that the fossil record offers important clues on~~
259 ~~the vulnerability of keystone marine species to climate change.~~ We contribute here to ~~their~~
260 ~~better understanding of the Pliocene fossil record~~ by reviewing the rich ~~and varied fossil~~
261 ~~record of Pliocene LMVs~~~~MM~~ of Tuscany, in Italy. In particular, we consider all reports of
262 Pliocene ~~cetaceans, sharks, sirenians and pinnipeds~~marine mammals and sharks and
263 revise taphonomy and ~~the~~ sedimentary facies associated with all ~~major~~known recent
264 findings, ~~framing~~setting them within a sequence stratigraphic framework. ~~At the same time~~
265 ~~we expand on~~ We also ~~expand knowledge on paleoenvironmental contextualisation~~ by
266 ~~considering the paleoecology of fossil invertebrates on a regional basis~~We also reconstruct
267 ~~the paleoenvironmental context and review data on a part of the marine ecosystem through~~

301
302 the paleoecology of fossil invertebrates on a regional basis, following a stratigraphic
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304 paleobiological approach that can be applied to both the recent and the distant geological
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306 past (Patzkowsky &and Holland₁₇ 2012). Published studies that have taken this direction are
307
308 still a few, examples concerning Jurassic ichthyosaurs, plesiosaurs and pliosaurs (McMullen
309
310 et al.₁₇ 2014), Cretaceous turtles, plesiosaurs, bony fish and sharks (Schemisser McKean
311
312 &and Gillette₁₇ 2015), Eocene archaeocetes, dugongssea cows and sharks (Peters et al.₁₇
313
314 2009), and Neogene whales, pinnipedsmarine mammals and sharks (Boessenecker et al.₁₇
315
316 2014). All of these papers record the co-occurrence of shelly faunas, only one undertaking
317
318 quantitative studies of the distribution of fossil invertebrates ~~associated with sedimentary~~
319
320 ~~facies~~ (Jurassic of the Sundance Formation: McMullen et al.₁₇ 2014₁₇; see also Danise &and
321
322 Holland₁₇ 2017). The benefits of an outcrop-scale sequence stratigraphic approach include:
323
324 (1) an independent record of relative sea-level change to test paleobiological hypotheses
325
326 (see also Pyenson &and Lindberg₁₇ 2011₁₇; Noakes et al.₁₇ 2013); (2) a chronostratigraphic
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328 scheme for high-resolution correlations; (3) a means to recognise minor and major breaks
329
330 of the record; (4) an ecological and sedimentary framework for taphofacies distribution
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332 (Patzkowsky &and Holland₁₇ 2012); and (5) an independent control of onshore-offshore
333
334 patterns of fossil assemblages (e.g., Tomašových et al.₁₇ 2014).

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337 ~~From a top-down approach that emphasises the role of large marine vertebrates (LMVs) as~~
338
339 ~~apex predators of their trophic web, r~~ Researchers that study the geologic history of marine
340
341 ecosystems have focused on patterns of ecological restructuring based on the taxonomy of
342
343 selected groups (e.g., Thorne et al.₁₇ 2011₁₇; Benton et al.₁₇ 2013₁₇; Scheyer et al.₁₇ 2014;
344
345 Fischer et al., 2016), at the expenses of a more holistic approach that includes functional
346
347 diversity and embraces as many ecosystem components as possible (Dineen et al.₁₇ 2014).
348
349 ~~This attitude should be reversed, similarly to~~ By analogy with ecologists ~~working on extant~~
350
351 ~~ecosystems~~ who shift focus from models based on single groups (e.g., Steeman et al.₁₇
352
353 2009) to an all-embracing vision of marine life (Lawton, 1994; Sergio et al.₁₇ 2014).
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362 connecting food web ecology with landscape ecology (Polis et al., 1997; Estes et al., 2011),
363 stratigraphic paleobiology can draw from the fossil record and offer multidimensional
364 insights on the complex geological history of modern marine ecosystems.
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368 After revising LMVs fossil MM hosted in major museums of Tuscany, both isolated and
369 articulated remains, we ~~then~~ focus on all fossil skeletons bones that ~~could~~ can be
370 stratigraphically (e.g., Bianucci et al., ~~1995~~, ~~1998~~, ~~2001~~; Tinelli, ~~2013~~) and
371 taphonomically framed (e.g., Dominici et al., ~~2009~~; Bianucci, ~~2010~~; Danise ~~&and~~ Dominici,
372 2014). ~~The systematics of MM lists for the~~ Mediterranean Pliocene ~~LMV~~ have been recently
373 ~~reviewed updated~~ (~~cetaceans marine mammals~~: Landini et al., 2005; Bianucci et al., 2009a;
374 Sorbi et al., 2012; ~~Bianucci &and Vomero, 2015~~; ~~elasmobranchs sharks~~: Marsili, 2006;
375 ~~sirenians~~: Sorbi et al. 2012). ~~ESpecies-level~~ ecological data, ~~are~~ available ~~from on~~ modern
376 ~~Mediterranean studies of apex predators consumers and mesocarnivores~~ (Pauly et al., 1998;
377 Cortés, 1999), with detailed information made available for Mediterranean species following
378 conservation concerns ~~(e.g., baleen and sperm whales marine mammals~~: Notarbartolo di
379 Sciara, ~~et al., 2003, 2008, 2016~~ ~~Pirotta et al. 2011)~~, with species-level data ~~(;~~ sharks:
380 Cavanagh ~~&and~~ Gibson, 2007), allowing for a significant detailed paleoecological evaluation
381 of the Tuscan fossil record. The actualistic approach is also viable for species of benthic
382 molluscs, about half of which are still extant in modern Mediterranean sea floors bottoms
383 (55% of extant species of Mediterranean and North Sea bivalves, excluding strictly brackish
384 and bathyal forms, i.e., 202 out of 367 species, survives from the Zanclean: Raffi et al.,
385 1985). The regional quantitative study of molluscan assemblages was the basis for an
386 independent assessment of paleoenvironments, paleoecology and paleobathymetry. A
387 revision ~~e~~ of abundance distributions of marine molluscs, the largest contributors to
388 Mediterranean Pliocene shell beds and a key component of Mesozoic and Cenozoic marine
389 ecosystems (Stanley, 1975; Vermeij, 1977), allowed to further explore the structure and
390 composition of ~~the benthic component of~~ Pliocene marine ecosystems, and reconstructing
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422 a paleobathymetric gradient (e.g., Scarponi [&and](#) Kowaleski, 2004) along which to frame
423 [LMVMM taphonomy occurrence](#). The present work must necessarily start with a review of
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425
426 the chronostratigraphy and physical stratigraphy of the Tuscan marine Pliocene.
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431 **1. Geological setting**

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435 The Pliocene succession of Tuscany was deposited in a complex setting characterized [sed](#)
436 by continental collision related to the later evolution of the Northern Apennines chain.
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438 According to a well-established hypothesis, the region, affected by shortening before the
439 Middle-Late Miocene, accommodated by NE-verging thrust and fold systems, underwent
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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 characterized [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](#)
Lazarotto, 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

481
482 bounded most basins through their infilling, only to be obliterated by younger parallel normal
483
484 fault systems, leaving an invariant stratigraphic onlap of the Pliocene successions onto the
485
486 basin margins. Despite a NW-SE distribution of the hinterland basins, the structural setting
487
488 is responsible for a NE-trending physiographic and paleogeographic gradient, where the FB
489
490 is closest, and the CB furthest, from offshore settings throughout the late orogenic phase,
491
492 with important implications for the facies architecture and the distribution of marine
493
494 vertebrates and shell beds. Differential active uplift of the basin shoulders during the
495
496 Pliocene, coupled with important erosional phases, resulted in a different preservation of the
497
498 original stratigraphic architecture. The infill during the Zanclean is generally
499
500 characterizedsed by relatively continuous open marine successions, the correlative fluvial-
501
502 coastal systems missing due to uplift and erosion of basin margins. On the other hand, the
503
504 Piacenzian infill is characterizedsed by genetically-connected, fluvial, coastal and shallow
505
506 marine facies tracts, particularly well-preserved in the EB, hinting to reduced uplift of the
507
508 marginal areas. The modern physiography of OOB, escaping the structurally-controlled
509
510 geometry of the other basins, mimics instead an original fluvial network developed during
511
512 the latest Messinian, flooded after the Salinity Crisis (Bossio et al., 1991; Benvenuti et al.,
513
514 2015), filled during the Pliocene, and finally disrupted by post-Pliocene uplift and erosion.
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516 This difference in the structural history also justifies the preservation in OOB of Zanclean
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518 fluvial and shallow marine facies (Fig. 2).
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525 1.1 Pliocene Stratigraphy

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530 The Neogene succession of Tuscany is up to 2000 m-thick, about half of which belongs to
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532 the uppermost Miocene-Pleistocene interval (Bossio et al., 2004; 1997; Benvenuti et al.,
533
534 2014). The Pliocene has been traditionally subdivided into three main informal
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536 lithostratigraphic units: continental conglomerates and sandstones at the base, overlain by
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541
542 the “Blue Clay Formation” (*Argille Azzurre*: Zanclean-lower Piacenzian), marking the post-
543
544 Messinian Mediterranean marine transgression and forming the thickest part of the basin
545
546 infill (e.g., Bossio et al., 1994; 1997; Ghinassi & Lazzarotto, 2005), and the “Upper
547
548 Sands” (*Sabbie superiori*: Piacenzian-Gelasian) and conglomerates, deposited during the
549
550 ensuing regression. Several finer lithostratigraphic units have been introduced to define the
551
552 local stratigraphy, resulting in a complex and largely informal lithostratigraphic terminology
553
554 which includes Zanclean lower “Blue Clays” and Zanclean-Piacenzian upper “Blue Clays”
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556 (Capezzuoli et al., 2015), the latter eventually further separated by the widespread
557
558 occurrence of Piacenzian carbonates (Nalin et al., 2016). The lower Zanclean (OOB:
559
560 Ghinassi, 2007; Nalin et al., 2010; Dominici et al., 2012) and the Piacenzian, are
561
562 characterised by the high-frequency alternation of coarse-grained and fine-grained facies,
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564 ranging from fluvial to marine shelf settings (Benvenuti et al., 1995; 2007; 2014; Martini
565
566 et al. 2011, Fig. 2). The dynamics of the Pliocene infilling are better-understood in the EB,
567
568 where six synthemms have been defined, each up to more than 200 m-thick, further
569
570 subdivided in a number of elementary and composite depositional sequences and
571
572 chronologically calibrated through marine biostratigraphy and continental vertebrate
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574 biochronology (Benvenuti & Del Conte, 2013; Benvenuti et al., 2014, with references).
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579 580 **2. Materials and methods**

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585 Stratigraphic sections were measured and described at several localities (Fig. 1). Siliciclastic
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587 and carbonate facies were described, subdivided into groups of facies based on lithology,
588
589 sedimentary structures and ichnology, and interpreted in terms of process and depositional
590
591 environment (Tab. 1). Each group represents a set of individual facies forming monogenic
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593 associations (in the sense of Mutti et al., 1994), i.e., the meter-scale stacking of facies which
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595 express the autocyclic behaviour of specific depositional systems within a given
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601 accommodation space (Benvenuti ~~&and~~ Del Conte, 2013). Sequence stratigraphic
602 concepts have been applied to reconstruct the dynamics of basin infills at a hierarchy of
603 scales, advancing hypotheses on controlling factors. The chronostratigraphic subdivision of
604 Benvenuti et al. (2014), which divides the Pliocene into six synthems, S1-S6 from older to
605 younger, was extended to all six Tuscan basins by referring to available biostratigraphic
606 schemes (Fig. 2). The sequence stratigraphic interpretation of S2 in OOB is based on Tinelli
607 (2013). Other parts of the S1-S3 succession were drawn based on available lithostratigraphic
608 literature (see below). Studies integrating sedimentary facies analysis, biostratigraphy and
609 magnetostratigraphy (Nalin et al., 2016) have helped correlating ~~several discontinuous~~
610 carbonate bodies typical of S4. The reader is referred to Benvenuti et al. (2007; 2014) for
611 details on facies analysis and sequence stratigraphic interpretation of synthems S3-S6.

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

624 On a second step, all fossil Tuscan Pliocene cetaceans ~~and other marine mammals (Sirenia,~~
625 Carnivora), sirenians and pinnipeds that could be framed within the available high-resolution
626 stratigraphic framework and associated with taphonomic data, were selected. At this step,
627

661
662 after excluding ~~isolated and smaller~~ unidentified MM remains, a dataset of ~~39 cases~~ 64
663 specimens (cetaceans $n = 3250$; ~~dugongsirenians~~ $n = 410$; pinnipeds $n = 24$) was
664
665 assembled. ~~Many of them were a~~ Associationed with shark teeth is frequent (55% of 25
666 cases according to Danise & Dominici, 2014 for the Italian Pliocene; see also Bianucci
667 et al., 2002, 2010). The majority of the 3964 specimens are part of included in the catalogue
668 of UFMSN, UPMSN, ~~and~~ AFMSN and MGGC, whereas a few are stored in smaller
669 collections of the municipalities of Montaione, Scandicci (Florence province), and Certaldo
670 (Pisa province), ~~and~~ one in a private property (Castello di Villa Banfi, near Montalcino, Siena
671 province), and one in the Museum National d'Histoire Naturelle in Paris (France). ~~Each one~~
672 of the 39 LMVs Whenever possible, large marine vertebrates was were coded by synthem (N
673 = 60) and depositional environment (N = 54). We analysed abundance distributions among
674 marine mammals, and species richness of marine mammals and sharks. To infer Pliocene
675 paleoecology, fossil taxa recognised in Tuscany were compared with their closest
676 descendants, focusing on the species today living in the North-Western Mediterranean Sea
677 (NWMS).

678
679 ~~Since a~~ All known LMVMM-bearing sedimentary facies are associated with a mollusc-
680 dominated benthic fauna. T, ~~the~~ third step of the analysis concerned a quantitative study of
681 shell beds, allowing: 1) to interpret the regional evolution from a perspective independent
682 from the sedimentary facies, and 2) to characterize ~~the~~ MM paleoenvironmental and
683 bathymetric distribution ~~of LMVs. Molluscs are a key component of Pliocene communities,~~
684 and 3) allowing to explore the structure of the benthic component of marine ecosystems and
685 to identify underlying environmental ~~factors~~ controls that underline the paleoenvironmental
686 distribution of LMVs. 72 Bulk samples were collected at major shell beds at bed resolution
687 throughout the succession and sieved with 1 mm mesh size. Fossils of bivalves, gastropods
688 and scaphopods were identified to species level. The minimum number of individuals was
689 calculated following standard approaches (see Patzkowsky & Holland, 2012), resulting
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722 in a richness of 525 species (S) and a total abundance of 64206 individuals (N). We coded
723 each fossil assemblage by synthem, tract of small-scale depositional sequence, and
724 depositional environment. Most samples belonged to facies types F2-F5 (Tab. 1; see also
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729 Tomašových et al.¹⁷ 2014). Facies F6 usually lacks macrofossils and allowed for the
730
731 collection of only one sample. No samples were collected in facies F1, lacking marine shells,
732
733 facies F7, mostly devoid shells, and facies F8, which is richly fossiliferous, but lacks
734
735 aragonite shells and is associated with specimens hardly extractable from the rock. The
736
737 resulting quantitative dataset served for statistical analyses on the distribution of species-
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739 level abundances on a siliciclastic shelf depositional system, performed with the software
740
741 Primer 6.0 (Clarke [and](#) Gorley, 2006). Analyses included clustering and nMDS ordination
742
743 techniques on a Bray-Curtis similarity matrix, of standardised, square-root transformed data
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745 (72 samples; S = 333 and N = 63518 after the exclusion of singletons). To test statistically
746
747 whether there is a significant difference between two or more groups of sampling units based
748
749 on sedimentary facies, we performed an analysis of similarity (ANOSIM). To interpret the
750
751 outcomes of the quantitative study and the significance of clusters we used species-level
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753 autoecologic information available for the most abundant species, based on the distribution
754
755 of extant forms. This information, retrieved from the Marine Biodiversity and Ecosystem
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757 Functioning EU website (MARBEF: www.marbef.org), included the average life depth of 23
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759 modern species that in our dataset had an overall abundance > 0.15%.
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764 765 **3. Results**

771 3.1. Unconformity-bounded units

775 3.1.1 Synthem S1: the early Zanclean transgression

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784 The Miocene-Pliocene transition, marking the return to marine conditions after the
785
786 Messinian salinity crisis (Krijgsman et al., 1999), is recorded in limited exposures of earliest
787
788 Zanclean, open marine mudstones resting both unconformably or conformably onto latest
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790 Messinian non-marine deposits (*Lago-Mare*), an isochronous boundary being dated in the
791
792 Mediterranean at 5.33 Ma (Roveri et al., 2014). Differences depend on the specific
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794 structurally-controlled distribution of hinterland basins, where an uplifting chain determined
795
796 the presence of thresholds delaying the early Zanclean marine flooding from inner (EB,
797
798 OOB: Benvenuti et al., 2015a) to outer hinterland basins (FB, VEB). In inner basins such
799
800 as EB, where S1 has been defined, continental deposition continued into the earliest
801
802 Zanclean, marine flooding occurring within the MPL1 biozone (references in Benvenuti et
803
804 al., 2015a). A chronostratigraphical equivalent of S1 is represented in FB and VEB (Bossio
805
806 et al., 1978) by an open-shelf mudstone, conformably resting on latest Messinian *Lago-*
807
808 *Mare* deposits (Roveri et al., 2014). An apparently analogous situation is documented in
809
810 OOB, where MPL1 shelfal mudstones of the early Zanclean (normal chron C3n) rest on a
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812 Messinian to basal Pliocene paleovalley fill (Benvenuti et al., 2015a).
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818 3.1.2 Synthem S2: Zanclean differential preservation

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822 Synthem S2, as recognized in the EB (Benvenuti et al. 2014), is represented by relatively
823
824 thin fluvial conglomerates unconformably resting on S1 (biozones MPL1-MPL2), capped by
825
826 S3 (biozone MPL4a: Bossio et al., 1993; 2001), comprising important stratigraphic gaps at
827
828 its base and top. On the other hand, in FB (Bossio et al., 1997), VEB (Bossio et al., 1994)
829
830 and SRB (Ghinassi & Lazzarotto, 2005), the same chronostratigraphic interval is
831
832 recorded by monotonous epibathyal mudstones several hundred meters thick, locally
833
834 intercalated with delta-front hyperpycnal sandstones and conglomerates. In a very broad
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842 sense, the concept of S2 is extended to these basins, by assuming that erosional
843
844 unconformities in EB pass to into correlative conformities in rapidly subsiding adjacent
845
846 basins, where thick successions could be accomodated. Apart from exceptions, no shells
847
848 were found in bathyal mudstone or in deltaic sandstone. In OOB, the same time span is
849
850 marked by a N-S facies gradient characterized ~~sed~~ by a single deepening-upward
851
852 succession, from fluvio-deltaic sandstone to shelfal mudstone, replaced by a succession
853
854 made of four distinct regressive-transgressive units in the Orcia valley to the north (Ghinassi,
855
856 2005; Benvenuti et al., 2015b). A laterally-continuous shell bed, with sharks remains and
857
858 skeletons and articulated bones of whales, ~~lugongsirenians~~ and ~~large bonyteleost~~ fishes
859
860 (Danise, 2010; Sorbi et al., 2012; Tinelli, 2013), marks a major transgressive surface
861
862 overlain by open shelf mudstones (Sorbi et al., 2012; Tinelli, 2013: biozone MPL2) that is
863
864 hypothetically traced along a NE-SW profile (Figs. 4, 5).
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870 3.1.3 Synthem S3: Zanclean-Piacenzian transition

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874 Synthem S3 is subdivided in EB into a lower and an upper interval (Benvenuti et al., 2014).
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876 The lower division is represented by deepening-upward, coarse-grained delta front system,
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878 overlain by an upper mudstone division from an open shelf setting. The upper part is rich
879
880 with shell beds, and occasional articulated whale skeletons, associated with shark teeth,
881
882 have been recovered (Danise ~~&and~~ Dominici, 2014). Similar shelf mudstones of the MPL4
883
884 biozone crop out in VEB and SRB (Bossio et al., 1993; Riforgiato et al., 2005) whereas
885
886 biostratigraphically equivalent mudstones in FB testify to an upper epibathyal
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888 paleoenvironment.
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893 3.1.4 Synthem S4: early Piacenzian warm climate and high sea-level

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902 | Synthem S4 (Benvenuti et al., 2014) has been recognizedsed in FB and VEB by facies
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904 | similarities and chronostratigraphic correlation. In EB, S4 comprises a lower interval
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906 | dominated by richly fossiliferous, massive mudstone or very-fine-grained sandstone
907
908 | (prodelta-inner shelf), overlain by bioclast-rich sandstones recording prograding mixed
909
910 | carbonate-clastic ramp, outcropping in the southeastern part of the Elsa valley. Equivalent
911
912 | deposits, also comprised in biozone MPL4b, are patchily distributed in FB, VEB, SRB, OOB
913
914 | and other basins of southern Tuscany (Ghinassi &and Nalin, 2010; Ghinassi, personal
915
916 | communication, 2015). The upper interval of S4 is formed by a succession of delta front
917
918 | sandstones, passing in EB eastern margin to a few tens of m-thick fluvial succession, hinting
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920 | at an original depositional gradient. S4 is apparently missing due to erosion north of San
921
922 | Gimignano (EB), and around Lajatico (VEB). Biostratigraphic data allow to refer S4 to the
923
924 | upper part of biozone MPL4b and the lower part of MPL5a, thus comprising the mid-lower
925
926 | part of the Piacenzian, globally characterizedsed between 3.264-3.025 Ma by warm climate
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928 | and relatively high sea level (Raymo et al., 2009; Dowsett et al., 2013; Prista et al., 2015).
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933 934 | 3.1.5 Synthem S5: mid-Piacenzian high-frequency sea level variation 935 936

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938 | Synthem S5, recognizedsed in EB and VEB, is bounded below by an erosional unconformity
939
940 | that cuts deeply into underlying units, bringing S5 directly on top of S3 (EB: log 15; VEB:
941
942 | logs 5-6 in Fig. 1). S5 is up to about 200 m in EB, where it has been subdivided into a
943
944 | hierarchy of small-scale depositional sequences (Benvenuti et al., 2007; Dominici et al.,
945
946 | 2008: see following paragraphs). Each composite depositional sequence forms a tens-of-
947
948 | m-thick asymmetric sedimentary cycle, composed by a deepening-upward part, from fluvial
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950 | or coastal coarse-grained sediments, to open shelf mudstones, sometimes topped by a
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952 | regressive shoreface or delta sandstone, other times directly overlain by the next sequence
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954 | through a sharp contact. Fluvial, lagoonalbrackish-water, and other intertidal deposits mark
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961
962 the lower part of each composite sequence, usually topped by a laterally-continuous shell
963 bed, from a few cm to a few dm-thick, representing a surface of transgression. Shell beds
964 are particularly well-developed around the middle part of sequences, where they separate
965 shoreface and delta sandstones from overlying open shelf mudstones, marking the time of
966 maximum flooding (MFS). Large marine vertebrates, including articulated whale skeletons
967 and large sharks (Danise [&and](#) Dominici, 2014), are often recovered both at MFS and
968 overlying mudstone (Fig. 1). Towards the north-eastern margin of EB, cyclothemic fluvial
969 conglomerates, sandstones and mudstones replace coastal and fully marine deposits,
970 testifying to an original facies gradient. In the central part of EB, composite sequences are
971 stacked to form a deepening-upward succession, with a topmost thick and laterally-
972 continuous open shelf mudstone interval, directly onlapping the S4-S5 basal unconformity
973 on the eastern EB (log 15, Fiano: Fig. 1).
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990 3.1.6 Synthem S6: Piacenzian-Gelasian climate change and regression

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994 As S5, synthem S6 is also built through a hierarchy of small-scale depositional sequences,
995 better expressed in EB, but also documented in SRB and CB. In EB, fluvial coarse-grained
996 sandstones fill a deep valley incised in S5 deposits (logs 8-10 in Fig. 1), resting on the basal
997 unconformity of S6. Intertidal or coastal lagoon deposits form the transgressive systems
998 tract of the composite depositional sequence. A laterally-continuous shell bed testifies to the
999 MFS of S6, topped by highstand shoreface and delta front sandstones. The Piacenzian-
1000 Gelasian boundary, corresponding to a major climatic transition from warmer-moister to
1001 colder-drier conditions (Benvenuti et al., 1995b; 2007), is marked by the Gauss-Matuyama
1002 reversal detected at Montopoli (Lindsay et al., 1980). Highstand marine sandstones are
1003 characterized [zed](#) by the recovery of two mysticete skeletons, at Montopoli (EB, see
1004 Capellini, 1905) and Sinalunga (CB, Fig. 7). Fully continental environments were established
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1022 throughout the Gelasian in all basins here under study (e.g., Benvenuti [&and](#) Del Conte,
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1024 2013; Benvenuti et al., 2014; Bianchi et al., 2015).
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1030 3.2 Sedimentary facies and facies associations 1031

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1034 Seven groups of siliciclastic facies and one group of carbonate facies, with very different
1035 fossil content, have been recognized (Tab. 1). Siliciclastic facies form a
1036 paleoenvironmental gradient from terrestrial to marine and, in the case of marine facies,
1037 from shallowest to deepest (Fig. 8a). Facies types are fluvial conglomerate and sandstone,
1038 and alluvial mudstone (F1); intertidal to very shallow subtidal mudstone and muddy
1039 sandstone (F2); shallow subtidal coarse- and medium-grained sandstone with sparse
1040 conglomerate (F3); deep subtidal muddy fine-grained sandstone (F4); open shelf sandy
1041 mudstone (F5); outer shelf to upper bathyal mudstone (F6); outer shelf and bathyal turbidite
1042 sandstone and conglomerate (F7). An eighth group is formed by facies deposited subtidally
1043 in limited mixed carbonatic-siliciclastic ramps (F8), irrespective of depth (Nalin et al., 2016).
1044 Facies F6-F7 are restricted to Zanclean deposits (synthems S1-S3); facies F5 and F8
1045 characterise the upper Zanclean-middle Piacenzian interval (synthems S3-S4); facies F1-
1046 F4 characterise the upper Piacenzian (synthems S5-S6). The OOB succession,
1047 characterised by facies F1-F4, is an exception within the Zanclean.
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1066 3.3 Elementary depositional sequences (EDS) 1067

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1070 Both fluvial (Benvenuti [&and](#) Del Conte, 2013) and marine facies groups (siliciclastics:
1071 Benvenuti et al., 2007; 2014; carbonates: Nalin et al., 2016) are stacked to form facies
1072 associations which record cyclic variations of depositional and environmental conditions in
1073 response to a change in accommodation space. Physical surfaces and the intervening
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1082 deposits allowed to subdivide depositional sequences in systems tracts (Benvenuti et al.,
1083 2007; Dominici et al., 2008). At the simplest scale, these hybrid facies associations form
1084 elementary depositional sequences, up to 10-20 m thick, in their turn stacked to form
1085 composite sequences (original concepts from Mutti et al., 1994). This hierarchy is
1086 particularly evident in synthem S5-S6, formed at a time of pronounced glacio-eustatic
1087 oscillations and expressed around coastal settings, where maximum facies contrast allows
1088 for the expression of subtle cycle of sea level variation (e.g., Benvenuti &and Dominici, 1992;
1089 Benvenuti et al., 2007; Dominici et al., 2008). Analogue sharp facies contrast within
1090 Zanclean EDS in OBB (Tinelli, 2013), but is otherwise absent in deeper sediments (facies
1091 F5-F7). EDSs have different expressions depending on the time interval and the
1092 sedimentary basin.
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1105 3.3.1 Zanclean EDS (synthems S1-S3)

1106 In most basins, deposition of synthems S1-S2-S3 takes place at outer-shelf or bathyal
1107 depths, well below the point on a depositional profile where the rate of relative sea level
1108 change is zero (equilibrium point). Here the sediment supply is not sufficient to fill the
1109 available accommodation space and an aggradational style of deposition prevails, with the
1110 result that in most Zanclean settings smaller cycles of sea level variations are not marked
1111 by a facies change. The sharp facies change recorded where the monotonous muddy
1112 deposition is interrupted by turbidite sandstone and conglomerate, is connected with
1113 synthem boundaries and major tectonic phases of restructuring of the region. LMVsMM and
1114 shell beds are practically absent. This situation reverses in the Orcia-Ombrone basin, where
1115 depths of deposition are shallower and EDS are expressed. At Arcille deltaic sandy
1116 conglomerates and sandstones (facies F3) are overlain by a fluvial cross-bedded sandstone
1117 (facies F1a), separated by a transgressive surface (TS) from an overlying bioturbated
1118 shallow marine sandstone. A *Haustator vermicularis* shell bed (Danise, 2010; Tinelli, 2013)
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1142 forms the MFS separating the shoreface sandstone from an open marine mudstone with
1143 scattered shells (facies F5), marking a sudden and prolonged deepening of the basin
1144 (biozone MPL2: Sorbi et al., 2012; Tinelli, 2013). The succession is topped by deposits from
1145 shallower depths, expression of the falling-stage (FSST), below the upper SB (Fig. 4).
1146 Similar small-scale depositional sequences, expressed through fining-upward cycles no less
1147 than 40 m-thick, are also present in synthem S3 at Case al Poggio, near Siena (biozones
1148 MPL3-MPL4a: Bianucci et al., 2001) and at Castelfiorentino (biozone MPL4b: Benvenuti et
1149 al., 2014).

1161 3.3.2 Piacenzian EDS (synthems S4-S6)

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1163 As depth of deposition shallows during the Piacenzian, and cycles of sea level variation
1164 widen, the cyclic stacking of EDS becomes the typical depositional theme (Benvenuti et al.,
1165 2007, 2014; Dominici et al., 2008). In FB, the northwesternmost basin, depths remain
1166 considerable and facies change is more subtle. Pliocene at Orciano Pisano is traditionally
1167 assigned to the “Blue Clays” formation (Bossio et al., 1997), but two distinct bodies were
1168 evidenced since the late nineteenth century (D’Ancona, 1867). The lower one is formed by
1169 grey claystone with very rare shells, the upper one by muddy, very-fine grained gray
1170 sandstone richly fossiliferous. The lower part of the latter interval outcrops at the foothill of
1171 the small town of Orciano Pisano, around the locality Case Nuove (Bianucci [and](#) Landini,
1172 2005; Berta et al., 2015). Here a laterally persistent shell bed is dominated by the turrillid
1173 *Archimediella spirata*, overlain by a 25 m-thick monotonous sandstone interval with
1174 intercalated shell beds or sparse shells, becoming muddier upward. The *Archimediella* shell
1175 bed is interpreted as the TS of an EDS, coinciding with the lower SB of a lower Piacenzian
1176 EDS. The overlying muddy fine-grained sandstone is the TST and HST (MPL5a: Dominici
1177 et al., 2009; Fig. 6). At shallower settings, in all basins to the East and South of FB, EDS of
1178 synthem S4 take the form of an alternation of mudstone and carbonate (facies F5 and F8:
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1202 Nalin et al., 2016), or mudstone and sandstone (facies F5 and F3-F4: Benvenuti et al., 2014;
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1204 biozone MPL5a). Middle and upper Piacenzian EDS form and alternation of coastal
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1206 mudstone and sandstone (facies F1-F2-F3: Benvenuti ~~&and~~ Dominici, 1992; Dominici,
1207
1208 1994), with MFS and HST marked by a shell bed topped by a lower shoreface sandstone,
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1210 or a shelf mudstone (facies F4-F5: Benvenuti et al., 2007; Dominici et al., 2008).
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1215 **43. Distribution of large marine vertebrates**

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1220 **3.4.1 Geographic distribution**

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1223 The MM geographic distribution ~~of all LMVs that could be assigned to a given locality and~~
1224 ~~sedimentary facies~~ is listed in Table 2. All LMVsMM that ~~were~~was geographically located,
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1226 irrespective of stratigraphy, ~~were~~was plotted in Fig. 3. The largest number were recovered
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1228 in FB in Northwestern Tuscany, with a peak at a few sites around the small town of Orciano
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1230 Pisano, in the Pisa province. This coincides with the highest number of known species,
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1232 including mammals, elasmobranchs, turtles, and large bony fishes ~~(see Bianucci & Landini~~
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1234 ~~2005, Marsili 2006)~~. LMVMM ~~abundance is also high~~is also abundant in the province of
1235
1236 Siena, around Volterra (VEB; Bianucci ~~&and~~ Landini 2005), and around San Quirico,
1237
1238 particularly rich with elasmobranchs according to the available data (SRB; Marsili, 2006). A
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1240 fourth basin with a consistent number of findings is OOB, where cetaceans, sharks,
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1242 ~~dugongsirenian~~s and large ~~bonyteleost~~ fishes have been unearthed.
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1248 **3.4.2 SMM stratigraphic distribution ~~of LMVs~~**

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1251 **3.4.2.1 Synthems S1-S2**

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1262 In the vicinity of Saline di Volterra, ~~provenance of a mandible with teeth of one of the sites~~
1263 ~~with remains of~~ *Pliophoca etrusca* (Berta et al., 2015) ~~and sperm whale (Tab. 2)~~, S1 is
1264 ~~represented by a bathyal mudstone (facies F6, biozone MPL1). Lower-middle Zanclean~~
1265 ~~LMVsMM are~~ otherwise absent, with the exception of S2 in OOB, where ~~the large marine~~
1266 ~~vertebrates~~ are concentrated ~~along the MFS at the maximum flooding interval~~, outcropping
1267 at Poggio alle Mura (Danise, 2010), Camigliano (Sorbi et al., 2012) and Arcille (Tinelli et
1268 al., 2012; Tinelli, 2013), in biozone MPL2. At Poggio alle Mura a slightly disarticulated
1269 ~~balaenopterid balaenid~~ whale skeleton (WOM1-1 in Tab. 2) has been excavated in contact
1270 with the laterally-persistent *Haustator* shell bed at the maximum flooding interval (Figs. 4, -
1271 5; Danise, 2010; Tinelli, 2013). At Camigliano and Arcille, tens of km from Poggio alle Mura,
1272 the *Haustator* shell bed is associated with other articulated skeletons and isolated ~~LMVMM~~
1273 remains, including ~~several specimens of the sirenian~~ *Metaxytherium subapenninum*
1274 (MOM21-1, MOM1-2-5), ~~large bony fishes, rays, and sharks~~ *Carcharias taurus*,
1275 *Carcharhinus* sp., *Galeocerdo cuvieri*, and *Squatina* sp. ~~sharks and rays~~ (Sorbi et al., 2012;
1276 Tinelli et al., 2012; Tinelli, 2013). ~~A partial skull of the delphinid~~ *Etruridelphis giulii*, with
1277 ~~right and left dentaries fractured, but nearly complete and with most teeth still in their alveoli~~
1278 ~~(DSi2-1 in Tab. 2), was recovered southeast of Siena, near Chianciano Terme (SRB) at the~~
1279 ~~top of a mudstone (facies F6) intercalated with turbiditic sandstone beds (Facies F7), topped~~
1280 ~~by a monotonous mudstone interval (upper Zanclean, uppermost part of biozone MPL3:~~
1281 ~~Bianucci et al., 2009b). In the same basin, two undetermined beaked whales and bones of~~
1282 ~~four different specimens attributed to~~ *Metaxytherium subapenninum* were found in the
1283 ~~middle of a fining-upward succession, at the boundary between biozones MPL3 and MPL4a~~
1284 ~~(Bianucci et al., 2001; WSi2-1-2 and MSi2-1-4 in Tab. 2), suggesting that findings at the two~~
1285 ~~SRB localities belong to the same MFS, in the upper part of S2. Four~~ Three specimens of
1286 ~~marine mammals were identified in Synthem S1, 13~~ seven in Synthem S2.
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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, WEI3-12). These strata are richly fossiliferous, with several shell beds with epifaunal cemented taxa, such as vermetid gastropods, oysters and corals (Facies F5), within a normal-polarity magnetostratigraphic interval (Gauss chron: Andrea Albanelli, personal communication, 1999). Based on physical stratigraphic correlation, this can be assigned to a lower Piacenzian HST. ~~Finally, aA dolphin skull of Hemisytrachelus 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, DWEI3-1-2 in Tab. 24). Overall, specimens of marine mammals attributed to Synthem S3 were sixeleveln (some are uncertain and may come from the upper part of S2: Tab. 2).~~

3.4.2.3 Synthem S4

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1382 Synthem S4 yielded the highest ~~number of the reviewed large marine vertebrates abundance~~
1383 ~~and species-richness of the Tuscan MM~~. In the Fine basin, the locality of Orciano Pisano is
1384 ~~and species-richness of the Tuscan MM~~. In the Fine basin, the locality of Orciano Pisano is
1385 represented in Table 2 by ~~nine~~18 records of whales, dolphins (a partial skeleton: Bianucci,
1386 1996; Bianucci et al., 2009), seals (Berta et al., 2015), tens of other ~~cetacean~~
1387 ~~specimens unidentified cetacean elements~~, hundreds of shark teeth and vertebrae (Fig. 3),
1388 and sea turtles, large bony fishes, and sea birds hosted in museum collections (Bianucci
1389 ~~& Landini, 2005; Marsili, 2007b; Cioppi and Dominici, 2011~~). In locality Case Nuove, a
1390 single middle Piacenzian ~~T~~~~stransgressive surface is known to have~~has yielded a whole,
1391 articulated whale skeleton (Figs. 4, 6), teeth of blue and white sharks and bones of sea birds
1392 (Dominici et al., 2009). From the same site come ~~ss a n-articulated seal~~ skeleton ~~of the monk~~
1393 ~~seal Pliophoca etrusca~~ (Berta et al., 2015~~4~~), and possibly many other museum specimens
1394 labelled “Orciano Pisano” ~~(e.g., Higgs et al., 2012)~~, suggesting that this ~~surface interval~~
1395 ~~isforms~~ the most prolific bonebed of the region ~~(Tab. 2)~~. A few cm above the *Archimediella*
1396 shell bed, glauconitic and deeply bioeroded whale bones (Danise, 2010), ~~associated~~ with
1397 ichnological evidence of the activity of *Osedax* bone-eating worms (~~see~~ Higgs et al., 2012),
1398 lie in a bioturbated muddy, fine-grained sandstone with a complex boxwork of *Ophiomorpha*
1399 and *Thalassinoides* trace fossils (Fig. 6), associated with a diverse paleocommunity of
1400 molluscs and other benthic invertebrates ~~from several trophic groups with complex trophic~~
1401 ~~connections~~ (Dominici et al., 2009; Danise et al., 2010). ~~In the adjacent~~At the boundary
1402 ~~between FB and~~ VEB, an incomplete ~~dolphin~~ skull and skeleton ~~of the dolphin Etruridelphis~~
1403 ~~giulii~~ was recovered near Lorenzana (Lawley, 1876; Bianucci, 1996; Bianucci et al., 2009~~b~~),
1404 at a locality associated with a muddy sandstone interval (facies F4) in synthem S4. An
1405 incomplete and ~~disarticulated mysticibalenopterid whale~~ete was recovered in a sandstone at
1406 San Gimignano, associated with pectinid bivalves (~~Fig. 7~~; facies F3; Elsa basin, EB: Danise
1407 ~~& Dominici, 2014~~), here tentatively assigned to the uppermost part of the synthem
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(WEI4-1 in Tab. 2). Overall, specimens of marine mammals attributed to Synthem S4 were 2728.

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; WEI5-1 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~~; ~~2014~~; Dominici et al., 2008; WEI5-2 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 reworking 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 WEI5-2, ~~in the middle of EB~~, lies in correspondence of an interval of low rates of sedimentation. In SRB, near

1501
1502 Castelnuovo Berardenga, shelfal mudstones (facies type F5) have yielded MM remains at
1503 a few localities. Delphinid remains were found at the “I Sodi” quarry and at Troiola (DSi5-1-
1504 2, in Tab. 2). Bones of a beaked whale and undetermined mysticetes are reported from
1505 Guistrigona (Manganelli and Benocci, 2014) and a fragmentary specimen of the monk seal
1506 *Pliophoca etrusca* from Castelnuovo Berardenga (Berta et al., 2015). A very rich shark
1507 fauna, including sawsharks, thresher, frilled, bluntnose sixgill, bramble, gulper, kitten, sand
1508 tiger, shorten mako, basking and requiem sharks, an association suggesting an upper slope
1509 paleoenvironment for the surroundings of Castelnuovo Berardenga Scalo (Cigala-Fulgosi et
1510 al., 2009; the same mudstone interval at the same locality has been interpreted as a shelfal
1511 deposit: Martini et al., 2016). Marine mammals identified in Synthem S5 were eight. Judging
1512 from historical accounts (Capellini, 1883), the killer whale *Orcinus citonensis* (DCh4-1) was
1513 recovered in a sandy unit lying on top of a thick mudstone interval (S3 or S4) and is
1514 tentatively assigned to S5. Specimens of marine mammals attributed to Synthem S5 were
1515 10.

1534 3.4.2.5 Synthem S6

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1538 A fairly complete skeleton of a large balaenid whale was recovered in the second half of the
1539 19th Century in the EB near Montopoli Valdarno (Capellini 1905), in open shelf strata
1540 attributable to the interval of maximum flooding of ~~Synthem~~ S6 (WEI6-1 in Tab. 2). The MFS
1541 of S6, of uppermost Piacenzian age, is marked in EB by a laterally continuous *Pteria*
1542 *phalenacea* shell bed, with a high-diversity association of macroinvertebrates, including a
1543 rich decapod paleocommunity (Garassino et al., 2012). In the ~~same locality~~ vicinity, near
1544 Palaia, a right whale (*Eubalena* sp.) was recovered in 1974 in sandy mudstones, in
1545 association with mollusc shells and teeth of the great white shark (*Carcharodon carcharias*:
1546 Bisconti, 2002; Sorbini et al., 2014). A tightly articulated balaenopterid skeleton was found
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1562 at Sinalunga (WCh4-1 in Tab. 2), in deltaic sandstones and conglomerates (Fig. 8). Marine
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1564 mammal specimens attributed to *Synthem S6* with some confidence were three.
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1567 1568 4.3 MM facies type distribution 1569

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1573 In an ideal deepening-up gradient, multi-element findings of marine mammals are very rare
1574 in intertidal and very shallow subtidal paleoenvironments (facies type F2, 1,5%: Fig. 9A),
1575 moderately represented in delta or shoreface sandstones (facies type F3, 4,6%), most
1576 abundant in sandy mudstone of open shelf settings (facies type F5, 87,70%), rare in outer
1577 shelf and bathyal sediments (facies type F6-F7, 6,21,5%). The most pristine and complete
1578 skeletons are associated with gravelly well-sorted sands from event sedimentation,
1579 suggesting a negative relationship between taphonomic loss and sedimentary processes at
1580 delta fronts. In the tightly articulated and pristine Sinalunga balaenopterid (WCh4-1 in S4-
1581 CB), the cortical surface of the tightly-connected vertebrae is practically intact, and carpal,
1582 metacarpal and phalanges of the flipper are in perfect anatomical connection, as if a sudden
1583 depositional event buried a fresh carcass (Fig. 8; similar pristine skeleton are found in deep
1584 water turbiditic succession: Stinnesbeck et al., 2014). Another pristine and tightly articulated
1585 skeleton, belonging to a killer whale (WCh3-1 in CB), was collected at Cetona in the second
1586 half of the 19th century, in a locality associated with sandstones, also possibly of deltaic
1587 origin. Large vertebrates embedded in fine-grained, muddy matrix (shelf deposit formed
1588 below storm wave base) and those associated with laterally-persistent shell beds
1589 (condensed deposits) are slightly disarticulated and fairly complete, showing signs of long
1590 permanence in a low energy, well-oxygenated seafloor before the final burial. Bioerosion of
1591 bones caused by phototrophic cyanobacteria and algae, heterotrophic fungi and bacteria
1592 (Orciano balaenopterid WFi4-1 in S4-FB), and eventually by whalebone-eating siboglinid
1593 worm of genus *Osedax* (on a ziphiid humerus, WFi4-14: Higgs et al., 2012), occurred at
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1622 condensed intervals, in association with glauconite (Danise, 2010). In one instance, a
1623 condensed shelly interval is traced for a few kilometers, connecting bioturbated shoreface
1624 sandstones yielding slightly disarticulated sirenian skeletons (MOM2-1, MOM2-2) and other
1625 MM (Tinelli, 2013), with open shelf deposits yielding slightly disarticulated whale remains
1626 (WOM2-1 in S2-OOB).

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1628 Regarding a sequence stratigraphic interpretation, pristine skeletons from delta front
1629 sediments can be part of the FSST (Fig. 4; or in an alternative interpretation it may belong
1630 to, of the early TST, when incised valleys are filled with coastal deposits). TST deposits
1631 account for 126,2% of cases (Fig. 9B). Much more frequently, articulated or slightly
1632 disarticulated skeletons are associated with the HST of the corresponding depositional
1633 sequence, lying above the MFS (956,9% of cases), or within the maximum flooding
1634 interval directly in coincidence with it, above a laterally-persistent shell bed (10,8%). Bone
1635 bioerosion is less pronounced in the late HST, when sedimentation rate increases
1636 (Castelfiorentino whale WEI3-2 in S3-EB).

1654 4.4 MM abundance and species-richness

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1659 Some taxa need revision, but a conservative estimate of the different morphologies suggest
1660 that at least 17 marine mammal species lived in the NWMS during the Pliocene (possibly
1661 more than 20, an estimate for the whole epoch, i.e., 5,332-2,588 Ma), against only 9
1662 presently living in the same area (plus two occasional visitors). Among the cetaceans, six
1663 families were present, against only five presently living in the Ligurian Sea (Tab. 3). The
1664 most abundant Pliocene species of Tuscany are the sirenian *Metaxytherium subapenninum*
1665 (N = 10), the dolphin *Etruridelphis giulii* (N = 7) and the delphinid *Hemisyntrachelus cortesii*
1666 (N = 5; Tab. 4). Overall abundance and species richness are not randomly distributed, but
1667 are maximum in Piacenzian strata of synthem S4, dated at 3.2-3.0 Ma (Tab. 2, Figs Fig-2,
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1682 9C-D2), particularly in the FB and VEB (Tab. 4). A species list of marine mammals summing
1683 up findingsfossils found around Orciano Pisano and at La Rocca, near Volterra, yields a
1684 species richness (S) of 11-1213. This Piacenzian peak in marine mammal diversity is
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1689 matched by the fossil record of sharks, also maximum near Orciano Pisano (S = 27), with a
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1691 second peak in S5, around Castelnuovo Berardenga (SRB, S = 16). Differently from the
1692
1693 marine mammals, showing a complete turnover from the Pliocene to the recent (Tab. 3),
1694
1695 34% of Pliocene shark species are still extant in the NWMS (Tabs. 5-6). Marine mammal
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1697 frequency and diversity gradually decreases in S5-S6.
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1704 **35. Paleoenvironment-fauna relations**

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1709 The paleoecology of Pliocene MM of Tuscany can be reconstructed by comparison with the
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1711 ecology of their modern relatives. This approach can be applied at the family or genus level
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1713 for marine mammals (Tab. 3), at the genus or species level for sharks (Tab. 5). With the
1714
1715 only exception of the sirenian *Metaxytherium subapenninum*, feeding on seagrasses
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1717 (Domining, 2001), and small demersal sharks (e.g., catsharks, frilled sharks), all MM studied
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1719 here are pelagic forms that had no direct connection to conditions at the seafloor (Tabs. 4
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1721 and 6). ~~With the exception of the few benthopelagic marine vertebrates (seals, dugongs),~~
1722
1723 many LMVs of the Pliocene of Tuscany were epipelagic (e.g., mysticetes, larger sharks) or
1724
1725 mesopelagic (e.g., sperm whales, ziphiids), ~~with no direct connection with the ecological~~
1726
1727 ~~conditions at the seafloor.~~ The paleoecology of benthic habitats informs however on the
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1729 situation of the overlying water column in terms of ~~ecological~~ factors that matter to the
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1731 distribution of ~~pelagic~~epipelagic and mesopelagic organisms. ~~These factors include, such~~
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1733 ~~as~~ water depth, salinity and nutrient levels. In the second place, since ~~all LMV~~all MM remains
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1735 after death ultimately sink to the seafloor, benthic paleoecology is also a means to
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1742 understand taphonomic controls on LMVMM distribution. Cluster analysis based on the
1743 distribution of mollusc species in 72 samples resulted in the identification of four main groups
1744 of ~~mollusc~~-samples, roughly corresponding to the four main facies types recognizedsed
1745 based on lithology and sedimentary structures (F2-F5 in Tab. 1). Clusters are formed by
1746 samples from outer shelf and upper slope (three samples), open shelf (34 samples),
1747 shoreface (23 samples), and transitional settings, such as brackish-water coastal lagoons
1748 and tidal flats (12 samples: see Supplement Material, Fig. S1). ANOSIM confirms that
1749 sedimentary facies type can broadly predict what benthic assemblage it will yield (Tab. 73;
1750 general $R = 0,632$). The difficulty to discriminate between upper and lower shoreface facies,
1751 and between shoreface and open shelf facies is confirmed by overlaps in sample distribution
1752 in the NMDS ordination diagram (Fig. 109A). Samples AG1, MON1 and MON2 allow to re-
1753 interpret the associated sandstones, originally included in upper shoreface facies type, as
1754 offshore deposits. The presence of gravels and cobbles intensely bioeroded by bivalves and
1755 polychaete (ichnofossils include *Gastrochaenolithes*, *Meandripolydora* and *Caulostrepsis*)
1756 and encrusted by balanids, oysters, serpulids, and bryozoans, suggests they are part of
1757 condensed beds resulting from transgressive pulses (hiatal concentrations). The
1758 relationship between facies type and mollusc association is broadly summarized
1759 in the following paragraphs (see online Supplement Information for a list of characterizing
1760 species).
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1784 35.1 Coastal lagoon, tidal flat and embayment

1785 Intertidal faunas are always associated with facies type F2 and are characterised by low-
1786 diversity associations, sometimes with less than 10 taxa and dominated by one or two
1787 species, including species today living in brackish waters of the Mediterranean, at intertidal
1788 or very shallow subtidal depths (e.g. *Cerastoderma edule*, *Nassarius reticulatus*,
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1801
1802 *Scrobicularia plana*: Pérès &and Picard, 1964). Facies type F2 is also associated with
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1804 samples having a species richness higher than the preceding and including species typical
1805
1806 of seagrass bottoms and known to withstand moderate changes of salinity. In only one
1807
1808 instance a LMVlarge vertebrate was associated with intertidal deposits. Interestingly, this
1809
1810 was (not a sirenian, but a balaenid, lying on top of large wood fragments-(: Bianucci, 1995;
1811
1812 Collareta et al., 2016; Fig. 98A).

1813 35.2 Upper shoreface

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1822 Facies type F3 is associated with a high-diversity assemblage representing a
1823
1824 paleocommunity dominated by suspension feeders adapted to shifting sandy bottoms, with
1825
1826 bivalves typical of modern shoreface sandy bottoms (e.g., families Glycymeridae, Tellinidae,
1827
1828 Donacidae and Veneridae). Among extinct species of this recurring assemblage, some are
1829
1830 large-sized or have very thick shells. Some species of this group indicate the presence of
1831
1832 vegetated bottoms. Small pyramidellid gastropods are parasitic on echinoderms, also typical
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1834 of the upper shoreface.
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1836 35.3 Lower shoreface

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1844 Species richness further increases in collections associated with facies type F4 (lower
1845
1846 shoreface). Species typical of this recurring assemblage include both suspension-feeding
1847
1848 and detritus-feeding bivalves and gastropods. The following gastropod families are usually
1849
1850 represented by several species: Trochidae, Rissoidae, Cerithiidae (from vegetated
1851
1852 bottoms), Naticidae, Muricidae, Turridae, Conidae, Terebridae, Bullidae, Cylichnidae
1853
1854 (carnivores), Pyramidellidae (echinoderm parasites). Many bivalve species occur in both
1855
1856 facies types F2 and F3. At three different sites and at different stratigraphic units LMVs
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1861
1862 were large marine vertebrates, including mysticetes, sirenians and sharks, were recovered
1863
1864 in association with shell beds dominated by the ~~turritellid and~~ gregarious turritellid gastropod
1865
1866 *Haustator vermicularis* (Fig. 6C-D).
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1871 35.4 Offshore and upper slope 1872 1873 1874

1875 Another important set of species recurred in facies type F5 (mudstone deposited in offshore
1876 bottoms at shelf depths). Among characterizing gastropods are the suspension feeders
1877
1878 (*Turritella tricarinata*, *Archimediella spirata* and *Petalochoncus intortus*), deposit feeders
1879
1880 (*Aporrhais uttingeriana*) and carnivores or scavengers (*Epitonium frondiculoides*, *Nassarius*
1881
1882 *semistriatus*, *Mitrella nassoides*). Also the bivalves occupy many different ecological niches
1883
1884 (e.g., infaunal detritus feeders, epifaunal suspension feeders, either free-living, byssate, or
1885
1886 cemented). Outer shelf and uppermost bathyal samples from F6 mudstones,
1887
1888 studied at only one location, are characterized sed by a separate set of carnivorous
1889
1890 gastropods and by a few small bivalve species. Ubiquitous molluscs include species found
1891
1892 from intertidal to outer shelf depths (e.g., *Corbula gibba*), and those preferential of open
1893
1894 marine waters, from lower shoreface to outer shelf. Most multi-element findings of marine
1895
1896 mammals are associated with sandy mudstones from open shelf settings, below storm wave
1897
1898 base (F5, 75-80% of occurrences; e.g., Orciano whale: Fig. 8A), also in association with an
1899
1900 *Archimediella spirata* shell bed (Fig. 6C-D). No molluscs were recovered in facies type F7,
1901
1902 with the exception of bathyal mudstone in the lowermost Pliocene of FB, associated with
1903
1904 sparse specimens of the gryphaeid epifaunal bivalve *Neopycnodonte navicularis* -(not
1905
1906 sampled).
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1914 35.5 Carbonate platform 1915 1916 1917 1918 1919 1920

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1922 A recurring benthic assemblage associated with the highly fossiliferous facies type F8, not
1923 included in the quantitative analysis, consists of the large pectinid bivalves *Gigantopecten*
1924 *latissima* and *Hinnites crispus* and by a mixture of photozoans (large benthic foraminifera),
1925
1926 hard-substrata dwellers (brachiopods, echinoderms), encrusters (red algae, bryozoa) and
1927
1928 bioeroders (clionid sponges). All fossil-rich carbonates are associated with synthem S4 , in
1929 the middle part of the Piacenzian (Fig. 2, see also Nalin et al., 2016).
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1937 **46. Paleodepths**

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1942 Multivariate techniques ~~can be~~ usefully applied to stratigraphic and paleobiologic
1943 analysis (Scarponi & Kowalewski, 2004). We used the results of the ordination analysis
1944 to estimate absolute depths of the final resting place of some LMV large vertebrates listed
1945 in Tab. 2. Samples in the NMDS ordination plot following a water depth gradient, with
1946 shallower samples to the left (low values of NMDS axis 1) and deeper samples to the right
1947 (high values of axis 1). Therefore, NMDS values of axis 1 can be used as a proxy for relative
1948 water depth. We calculated absolute palaeodepths by fitting a logarithmic regression curve
1949 between absolute paleodepth of 23 modern species (data from MARBEF database),
1950 common in our dataset, and the values on NMDS axis 1 (Supplement Material: Tabs. S1-
1951 S4). The regression analysis, with $R^2 = 0.813$, indicates that scores along the nMDS main
1952 axis are a good predictor of the preferred depth for the 23 modern species (Fig. 910B, inset),
1953 thus supporting the bathymetric interpretation. This allowed to estimate the absolute depth
1954 of the 72 ~~mollusc~~ samples, which ranged from 0.4 m to 365 m, i.e., from intertidal to upper
1955 slope depths (Fig. 109B). ~~These results are,~~ in accordance with a previous estimate of
1956 absolute paleodepths, ~~carried out~~ in the upper part of the Pliocene ~~succession~~ of EB, ~~and~~
1957 based on counts of foraminifera. ~~(Dominici et al., 2007).~~ ~~According to the present estimates,~~
1958 ~~F~~ Facies type F2 is deposited at 0-105 m depth ~~(mostly 0-5 m)~~, F3 at 3-30 m, F4 at 10-100
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1982 m, and F5 at 40-300 m, F5 at around 350 m depth (only one sample: Fig. 910B). The position
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1984 of fossil cetaceans, dugongsirenians, pinnipeds and large sharks (respectively W, M, P and
1985
1986 S, N = 13) was plotted near the corresponding shell bed in the NMDS ordination. The
1987
1988 resulting pattern shows that all large mammalsMM considered, associated with open shelf
1989
1990 settings and with facies types F4-F5, cluster around a depth of about 100 m, spanning 30-
1991
1992 300 m (Fig. 9B).

1993 1994 1995 1996 1997 **5. Interpretation**

1998
1999 ~~Large marine vertebrates are nearly unrecorded in synthem S1-2 (Zanclean, mostly bathyal~~
2000
2001 ~~mudstone and turbiditic sandstone), notwithstanding these successions are the thickest, but~~
2002
2003 ~~they are recovered in S2 in OOB (shoreface and open shelf deposits). LMVs are abundant~~
2004
2005 ~~in synthems S3-5, peaking in synthem S4 (middle part of the Piacenzian), with intermediate~~
2006
2007 ~~abundances in synthem S6 (upper Piacenzian-lowermost Gelasian). In an ideal deepening-~~
2008
2009 ~~up gradient, multi-element findings of marine mammals are very rare in intertidal and very~~
2010
2011 ~~shallow subtidal paleoenvironments (facies type F2: one instance in Bianucci, 1995, out of~~
2012
2013 ~~39 cases explored), moderately represented in delta or shoreface sandstones (facies type~~
2014
2015 ~~F3), most abundant in sandy mudstone of open shelf settings (facies type F5, 77% of~~
2016
2017 ~~occurrences: Fig. 8A; e.g., Orciano whale: Figs. 4, 6), nearly absent in outer shelf and~~
2018
2019 ~~bathyal sediments (Saline di Volterra seal, PEr1-1 in S1-VB; Lucciolabella dolphin, WSi2-1~~
2020
2021 ~~in S3-SB). Regarding their taphonomy, the most pristine and complete skeletons are~~
2022
2023 ~~associated with gravelly well-sorted sands from event sedimentation, suggesting a negative~~
2024
2025 ~~relationship between taphonomic loss and sedimentary processes at delta fronts. In the~~
2026
2027 ~~tightly articulated and pristine Sinalunga balaenopterid (WCh4-1 in S4-CB), the cortical~~
2028
2029 ~~surface of the tightly-connected vertebrae is practically intact, and carpal, metacarpal and~~
2030
2031 ~~phalanges of the flipper are in perfect anatomical connection, as if a sudden depositional~~
2032
2033 ~~event buried a fresh carcass (Fig. 7; similar pristine skeleton are found in deep water~~
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2042 turbiditic succession: Stinnesbeck et al. 2014). Another pristine and tightly articulated
2043 skeleton, belonging to a killer whale (WCh3-1 in S4-CB), was collected at Cetona in the
2044 second half of the 19th century, in a locality associated with sandstones, also possibly of
2045 deltaic origin. LMVs embedded in a fine-grained, muddy matrix (shelf deposit formed below
2046 storm wave base) and those associated with laterally-persistent shell beds (condensed
2047 deposits) are slightly disarticulated and fairly complete, showing signs of long permanence
2048 in a low energy, well-oxygenated seafloor before the final burial. Bioerosion of bones caused
2049 by phototrophic cyanobacteria and algae, heterotrophic fungi and bacteria (Orciano
2050 balaeopterid WFi4-1 in S4-FB), and eventually by whalebone-eating siboglinid worm of
2051 genus *Osedax* (on a ziphiid humerus: Higgs et al. 2012), occurred at condensed intervals,
2052 in association with glauconite (Danise 2010). In one instance, a condensed shelly interval is
2053 traced for a few kilometers, connecting bioturbated shoreface sandstones yielding slightly
2054 disarticulated dugong skeletons (MOm2-1, MOm2-2) and other LMVs (Tinelli, 2013), with
2055 open shelf deposits yielding slightly disarticulated whale remains (WOm2-1 in S2-OOB).
2056
2057 Regarding a sequence stratigraphic interpretation, pristine skeletons from delta front
2058 sediments can be part of the FSST (Fig. 4; or in alternative interpretation, of the early TST,
2059 when incised valleys are filled with coastal deposits). TST deposits account for 12% of
2060 cases. Much more frequently, slightly disarticulated skeletons are associated with the HST
2061 of the corresponding depositional sequence, lying above the MFS (69% of cases), or directly
2062 in coincidence with it, above a laterally-persistent shell bed (10%). Bone bioerosion is less
2063 pronounced in the late HST, when sedimentation rate increases (Castelfiorentino whale
2064 WEI3-2 in S3-EB).
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2091 **67. DiscussionFactors of the Pliocene NWMS marine**

2092 **megafauna fossil record**

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2102 The detailed sequence-stratigraphic framework and the abundant shell beds, offering an
2103 independent check on sedimentary facies distribution by benthic paleoecology, allows also
2104 to explore factors behind MM geographic and stratigraphic distribution, and to sort out
2105 evolutionary, ecological, and taphonomic drivers of this particular fossil record. NWMS
2106 Pliocene distribution can be compared with similar studies in different settings and at
2107 different times, to draw conclusions on the general quality of MM fossil record.
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2117 7.1 Evolutionary control

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2122 Available data allow a meaningful comparison of NWMS MM diversity across the Pliocene,
2123 particularly detailed for marine mammals (Fig. 9D). Although the study suggests a facies
2124 control on MM distribution, with large vertebrate MM remains being generally
2125 connected associated with late TST-HST muddy sandstones and mudstones from lower
2126 shoreface and offshore shelf paleosettings, the temporal pattern of biodiversity recorded on
2127 a regional basis should in part likely represent reflects also a paleobiologic phenomenon,
2128 since lower shoreface and offshore shelf sediments are represented in all synthem. Marine
2129 mammals are unrecorded in the thickest part of synthem S1-2 (Zanclean, mostly bathyal
2130 mudstone and turbiditic sandstone), but they are present in S2, in OOB (Zanclean shoreface
2131 and open shelf deposits) and SRB (Zanclean upper slope deposits). MM is
2132 uncommon gradually rises in S3, at the upper Zanclean-lower Piacenzian, whereas it
2133 suddenly peaks in synthem S4, where species richness of both marine mammals and sharks
2134 is highest. S5 reflects a lower diversity of marine mammals, but still a high diversity of sharks,
2135 while values of both groups drop to the lowest abundance and species richness in S6, during
2136 the upper Piacenzian-lowermost Gelasian (Fig. 9D).
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2153 The S4 diversity peak coincides with the middle part (3.264–3.025 Ma) of the Piacenzian, a
2154 time interval in which the earth experienced global average temperature 1.84 °C-3.60 °C
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2162 warmer than the pre-industrial period (Dowsett et al., 2013). Climatic impact is testified by
2163 the widespread occurrence of carbonate deposits in S4 (Fig. 2), with sedimentary facies
2164 indicative of warm-temperate to subtropical conditions, with summer sea-surface
2165 temperature considerably warmer than 20°C and winter temperatures colder than 20°C
2166 (Nalin et al., 2016). This suggests a causative link between global climate and biodiversity,
2167 S4 diversity peak recording a global phenomenon, possibly an increase of speciation rate
2168 connected with global warming. Similarly, we propose that the lower diversities recorded at
2169 S5-S6 are the regional expression of an increase in extinction rate related to climatic cooling
2170 and global sea-level drop, ultimately leading to the global MM extinction event recorded on
2171 a coarser scale at the Pliocene-Pleistocene boundary (Pimiento et al., 2017): the finer
2172 stratigraphic resolution adopted here suggests a stepwise extinction event. NWMS data also
2173 point to a selective effect, extinction being recorded by marine mammals, with a 100%
2174 regional turnover between Pliocene and Recent (Tab. 3), but not as much by the shark
2175 fauna, with 34% of the species still living in the Mediterranean, while still others have shrank
2176 their distribution to subtropical latitudes. Also the Piacenzian teleost fish fauna (Cigala
2177 Fulgosi et al., 2009) and the benthic mollusks (Raffi et al., 1985) show a high percentage
2178 of holdovers, suggesting that marine mammals have been particularly prone to climatic
2179 change (see also Steeman et al., 2009).

2180 Estimates of body size in Pliocene mysticetes of Tuscany, with several specimens reaching
2181 10 m (Danise and Dominici, 2014: seven specimens in Tab. 1), are comparable to global
2182 values derived from the literature for this time interval (Lambert et al., 2010), confirming that
2183 NWMS baleen whales were larger than their Miocene analogues, and smaller than modern
2184 forms. As with regard to odontocetes, the most common Pliocene delphinid, *Etruridelphis*,
2185 was larger than the modern analogue *Stenella* (Bianucci et al., 2009b). The same is true for
2186 *Hemisyntrachelus cortesii*, larger than modern *Tursiops* (Bianucci, 1997a). On the other
2187 hand, the largest extant delphinid *Orcinus orca*, reaching 9 m, is about twice as long as

2221
2222 *Orcinus citonensis* (Heyning and Dahlheim, 1988). The high percent of holdover points to a
2223 more conservative figure for larger sharks (Tab. 5), but the presence in the Pliocene of the
2224 gigantic *Carcharocles megalodon* and some large thermophilic species today restricted to
2225 lower latitudes suggests that impoverishment of the fauna is coupled with an average
2226 decrease in size (Marsili, 2008). Comparing sizes suggests an overall restructuring of
2227 NWMS MM during the last three million years (see also Bisconti, 2009).

2234
2235 ~~The geographic and stratigraphic distribution of large marine vertebrates in the fossil record,~~
2236 ~~as that of any other key elements of marine ecosystems, depends on ecological (i.e., the~~
2237 ~~production of organic parts) and taphonomic factors (their preservation). The detailed~~
2238 ~~sequence-stratigraphic framework available for the very thick Pliocene succession of~~
2239 ~~Tuscany, and the abundant shell beds that offer an independent check on sedimentary~~
2240 ~~facies distribution by benthic paleoecology, allow to explore ecological and taphonomic~~
2241 ~~drivers on the distribution of Northwestern Mediterranean LMVs. In its turn, this can be~~
2242 ~~compared with similar studies in different settings and at different times, to draw conclusions~~
2243 ~~on the general quality of LMV fossil record.~~

2256 67.21 Ecological control

2259 Marine

2260
2261 The composition of the Pliocene NWMS MM is affected in the first place by the availability
2262 of food. At the lowest trophic level, inferring from the ecology of the modern MM (Tabs. 3,
2263 5), we found herbivore sirenians feeding on seagrasses (trophic level, TL = 2,0), all others
2264 being carnivores, thus having TL > 3,0 (Fig. 1211). The lowermost levels among the
2265 carnivores were occupied by baleen whales and whale sharks (TL = 3,2-3,4), filter-feeding
2266 on pelagic crustaceans and fishes (krill). Roughsharks, catsharks, and houndsharks, with
2267 many species living in the modern Mediterranean, have a relatively species-poor Pliocene
2268 record, probably due to a preservation bias related to their small size. At TL = 3,7-4,0 were

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2282 one species of catshark and a monk seal, both feeding near the seafloor on crustaceans,
2283 teleost fishes and cephalopods. At TL = 4,1 were sandbar, tiger and blue sharks, feeding on
2284 teleost fishes, cephalopods and on marine mammals. At the same level, in slope
2285 environments, kitefin sharks mainly fed on other sharks. The majority of MM species were
2286 found at TL = 4,2, with smaller odontocetes (three species) and 11 species of sharks,
2287 including several requiem sharks, a houndshark and a hammerhead. Larger dephinids,
2288 sperm whales, beaked whales, together with mackerel, sand and sand tiger sharks,
2289 occupied high trophic levels (TL = 4,3), followed at the top of the global NWMS food web by
2290 white shark, megalodon shark, one species of sevengill shark (genus *Notorynchus*), and
2291 killer whales, all feeding on marine mammals and smaller sharks (TL = 4,4-4,7). With no
2292 exception, all highest levels encountered in modern NWMS offshore pelagic and nearshore
2293 communities were occupied during the Pliocene by an analogous MM, often by the same
2294 species (large sharks), or by congeneric or con-familial species (marine mammals: Tab. 3,
2295 5). The Pliocene pelagic ecosystem, typified by the mid-Piacenzian S4 association, must
2296 have been however trophically more diversified (Fig. 11), including aquatic megaherbivores,
2297 several balaenid filter feeders, larger and more diverse dolphins, and sharks species today
2298 extinct (e.g., *Carcharocles megalodon*) or restricted to tropical seas (e.g., *Galeocerdo*
2299 *cuvier*). With the exception of TL = 2, all Pliocene NWMS MM were either apex predators of
2300 their community, or mesopredators, occupying trophic positions below apex predators. The
2301 definitions of apex predators (or top predators) and mesopredators are relative and to an
2302 extent context-dependent (species that in a context are apex predators, in another are
2303 mesopredators, e.g., Estes et al., 1998). Since predation is a trophic interaction in which
2304 one animal (predator) consumes another (prey) as a source of energy (food), irrespective of
2305 the means by which this is accomplished (Lourenço et al., 2013), filter-feeding baleen
2306 whales can be considered apex-predators of their community (e.g., Lewiston et al., 2004;
2307 Notarbartolo di Sciara et al., 2016). Among sharks, 68% of living Mediterranean
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2342 elasmobranches are ranked as top predators, with a trophic level of 4 or more (Goffredo and
2343 Dubinsky, 2014, including superorder Batoidea, against 22% of teleost fishes), an estimate
2344 that can be extended to Pliocene NWMS MM. Relationships between apex predators and
2345 mesopredators are complex and hard to define in ecology, involving predation on other
2346 predators (intraguild predation, combining competition and predation: Polis et al., 1989),
2347 where consumption and competition need to be proved (Lourenço et al., 2013). In the
2348 Mediterranean Pliocene, paleontological evidences of carnivores serving as food to MM
2349 include killing of prey (Bianucci et al., 2010) and scavenging (Cigala Fulgosi, 1990; Bianucci
2350 et al., 2002; Dominici et al., 2009). The occurrence of intraguild predation must have been
2351 far more extended than what taphonomy can prove, however, given a Pliocene diversity of
2352 NWMS very large raptorial feeders higher than the modern, including the killer whale
2353 *Orcinus citonensis*, the large delphinid *Hemisyntrochelus cortesii* (phylogenetically related
2354 to the modern killer whale: Murakami et al., 2014), the white shark *Carcharodon carcharias*,
2355 the largest shark of all times *Carcharocles magalodon* (Marsili, 2008), and a diverse
2356 association of smaller carnivores, including monk seal, delphinids and sharks with $4,0 < TL$
2357 $< 4,2$ (Tab. 3, 5), candidate prey for larger raptorial feeders. This interaction likely exerted
2358 in its turn a control on community structure at lower trophic levels through processes like
2359 “mesopredator release” and trophic cascades (Roemer et al., 2009), eventually linking
2360 pelagic and nearshore communities, including benthic animals and plants, like in many
2361 modern ecosystems (Estes et al., 2011, 2016), down to slope depths (e.g., Parrish, 2009).
2362 Large raptorial feeders could exert a control on the diversity of the filter-feeding MM, like it
2363 has been suggested on a global scale since the Miocene (Lambert et al., 2010), and for the
2364 Pliocene by Bisconti (2003), when baleen whales were more diversified, both in terms of
2365 species richness, size range, and feeding strategies, including both skim- and lunge-filter
2366 feeding (respectively balaenid and balaenopterid whales: Berta et al., 2016; Hocking et al.,
2367 2017), minimising competition for food and diversifying spatial niches (see also Marx et al.,
2368 2017), minimising competition for food and diversifying spatial niches (see also Marx et al.,
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2400 2017), minimising competition for food and diversifying spatial niches (see also Marx et al.,

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2402 2017, for the upper Miocene). A further important top-down control on community structure
2403 is suggested by modern studies on the role of baleen and sperm whales as nutrient vectors,
2404 both in horizontal (during seasonal migration) and vertical direction (during daily feeding
2405 migration: Roman and McCarthy, 2010), a process particularly important in oligotrophic seas
2406 (Alleger et al., 2017), like large sectors of the Mediterranean. Finally (literally, after death),
2407 MM becomes a detrital sources of energy and habitat for deep sea whale-fall communities
2408 (Roman et al., 2014; Smith et al., 2015), with paleontological evidence available for the
2409 NWMS (Dominici et al., 2009; Higgs et al., 2012; Baldanza et al., 2013).

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2419 Much evidence suggests that a bottom-up control on the structure of NWMS MM community
2420 was exerted by wind-driven upwelling currents, through enhanced oceanic productivity and
2421 concentration of preys. Over geologic time, these factors may have exerted a selection
2422 favoring large size, triggering the Plio-Pleistocene emergence of whale gigantism in several
2423 lineages (Slater et al., 2017). The largest among marine top predators can travel long
2424 distances and cross oceans, but tend to congregate in shallow waters with abundant prey.

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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

(Tab. 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 (Jørgensen 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 Ssea (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,

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2522 allowing to minimise competition with other large filter feeders (see Friedlaender et al.,
2523 2014). ~~Among the odontoceti,~~ The sperm whale *Physeter macrocephalus* uses habitat
2524 across a range of depths and a specialised diet (Rendell and Frantzis, 2016), gathering
2525 along ~~NWMed~~NWMS steeper slopes, where water currents allows for higher trophic level
2526 biomass (Pirota et al., 2011). ~~Beaked whales are particularly abundant in the Ligurian~~
2527 Sea and central Tyrrhenian Sea, preferring submarine canyons at slope depths (Podestà et
2528 al., 2016). ~~The largest among common Mediterranean delphinids, *Grampus griseus*, is~~
2529 frequent in the Ligurian and Thyrrhenian seas where it forages on cephalopods at depths
2530 300-1500, where upwelling currents are most effective (Azzellino et al., 2016).

2541 The ~~NWMed~~NWMS existed as a Liguro-Provençal back-arc oceanic basin since the upper
2542 Miocene, when Sardinia rotated to its present position (Gattacceca et al., 2007), and in
2543 coincidence with the formation of the hinterland basins here under study (Muttoni et al.,
2544 2001), justifying the assumption that the modern ~~NWMed~~NWMS trophic regime is a feature
2545 that dates back at least to the upper Miocene. ~~Past eutrophic conditions are testified in~~
2546 Tuscany by ~~Consistenly,~~ diatomites deposited in Tuscany during the Messinian, before the
2547 salinity crisis (Bossio et al., 1997; Roveri et al., 2014), indicate that high productivity was
2548 a primitive feature of the Ligurian Sea ~~and by t.~~ Paleontological evidences include the very
2549 high diversity and abundance of Pliocene LMVsMM in FB, the closest to modern upwelling
2550 areas (Fig. 3), and the association of several MM with “*Turritella* beds”, turritellic
2551 gastropods showing gregarious habit and high abundance in areas of high primary
2552 productivity (Allmon, 1988). Both a comparison with the modern and paleoecologic data
2553 strongly suggest that, ~~particularly at times of transgression, maximum flooding and~~
2554 highstand, a wedge of ~~NWMed~~NWMS nutrient-rich waters intersecting the Tuscan shelf
2555 would have positively affected the general biomass ~~exerted a strong bottom-up control~~ on
2556 community structure through mixing and upwelling of nutrients, stimulation of phytoplankton
2557 blooms, followed by zooplankton increase, while nekton and vertebrates tracked plankton

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2582 concentrations, as is typical of modern upwelling systems throughout the world (Polis et al.,
2583 1997). High surface primary productivity in the study area during the Pliocene would have
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2585 caused a concentration of ~~food~~detritus-falls, supporting a diverse community of deep-sea
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2587 scavengers.
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2592 67.32 Taphonomic control

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2597 Taphonomic data on articulation and completeness of MM specimens are available for large
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2599 mammals, the shark record being formed mainly by isolated teeth collected through
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2601 superficial picking during the years (Cigala Fulgosi et al., 2009), with only a few
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2603 contextualised studies (e.g., Bianucci et al., 2002; Dominici et al., 2009). Our record includes
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2605 several marine mammals with a high degree of articulation (14%) and completeness (27%),
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2607 or with at least cranial and post-cranial elements of the same individual (38%). All articulated
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2609 specimens and the most complete skeletons are associated with shelf mudstones, usually
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2611 forming the HST of the relative depositional sequence (Tab. 2), with two exceptions, one
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2613 associated with delta-front, coarse-grained beds (WCh6-1, Fig. 6), another from outer shelf
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2615 or upper slope sediments (DSi2-1). These data point to a strong environmental control on
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2617 the quality of the MM fossil record, at least concerning articulation and completeness of
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2619 skeletons, very shallow and very deep (bathyal) depths being generally unfavourable to the
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2621 preservation of MM bones (Fig. 9A). To explain these results, hypotheses are based on the
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2623 available data on carcasses of MM in modern marine environments.
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2628 The biostratinomy of lung-breathing marine mammals depends on water depth (Allison et
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2630 al. 1991; Smith et al., 2005). The vast majority of mammals are negatively buoyant and sink
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2632 after death, but in shallow waters the low hydrostatic pressure allows putrefaction gases to
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2634 develop and carcasses to resurface. Skeletons are scavenged (Dicken, 2008) and
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2636 disintegrate while floating, leading to the preferential deposition of isolated bones. At deeper
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2641 settings, where high hydrostatic pressure allows the carcass to lay relatively undisturbed on
2642 the seafloor, the skeleton becomes only slightly disarticulated after soft tissue removal
2643 (Reisdorf et al., 2012). The subsequent fate of deep-water, disarticulated skeletons depends
2644 on the nature of the scavenging fauna and other elements of the whale-fall community, and
2645 on the time of exposure on the seafloor (Boessenecker et al. 2014). At depths deeper than
2646 the slope breaks, where sedimentation rate is very low, carcasses are exposed for a long
2647 time and the skeleton is rapidly disintegrated. Time-series analyses carried out at modern
2648 whale-fall communities at slope depths (range 382-2893 m: Lundsén et al., 2010) suggests
2649 that carcasses up to 17 m are rapidly degraded, with the deepest whale carcasses
2650 disappearing after only seven years of exposure on the sea floor. Larger skeletons may
2651 persist on deeper settings for decades, but if not buried, they also ultimately undergo
2652 complete destruction. Although environmental forcing triggered by higher temperatures,
2653 active currents and sediment transport, clearly plays a role, a specialized whale-fall
2654 fauna rapidly consumes both soft and mineralized tissues. This fauna is
2655 characterized by low diversity and high abundance of microorganisms, most likely as a
2656 result of both specialization to nutrient enrichment and high growth rates. Whale-fall
2657 habitats likely undergo a temporal microbial succession from primarily heterotrophic to more
2658 heterotrophic/chemosynthetic metabolisms until the whale biomass is completely exploited
2659 (Smith et al., 2015). Of all the specialized taxa, bone-eating polychaetes of genus
2660 *Osedax*, with their soft root-like tissues that erode the bones to access nutrients
2661 (Tresguerres et al., 2013; Minamoto et al., 2017), are the primary cause of bone
2662 disintegration, particularly of denser bones (Higgs et al., 2011). Found also at shelf depths,
2663 but invariably in low abundance (Huusgaard et al., 2012; Higgs et al., 2014b), bone-eating
2664 worms occur in high numbers in the deep sea (Smith et al., 2015) where they act as
2665 biodiversity regulators (Alfaro-Lucas et al., 2017). The general paucity of novel taxa on
2666 shallow-water whale falls suggests that species-rich, specialized whale-fall communities

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2702 develop only in the food-poor deep sea. Accordingly, among new animal species described
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2704 in the recent literature from whale falls, only about 10% have been found on whale remains
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2706 at depths of less than 260 m (12 out of 129 new species: Smith et al., 2015). Of all ~~large~~
2707 ~~marine vertebrates~~MM investigated so far, only whales are known to host a whale-fall
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2709 community, but also carcasses of large elasmobranchs undergo rapid destruction ~~on the~~
2710 ~~deep sea~~at bathyal depths, teeth being all that eventually remains (Higgs et al., 2014a; teeth
2711 are also lost by sharks during feeding: Pokines and Symes, 2013). As a consequence, over
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2713 geological time no large marine vertebrate is expected to be recovered at depths greater
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2715 than the shelf break. On the opposite side, the lack of a biota ~~specialized~~sed in exploiting
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2717 large organic falls, coupled with higher rates of deposition in proximity of sediment sources,
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2719 make it more probable that ~~articulated, or only partially disarticulated~~the most articulated
2720 and complete whale skeletons become part of the fossil record of shelf settings below storm
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2722 wave base.
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2734 **78. Comparison with other studies**

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2739 The study of sedimentary facies uncovers some environmental factors that directly control
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2741 the taphonomy of large marine vertebrates. Such abiotic drivers include water pressure,
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2743 wave energy and sedimentation rate — three factors ~~summarized~~sed by water depth, and
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2745 upwelling, bringing to the surface deep sea nutrients and concentrating preys. The
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2747 taphonomic pathway of large marine carcasses is also driven by biotic factors that change
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2749 in geological time in response to coevolution between bacteria, scavengers and their
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2751 substrates. We now explore the multifaceted nature of ~~LMVMM~~MM taphonomy by reviewing
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2753 Mesozoic and Cenozoic studies ~~comparable to ours~~where sufficient data for stratigraphic
2754 paleobiology are available.
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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 ~~dugongsirenians~~ 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 LMVsMM 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

2821
2822 rich in glauconite, suggesting long exposure on the sea-floor (Louwye et al., 2010). Bones
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2824 are concentrated at the base of a coarsening-upward succession, on top of shallow marine,
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2826 coarse-grained sandstone, suggesting this is a surface of maximum flooding. An association
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2828 of LMVsMM taxonomically comparable to ~~those~~that here under study is encountered in the
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2830 Mio-Pliocene of the Purisima Formation, in Central California. Taphofacies differ in some
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2832 aspects. The Pliocene of California yields laterally persistent bonebeds with polished and
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2834 phosphatised bones, and abundant phosphate nodules that are absent in Tuscany,
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2836 indicating times of higher sediment starvation during transgressive pulses, in an area of
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2838 much stronger nutrient content (the California Current system is a northern-hemisphere
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2840 analogue of the Peruvian upwelling system, associated with the economically most
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2842 important fish stocks in the world: Mann &and Lazier₁₇, 2006). Shoreface deposits indicate
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2844 stronger wave energy, and the preferential absence of molluscs in bonebeds indicates
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2846 chemical destruction of carbonate shells (Boessenecker et al.₁₇, 2014, in a quantitative MM
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2848 taphonomic study ~~that includes isolated LMV fragments~~). Episodic sedimentation, however,
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2850 causes the preferential preservation of articulated remains in the Californian offshore as in
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2852 the Pliocene of NWMedNWMS. The late Miocene Pisco Formation in Perú offers another,
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2854 more extreme example of LMVMM taphonomy in a eutrophic setting. Here almost two
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2856 hundred cetaceans, pinnipeds, and sharks were described in an exceptional state of
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2858 preservation (Bianucci et al.₁, 2015), within a monotonous succession of finely laminated
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2860 white diatomites (Di Celma et al.₁, 2015), suggesting very high primary productivity in an area
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2862 of intense upwelling and volcanic activity. Algal blooms sustained high biomass of apex
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2864 predators (see Marx &and Uhen₁, 2010), triggering at the same time anoxic conditions at the
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2866 seafloor where LMVMM carcasses remained intact (Brand et al.₁, 2004₁₇; see also Gioncada
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2868 et al.₁, 2016; Marx et al., 2017, also in offshore paleosettings). Finally, the stratigraphic
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2870 distribution of Pliocene cetaceans in western Emilia (Italy) shows an uneven distribution of
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2872 findings (N = 24, dolphins and baleen whales) and a strong positive correlation with offshore
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2882 mudstones (no findings in shoreface sandstones, rare occurrences in epibathyal
2883 mudstones: Freschi and Cau, 2016), paralleling the distribution of Tuscan Pliocene MM.
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2888 78.2 Biotic factors

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2893 Many reviews of Triassic (Camp, 1980; Hogler, 1992; Motani et al., 2008; Hu et al., 2011;
2894 Liu et al., 2014) and Early Jurassic marine reptiles (Benton & Taylor, 1984) report mostly
2895 good preservation and a high degree of completeness and articulation of skeletal material.
2896 This record might be partially controlled by prevailing anoxic or dysoxic conditions in the
2897 bottom waters of many Mesozoic fossiliferous deposits (e.g., Middle Triassic Besano and
2900 Guangling Formations, Lower Jurassic Blue Lias and Posidonia Shale Formations), which
2901 precluded organism activity within the sediment, and prevented predation or scavenging of
2902 the carcasses on the sea bottom (Beardmore & Furrer, 2016). Evidence of advanced
2903 levels of disarticulation or bone degradation (Martill, 1985; sauropterygians, crocodylians,
2904 ichthyosaurs and fishes from the Middle Jurassic Oxford Clay Formation), is mostly
2905 attributed to physical factors (e.g., weathering on the sea floor). Up to the early-Late
2906 Cretaceous, biological activity is testified by circumstantial evidence of scavenging
2907 (*Hybodus* teeth associated with marine reptile skeletons, Martill et al., 1994), and by the
2908 more common occurrence of microbial mats, grazers and encrusters (Martill, 1987; Meyer,
2909 2011; Danise et al., 2014; Reolid et al., 2015), but lack traces of bone-eating worms and
2910 sulphophilic fauna typical of modern whale falls. The siboglinid *Osedax* is an evolutionary
2911 novelty in possessing a root system that hosts heterotrophic mutualists and secretes bone-
2912 dissolving acids (Tresguerres et al., 2013; Miyamoto et al., 2017), and an ecosystem
2913 engineer (Alfaro-Lucas et al., 2017). Genus *Osedax* is today associated with whale falls
2914 worldwide (Taboada et al., 2015), but its impact on LMVMM has changed in time. The oldest
2915 trace fossils attributable to a bone-eating fauna is found on early-Late Cretaceous plesiosaur
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2942 and sea turtle bones (about 100 Ma: Danise &and Higgs, 2015). Time estimates suggest
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2944 that *Osedax* diverged from other siboglinids in the Middle Cretaceous (around 108 Ma:
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2946 Taboada et al., 2015). However, if the bone-eating worm lives also on the bones of birds
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2948 and terrestrial mammals (Rouse et al., 2011), its global nature and high species diversity in
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2950 modern oceans suggest that whale falls, as complex and species-rich habitats, have been
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2952 the most important biodiversity generators (Higgs et al., 2014b; Smith et al., 2015). And
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2954 although the first appearance of *Osedax* is concomitant with the occurrence of large marine
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2956 reptiles and teleost fishes in the oceans, long before whale evolution, and although their
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2958 distribution is not limited to large carcasses (Pyenson and Haas, 2007), the radiation of
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2960 ocean-going mysticetes at the Oligocene onset of the Antarctic Circumpolar Current
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2962 (Fordyce, 2003) clearly increased available substrata worldwide. The steady increase of
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2964 cetacean size during the Neogene, with a dramatic pulse in the last five million years, when
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2966 Neoceti surpassed 10 m length and reached 30 m in the Pleistocene (Lambert et al., 2010;
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2968 Slater et al., 2017), would have thus triggered a second and more massive radiation of bone-
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2970 eating worms (Kiel and Goedert, 2006). Consistently with this hypothesis, the preferential
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2972 distribution of modern *Osedax* in high latitude settings worldwide (Taboada et al., 2015)
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2974 suggests that biodiversity hotspots coincide with the feeding grounds of larger cetaceans.
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2976 Other bone-eaters of modern deep water whale-fall ecosystem belong to the group of
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2978 abyssochrysid snails, with fossils found on Late Cretaceous plesiosaur bones (Kaim et al.
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2980 2008) and sea turtle bones (within a chemosynthesis-based association: Jenkins et al.,
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2982 2017). Modern abyssochrysid whalebone-eaters of genus *Rubyspira*, hosting a specific
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2984 and exclusive microbiome (Aronson et al., 2017), split during the upper Eocene/lower
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2986 Oligocene (Johnson et al., 2010). Like for *Osedax*, sSpecies of *Rubyspira* likely benefited
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2988 too from the radiation of ocean-going whales. Although scanty, available evidence on the
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2990 geological history of bone-eaters thus makes the ephemeral nature of large carcasses in
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3002 modern deep seas — and their absence in bathyal deposits of the Pliocene of
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3004 NWMedNWMS — a larger-than-life model for the Mesozoic and the early Paleogene.
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3008 E9. Conclusions

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3013 1) Sedimentary facies in the Pliocene of Tuscany are vertically stacked to form small-scale
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3015 depositional sequences particularly in the upper half, Piacenzian part of the succession,
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3017 with laterally-continuous shell beds marking transgressive surfaces and ~~the~~
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3019 surface intervals of maximum flooding. Small-scale sedimentary sequences are stacked
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3021 to form six major, unconformity-bounded stratigraphic units (synthems) of regional
3022
3023 extension, forming a high-resolution framework to study the chronostratigraphic
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3025 distribution of marine megafauna (MM).
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3028 2) Sedimentary facies Benthic biotopes, identified through a quantitative study of a large
3029
3030 mollusk mollusc dataset, can be arranged to form an ideal onshore-offshore, bathymetric
3031
3032 gradient, connecting terrestrial environments with deep sea epibathyal bottoms,
3033
3034 consistently with the distribution of sedimentary facies. BonesMM remains of large
3035
3036 marine vertebrates and shell beds are present in all marine paleoenvironments, but their
3037
3038 distribution is uneven.
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3041 2) The fossil record of large vertebrates, including marine mammals (abundance data) and
3042
3043 larger sharks (presence-absence data), is particularly rich in sediments deposited
3044
3045 between storm wave base and ~~the~~ shelf break, moderately rich in shoreface sediments,
3046
3047 very poor in epibathyal sediments. Paleobathymetric estimates suggest that a peak of
3048
3049 abundance of better preserved skeletons occurs around 100 m depth, within the 30-300
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3051 m range.
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3054 3) Species richness of MM and abundance of marine mammal remains steadily increase
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3056 during the Zanclean, reaching a peak in synthem 4, possibly as a response to the mid-
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3062 Piacenzian warm period, and gradually decrease until reaching a minimum in proximity
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3064 of the Plio-Pleistocene boundary.
3065

3066 4) Comparison with ecological data on a global scale, paleogeographic and topographic
3067 considerations on the North-Western Mediterranean Sea (NWMS)Mediterranean
3068 paleogeography, and the frequentoccasional association of Pliocene large marine
3069 vertebratesMM with Turritella beds, suggest that upwelling and high-nutrient conditions
3070 in the Northwestern Mediterranean offshore sustained during the Pliocene a rich
3071 community of apex predators and mesopredators. Higher taxonomic MM diversity in the
3072 NWMS during the Pliocene, suggests higher niche-partitioning. with respect to the
3073 modern NWMS and a top-down control on community structure.
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3083 5) A comparison with studies on the biota exploiting tissues of large food particles sunken
3084 on the seafloor, both modern and ancient, suggests that the poor epibathyal record of
3085 Pliocene larger vertebrates of Tuscany may be caused by the destructive action of bone-
3086 eating invertebrates. This biotic driver of the marine vertebrate fossil record was less
3087 efficient before the radiation of ocean-going whales in the late Eocene-lower Oligocene.
3088 On the other hand, bone-eaters played a major taphonomic role on a global scale after
3089 the Pliocene-Pleistocene increase in whale size.
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3098 6) Due to resurfacing of carcasses in shallow waters, the taphonomy of large marine
3099 vertebratesMM fossil record through the Mesozoic-Cenozoic isreviewed through
3100 stratigraphic paleobiology shows a strong facies control, being more continuous
3101 comparable through the Mesozoic-Cenozoic in rocks formeddeposited below storm wave
3102 base and above the shelf-slope break during sea-level transgressions and highstands.
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3124 knowledge of fossiliferous Pliocene outcrops of Tuscany.
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5306 **Figure and table captions:**
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5309
5310 Fig. 1 - Location of sedimentary logs within the largest Pliocene basins of Tuscany. Fine
5311 Basin (FB): Pagliana (1), Pieve Vecchia (2) and Orciano Pisano (3). Volterra-Era Basin
5312 (VEB): Parlascio (4), Lajatico (5), Fabbrica (6) and Volterra (7). Era Basin (EB): San Lorenzo
5313 (8), La Serra (9), Poggio al lupo (10), San Maiano (11), Canneto (12), Casenuove (13),
5314 Castelfiorentino (14), Fiano (15) and San Gimignano (16). Orcia-Ombrone Basin: Arcille (17)
5315 and Poggio alle Mura (18). Siena-Radicofani Basin (SRB): Siena (19), [Monteaperto \(20\),](#)
5316 [Castelnuovo Berardenga \(21\),](#) ~~and Radicofani (21,22)~~ [and Fastelli \(23\).](#) Chiana Basin (CB):
5317 Sinalunga (24), Cetona (25) and Allerona (26).
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5329 Fig. 2 - Pliocene stratigraphy of Tuscany, [see Fig. 1 for the location of numbered sections.](#)
5330 [All logs measured and described by the authors, except Volterra \(log 7: Bianucci et al. 1998\),](#)
5331 [Arcille \(log 17: Tinelli et al., 2012; Tinelli, 2013\), Siena \(log 19: Bianucci et al., 2001\),](#)
5332 [Monteaperto \(log 20: Martini et al., 2011\), Castelnuovo Berardenga \(log 21: Martini et al.,](#)
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5342 2016) and Radicofani (log 22: Ghinassi and Lazzarotto, 2005)(chronostratigraphy based on
5343 biostratigraphic data from several sources, see main text). See Fig. 1 for the location of
5344 numbered logs. (Chronostratigraphy of localities 25 (Poltriciano, Cetona: Capellini, 1883)
5345 and 26 (Allerona: Danise, 2010) are unknown logs 21-23 not shown). Correlation between
5346 sections is also shown as boundaries of planktonic foraminifera biozones (dashed lines),
5347 following the scheme of Sprovieri (1992), based on available biostratigraphic studies for
5348 each basin (see main text for relevant references).
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5359 Fig. 3 - NumberAbundance of fossil large marine vertebrateMM records in major museums
5360 of Tuscany catalogues, distributed by locality of provenance. Each record ranges from a
5361 single fragment or single tooth, to a quasi-articulated, nearly complete skeleton. A: whales
5362 and dolphinsmasticates and odontocetes; B: large sharks; C: dugongssirenians — manscuba
5363 diver for scale in each figure. Symbols for basins as in Fig. 1.
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5372 Fig. 4 - Detailed sedimentary logs measured at three localities, representing three different
5373 stratigraphic contexts for the large marine vertebrate fossil record of the Tuscan Pliocene.
5374 The succession at Orciano Pisano is included in synthem S3-S4 of FB, at Arcille-Poggio
5375 alle Mura-Camigliano in synthem S2 of OOB, at Sinalunga in synthem S6 of CB. See Figs.1-
5376 2 for the location of the numbered localities and references in the main text for facies
5377 analysis and sequence stratigraphy of synthem S5. Arcille log from Tinelli et al., 2012, and
5378 Tinelli, 2013.
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5389 Fig. 5 - Taphonomy of large marine vertebrates at Poggio alle Mura (Figs. 5A-5D) and Arcille
5390 (Fig. 5E, see Fig. 4 for the sequence stratigraphic and sedimentary context; plan view of the
5391 sirenian skeleton is modified from Tinelli et al., 2012), synthem S2. A: Plan view of the
5392 Poggio alle Mura undetermined balaenopterid. Parts of the skeleton are quasi-articulated,
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5402 others are scattered, but not far from the original position. B: Quasi-articulated vertebrae of
5403 the same specimen, lying on top of a *Haustator* shell bed. C: Side view of a vertebra on top
5404 of the densely-packed shell bed. D: Detail of the shell bed, in top view. The turrilline
5405 gastropod *Haustator vermicularis* is visible in the upper left, a large fragment of wood in the
5406 lower right, with the inchnofossil *Teredolithes* produced by wood-dwelling teredinid bivalves,
5407 in the centre of the photograph. E: Plan view of one of the Arcille dugongsirenian specimens,
5408 belonging to the species of *Metaxitherium appennicum*. Same scale as in 5A, the arrows
5409 points to the North.
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5421 Fig. 6 - Taphonomy of a 10m-long, undetermined balaenopterid at Orciano Pisano (see Fig.
5422 4 for the sequence stratigraphic and sedimentary context), synthem 4. A: Planimetry of the
5423 quasi-articulated and nearly complete skeleton. B: Detail of the central part of the skeleton
5424 in the field. The cortex layer of vertebrae and flipper bones is badly consumed, whereas
5425 some of the costae are still pristine. C: Lateral view of a turrillid shell bed, below, and the
5426 surface where the whale skeleton lied (dashed line), about 15 cm above the shell bed. The
5427 sediment is a very fine-grained silty sand, completely bioturbated (large vertical burrows are
5428 visible). D: Top view detail of the turrillid shell bed. At the center a valve of *Yoldia nitida*,
5429 surrounded by a few specimens of the turrillid *Archimediella spirata*.
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5442 Fig. 7 - Taphonomy of an incomplete, undetermined mystecete at Castel San Gimignano,
5443 synthem 4, comprising articulated torso elements. A: Planimetry of the articulated elements.
5444 B: Detail of one of the limbs in the field (trowel for scale = 22 cm): humerus, radius and ulna
5445 are in anatomical relationship; the cortex layer is well preserved, suggesting quick burial of
5446 the carcass. C: Bones of the chest region; on the background the massive sandstone
5447 associated with the fossil whale. Articulated shoreface pectinid bivalves (*Pecten*
5448 *flabelliformis*) were interspersed in the sandstone (photographs by Fabio Cozzini, 1985).
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5464 Fig. [87](#) - Taphonomy of a 5m-long, undetermined balaenopterid at Sinalunga (see Fig. 4 for
5465 a tentative sequence stratigraphic interpretation), synthem 6. A: Oblique view of the fully
5466 articulated skeleton lying in a gravelly sandstone, stratified in the lower part, massive in the
5467 upper. Vertebrae are tightly connected as if in life. B: Plan view of the flipper, with carpals,
5468 metacarpals and phalanges in perfect anatomical connection. C: The gravelly sandstone
5469 lies above a bioturbated muddy sandstone, with vertical burrows (*Ophiomorpha*). D: The
5470 lower part of the unit with the whale skeleton is formed by three fining-upward beds. Each
5471 bed grades from gravel to medium-grained sand. Articulated and empty shoreface bivalves
5472 (e.g., *Callista chione*), not in life position, are interspersed with the coarse gravel.
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5485 Fig. [98](#) - Quantitative analysis of the facies type and sequence stratigraphic distribution of
5486 large marine vertebrates, Pliocene of Tuscany (N=39, see Tab. 2). A: The vast majority of
5487 cases (77%) are associated with fine-grained muddy sediments of the shelf, a few are found
5488 in deltaic coarse-grained strata. B: Most [LMVsMM](#) (69%) [are](#) found in highstand deposits,
5489 a few in proximity of the maximum flooding interval, or in transgressive deposits.
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5498 Fig. [109](#) - NMDS ordination of bulk samples (N=72, see Fig. 2 for their stratigraphic
5499 position), based on the distribution of standardised abundances of 329 mollusc species
5500 (further explanation on multivariate techniques in the main text). A: Samples are subdivided
5501 based on the associated sedimentary facies types (F2-F5 in Tab. 1). The main axis ordines
5502 samples along a paleodepth gradient, from shallowest to deepest, moving from the left to
5503 the right side of the bivariate plot. B: Same ordination, with an estimate of absolute
5504 paleodepth of each sample based on score along the main axis and calibrated through the
5505 average modern depth distribution of 23 extant species characterising the Pliocene dataset
5506 (abundance > 0.15%, see text; regression logarithmic curve in the inset). Vertebrates
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5522 recovered in proximity of some of the samples (N=_13) are plotted on the diagram,
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5524 confirming that, on average, the LMVMM fossil record is concentrated on the open shelf at
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5526 an estimated depth of 30-300 m (M=dugongs sirenians; S=sharks; P=pinnipeds; W=
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5528 whales).

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5532 Fig. 11 - Occupancy of trophic levels by Pliocene marine mammals and sharks in the north-
5533 western Mediterranean, expressed by number of species per trophic level (see Tabs 3, 5 for
5534 explanation and references). This figure, summing up data for the whole epoch, spanning
5535 circa 2,8 My, closely matches the association found in one single synthem S4, of much
5536 shorter duration (mid-Piacenzian, 3-4 hundred thousand years).
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5545 Tab. 1 - Sedimentary facies types.
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5550 Tab. 2 - Stratigraphic, taphonomic and paleoenvironmental framework for Pliocene large
5551 marine vertebratesmarine mammals recovered ofin Tuscany, with abundance data (N=
5552 3964). A: Highly-aArticulated and quasi-articulated skeleton; C: Highly-eComplete and quasi-
5553 complete skeleton; C+PC: Cranial and post-cranial bonesremains.
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5560 Tab. 3 - Paleoecology of Pliocene large mammals compared toand ecology of modern
5561 NWMS analogues.
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5567 Tab. 4 - Geographic distribution of Pliocene large mammals in Tuscany.
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5571 Tab. 5 . Paleoecology of Pliocene sharks compared toand ecology of modern NWMS
5572 analogues.
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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 paleoenvironments 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 paleoenvironments 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

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73 destruction. An estimate of paleobathymetries based on multivariate techniques suggests
74 that the preferential depth for the inclusion of MM in the fossil record was 30-300 m. The
75 results are compared with major Mesozoic and Cenozoic MM records worldwide. Available
76 evidence suggests that the late Neogene radiation of large whales, true ecosystem
77 engineers, and their size increase, triggered the radiation of a bone-eating fauna that
78 hampered, and hampers, MM preservation in the deep sea. Stratigraphic paleobiology and
79 an ecosystem-level approach deliver useful insights in the nature of the fossil record.
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101 **1. Introduction**

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108 The modern marine megafauna (MM) includes all marine mammals, seabirds, sea turtles
109 and sharks, apex consumers that influence their associated ecosystems (Lewison et al.,
110 2004), both pelagic and nearshore, through top-down forcing and trophic cascades, and
111 now severely affected by human impact (Estes et al., 1998, 2011, 2016). On a
112 macroevolutionary scale, predation pressure has shaped the evolution of marine preys, with
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122 feedbacks on predators, setting the stage for the Mesozoic marine revolution (Vermeji, 1977;
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124 Chen and Benton, 2012; Benton et al., 2013). The new ecosystem structure started in the
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126 the Early and Middle Triassic with several lineages of Actinopterygian fishes (Chen and
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128 Benton, 2012), continuing with marine reptiles possessing feeding styles (Fröbisch et al.,
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130 2013; Motani et al., 2015; but see also Motani et al., 2013) and reproductive adaptations
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132 (Motani et al., 2014) of modern type. Triassic and Jurassic novelties underwent a prolonged
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134 crisis during the Cretaceous, with the gradual extinction of plesiosaurians, mosasaurs
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136 (Benson et al., 2010) and ichthyosaurs (Fischer et al., 2016), and a diversity drop of sharks
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138 (Guinot et al., 2012). A marine megafauna of comparable size returned in the Paleogene,
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140 with the new diversification of neoselachian elasmobranchs (Kriwet and Benton, 2004) and
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142 the evolution of large marine mammals: Eocene archaeocetes (Uhen, 2008, Gingerich et
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144 al., 2009) and Oligocene odontocetes and mysticetes (Gingerich, 2005; Marx and Uhen
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146 2010, Berta, 2012; Marx et al., 2016) empowered by high metabolic rates and new anatomic
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148 features (Armfield et al., 2013). Among the largest vertebrates of all times, after a dramatic
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150 size increase at the outset of glacial age (Marx et al., 2016; Bisconti et al., 2017; Slater et
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152 al., 2017), baleen and sperm whales are among today's ocean's ecosystem engineers
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154 (Roman et al., 2014) with which to compare their Mesozoic analogues (Smith et al., 2016).
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157 Notwithstanding a crucial role in ecology and evolution, the nature and distribution of the
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159 MM fossil record has been less explored, compared to that of marine invertebrates and
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161 terrestrial vertebrates. Available data suggest a strong correlation between taxic diversity
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163 and the number of marine fossiliferous formations, resulting in megabiases in the fossil
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165 record (e.g., Cretaceous: Benson et al., 2010). Within its vast history, studies on the
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167 geologically recent marine megafauna offer important insights, considering our better
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169 knowledge of: 1) geological setting, in terms of outcrop extent and high-resolution
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171 stratigraphy; 2) ecologic role played by individual species, whether extant or extinct, in terms
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173 of habitat, trophic role, life histories and population structure, thanks to a comparison with
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182 extant descendants, or close relatives; 3) MM taphonomy, based on actuopaleontology. A
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184 recent global study revealed that MM extinction peaked in the late Pliocene, between 3.8
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186 and 2.4Ma, linked to the sudden drop in the extension of nearshore environments after a
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188 large sea level regression (Pimiento et al., 2017), confirming that the fossil record offers
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190 important clues on the vulnerability of keystone marine species to climate change. We
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192 contribute here to a better understanding of the Pliocene fossil record by reviewing the rich
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194 MM of Tuscany, in Italy. In particular, we consider all reports of Pliocene marine mammals
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196 and sharks and revise taphonomy and sedimentary facies associated with all known
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198 findings, setting them within a sequence stratigraphic framework. We also reconstruct the
199
200 paleoenvironmental context and review data on a part of the marine ecosystem through the
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202 paleoecology of fossil invertebrates on a regional basis, following a stratigraphic
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204 paleobiological approach that can be applied to both the recent and the distant geological
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206 past (Patzkowsky and Holland, 2012). Published studies that have taken this direction are
207
208 still a few, examples concerning Jurassic ichthyosaurs, plesiosaurs and pliosaurs (McMullen
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210 et al., 2014), Cretaceous turtles, plesiosaurs, bony fish and sharks (Schemisser McKean
211
212 and Gillette, 2015), Eocene archaeocetes, sea cows and sharks (Peters et al. 2009), and
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214 Neogene marine mammals and sharks (Boessenecker et al., 2014). All of these papers
215
216 record the co-occurrence of shelly faunas, only one undertaking quantitative studies of the
217
218 distribution of fossil invertebrates (Jurassic of the Sundance Formation: McMullen et al.,
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220 2014, see also Danise and Holland, 2017). The benefits of an outcrop-scale sequence
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222 stratigraphic approach include: (1) an independent record of relative sea-level change to
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224 test paleobiological hypotheses (see also Pyenson and Lindberg, 2011; Noakes et al.,
225
226 2013); (2) a chronostratigraphic scheme for high-resolution correlations; (3) a means to
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228 recognise minor and major breaks of the record; (4) an ecological and sedimentary
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230 framework for taphofacies distribution (Patzkowsky and Holland, 2012); and (5) an
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241 independent control of onshore-offshore patterns of fossil assemblages (e.g., Tomašových
242 et al., 2014).
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246 Researchers that study the geologic history of marine ecosystems have focused on patterns
247 of ecological restructuring based on the taxonomy of selected groups (e.g., Thorne et al.,
248 2011; Benton et al., 2013; Scheyer et al., 2014; Fischer et al., 2016), at the expenses of a
249 more holistic approach that includes functional diversity and embraces as many ecosystem
250 components as possible (Dineen et al., 2014). By analogy with ecologists who shift focus
251 from models based on single groups (e.g., Steeman et al., 2009) to an all-embracing vision
252 of marine life (Lawton, 1994; Sergio et al., 2014), connecting food web ecology with
253 landscape ecology (Polis et al., 1997; Estes et al., 2011), stratigraphic paleobiology can
254 draw from the fossil record and offer multidimensional insights on the complex geological
255 history of modern marine ecosystems.
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267 After revising fossil MM hosted in major museums of Tuscany, both isolated and articulated
268 remains, we focus on all fossil bones that can be stratigraphically (e.g., Bianucci et al., 1995,
269 1998, 2001; Tinelli, 2013) and taphonomically framed (e.g., Dominici et al., 2009; Bianucci,
270 2010; Danise and Dominici, 2014). MM lists for the Mediterranean Pliocene have been
271 recently updated (marine mammals: Landini et al., 2005; Bianucci et al., 2009a; Sorbi et al.,
272 2012; Bianucci and Vomero, 2014; sharks: Marsili, 2006). Species-level ecological data are
273 available on modern apex consumers and mesocarnivores (Pauly et al., 1998; Cortés,
274 1999), with detailed information made available for Mediterranean species following
275 conservation concerns (marine mammals: Notarbartolo di Sciara et al., 2016; sharks:
276 Cavanagh and Gibson, 2007), allowing for a detailed paleoecological evaluation of the
277 Tuscan fossil record. The actualistic approach is also viable for species of benthic molluscs,
278 about half of which are still extant in modern Mediterranean bottoms (55% of extant species
279 of Mediterranean and North Sea bivalves, excluding strictly brackish and bathyal forms, i.e.,
280 202 out of 367 species, survives from the Zanclean: Raffi et al., 1985). The regional
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301 quantitative study of molluscan assemblages was the basis for an independent assessment
302 of paleoenvironments, paleoecology and paleobathymetry. A revision of abundance
303 of paleoenvironments, paleoecology and paleobathymetry. A revision of abundance
304 distributions of marine molluscs, the largest contributors to Mediterranean Pliocene shell
305 beds and a key component of Mesozoic and Cenozoic marine ecosystems (Stanley, 1975;
306 Vermeij, 1977), allowed to further explore the structure and composition of Pliocene marine
307 ecosystems, and reconstruct a paleobathymetric gradient (e.g., Scarponi and Kowaleski,
308 2004) along which to frame MM occurrence. The present work must necessarily start with a
309 review of the chronostratigraphy and physical stratigraphy of the Tuscan marine Pliocene.
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321 **1. Geological setting**

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326 The Pliocene succession of Tuscany was deposited in a complex setting characterised by
327 continental collision related to the later evolution of the Northern Apennines chain. According
328 to a well-established hypothesis, the region, affected by shortening before the Middle-Late
329 Miocene, accommodated by NE-verging thrust and fold systems, underwent crustal
330 extension during the late Neogene and the Quaternary (DeCelles, 2012; Fig. 1). Crustal
331 extension generated differential subsidence in a series of normal-fault controlled hinterland
332 sedimentary basins, filled throughout by continental and shallow marine, mostly clastic
333 successions (Martini and Sagri, 1993; Pascucci et al., 2006; Brogi, 2011). An alternative
334 hypothesis places the late orogenic hinterland basins in a more complex tectonic setting
335 characterised by the alternation of compressive, extensional and transcurrent stress fields
336 (Benvenuti et al., 2014; Bonini et al., 2014).
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349 The Neogene Tuscan basins considered in this work include, from West to East, and from
350 North to South, the Fine Basin (FB; Bossio et al., 1997), the Volterra-Era Basin (VEB; Bossio
351 et al., 1994), The Elsa Basin (EB; Benvenuti et al., 2014), the Ombrone-Orcia Basin (OOB;
352 Bossio et al., 1991; Nalin et al., 2010), the Siena-Radicofani Basin (SRB; Ghinassi and
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362 Lazzarotto, 2005; Martini et al., 2011, 2016), and the Chiana Basin (CB; Fig. 1: Pesa Basin
363 not considered here). With one exception (OOB, see below), these basins show a shape
364 conditioned by the structural and physiographic features of the inner portion of the Northern
365 Apennines. Their NW-SE general elongation reflects the trend of the thrust-related anticline
366 ridges developed during earlier collisional stages. These compressive structures have
367 bounded most basins through their infilling, only to be obliterated by younger parallel normal
368 fault systems, leaving an invariant stratigraphic onlap of the Pliocene successions onto the
369 basin margins. Despite a NW-SE distribution of the hinterland basins, the structural setting
370 is responsible for a NE-trending physiographic and paleogeographic gradient, where the FB
371 is closest, and the CB furthest, from offshore settings throughout the late orogenic phase,
372 with important implications for the facies architecture and the distribution of marine
373 vertebrates and shell beds. Differential active uplift of the basin shoulders during the
374 Pliocene, coupled with important erosional phases, resulted in a different preservation of the
375 original stratigraphic architecture. The infill during the Zanclean is generally characterised
376 by relatively continuous open marine successions, the correlative fluvial-coastal systems
377 missing due to uplift and erosion of basin margins. On the other hand, the Piacenzian infill
378 is characterised by genetically-connected, fluvial, coastal and shallow marine facies tracts,
379 particularly well-preserved in the EB, hinting to reduced uplift of the marginal areas. The
380 modern physiography of OOB, escaping the structurally-controlled geometry of the other
381 basins, mimics instead an original fluvial network developed during the latest Messinian,
382 flooded after the Salinity Crisis (Bossio et al., 1991; Benvenuti et al., 2015), filled during the
383 Pliocene, and finally disrupted by post-Pliocene uplift and erosion. This difference in the
384 structural history also justifies the preservation in OOB of Zanclean fluvial and shallow
385 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 lithostratigraphic 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 lithostratigraphic units have been introduced to define the local stratigraphy, resulting in a complex and largely informal lithostratigraphic 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

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482 Stratigraphic sections were measured and described at several localities (Fig. 1). Siliciclastic
483 and carbonate facies were described, subdivided into groups of facies based on lithology,
484 sedimentary structures and ichnology, and interpreted in terms of process and depositional
485 environment (Tab. 1). Each group represents a set of individual facies forming monogenic
486 associations (in the sense of Mutti et al., 1994), i.e., the meter-scale stacking of facies which
487 express the autocyclic behaviour of specific depositional systems within a given
488 accommodation space (Benvenuti and Del Conte, 2013). Sequence stratigraphic concepts
489 have been applied to reconstruct the dynamics of basin infills at a hierarchy of scales,
490 advancing hypotheses on controlling factors. The chronostratigraphic subdivision of
491 Benvenuti et al. (2014), which divides the Pliocene into six synthem, S1-S6 from older to
492 younger, was extended to all six Tuscan basins by referring to available biostratigraphic
493 schemes (Fig. 2). The sequence stratigraphic interpretation of S2 in OOB is based on Tinelli
494 (2013). Other parts of the S1-S3 succession were drawn based on available lithostratigraphic
495 literature (see below). Studies integrating sedimentary facies analysis, biostratigraphy and
496 magnetostratigraphy (Nalin et al., 2016) have helped correlating carbonate bodies typical of
497 S4. The reader is referred to Benvenuti et al. (2007; 2014) for details on facies analysis and
498 sequence stratigraphic interpretation of synthem S3-S6.

499 First, data on the geographic distribution of fossil marine mammals, large sharks and
500 sirenians were largely based on collections housed at the Natural History museums of the
501 University of Florence (UFMSN), University of Pisa (UPMSN), and Accademia de' Fisiocritici
502 of Siena (AFMSN), the three largest collections of Tuscany, and at the Geological Museum
503 Giovanni Capellini, Bologna University (MGGC). In particular, counts of cetaceans were
504 based on UFMSN collections (Mysticeti and Odontoceti, N = 142), large shark on the sum
505 of UFMSN, UPMSN and AFMSN collections (Carcharhiniformes and Lamniformes, N = 337,
506 data synthesised from Marsili, 2006), sirenians from all reports in Tab. 2 (N = 10). Each
507 record is formed either by a single element (e.g., whale bone, shark tooth), by a few
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542 elements of the same individual, or by a whole, quasi-articulated skeletons. A large
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544 proportion of this dataset lacks precise location, allowing only for some crude stratigraphic
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546 attribution (Fig. 3).
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549 On a second step, all fossil Tuscan Pliocene cetaceans, sirenians and pinnipeds that could
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551 be framed within the available high-resolution stratigraphic framework and associated with
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553 taphonomic data, were selected. At this step, after excluding unidentified MM remains, a
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555 dataset of 64 specimens (cetaceans N = 50; sirenians N = 10; pinnipeds N = 4) was
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557 assembled. Association with shark teeth is frequent (55% of 25 cases according to Danise
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559 and Dominici 2014 for the Italian Pliocene; see also Bianucci et al. 2002, 2010). The majority
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561 of the 64 specimens are included in the catalogue of UFMSN, UPMSN, AFMSN and MGGC,
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563 whereas a few are stored in smaller collections of the municipalities of Montaione, Scandicci
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565 (Florence province), and Certaldo (Pisa province), one in a private property (Castello di Villa
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567 Banfi, near Montalcino, Siena province), and one in the Museum National d'Histoire
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569 Naturelle in Paris (France). Whenever possible, large marine vertebrates were coded by
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571 synthem (N = 60) and depositional environment (N = 54). We analysed abundance
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573 distributions among marine mammals, and species richness of marine mammals and
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575 sharks. To infer Pliocene paleoecology, fossil taxa recognised in Tuscany were compared
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577 with their closest descendants, focusing on the species today living in the North-Western
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579 Mediterranean Sea (NWMS).
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583 All known MM-bearing sedimentary facies are associated with a mollusc-dominated benthic
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585 fauna. The third step of the analysis concerned a quantitative study of shell beds, allowing:
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587 1) to interpret the regional evolution from a perspective independent from the sedimentary
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589 facies, 2) to characterise MM paleoenvironmental and bathymetric distribution, and 3) to
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591 explore the structure of the benthic component of marine ecosystems and to identify
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593 underlying environmental controls. 72 Bulk samples were collected at major shell beds at
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595 bed resolution throughout the succession and sieved with 1 mm mesh size. Fossils of
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601 bivalves, gastropods and scaphopods were identified to species level. The minimum number
602 of individuals was calculated following standard approaches (see Patzkowsky and Holland,
603 2012), resulting in a richness of 525 species (S) and a total abundance of 64206 individuals
604 (N). We coded each fossil assemblage by synthem, tract of small-scale depositional
605 sequence, and depositional environment. Most samples belonged to facies types F2-F5
606 (Tab. 1; see also Tomašových et al., 2014). Facies F6 usually lacks macrofossils and
607 allowed for the collection of only one sample. No samples were collected in facies F1,
608 lacking marine shells, facies F7, mostly devoid shells, and facies F8, which is richly
609 fossiliferous, but lacks aragonite shells and is associated with specimens hardly extractable
610 from the rock. The resulting quantitative dataset served for statistical analyses on the
611 distribution of species-level abundances on a siliciclastic shelf depositional system,
612 performed with the software Primer 6.0 (Clarke and Gorley, 2006). Analyses included
613 clustering and nMDS ordination techniques on a Bray-Curtis similarity matrix, of
614 standardised, square-root transformed data (72 samples; S = 333 and N = 63518 after the
615 exclusion of singletons). To test statistically whether there is a significant difference between
616 two or more groups of sampling units based on sedimentary facies, we performed an
617 analysis of similarity (ANOSIM). To interpret the outcomes of the quantitative study and the
618 significance of clusters we used species-level autoecologic information available for the
619 most abundant species, based on the distribution of extant forms. This information, retrieved
620 from the Marine Biodiversity and Ecosystem Functioning EU website (MARBEF:
621 www.marbef.org), included the average life depth of 23 modern species that in our dataset
622 had an overall abundance > 0.15%.

651 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 (Krijgsman 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)

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722 and SRB (Ghinassi and Lazzarotto, 2005), the same chronostratigraphic interval is recorded
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724 by monotonous epibathyal mudstones several hundred meters thick, locally intercalated with
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726 delta-front hyperpycnal sandstones and conglomerates. In a very broad sense, the concept
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728 of S2 is extended to these basins, by assuming that erosional unconformities in EB pass to
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730 into correlative conformities in rapidly subsiding adjacent basins, where thick successions
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732 could be accommodated. Apart from exceptions, no shells were found in bathyal mudstone or
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734 in deltaic sandstone. In OOB, the same time span is marked by a N-S facies gradient
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736 characterised by a single deepening-upward succession, from fluvio-deltaic sandstone to
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738 shelfal mudstone, replaced by a succession made of four distinct regressive-transgressive
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740 units in the Orcia valley to the north (Ghinassi, 2005; Benvenuti et al., 2015b). A laterally-
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742 continuous shell bed, with sharks remains and skeletons and articulated bones of whales,
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744 sirenians and large teleost fishes (Danise, 2010; Sorbi et al., 2012; Tinelli, 2013), marks a
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746 major transgressive surface overlain by open shelf mudstones (Sorbi et al., 2012; Tinelli,
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748 2013: biozone MPL2) that is hypothetically traced along a NE-SW profile (Figs. 4, 5).
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754 3.1.3 Synthem S3: Zanclean-Piacenzian transition

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758 Synthem S3 is subdivided in EB into a lower and an upper interval (Benvenuti et al., 2014).
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760 The lower division is represented by deepening-upward, coarse-grained delta front system,
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762 overlain by an upper mudstone division from an open shelf setting. The upper part is rich
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764 with shell beds, and occasional articulated whale skeletons, associated with shark teeth,
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766 have been recovered (Danise and Dominici, 2014). Similar shelf mudstones of the MPL4
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768 biozone crop out in VEB and SRB (Bossio et al., 1993; Riforgiato et al., 2005) whereas
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770 biostratigraphically equivalent mudstones in FB testify to an upper epibathyal
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772 paleoenvironment.
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782 3.1.4 Synthem S4: early Piacenzian warm climate and high sea-level
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786 Synthem S4 (Benvenuti et al., 2014) has been recognised in FB and VEB by facies
787 similarities and chronostratigraphic correlation. In EB, S4 comprises a lower interval
788 dominated by richly fossiliferous, massive mudstone or very-fine-grained sandstone
789 (prodelta-inner shelf), overlain by bioclast-rich sandstones recording prograding mixed
790 carbonate-clastic ramp, outcropping in the southeastern part of the Elsa valley. Equivalent
791 deposits, also comprised in biozone MPL4b, are patchily distributed in FB, VEB, SRB, OOB
792 and other basins of southern Tuscany (Ghinassi and Nalin, 2010; Ghinassi, personal
793 communication, 2015). The upper interval of S4 is formed by a succession of delta front
794 sandstones, passing in EB eastern margin to a few tens of m-thick fluvial succession, hinting
795 at an original depositional gradient. S4 is apparently missing due to erosion north of San
796 Gimignano (EB), and around Lajatico (VEB). Biostratigraphic data allow to refer S4 to the
797 upper part of biozone MPL4b and the lower part of MPL5a, thus comprising the mid-lower
798 part of the Piacenzian, globally characterised between 3.264-3.025 Ma by warm climate and
799 relatively high sea level (Raymo et al., 2009; Dowsett et al., 2013; Prista et al., 2015).
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818 3.1.5 Synthem S5: mid-Piacenzian high-frequency sea level variation
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822 Synthem S5, recognised in EB and VEB, is bounded below by an erosional unconformity
823 that cuts deeply into underlying units, bringing S5 directly on top of S3 (EB: log 15; VEB:
824 logs 5-6 in Fig. 1). S5 is up to about 200 m in EB, where it has been subdivided into a
825 hierarchy of small-scale depositional sequences (Benvenuti et al., 2007; Dominici et al.,
826 2008: see following paragraphs). Each composite depositional sequence forms a tens-of-
827 m-thick asymmetric sedimentary cycle, composed by a deepening-upward part, from fluvial
828 or coastal coarse-grained sediments, to open shelf mudstones, sometimes topped by a
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842 regressive shoreface or delta sandstone, other times directly overlain by the next sequence
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844 through a sharp contact. Fluvial, brackish-water, and other intertidal deposits mark the lower
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846 part of each composite sequence, usually topped by a laterally-continuous shell bed, from
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848 a few cm to a few dm-thick, representing a surface of transgression. Shell beds are
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850 particularly well-developed around the middle part of sequences, where they separate
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852 shoreface and delta sandstones from overlying open shelf mudstones, marking the time of
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854 maximum flooding (MFS). Large marine vertebrates, including articulated whale skeletons
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856 and large sharks (Danise and Dominici, 2014), are often recovered both at MFS and
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858 overlying mudstone (Fig. 1). Towards the north-eastern margin of EB, cyclothemic fluvial
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860 conglomerates, sandstones and mudstones replace coastal and fully marine deposits,
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862 testifying to an original facies gradient. In the central part of EB, composite sequences are
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864 stacked to form a deepening-upward succession, with a topmost thick and laterally-
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866 continuous open shelf mudstone interval, directly onlapping the S4-S5 basal unconformity
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868 on the eastern EB (log 15, Fiano: Fig. 1).
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874 3.1.6 Synthem S6: Piacenzian-Gelasian climate change and regression

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878 As S5, synthem S6 is also built through a hierarchy of small-scale depositional sequences,
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880 better expressed in EB, but also documented in SRB and CB. In EB, fluvial coarse-grained
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882 sandstones fill a deep valley incised in S5 deposits (logs 8-10 in Fig. 1), resting on the basal
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884 unconformity of S6. Intertidal or coastal lagoon deposits form the transgressive systems
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886 tract of the composite depositional sequence. A laterally-continuous shell bed testifies to the
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888 MFS of S6, topped by highstand shoreface and delta front sandstones. The Piacenzian-
889
890 Gelasian boundary, corresponding to a major climatic transition from warmer-moister to
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892 colder-drier conditions (Benvenuti et al., 1995b; 2007), is marked by the Gauss-Matuyama
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894 reversal detected at Montopoli (Lindsay et al., 1980). Highstand marine sandstones are
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901 characterised by the recovery of two mysticete skeletons, at Montopoli (EB, see Capellini,
902 1905) and Sinalunga (CB, Fig. 7). Fully continental environments were established
903 throughout the Gelasian in all basins here under study (e.g., Benvenuti and Del Conte, 2013;
904 Benvenuti et al., 2014; Bianchi et al., 2015).
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914 3.2 Sedimentary facies and facies associations 915

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919 Seven groups of siliciclastic facies and one group of carbonate facies, with very different
920 fossil content, have been recognised (Tab. 1). Siliciclastic facies form a paleoenvironmental
921 gradient from terrestrial to marine and, in the case of marine facies, from shallowest to
922 deepest (Fig. 8a). Facies types are fluvial conglomerate and sandstone, and alluvial
923 mudstone (F1); intertidal to very shallow subtidal mudstone and muddy sandstone (F2);
924 shallow subtidal coarse- and medium-grained sandstone with sparse conglomerate (F3);
925 deep subtidal muddy fine-grained sandstone (F4); open shelf sandy mudstone (F5); outer
926 shelf to upper bathyal mudstone (F6); outer shelf and bathyal turbidite sandstone and
927 conglomerate (F7). An eighth group is formed by facies deposited subtidally in limited mixed
928 carbonatic-siliciclastic ramps (F8), irrespective of depth (Nalin et al., 2016). Facies F6-F7
929 are restricted to Zanclean deposits (synthems S1-S3); facies F5 and F8 characterise the
930 upper Zanclean-middle Piacenzian interval (synthems S3-S4); facies F1-F4 characterise the
931 upper Piacenzian (synthems S5-S6). The OOB succession, characterised by facies F1-F4,
932 is an exception within the Zanclean.
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950 3.3 Elementary depositional sequences (EDS) 951

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954 Both fluvial (Benvenuti and Del Conte, 2013) and marine facies groups (siliciclastics:
955 Benvenuti et al., 2007; 2014; carbonates: Nalin et al., 2016) are stacked to form facies
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962 associations which record cyclic variations of depositional and environmental conditions in
963 response to a change in accommodation space. Physical surfaces and the intervening
964 deposits allowed to subdivide depositional sequences in systems tracts (Benvenuti et al.,
965 2007; Dominici et al., 2008). At the simplest scale, these hybrid facies associations form
966 elementary depositional sequences, up to 10-20 m thick, in their turn stacked to form
967 composite sequences (original concepts from Mutti et al., 1994). This hierarchy is
968 particularly evident in synthem S5-S6, formed at a time of pronounced glacio-eustatic
969 oscillations and expressed around coastal settings, where maximum facies contrast allows
970 for the expression of subtle cycle of sea level variation (e.g., Benvenuti and Dominici, 1992;
971 Benvenuti et al., 2007; Dominici et al., 2008). Analogue sharp facies contrast within
972 Zanclean EDS in OBB (Tinelli, 2013), but is otherwise absent in deeper sediments (facies
973 F5-F7). EDSs have different expressions depending on the time interval and the
974 sedimentary basin.

991 3.3.1 Zanclean EDS (synthems S1-S3)

992 In most basins, deposition of synthems S1-S2-S3 takes place at outer-shelf or bathyal
993 depths, well below the point on a depositional profile where the rate of relative sea level
994 change is zero (equilibrium point). Here the sediment supply is not sufficient to fill the
995 available accommodation space and an aggradational style of deposition prevails, with the
996 result that in most Zanclean settings smaller cycles of sea level variations are not marked
997 by a facies change. The sharp facies change recorded where the monotonous muddy
998 deposition is interrupted by turbidite sandstone and conglomerate, is connected with
999 synthem boundaries and major tectonic phases of restructuring of the region. MM and shell
1000 beds are practically absent. This situation reverses in the Orcia-Ombrore basin, where
1001 depths of deposition are shallower and EDS are expressed. At Arcille deltaic sandy
1002 conglomerates and sandstones (facies F3) are overlain by a fluvial cross-bedded sandstone
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1022 (facies F1a), separated by a transgressive surface (TS) from an overlying bioturbated
1023 shallow marine sandstone. A *Haustator vermicularis* shell bed (Danise, 2010; Tinelli, 2013)
1024 forms the MFS separating the shoreface sandstone from an open marine mudstone with
1025 scattered shells (facies F5), marking a sudden and prolonged deepening of the basin
1026 (biozone MPL2: Sorbi et al., 2012; Tinelli, 2013). The succession is topped by deposits from
1027 shallower depths, expression of the falling-stage (FSST), below the upper SB (Fig. 4).
1028 Similar small-scale depositional sequences, expressed through fining-upward cycles no less
1029 than 40 m-thick, are also present in synthem S3 at Case al Poggio, near Siena (biozones
1030 MPL3-MPL4a: Bianucci et al., 2001) and at Castelfiorentino (biozone MPL4b: Benvenuti et
1031 al., 2014).
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1045 3.3.2 Piacenzian EDS (synthems S4-S6)

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1047 As depth of deposition shallows during the Piacenzian, and cycles of sea level variation
1048 widen, the cyclic stacking of EDS becomes the typical depositional theme (Benvenuti et al.,
1049 2007, 2014; Dominici et al., 2008). In FB, the northwesternmost basin, depths remain
1050 considerable and facies change is more subtle. Pliocene at Orciano Pisano is traditionally
1051 assigned to the “Blue Clays” formation (Bossio et al., 1997), but two distinct bodies were
1052 evidenced since the late nineteenth century (D’Ancona, 1867). The lower one is formed by
1053 grey claystone with very rare shells, the upper one by muddy, very-fine grained gray
1054 sandstone richly fossiliferous. The lower part of the latter interval outcrops at the foothill of
1055 the small town of Orciano Pisano, around the locality Case Nuove (Bianucci and Landini,
1056 2005; Berta et al., 2015). Here a laterally persistent shell bed is dominated by the turritellid
1057 *Archimediella spirata*, overlain by a 25 m-thick monotonous sandstone interval with
1058 intercalated shell beds or sparse shells, becoming muddier upward. The *Archimediella* shell
1059 bed is interpreted as the TS of an EDS, coinciding with the lower SB of a lower Piacenzian
1060 EDS. The overlying muddy fine-grained sandstone is the TST and HST (MPL5a: Dominici
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1082 et al., 2009; Fig. 6). At shallower settings, in all basins to the East and South of FB, EDS of
1083
1084 synthem S4 take the form of an alternation of mudstone and carbonate (facies F5 and F8:
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1086 Nalin et al., 2016), or mudstone and sandstone (facies F5 and F3-F4: Benvenuti et al., 2014;
1087
1088 biozone MPL5a). Middle and upper Piacenzian EDS form and alternation of coastal
1089
1090 mudstone and sandstone (facies F1-F2-F3: Benvenuti and Dominici, 1992; Dominici, 1994),
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1092 with MFS and HST marked by a shell bed topped by a lower shoreface sandstone, or a shelf
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1094 mudstone (facies F4-F5: Benvenuti et al., 2007; Dominici et al., 2008).
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1099 **4. Distribution of large marine vertebrates**

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1101 **4.1 Geographic distribution**

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1105 The MM geographic distribution is listed in Table 2. All MM that was geographically located,
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1107 irrespective of stratigraphy, was plotted in Fig. 3. The largest number were recovered in FB
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1109 in Northwestern Tuscany, with a peak at a few sites around the small town of Orciano
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1111 Pisano, in the Pisa province. This coincides with the highest number of known species,
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1113 including mammals, elasmobranchs, turtles, and large bony fishes. MM is also abundant in
1114
1115 the province of Siena, around Volterra (VEB; Bianucci and Landini 2005), and around San
1116
1117 Quirico, particularly rich with elasmobranchs according to the available data (SRB; Marsili,
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1119 2006). A fourth basin with a consistent number of findings is OOB, where cetaceans, sharks,
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1121 sirenians and large teleost fishes have been unearthed.
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1128 **4.2 MM stratigraphic distribution**

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1130 **4.2.1 Synthems S1-S2**

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1142 In the vicinity of Saline di Volterra, one of the sites with remains of *Pliophoca etrusca* (Berta
1143 et al. 2015) and sperm whale (Tab. 2), S1 is represented by a bathyal mudstone (facies F6,
1144 biozone MPL1). Lower-middle Zanclean MM is otherwise absent, with the exception of S2
1145 in OOB, where large marine vertebrates are concentrated at the maximum flooding interval,
1146 outcropping at Poggio alle Mura (Danise, 2010), Camigliano (Sorbi et al., 2012) and Arcille
1147 (Tinelli et al., 2012; Tinelli, 2013), in biozone MPL2. At Poggio alle Mura a slightly
1148 disarticulated balaenid whale skeleton (WOM1-1 in Tab. 2) has been excavated in contact
1149 with the laterally-persistent *Haustator* shell bed at the maximum flooding interval (Figs. 4, 5;
1150 Danise, 2010; Tinelli, 2013). At Camigliano and Arcille, tens of km from Poggio alle Mura,
1151 the *Haustator* shell bed is associated with other articulated skeletons and isolated MM
1152 remains, including several specimens of the sirenian *Metaxytherium subapenninum*
1153 (MOM2-1-5), large bony fishes, rays, and sharks *Carcharias taurus*, *Carcharhinus* sp.,
1154 *Galeocerdo cuvieri*, and *Squatina* sp. (Sorbi et al., 2012; Tinelli et al., 2012; Tinelli, 2013).
1155 A partial skull of the delphinid *Etruridelphis giulii*, with right and left dentaries fractured, but
1156 nearly complete and with most teeth still in their alveoli (DSi2-1 in Tab. 2), was recovered
1157 southeast of Siena, near Chianciano Terme (SRB) at the top of a mudstone (facies F6)
1158 intercalated with turbiditic sandstone beds (Facies F7), topped by a monotonous mudstone
1159 interval (upper Zanclean, uppermost part of biozone MPL3: Bianucci et al., 2009b). In the
1160 same basin, two undetermined beaked whales and bones of four different specimens
1161 attributed to *Metaxytherium subapenninum* were found in the middle of a fining-upward
1162 succession, at the boundary between biozones MPL3 and MPL4a (Bianucci et al., 2001;
1163 WSi2-1-2 and MSi2-1-4 in Tab. 2), suggesting that findings at the two SRB localities belong
1164 to the same MFS, in the upper part of S2. Three specimens of marine mammals were
1165 identified in Synthem S1, seven in Synthem S2.

1195 4.2.2 Synthem S3

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1204 The upper part of S3 yielded an articulated and well-preserved balenopterid skeleton found
1205 in a 30 m-thick mudstone succession at Castelfiorentino, in the Elsa basin (EB, WEI3-1).
1206
1207 These strata are richly fossiliferous, with several shell beds with epifaunal cemented taxa,
1208
1209 such as vermetid gastropods, oysters and corals (Facies F5), in a normal-polarity
1210
1211 magnetostratigraphic interval (Gauss chron: Andrea Albianelli, personal communication,
1212
1213 1999). Based on physical stratigraphic correlation, this can be assigned to a lower
1214
1215 Piacenzian HST. A skull of *Hemisyntrachelus* sp. (Aldinucci et al., 2011) and partly
1216
1217 articulated vertebrae and costae of a dolphin skeleton (Arbeid et al., 2015) were recently
1218
1219 excavated a few hundred meters apart one from the other, along a monotonous mudstone
1220
1221 S3 succession intercalated with several *Ostrea* and *Serpulorbis* shell beds, near Certaldo
1222
1223 (facies F5, DEI3-1-2 in Tab. 2). Overall, specimens of marine mammals attributed to
1224
1225 Synthem S3 were eleven (some are uncertain and may come from the upper part of S2:
1226
1227 Tab. 2).
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1234 4.2.3 Synthem S4 1235 1236 1237

1238 Synthem S4 yielded the highest abundance and species-richness of the Tuscan MM. In the
1239
1240 Fine basin, the locality of Orciano Pisano is represented in Table 2 by 18 records of whales,
1241
1242 dolphins (a partial skeleton: Bianucci, 1996; Bianucci et al., 2009), seals (Berta et al., 2015),
1243
1244 tens of other unidentified cetacean elements, hundreds of shark teeth and vertebrae (Fig.
1245
1246 3), and sea turtles, large bony fishes, and sea birds hosted in museum collections (Bianucci
1247
1248 and Landini, 2005; Marsili, 2007b; Cioppi and Dominici, 2011). In locality Case Nuove, a
1249
1250 single middle Piacenzian transgressive surface has yielded a whole, articulated whale
1251
1252 skeleton (Figs. 4, 6), teeth of blue and white sharks and bones of sea birds (Dominici et al.,
1253
1254 2009). From the same site comes a skeleton of the monk seal *Pliophoca etrusca* (Berta et
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1261
1262 al., 2015), and possibly many other museum specimens labelled “Orciano Pisano”,
1263
1264 suggesting that this interval forms the most prolific bonebed of the region (Tab. 2). A few cm
1265
1266 above the *Archimediella* shell bed, glauconitic and deeply bioeroded whale bones (Danise,
1267
1268 2010), associated with ichnological evidence of the activity of *Osedax* bone-eating worms
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1270 (see Higgs et al., 2012), lie in a bioturbated muddy, fine-grained sandstone with a complex
1271
1272 boxwork of *Ophiomorpha* and *Thalassinoides* trace fossils (Fig. 6), associated with a diverse
1273
1274 paleocommunity of molluscs and other benthic invertebrates with complex trophic
1275
1276 connections (Dominici et al., 2009; Danise et al., 2010). At the boundary between FB and
1277
1278 VEB, an incomplete skull and skeleton of the dolphin *Etruridelphis giulii* was recovered near
1279
1280 Lorenzana (Lawley, 1876; Bianucci, 1996; Bianucci et al., 2009b), at a locality associated
1281
1282 with a muddy sandstone interval (facies F4) in synthem S4. An incomplete and articulated
1283
1284 mysticete was recovered in a sandstone at San Gimignano, associated with pectinid
1285
1286 bivalves (Fig. 7; facies F3; Elsa basin, EB: Danise and Dominici, 2014), here tentatively
1287
1288 assigned to the uppermost part of the synthem (WEI4-1 in Tab. 2). Overall, specimens of
1289
1290 marine mammals attributed to Synthem S4 were 28.
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1296 4.2.4 Synthem S5

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1300 The next MM richer stratigraphic interval are Piacenzian deposits of synthem S5. An
1301
1302 incomplete and disarticulated balaenid skeleton was found in intertidal deposits of the lower
1303
1304 part of the synthem, at Casenuove (facies F2, EB; Bianucci et al., 1995; Collareta et al.,
1305
1306 2016; WEI5-1 in Tab. 2). A large balaenid was recovered higher up section, a few meters
1307
1308 above a laterally-continuous very thick and complex *Haustator vermicularis* shell bed, up to
1309
1310 2 m-thick (Benvenuti et al., 1995a), traced laterally for 2 km to the east of San Miniato
1311
1312 (“*Turritella strata*”, De Stefani, 1874), and forming a surface of transgression within the TST
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1314 of S5 (Benvenuti et al., 2007; 2014; Dominici et al., 2008). The MFS is formed by a
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1321
1322 *Glycymeris insubricus* shell bed, separating around San Miniato shoreface sandstone
1323
1324 (facies F3 or F4) from offshore mudstone (F5; Benvenuti et al., 2007). The balaenid skeleton
1325
1326 was almost articulated and bioeroded, closely associated with teeth of the great white shark
1327
1328 and other scavengers (Borselli and Cozzini, 1992; Bianucci et al., 2002; Danise and
1329
1330 Dominici, 2014), in the early HST of synthem S5 (Benvenuti et al., 2007; Dominici et al.,
1331
1332 2008; WEI5-2 in Tab. 2). The *Glycymeris* shell bed can be traced laterally for several km. In
1333
1334 the vicinity of Fiano, it includes bioeroded and encrusted gravels inherited from underlying
1335
1336 successions, interpreted as revinement deposits. The interval of maximum flooding is
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1338 marked by the stacking of at least three distinct shell beds, all including a high-diversity
1339
1340 association with bioeroded and encrusted shells. This situation suggests that balaenid
1341
1342 WEI5-2 lies in correspondence of an interval of low rates of sedimentation. In SRB, near
1343
1344 Castelnuovo Berardenga, shelfal mudstones (facies type F5) have yielded MM remains at
1345
1346 a few localities. Delphinid remains were found at the “I Sodi” quarry and at Troiola (DSi5-1-
1347
1348 2, in Tab. 2). Bones of a beaked whale and undetermined mysticetes are reported from
1349
1350 Guistrigona (Manganelli and Benocci, 2014) and a fragmentary specimen of the monk seal
1351
1352 *Pliophoca etrusca* from Castelnuovo Berardenga (Berta et al., 2015). A very rich shark
1353
1354 fauna, including sawsharks, thresher, frilled, bluntnose sixgill, bramble, gulper, kitten, sand
1355
1356 tiger, shorten mako, basking and requiem sharks, an association suggesting an upper slope
1357
1358 paleoenvironment for the surroundings of Castelnuovo Berardenga Scalo (Cigala-Fulgosi et
1359
1360 al., 2009; the same mudstone interval at the same locality has been interpreted as a shelfal
1361
1362 deposit: Martini et al., 2016). Judging from historical accounts (Capellini, 1883), the killer
1363
1364 whale *Orcinus citonensis* (DCh4-1) was recovered in a sandy unit lying on top of a thick
1365
1366 mudstone interval (S3 or S4) and is tentatively assigned to S5. Specimens of marine
1367
1368 mammals attributed to Synthem S5 were 10.

1375 4.2.5 Synthem S6

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1384 A fairly complete skeleton of a large balaenid whale was recovered in the second half of the
1385
1386 19th Century in the EB near Montopoli Valdarno (Capellini 1905), in open shelf strata
1387
1388 attributable to the interval of maximum flooding of S6 (WEI6-1 in Tab. 2). The MFS of S6, of
1389
1390 uppermost Piacenzian age, is marked in EB by a laterally continuous *Pteria phalenacea*
1391
1392 shell bed, with a high-diversity association of macroinvertebrates, including a rich decapod
1393
1394 paleocommunity (Garassino et al., 2012). In the vicinity, near Palaia, a right whale (*Eubalena*
1395
1396 sp.) was recovered in 1974 in sandy mudstones, in association with mollusc shells and teeth
1397
1398 of the great white shark (*Carcharodon carcharias*: Bisconti, 2002; Sorbini et al., 2014). A
1399
1400 tightly articulated balaenopterid skeleton was found at Sinalunga (WCh4-1 in Tab. 2), in
1401
1402 deltaic sandstones and conglomerates (Fig. 8). Marine mammal specimens attributed to
1403
1404 Synthem S6 were three.
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1410 4.3 MM facies type distribution 1411 1412 1413 1414

1415 In an ideal deepening-up gradient, multi-element findings of marine mammals are very rare
1416
1417 in intertidal and very shallow subtidal paleoenvironments (facies type F2, 1,5%: Fig. 9A),
1418
1419 moderately represented in delta or shoreface sandstones (facies type F3, 4,6%), most
1420
1421 abundant in sandy mudstone of open shelf settings (facies type F5, 70%), rare in outer shelf
1422
1423 and bathyal sediments (facies type F6-F7, 1,5%). The most pristine and complete skeletons
1424
1425 are associated with gravelly well-sorted sands from event sedimentation, suggesting a
1426
1427 negative relationship between taphonomic loss and sedimentary processes at delta fronts.
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1430 In the tightly articulated and pristine Sinalunga balaenopterid (WCh4-1 in S4-CB), the
1431
1432 cortical surface of the tightly-connected vertebrae is practically intact, and carpal,
1433
1434 metacarpal and phalanges of the flipper are in perfect anatomical connection, as if a sudden
1435
1436 depositional event buried a fresh carcass (Fig. 8; similar pristine skeleton are found in deep
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1442 water turbiditic succession: Stinnesbeck et al., 2014). Another pristine and tightly articulated
1443
1444 skeleton, belonging to a killer whale (WCh3-1 in CB), was collected at Cetona in the second
1445
1446 half of the 19th century, in a locality associated with sandstones, also possibly of deltaic
1447
1448 origin. Large vertebrates embedded in fine-grained, muddy matrix (shelf deposit formed
1449
1450 below storm wave base) and those associated with laterally-persistent shell beds
1451
1452 (condensed deposits) are slightly disarticulated and fairly complete, showing signs of long
1453
1454 permanence in a low energy, well-oxygenated seafloor before the final burial. Bioerosion of
1455
1456 bones caused by phototrophic cyanobacteria and algae, heterotrophic fungi and bacteria
1457
1458 (Orciano balaenopterid WFi4-1 in S4-FB), and eventually by whalebone-eating siboglinid
1459
1460 worm of genus *Osedax* (on a ziphiid humerus, WFi4-14: Higgs et al., 2012), occurred at
1461
1462 condensed intervals, in association with glauconite (Danise, 2010). In one instance, a
1463
1464 condensed shelly interval is traced for a few kilometers, connecting bioturbated shoreface
1465
1466 sandstones yielding slightly disarticulated sirenian skeletons (MOM2-1, MOM2-2) and other
1467
1468 MM (Tinelli, 2013), with open shelf deposits yielding slightly disarticulated whale remains
1469
1470 (WOM2-1 in S2-OOB).
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1472
1473 Regarding a sequence stratigraphic interpretation, pristine skeletons from delta front
1474
1475 sediments can be part of the FSST (Fig. 4; in an alternative interpretation it may belong to
1476
1477 the early TST, when incised valleys are filled with coastal deposits). TST deposits account
1478
1479 for 6,2% of cases (Fig. 9B). Much more frequently, articulated or slightly disarticulated
1480
1481 skeletons are associated with the HST of the corresponding depositional sequence, lying
1482
1483 above the MFS (56,9% of cases), or within the maximum flooding interval, above a laterally-
1484
1485 persistent shell bed (10,8%). Bone bioerosion is less pronounced in the late HST, when
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1487 sedimentation rate increases (Castelfiorentino whale WEI3-2 in S3-EB).
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1491 1492 1493 4.4 MM abundance and species-richness 1494 1495 1496 1497 1498 1499 1500

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1502 Some taxa need revision, but a conservative estimate of the different morphologies suggest
1503 that at least 17 marine mammal species lived in the NWMS during the Pliocene (possibly
1504 more than 20, an estimate for the whole epoch, i.e., 5,332-2,588 Ma), against nine presently
1505 living in the same area (plus two occasional visitors). Among the cetaceans, six families
1506 were present, against only five presently living in the Ligurian Sea (Tab. 3). The most
1507 abundant Pliocene species of Tuscany are the sirenian *Metaxytherium subapenninum* (N =
1508 10), the dolphin *Etruridelphis giulii* (N = 7) and the delphinid *Hemisyntrachelus cortesii* (N =
1509 5: Tab. 4). Overall abundance and species richness are not randomly distributed, but are
1510 maximum in Piacenzian strata of synthem S4, dated at 3.2-3.0 Ma (Tab. 2, Figs 2, 9C-D),
1511 particularly in the FB and VEB (Tab. 4). A species list of marine mammals summing up
1512 fossils found around Orciano Pisano and at La Rocca, near Volterra, yields a species
1513 richness (S) of 13. This Piacenzian peak in marine mammal diversity is matched by the fossil
1514 record of sharks, also maximum near Orciano Pisano (S = 27), with a second peak in S5,
1515 around Castelnuovo Berardenga (SRB, S = 16). Differently from the marine mammals,
1516 showing a complete turnover from the Pliocene to the recent (Tab. 3), 34% of Pliocene shark
1517 species are still extant in the NWMS (Tabs. 5-6). Marine mammal frequency and diversity
1518 gradually decreases in S5-S6.
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1541 **5. Paleoenvironment-fauna relations**

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1546 The paleoecology of Pliocene MM of Tuscany can be reconstructed by comparison with the
1547 ecology of their modern relatives. This approach can be applied at the family or genus level
1548 for marine mammals (Tab. 3), at the genus or species level for sharks (Tab. 5). With the
1549 only exception of the sirenian *Metaxytherium subapenninum*, feeding on seagrasses
1550 (Domining, 2001), and small demersal sharks (e.g., catsharks, frilled sharks), all MM studied
1551 here are pelagic forms that had no direct connection to conditions at the seafloor (Tabs. 4
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1562 and 6). The paleoecology of benthic habitats informs however on the situation of the
1563
1564 overlying water column in terms of factors that matter to the distribution of pelagic
1565
1566 organisms, such as water depth, salinity and nutrient levels. In the second place, since all
1567
1568 MM remains after death ultimately sink to the seafloor, benthic paleoecology is also a means
1569
1570 to understand taphonomic controls on MM distribution. Cluster analysis based on the
1571
1572 distribution of mollusc species in 72 samples resulted in the identification of four main groups
1573
1574 of samples, roughly corresponding to the four main facies types recognised based on
1575
1576 lithology and sedimentary structures (F2-F5 in Tab. 1). Clusters are formed by samples from
1577
1578 outer shelf and upper slope (three samples), open shelf (34 samples), shoreface (23
1579
1580 samples), and transitional settings, such as brackish-water coastal lagoons and tidal flats
1581
1582 (12 samples: see Supplement Material, Fig. S1). ANOSIM confirms that sedimentary facies
1583
1584 type can broadly predict what benthic assemblage it will yield (Tab. 7; general $R = 0,632$).
1585
1586 The difficulty to discriminate between upper and lower shoreface facies, and between
1587
1588 shoreface and open shelf facies is confirmed by overlaps in sample distribution in the NMDS
1589
1590 ordination diagram (Fig. 10A). Samples AG1, MON1 and MON2 allow to re-interpret the
1591
1592 associated sandstones, originally included in upper shoreface facies type, as offshore
1593
1594 deposits. The presence of gravels and cobbles intensely bioeroded by bivalves and
1595
1596 polychaete (ichnofossils include *Gastrochaenolithes*, *Meandripolydora* and *Caulostrepsis*)
1597
1598 and encrusted by balanids, oysters, serpulids, and bryozoans, suggests they are part of
1599
1600 condensed beds resulting from transgressive pulses (hiatal concentrations). The
1601
1602 relationship between facies type and mollusc association is broadly summarised in the
1603
1604 following paragraphs (see online Supplement Information for a list of characterising
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1606 species).
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1613 5.1 Coastal lagoon, tidal flat and embayment 1614 1615 1616 1617 1618 1619 1620

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1622 Intertidal faunas are always associated with facies type F2 and are characterised by low-
1623
1624 diversity associations, sometimes with less than 10 taxa and dominated by one or two
1625
1626 species, including species today living in brackish waters of the Mediterranean, at intertidal
1627
1628 or very shallow subtidal depths (e.g. *Cerastoderma edule*, *Nassarius reticulatus*,
1629
1630 *Scrobicularia plana*: Pérés and Picard, 1964). Facies type F2 is also associated with
1631
1632 samples having a species richness higher than the preceding and including species typical
1633
1634 of seagrass bottoms and known to withstand moderate changes of salinity. In only one
1635
1636 instance a large vertebrate was associated with intertidal deposits (a balaenid, lying on top
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1638 of large wood fragments: Bianucci, 1995; Collareta et al., 2016).
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1641 1642 1643 5.2 Upper shoreface 1644 1645 1646 1647

1648 Facies type F3 is associated with a high-diversity assemblage representing a
1649
1650 paleocommunity dominated by suspension feeders adapted to shifting sandy bottoms, with
1651
1652 bivalves typical of modern shoreface sandy bottoms (e.g., families Glycymeridae, Tellinidae,
1653
1654 Donacidae and Veneridae). Among extinct species of this recurring assemblage, some are
1655
1656 large-sized or have very thick shells. Some species of this group indicate the presence of
1657
1658 vegetated bottoms. Small pyramidellid gastropods are parasitic on echinoderms, also typical
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1660 of the upper shoreface.
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1665 1666 5.3 Lower shoreface 1667 1668 1669

1670 Species richness further increases in collections associated with facies type F4 (lower
1671
1672 shoreface). Species typical of this recurring assemblage include both suspension-feeding
1673
1674 and detritus-feeding bivalves and gastropods. The following gastropod families are usually
1675
1676 represented by several species: Trochidae, Rissoidae, Cerithiidae (from vegetated
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1681
1682 bottoms), Naticidae, Muricidae, Turridae, Conidae, Terebridae, Bullidae, Cylichnidae
1683
1684 (carnivores), Pyramidellidae (echinoderm parasites). Many bivalve species occur in both
1685
1686 facies types F2 and F3. At three different sites and at different stratigraphic units large
1687
1688 marine vertebrates, including mysticetes, sirenians and sharks, were recovered in
1689
1690 association with shell beds dominated by the gregarious turritellid gastropod *Haustator*
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1692 *vermicularis* (Fig. 6C-D).
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1697 5.4 Offshore and upper slope 1698 1699 1700

1701
1702 Another important set of species recurred in facies type F5 (mudstone deposited in offshore
1703
1704 bottoms at shelf depths). Among characterising gastropods are the suspension feeders
1705
1706 (*Turritella tricarinata*, *Archimediella spirata* and *Petalochoncus intortus*), deposit feeders
1707
1708 (*Aporrhais uttingeriana*) and carnivores or scavengers (*Epitonium frondiculoides*, *Nassarius*
1709
1710 *semistriatus*, *Mitrella nassoides*). Also the bivalves occupy many different ecological niches
1711
1712 (e.g., infaunal detritus feeders, epifaunal suspension feeders, either free-living, byssate, or
1713
1714 cemented). Outer shelf and uppermost bathyal sediments from F6 mudstones, studied at
1715
1716 only one location, are characterised by a separate set of carnivorous gastropods and by a
1717
1718 few small bivalve species. Ubiquitous molluscs include species found from intertidal to outer
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1720 shelf depths (e.g., *Corbula gibba*), and those preferential of open marine waters, from lower
1721
1722 shoreface to outer shelf. Most multi-element findings of marine mammals are associated
1723
1724 with sandy mudstones from open shelf settings, below storm wave base, also in association
1725
1726 with an *Archimediella spirata* shell bed (Fig. 6C-D). No molluscs were recovered in facies
1727
1728 type F7, with the exception of bathyal mudstone in the lowermost Pliocene of FB, associated
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1730 with sparse specimens of the gryphaeid epifaunal bivalve *Neopycnodonte navicularis* (not
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1732 sampled).
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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 protozoans (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

1801
1802 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
1803
1804 350 m depth (only one sample: Fig. 10B). The position of fossil cetaceans, sirenians,
1805
1806 pinnipeds and large sharks (respectively W, M, P and S, N = 13) was plotted near the
1807
1808 corresponding shell bed in the NMDS ordination. The resulting pattern shows that all MM
1809
1810 considered, associated with open shelf settings and with facies types F4-F5, cluster around
1811
1812 -100 m, spanning -30-300 m.
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1815 1816 **7. Factors of the Pliocene NWMS marine megafauna fossil** 1817 1818 **record** 1819 1820 1821 1822 1823 1824

1825 The detailed sequence-stratigraphic framework and the abundant shell beds, offering an
1826
1827 independent check on sedimentary facies distribution by benthic paleoecology, allows also
1828
1829 to explore factors behind MM geographic and stratigraphic distribution, and to sort out
1830
1831 evolutionary, ecological, and taphonomic drivers of this particular fossil record. NWMS
1832
1833 Pliocene distribution can be compared with similar studies in different settings and at
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1835 different times, to draw conclusions on the general quality of MM fossil record.
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1839 1840 **7.1 Evolutionary control** 1841 1842 1843

1844 Available data allow a meaningful comparison of NWMS MM diversity across the Pliocene,
1845
1846 particularly detailed for marine mammals (Fig. 9D). Although the study suggests a facies
1847
1848 control, with MM remains being generally associated with late TST-HST muddy sandstones
1849
1850 and mudstones from lower shoreface and offshore shelf paleosettings, the temporal pattern
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1852 of biodiversity recorded on a regional basis likely reflects also a paleobiologic phenomenon,
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1854 since lower shoreface and offshore shelf sediments are represented in all synthems. Marine
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1862 mammals are unrecorded in the thickest part of synthem S1-2 (Zanclean, mostly bathyal
1863 mudstone and turbiditic sandstone), but they are present in S2, in OOB (Zanclean shoreface
1864 and open shelf deposits) and SRB (Zanclean upper slope deposits). MM gradually rises in
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1866
1867
1868 S3, at the upper Zanclean-lower Piacenzian, whereas it suddenly peaks in synthem S4,
1869
1870 where species richness of both marine mammals and sharks is highest. S5 reflects a lower
1871
1872 diversity of marine mammals, but still a high diversity of sharks, while values of both groups
1873
1874 drop to the lowest abundance and species richness in S6, during the upper Piacenzian-
1875
1876 lowermost Gelasian (Fig. 9D).
1877
1878

1879 The S4 diversity peak coincides with the middle part (3.264–3.025 Ma) of the Piacenzian, a
1880
1881 time interval in which the earth experienced global average temperature 1.84 °C-3.60 °C
1882
1883 warmer than the pre-industrial period (Dowsett et al., 2013). Climatic impact is testified by
1884
1885 the widespread occurrence of carbonate deposits in S4 (Fig. 2), with sedimentary facies
1886
1887 indicative of warm-temperate to subtropical conditions, with summer sea-surface
1888
1889 temperature considerably warmer than 20°C and winter temperatures colder than 20°C
1890
1891 (Nalin et al., 2016). This suggests a causative link between global climate and biodiversity,
1892
1893 S4 diversity peak recording a global phenomenon, possibly an increase of speciation rate
1894
1895 connected with global warming. Similarly, we propose that the lower diversities recorded at
1896
1897 S5-S6 are the regional expression of an increase in extinction rate related to climatic cooling
1898
1899 and global sea-level drop, ultimately leading to the global MM extinction event recorded on
1900
1901 a coarser scale at the Pliocene-Pleistocene boundary (Pimiento et al., 2017): the finer
1902
1903 stratigraphic resolution adopted here suggests a stepwise extinction event. NWMS data also
1904
1905 point to a selective effect, extinction being recorded by marine mammals, with a 100%
1906
1907 regional turnover between Pliocene and Recent (Tab. 3), but not as much by the shark
1908
1909 fauna, with 34% of the species still living in the Mediterranean, while still others have shrank
1910
1911 their distribution to subtropical latitudes. Also the Piacenzian teleost fish fauna (Cigala
1912
1913 Fulgosi et al., 2009) and benthic molluscs (Raffi et al., 1985) show a high percentage of
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1922 holdovers, suggesting that marine mammals have been particularly prone to climatic change
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1924 (see also Steeman et al., 2009).
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1926 Estimates of body size in Pliocene mysticetes of Tuscany, with several specimens reaching
1927 10 m (Danise and Dominici, 2014: seven specimens in Tab. 1), are comparable to global
1928 values derived from the literature for this time interval (Lambert et al., 2010), confirming that
1929 NWMS baleen whales were larger than their Miocene analogues, and smaller than modern
1930 forms. As with regard to odontocetes, the most common Pliocene delphinid, *Etruridelphis*,
1931 was larger than the modern analogue *Stenella* (Bianucci et al., 2009b). The same is true for
1932 *Hemisyntrachelus cortesii*, larger than modern *Tursiops* (Bianucci, 1997a). On the other
1933 hand, the largest extant delphinid *Orcinus orca*, reaching 9 m, is about twice as long as
1934 *Orcinus citonensis* (Heyning and Dahlheim, 1988). The high percent of holdover points to a
1935 more conservative figure for larger sharks (Tab. 5), but the presence in the Pliocene of the
1936 gigantic *Carcharocles megalodon* and some large thermophilic species today restricted to
1937 lower latitudes suggests that impoverishment of the fauna is coupled with an average
1938 decrease in size (Marsili, 2008). Comparing sizes suggests an overall restructuring of
1939 NWMS MM during the last three million years (see also Bisconti, 2009).
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1957 7.2 Ecological control 1958 1959 1960 1961 1962

1963 The composition of the Pliocene NWMS MM is affected in the first place by the availability
1964 of food. At the lowest trophic level, inferring from the ecology of the modern MM (Tabs. 3,
1965 5), we found herbivore sirenians feeding on seagrasses (trophic level, TL = 2,0), all others
1966 being carnivores, thus having TL > 3,0 (Fig. 11). The lowermost levels among the carnivores
1967 were occupied by baleen whales and whale sharks (TL = 3,2-3,4), filter-feeding on pelagic
1968 crustaceans and fishes (krill). Roughsharks, catsharks, and houndsharks, with many
1969 species living in the modern Mediterranean, have a relatively species-poor Pliocene record,
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1982 probably due to a preservation bias related to their small size. At TL = 3,7-4,0 were one
1983
1984 species of catshark and a monk seal, both feeding near the seafloor on crustaceans, teleost
1985
1986 fishes and cephalopods. At TL = 4,1 were sandbar, tiger and blue sharks, feeding on teleost
1987
1988 fishes, cephalopods and on marine mammals. At the same level, in slope environments,
1989
1990 kitefin sharks mainly fed on other sharks. The majority of MM species were found at TL =
1991
1992 4,2, with smaller odontocetes (three species) and 11 species of sharks, including several
1993
1994 requiem sharks, a houndshark and a hammerhead. Larger dephinids, sperm whales,
1995
1996 beaked whales, together with mackerel, sand and sand tiger sharks, occupied high trophic
1997
1998 levels (TL = 4,3), followed at the top of the global NWMS food web by white shark,
1999
2000 megalodon shark, one species of sevengill shark (genus *Notorynchus*), and killer whales,
2001
2002 all feeding on marine mammals and smaller sharks (TL = 4,4-4,7). With no exception, all
2003
2004 highest levels encountered in modern NWMS offshore pelagic and nearshore communities
2005
2006 were occupied during the Pliocene by an analogous MM, often by the same species (large
2007
2008 sharks), or by congeneric or con-familial species (marine mammals: Tab. 3, 5). The Pliocene
2009
2010 pelagic ecosystem, typified by the mid-Piacenzian S4 association, must have been however
2011
2012 trophically more diversified (Fig. 11), including aquatic megaherbivores, several balaenid
2013
2014 filter feeders, larger and more diverse dolphins, and sharks species today extinct (e.g.,
2015
2016 *Carcharocles megalodon*) or restricted to tropical seas (e.g., *Galeocerdo cuvier*). With the
2017
2018 exception of TL = 2, all Pliocene NWMS MM were either apex predators of their community,
2019
2020 or mesopredators, occupying trophic positions below apex predators. The definitions of apex
2021
2022 predators (or top predators) and mesopredators are relative and to an extent context-
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2024 dependent (species that in a context are apex predators, in another are mesopredators, e.g.,
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2026 Estes et al., 1998). Since predation is a trophic interaction in which one animal (predator)
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2028 consumes another (prey) as a source of energy (food), irrespective of the means by which
2029
2030 this is accomplished (Lourenço et al., 2013), filter-feeding baleen whales can be considered
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2032 apex-predators of their community (e.g., Lewiston et al., 2004; Notarbartolo di Sciara et al.,
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2042 2016). Among sharks, 68% of living Mediterranean elasmobranches are ranked as top
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2044 predators, with a trophic level of 4 or more (Goffredo and Dubinsky, 2014, including
2045
2046 superorder Batoidea, against 22% of teleost fishes), an estimate that can be extended to
2047
2048 Pliocene NWMS MM. Relationships between apex predators and mesopredators are
2049
2050 complex and hard to define in ecology, involving predation on other predators (intraguild
2051
2052 predation, combining competition and predation: Polis et al., 1989), where consumption and
2053
2054 competition need to be proved (Lourenço et al., 2013). In the Mediterranean Pliocene,
2055
2056 paleontological evidences of carnivores serving as food to MM include killing of prey
2057
2058 (Bianucci et al., 2010) and scavenging (Cigala Fulgosi, 1990; Bianucci et al., 2002; Dominici
2059
2060 et al., 2009). The occurrence of intraguild predation must have been far more extended than
2061
2062 what taphonomy can prove, however, given a Pliocene diversity of NWMS very large
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2064 raptorial feeders higher than the modern, including the killer whale *Orcinus citonensis*, the
2065
2066 large delphinid *Hemisyntrachelus cortesii* (phylogenetically related to the modern killer
2067
2068 whale: Murakami et al., 2014), the white shark *Carcharodon carcharias*, the largest shark
2069
2070 of all times *Carcharocles magalodon* (Marsili, 2008), and a diverse association of smaller
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2072 carnivores, including monk seal, delphinids and sharks with $4,0 < TL < 4,2$ (Tab. 3, 5),
2073
2074 candidate prey for larger raptorial feeders. This interaction likely exerted in its turn a control
2075
2076 on community structure at lower trophic levels through processes like “mesopredator
2077
2078 release” and trophic cascades (Roemer et al., 2009), eventually linking pelagic and
2079
2080 nearshore communities, including benthic animals and plants, like in many modern
2081
2082 ecosystems (Estes et al., 2011, 2016), down to slope depths (e.g., Parrish, 2009). Large
2083
2084 raptorial feeders could exert a control on the diversity of the filter-feeding MM, like it has
2085
2086 been suggested on a global scale since the Miocene (Lambert et al., 2010), and for the
2087
2088 Pliocene by Bisconti (2003), when baleen whales were more diversified, both in terms of
2089
2090 species richness, size range, and feeding strategies, including both skim- and lunge-filter
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2092 feeding (respectively balaenid and balaenopterid whales: Berta et al., 2016; Hocking et al.,
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2101
2102 2017), minimising competition for food and diversifying spatial niches (see also Marx et al.,
2103
2104 2017, for the upper Miocene). A further important top-down control on community structure
2105
2106 is suggested by modern studies on the role of baleen and sperm whales as nutrient vectors,
2107
2108 both in horizontal (during seasonal migration) and vertical direction (during daily feeding
2109
2110 migration: Roman and McCarthy, 2010), a process particularly important in oligotrophic seas
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2112 (Alleger et al., 2017), like large sectors of the Mediterranean. Finally (literally, after death),
2113
2114 MM becomes a detrital sources of energy and habitat for deep sea whale-fall communities
2115
2116 (Roman et al., 2014; Smith et al., 2015), with paleontological evidence available for the
2117
2118 NWMS (Dominici et al., 2009; Higgs et al., 2012; Baldanza et al., 2013).

2119
2120 Much evidence suggests that a bottom-up control on the structure of NWMS MM community
2121
2122 was exerted by wind-driven upwelling currents, through enhanced oceanic productivity and
2123
2124 concentration of preys. Over geologic time, these factors may have exerted a selection
2125
2126 favoring large size, triggering the Plio-Pleistocene emergence of whale gigantism in several
2127
2128 lineages (Slater et al., 2017). The largest among marine top predators can travel long
2129
2130 distances and cross oceans, but tend to congregate in shallow waters with abundant prey.
2131
2132 Baleen whales, abundant in boreal eutrophic waters (Woodley and Gaskin, 1996), with
2133
2134 population size under the control of food availability (Croll et al., 2005), always require high
2135
2136 prey density for efficient bulk filter feeding (Goldbogen et al., 2011). Six different species of
2137
2138 mysticetes currently foraging in the Southern ocean, among which the largest animals that
2139
2140 have ever lived in world oceans, exploit the high biomass of Antarctic krill, their main food
2141
2142 resource. Great white sharks are abundant in the offshore of California (Jorgensen et al.,
2143
2144 2010), Australia-New Zealand, South Africa, and in the Mediterranean (Bonfil et al., 2005),
2145
2146 clustering in proximity of seal colonies, including monk seals. The distribution in the modern
2147
2148 Mediterranean is no exception to general rule, only in a smaller scale, with large sharks and
2149
2150 marine mammals congregating in productive areas, such as the Strait of Sicily and the
2151
2152 Balearic Archipelago (Tabs. 3, 5), with the second largest animal on earth, the fin whale,
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2161
2162 showing a movement pattern that parallels seasonal variability in available feeding habitat
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2164 (Notarbartolo di Sciara, 2016), contributing to the horizontal transfer of nutrients. Tuscany
2165
2166 faces the Ligurian Sea, where a deep-water upwelling current coming from Southeast
2167
2168 convects nutrients to the water surface, leading to high levels of primary productivity in its
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2170 western sectors, extending westward to the Provençal and Balearic Seas, with spring algal
2171
2172 blooms. These waters host different trophic regimes in an otherwise oligotrophic
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2174 Mediterranean Sea (Lazzari et al., 2012; Melanotte-Rizzoli et al., 2014; Stambler, 2014).
2175
2176 Supporting a conspicuous biomass of zooplankton (Cuzin-Roudy 2011), the Ligurian Sea
2177
2178 sustains large populations of fin whales (*Balaenoptera physalis*) and striped dolphins
2179
2180 (*Stenella coeruleoalba*: Notarbartolo di Sciara et al., 2008). Mediterranean-resident fin
2181
2182 whales have adapted to exploit localised mesoscale hotspots of productivity that are highly
2183
2184 variable in space and time (Notarbartolo di Sciara et al., 2016), feeding behaviors possibly
2185
2186 mediated by the depth of prey and species-specific behaviours, allowing to minimise
2187
2188 competition with other large filter feeders (see Friedlaender et al., 2014). The sperm whale
2189
2190 *Physeter macrocephalus* uses habitat across a range of depths and a specialised diet
2191
2192 (Rendell and Frantzis, 2016), gathering along NWMS steeper slopes, where water currents
2193
2194 allows for higher trophic level biomass (Pirodda et al., 2011). Beaked whales are particularly
2195
2196 abundant in the Ligurian Sea and central Tyrrhenian Sea, preferring submarine canyons at
2197
2198 slope depths (Podestà et al., 2016). The largest among common Mediterranean delphinids,
2199
2200 *Grampus griseus*, is frequent in the Ligurian and Thyrrhenian seas where it forages on
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2202 cephalopods at depths 300-1500, where upwelling currents are most effective (Azzellino et
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2204 al., 2016).
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2209 The NWMS existed as a Liguro-Provençal back-arc oceanic basin since the upper Miocene,
2210
2211 when Sardinia rotated to its present position (Gattacceca et al., 2007), and in coincidence
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2213 with the formation of the hinterland basins here under study (Muttoni et al., 2001), justifying
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2215 the assumption that the modern NWMS trophic regime is a feature that dates back at least
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2222 to the upper Miocene. Consistently, diatomites deposited in Tuscany during the Messinian,
2223
2224 before the salinity crisis (Bossio et al., 1997; Roveri et al., 2014), indicate that high
2225
2226 productivity was a primitive feature of the Ligurian Sea. Paleontological evidences include
2227
2228 the high diversity and abundance of Pliocene MM in FB, the closest to modern upwelling
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2230 areas (Fig. 3), and the association of several MM with “*Turritella* beds”, turritelline
2231
2232 gastropods showing gregarious habit and high abundance in areas of high primary
2233
2234 productivity (Allmon, 1988). Both a comparison with the modern and paleoecologic data
2235
2236 strongly suggest that a wedge of NWMS nutrient-rich waters intersecting the Tuscan shelf
2237
2238 exerted a strong bottom-up control on community structure through mixing and upwelling of
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2240 nutrients, stimulation of phytoplankton blooms, followed by zooplankton increase, while
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2242 nekton and vertebrates tracked plankton concentrations, as is typical of modern upwelling
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2244 systems throughout the world (Polis et al., 1997). High surface primary productivity in the
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2246 study area during the Pliocene would have caused a concentration of detritus-falls,
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2248 supporting a diverse community of deep-sea scavengers.
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2254 7.3 Taphonomic control 2255 2256 2257 2258

2259 Taphonomic data on articulation and completeness of MM specimens are available for large
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2261 mammals, the shark record being formed mainly by isolated teeth collected through
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2263 superficial picking during the years (Cigala Fulgosi et al., 2009), with only a few
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2265 contextualised studies (e.g., Bianucci et al., 2002; Dominici et al., 2009). Our record includes
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2267 several marine mammals with a high degree of articulation (14%) and completeness (27%),
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2269 or with at least cranial and post-cranial elements of the same individual (38%). All articulated
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2271 specimens and the most complete skeletons are associated with shelf mudstones, usually
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2273 forming the HST of the relative depositional sequence (Tab. 2), with two exceptions, one
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2275 associated with delta-front, coarse-grained beds (WCh6-1, Fig. 6), another from outer shelf
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2282 or upper slope sediments (DSi2-1). These data point to a strong environmental control on
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2284 the quality of the MM fossil record, at least concerning articulation and completeness of
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2286 skeletons, very shallow and very deep (bathyal) depths being generally unfavourable to the
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2288 preservation of MM bones (Fig. 9A). To explain these results, hypotheses are based on the
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2290 available data on carcasses of MM in modern marine environments.
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2293 The biostratinomy of lung-breathing marine mammals depends on water depth (Allison et
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2295 al. 1991; Smith et al., 2005). The vast majority of mammals are negatively buoyant and sink
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2297 after death, but in shallow waters the low hydrostatic pressure allows putrefaction gases to
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2299 develop and carcasses to resurface. Skeletons are scavenged (Dicken, 2008) and
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2301 disintegrate while floating, leading to the preferential deposition of isolated bones. At deeper
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2303 settings, where high hydrostatic pressure allows the carcass to lay relatively undisturbed on
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2305 the seafloor, the skeleton becomes only slightly disarticulated after soft tissue removal
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2307 (Reisdorf et al., 2012). The subsequent fate of deep-water, disarticulated skeletons depends
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2309 on the nature of the scavenging fauna and other elements of the whale-fall community, and
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2311 on the time of exposure on the seafloor (Boessenecker et al. 2014). At depths deeper than
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2313 the slope breaks, where sedimentation rate is very low, carcasses are exposed for a long
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2315 time and the skeleton is rapidly disintegrated. Time-series analyses carried out at modern
2316
2317 whale-fall communities at slope depths (range 382-2893 m: Lundsén et al., 2010) suggests
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2319 that carcasses up to 17 m are rapidly degraded, with the deepest whale carcasses
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2321 disappearing after only seven years of exposure on the sea floor. Larger skeletons may
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2323 persist on deeper settings for decades, but if not buried, they also ultimately undergo
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2325 complete destruction. Although environmental forcing triggered by higher temperatures,
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2327 active currents and sediment transport, clearly plays a role, a specialised whale-fall fauna
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2329 rapidly consumes both soft and mineralised tissues. This fauna is characterised by low
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2331 diversity and high abundance of microorganisms, most likely as a result of both
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2333 specialisation to nutrient enrichment and high growth rates. Whale-fall habitats likely
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2342 undergo a temporal microbial succession from primarily heterotrophic to more
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2344 heterotrophic/chemosynthetic metabolisms until the whale biomass is completely exploited
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2346 (Smith et al., 2015). Of all the specialised taxa, bone-eating polychaetes of genus *Osedax*,
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2348 with their soft root-like tissues that erode the bones to access nutrients (Tresguerres et al.,
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2350 2013; Minamoto et al., 2017), are the primary cause of bone disintegration, particularly of
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2352 denser bones (Higgs et al., 2011). Found also at shelf depths, but invariably in low
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2354 abundance (Huusgaard et al., 2012; Higgs et al., 2014b), bone-eating worms occur in high
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2356 numbers in the deep sea (Smith et al., 2015) where they act as biodiversity regulators
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2358 (Alfaro-Lucas et al., 2017). The general paucity of novel taxa on shallow-water whale falls
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2360 suggests that species-rich, specialised whale-fall communities develop only in the food-poor
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2362 deep sea. Accordingly, among new animal species described in the recent literature from
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2364 whale falls, only about 10% have been found on whale remains at depths of less than 260
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2366 m (12 out of 129 new species: Smith et al., 2015). Of all MM investigated so far, only whales
2367
2368 are known to host a whale-fall community, but also carcasses of large elasmobranchs
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2370 undergo rapid destruction at bathyal depths, teeth being all that eventually remains (Higgs
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2372 et al., 2014a; teeth are also lost by sharks during feeding: Pokines and Symes, 2013). As a
2373
2374 consequence, over geological time no large marine vertebrate is expected to be recovered
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2376 at depths greater than the shelf break. On the opposite side, the lack of a biota specialised
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2378 in exploiting large organic falls, coupled with higher rates of deposition in proximity of
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2380 sediment sources, make it more probable that the most articulated and complete whale
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2382 skeletons become part of the fossil record of shelf settings below storm wave base.
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2389 **8. Comparison with other studies**

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2394 The study of sedimentary facies uncovers some environmental factors that directly control
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2396 the taphonomy of large marine vertebrates. Such abiotic drivers include water pressure,
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2402 wave energy and sedimentation rate — three factors summarised by water depth, and
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2404 upwelling, bringing to the surface deep sea nutrients and concentrating preys. The
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2406 taphonomic pathway of large marine carcasses is also driven by biotic factors that change
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2408 in geological time in response to coevolution between bacteria, scavengers and their
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2410 substrates. We now explore the multifaceted nature of MM taphonomy by reviewing
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2412 Mesozoic and Cenozoic studies where sufficient data for stratigraphic paleobiology are
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2414 available.
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2419 8.1 Abiotic factors 2420 2421 2422 2423

2424 According to one of the few previous studies on the sequence stratigraphic distribution of
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2426 MM, Jurassic ichthyosaurs, plesiosaurs, and pliosaurs of the Sundance Seaway, in North
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2428 America, display facies control and are found primarily in offshore mudstone and at
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2430 condensed intervals at the maximum flooding surface, rather than shoreface and estuarine
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2432 sandstone (McMullen et al., 2014). Taphonomic data on Upper Cretaceous marine reptiles
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2434 and large fishes suggest that partially articulated and disarticulated skeletons are associated
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2436 with little biological activity and relatively rapid burial by muddy sediments, deposited in the
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2438 North American seaway during an interval of maximum flooding (Schemisser McKean and
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2440 Gillette, 2015). Upper Cretaceous mosasaur remains are particularly concentrated in fine-
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2442 grained shelf deposits in Europe (Jagt and Jagt-Yazykova, 2016). Complete, partially
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2444 articulated whale skeletons of archaeocetes, together with bones and teeth of sirenians and
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2446 sharks, are abundant in offshore marine flooding surfaces (MFS) in the Priabonian late TST
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2448 of Egypt. In a further parallelism with the Pliocene of Tuscany, Late Eocene well-articulated
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2450 whales are associated with rapidly accumulating shoreface sediments of the FSST,
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2452 comprising “*Turritella* shell beds” (Peters et al., 2009). During the Oligocene, eomysticete
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2454 whale bones were deposited at shelf depth below storm wave base. The occurrence of
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2461 sparse traces attributed to *Osedax* and the association with a glauconitic limestone testify
2462 to the exposure of bones on the seafloor without undergoing complete destruction
2463 (Boessenecker and Fordyce, 2014), in a manner similar to MM at Orciano (see Danise et
2464 al., 2010; Higgs et al., 2012). Burdigalian/Langhian MM recovered in the Antwerpen Sands,
2465 in Belgium (including isolated remains of a baleen whale, several odontocetes and a
2466 pinniped) are fragmented, worn and associated with clayey sandstone rich in glauconite,
2467 suggesting long exposure on the sea-floor (Louwye et al., 2010). Bones are concentrated
2468 at the base of a coarsening-upward succession, on top of shallow marine, coarse-grained
2469 sandstone, suggesting this is a surface of maximum flooding. An association of MM
2470 taxonomically comparable to that here under study is encountered in the Mio-Pliocene of
2471 the Purisima Formation, in Central California. Taphofacies differ in some aspects. The
2472 Pliocene of California yields laterally persistent bonebeds with polished and phosphatised
2473 bones, and abundant phosphate nodules that are absent in Tuscany, indicating times of
2474 higher sediment starvation during transgressive pulses, in an area of much stronger nutrient
2475 content (the California Current system is a northern-hemisphere analogue of the Peruvian
2476 upwelling system, associated with the economically most important fish stocks in the world:
2477 Mann and Lazier, 2006). Shoreface deposits indicate stronger wave energy, and the
2478 preferential absence of molluscs in bonebeds indicates chemical destruction of carbonate
2479 shells (Boessenecker et al., 2014, in a quantitative MM taphonomic study). Episodic
2480 sedimentation, however, causes the preferential preservation of articulated remains in the
2481 Californian offshore as in the Pliocene of NWMS. The late Miocene Pisco Formation in Perù
2482 offers another, more extreme example of MM taphonomy in a eutrophic setting. Here almost
2483 two hundred cetaceans, pinnipeds, and sharks were described in an exceptional state of
2484 preservation (Bianucci et al., 2015), within a monotonous succession of finely laminated
2485 white diatomites (Di Celma et al., 2015), suggesting very high primary productivity in an area
2486 of intense upwelling and volcanic activity. Algal blooms sustained high biomass of apex
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2522 predators (see Marx and Uhen, 2010), triggering at the same time anoxic conditions at the
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2524 seafloor where MM carcasses remained intact (Brand et al., 2004; see also Gioncada et al.,
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2526 2016; Marx et al., 2017, also in offshore paleosettings). Finally, the stratigraphic distribution
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2528 of Pliocene cetaceans in western Emilia (Italy) shows an uneven distribution of findings (N
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2530 = 24, dolphins and baleen whales) and a strong positive correlation with offshore mudstones
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2532 (no findings in shoreface sandstones, rare occurrences in epibathyal mudstones: Freschi
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2534 and Cau, 2016), paralleling the distribution of Tuscan Pliocene MM.
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2539 8.2 Biotic factors 2540 2541 2542 2543

2544 Many reviews of Triassic (Camp, 1980; Hogler, 1992; Motani et al., 2008; Hu et al., 2011;
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2546 Liu et al., 2014) and Early Jurassic marine reptiles (Benton and Taylor, 1984) report mostly
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2548 good preservation and a high degree of completeness and articulation of skeletal material.
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2550 This record might be partially controlled by prevailing anoxic or dysoxic conditions in the
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2552 bottom waters of many Mesozoic fossiliferous deposits (e.g., Middle Triassic Besano and
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2554 Guangling Formations, Lower Jurassic Blue Lias and Posidonia Shale Formations), which
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2556 precluded organism activity within the sediment, and prevented predation or scavenging of
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2558 the carcasses on the sea bottom (Beardmore and Furrer, 2016). Evidence of advanced
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2560 levels of disarticulation or bone degradation (Martill, 1985; sauropterygians, crocodylians,
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2562 ichthyosaurs and fishes from the Middle Jurassic Oxford Clay Formation), is mostly
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2564 attributed to physical factors (e.g., weathering on the sea floor). Up to the early-Late
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2566 Cretaceous, biological activity is testified by circumstantial evidence of scavenging
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2568 (*Hybodus* teeth associated with marine reptile skeletons, Martill et al., 1994), and by the
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2570 more common occurrence of microbial mats, grazers and encrusters (Martill, 1987; Meyer,
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2572 2011; Danise et al., 2014; Reolid et al., 2015), but lack traces of bone-eating worms and
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2574 sulphophilic fauna typical of modern whale falls. The siboglinid *Osedax* is an evolutionary
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2582 novelty in possessing a root system that hosts heterotrophic mutualists and secretes bone-
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2584 dissolving acids (Tresguerres et al., 2013; Miyamoto et al., 2017), and an ecosystem
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2586 engineer (Alfaro-Lucas et al., 2017). Genus *Osedax* is today associated with whale falls
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2588 worldwide (Taboada et al., 2015), but its impact on MM has changed in time. The oldest
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2590 trace fossils attributable to a bone-eating fauna is found on early-Late Cretaceous plesiosaur
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2592 and sea turtle bones (about 100 Ma: Danise and Higgs, 2015). Time estimates suggest that
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2594 *Osedax* diverged from other siboglinids in the Middle Cretaceous (around 108 Ma: Taboada
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2596 et al., 2015). However, if the bone-eating worm lives also on the bones of birds and terrestrial
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2598 mammals (Rouse et al., 2011), its global nature and high species diversity in modern oceans
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2600 suggest that whale falls, as complex and species-rich habitats, have been the most
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2602 important biodiversity generators (Higgs et al., 2014b; Smith et al., 2015). And although the
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2604 first appearance of *Osedax* is concomitant with the occurrence of large marine reptiles and
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2606 teleost fishes in the oceans, long before whale evolution, and although their distribution is
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2608 not limited to large carcasses (Pyenson and Haas, 2007), the radiation of ocean-going
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2610 mysticetes at the Oligocene onset of the Antarctic Circumpolar Current (Fordyce, 2003)
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2612 clearly increased available substrata worldwide. The steady increase of cetacean size
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2614 during the Neogene, with a dramatic pulse in the last five million years, when Neoceti
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2616 surpassed 10 m length and reached 30 m in the Pleistocene (Lambert et al., 2010; Slater et
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2618 al., 2017), would have thus triggered a second and more massive radiation of bone-eating
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2620 worms (Kiel and Goedert, 2006). Consistently with this hypothesis, the preferential
2621
2622 distribution of modern *Osedax* in high latitude settings worldwide (Taboada et al., 2015)
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2624 suggests that biodiversity hotspots coincide with the feeding grounds of larger cetaceans.
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2626 Other bone-eaters of modern deep water whale-fall ecosystem belong to the group of
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2628 abyssochrysid snails, with fossils found on Late Cretaceous plesiosaur (Kaim et al. 2008)
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2630 and sea turtle bones (within a chemosynthesis-based association: Jenkins et al., 2017).
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2632 Modern abyssochrysid whalebone-eaters of genus *Rubyspira*, hosting a specific and
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2642 exclusive microbiome (Aronson et al., 2017), split during the upper Eocene/lower Oligocene
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2644 (Johnson et al., 2010). Species of *Rubyspira* benefited too from the radiation of ocean-going
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2646 whales. Although scanty, available evidence on the geological history of bone-eaters thus
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2648 makes the ephemeral nature of large carcasses in modern deep seas — and their absence
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2650 in bathyal deposits of the Pliocene of NWMS — a larger-than-life model for the Mesozoic
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2652 and the early Paleogene.
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2657 **9. Conclusions**

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2662 1) Sedimentary facies in the Pliocene of Tuscany are vertically stacked to form small-scale
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2664 depositional sequences particularly in the upper half, Piacenzian part of the succession,
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2666 with laterally-continuous shell beds marking transgressive surfaces and intervals of
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2668 maximum flooding. Small-scale sedimentary sequences are stacked to form six major,
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2670 unconformity-bounded stratigraphic units (synthems) of regional extension, forming a
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2672 high-resolution framework to study the chronostratigraphic distribution of marine
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2674 megafauna (MM).
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2677 2) Benthic biotopes, identified through a quantitative study of a large mollusc dataset, can
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2679 be arranged to form an ideal onshore-offshore, bathymetric gradient, connecting
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2681 terrestrial environments with deep sea epibathyal bottoms, consistently with the
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2683 distribution of sedimentary facies. MM remains and shell beds are present in all marine
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2685 paleoenvironments, but their distribution is uneven. The fossil record of large vertebrates,
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2687 including marine mammals (abundance data) and sharks (presence-absence data), is
2688
2689 particularly rich in sediments deposited between storm wave base and shelf break,
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2691 moderately rich in shoreface sediments, very poor in epibathyal sediments.
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2693 Paleobathymetric estimates suggest that a peak of abundance of better preserved
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2695 skeletons occurs around 100 m depth, within the 30-300 m range.
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- 3) Species-richness 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 boundary.
 - 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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2764 knowledge of fossiliferous Pliocene outcrops of Tuscany.
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4785 **Figure and table captions:**
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4789 Fig. 1 - Location of sedimentary logs within the largest Pliocene basins of Tuscany. Fine
4790 Basin (FB): Pagliana (1), Pieve Vecchia (2) and Orciano Pisano (3). Volterra-Era Basin
4791 (VEB): Parlascio (4), Lajatico (5), Fabbrica (6) and Volterra (7). Era Basin (EB): San Lorenzo
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4793 (8), La Serra (9), Poggio al lupo (10), San Maiano (11), Canneto (12), Casenuove (13),
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4802 Castelfiorentino (14), Fiano (15) and San Gimignano (16). Orcia-Ombrone Basin: Arcille (17)
4803 and Poggio alle Mura (18). Siena-Radicofani Basin (SRB): Siena (19), Monteaperto (20),
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4805 Castelnovo Berardenga (21), Radicofani (22) and Fastelli (23). Chiana Basin (CB):
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4807 Sinalunga (24), Cetona (25) and Allerona (26).
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4813 Fig. 2 - Pliocene stratigraphy of Tuscany, see Fig. 1 for the location of numbered sections.
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4815 All logs measured and described by the authors, except Volterra (log 7: Bianucci et al. 1998),
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4817 Arcille (log 17: Tinelli et al., 2012; Tinelli, 2013), Siena (log 19: Bianucci et al., 2001),
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4819 Monteaperto (log 20: Martini et al., 2011), Castelnovo Berardenga (log 21: Martini et al.,
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4821 2016) and Radicofani (log 22: Ghinassi and Lazzarotto, 2005). Chronostratigraphy of
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4823 localities 25 (Poltriciano, Cetona: Capellini, 1883) and 26 (Allerona: Danise, 2010) are
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4825 unknown. Correlation between sections is also shown as boundaries of planktonic
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4827 foraminifera biozones (dashed lines), following the scheme of Sprovieri (1992), based on
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4829 available biostratigraphic studies for each basin (see main text for relevant references).
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4835 Fig. 3 - Abundance of fossil MM records in major museums of Tuscany, distributed by locality
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4837 of provenance. Each record ranges from a single fragment or tooth, to articulated, nearly
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4839 complete skeleton. A: masticates and odontocetes; B: large sharks; C: sirenians — scuba
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4841 diver for scale in each figure. Symbols for basins as in Fig. 1.
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4846 Fig. 4 - Detailed sedimentary logs measured at three localities, representing three different
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4848 stratigraphic contexts for the large marine vertebrate fossil record of the Tuscan Pliocene.
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4850 The succession at Orciano Pisano is included in synthems S3-S4 of FB, at Arcille-Poggio
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4852 alle Mura-Camigliano in synthem S2 of OOB, at Sinalunga in synthem S6 of CB. See Figs.1-
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4854 2 for the location of the numbered localities and references in the main text for facies
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4862 analysis and sequence stratigraphy of synthem S5. Arcille log from Tinelli et al., 2012, and
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4864 Tinelli, 2013.
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4868 Fig. 5 - Taphonomy of large marine vertebrates at Poggio alle Mura (Figs. 5A-5D) and Arcille
4869 (Fig. 5E, see Fig. 4 for the sequence stratigraphic and sedimentary context; plan view of the
4870 sirenian skeleton is modified from Tinelli et al., 2012), synthem S2. A: Plan view of the
4871 Poggio alle Mura undetermined balaenopterid. Parts of the skeleton are quasi-articulated,
4872 others are scattered, but not far from the original position. B: Quasi-articulated vertebrae of
4873 the same specimen, lying on top of a *Haustator* shell bed. C: Side view of a vertebra on top
4874 of the densely-packed shell bed. D. Detail of the shell bed, in top view. The turritelline
4875 gastropod *Haustator vermicularis* is visible in the upper left, a large fragment of wood in the
4876 lower right, with the inchnofossil *Teredolithes* produced by wood-dwelling teredinid bivalves,
4877 in the centre of the photograph. E: Plan view of one of the Arcille sirenian specimens of
4878 *Metaxitherium appenninicum*. Same scale as in 5A, the arrows points to the North.
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4894 Fig. 6 - Taphonomy of a 10m-long, undetermined balaenopterid at Orciano Pisano (see Fig.
4895 4 for the sequence stratigraphic and sedimentary context), synthem 4. A: Planimetry of the
4896 quasi-articulated and nearly complete skeleton. B: Detail of the central part of the skeleton
4897 in the field. The cortex layer of vertebrae and flipper bones is badly consumed, whereas
4898 some of the costae are still pristine. C: Lateral view of a turritellid shell bed, below, and the
4899 surface where the whale skeleton lied (dashed line), about 15 cm above the shell bed. The
4900 sediment is a very fine-grained silty sand, completely bioturbated (large vertical burrows are
4901 visible). D: Top view detail of the turritellid shell bed. At the center a valve of *Yoldia nitida*,
4902 surrounded by a few specimens of the turritellid *Archimediella spirata*.
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4922 Fig. 7 - Taphonomy of an incomplete, undetermined mystecete at Castel San Gimignano,
4923 synthem 4, comprising articulated torso elements. A: Planimetry of the articulated elements.
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4925 B: Detail of one of the limbs in the field (trowel for scale = 22 cm): humerus, radius and ulna
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4927 are in anatomical relationship; the cortex layer is well preserved, suggesting quick burial of
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4929 the carcass. C: Bones of the chest region; on the background the massive sandstone
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4931 associated with the fossil whale. Articulated shoreface pectinid bivalves (*Pecten*
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4933 *flabelliformis*) were interspersed in the sandstone (photographs by Fabio Cozzini, 1985).
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4939 Fig. 8 - Taphonomy of a 5m-long, undetermined balaenopterid at Sinalunga (see Fig. 4 for
4940 a tentative sequence stratigraphic interpretation), synthem 6. A: Oblique view of the fully
4941 articulated skeleton lying in a gravelly sandstone, stratified in the lower part, massive in the
4942 upper. Vertebrae are tightly connected as if in life. B: Plan view of the flipper, with carpals,
4943 metacarpals and phalanges in perfect anatomical connection. C: The gravelly sandstone
4944 lies above a bioturbated muddy sandstone, with vertical burrows (*Ophiomorpha*). D: The
4945 lower part of the unit with the whale skeleton is formed by three fining-upward beds. Each
4946 bed grades from gravel to medium-grained sand. Articulated and empty shoreface bivalves
4947 (e.g., *Callista chione*), not in life position, are interspersed with the coarse gravel.
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4960 Fig. 9 - Quantitative analysis of the facies type and sequence stratigraphic distribution of
4961 large marine vertebrates, Pliocene of Tuscany (N = 39, see Tab. 2). A: The vast majority of
4962 cases (77%) are associated with fine-grained muddy sediments of the shelf, a few are found
4963 in deltaic coarse-grained strata. B: Most MM (69%) is found in highstand deposits, a few in
4964 proximity of the maximum flooding interval, or in transgressive deposits.
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4973 Fig. 10 - NMDS ordination of bulk samples (N = 72, see Fig. 2 for their stratigraphic position),
4974 based on the distribution of standardised abundances of 329 mollusc species (further
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4982 explanation on multivariate techniques in the main text). A: Samples are subdivided based
4983 on the associated sedimentary facies types (F2-F5 in Tab. 1). The main axis ordinales
4984 samples along a paleodepth gradient, from shallowest to deepest, moving from the left to
4985 the right side of the bivariate plot. B: Same ordination, with an estimate of absolute
4986 paleodepth of each sample based on score along the main axis and calibrated through the
4987 average modern depth distribution of 23 extant species characterising the Pliocene dataset
4988 (abundance > 0.15%, see text; regression logarithmic curve in the inset). Vertebrates
4989 recovered in proximity of some of the samples (N = 13) are plotted on the diagram,
4990 confirming that, on average, the MM fossil record is concentrated on the open shelf at an
4991 estimated depth of 30-300 m (M = sirenians; S = sharks; P = pinnipeds; W = whales).
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5006 Fig. 11 - Occupancy of trophic levels by Pliocene marine mammals and sharks in the north-
5007 western Mediterranean, expressed by number of species per trophic level (see Tabs 3, 5 for
5008 explanation and references). This figure, summing up data for the whole epoch, spanning
5009 circa 2,8 My, closely matches the association found in one single synthem S4, of much
5010 shorter duration (mid-Piacenzian, 3-4 hundred thousand years).
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5018 Tab. 1 - Sedimentary facies types.
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5022 Tab. 2 - Stratigraphic, taphonomic and paleoenvironmental framework for Pliocene marine
5023 mammals recovered in Tuscany, with abundance data (N = 64). A: Articulated and quasi-
5024 articulated skeleton; C: Complete and quasi-complete skeleton; C+PC: Cranial and post-
5025 cranial remains.
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5033 Tab. 3 - Paleoecology of Pliocene large mammals and ecology of modern NWMS
5034 analogues.
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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

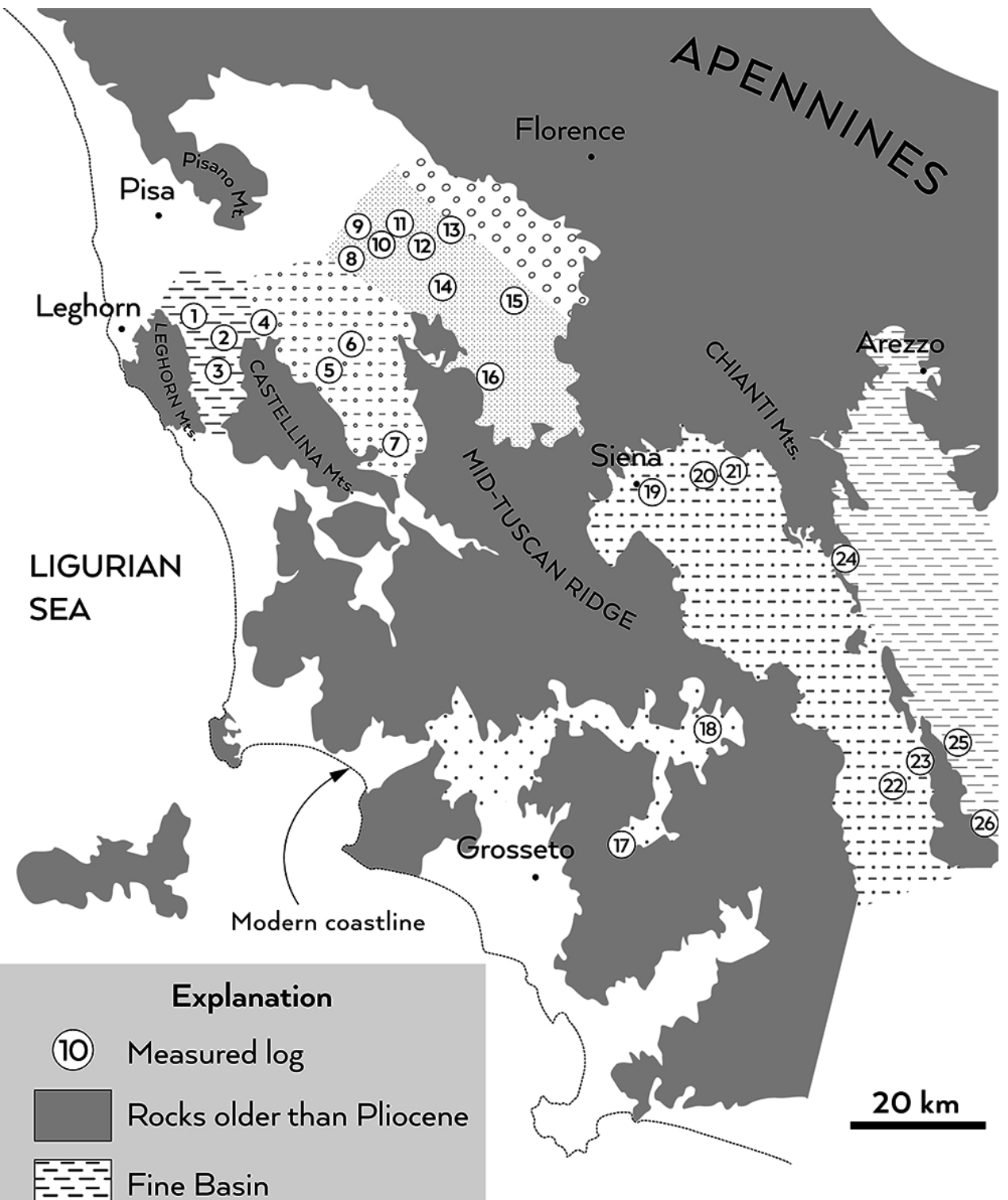
Fig. S1 - Dendrogram resulting from cluster analysis of a dataset of 336 species distributed in 72 samples (standardised abundance, square-root transformed, Bray-Curtis similarity).

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.



Explanation

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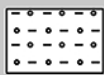
Measured log



Rocks older than Pliocene



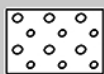
Fine Basin



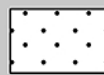
Volterra-Era Basin



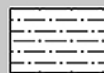
Elsa Basin



Pesa Basin



Ombrone-Orcia Basin



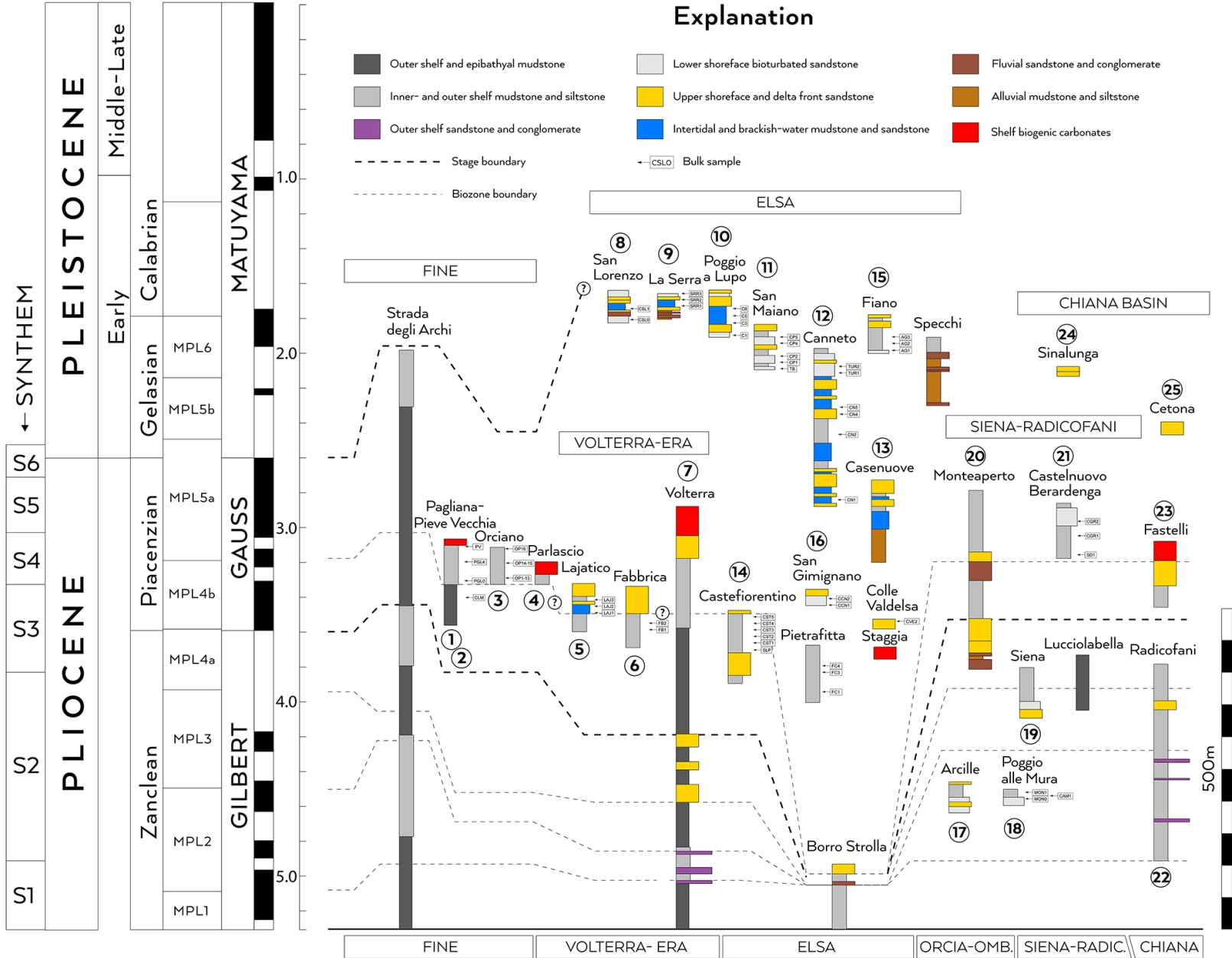
Siena-Radicofani Basin

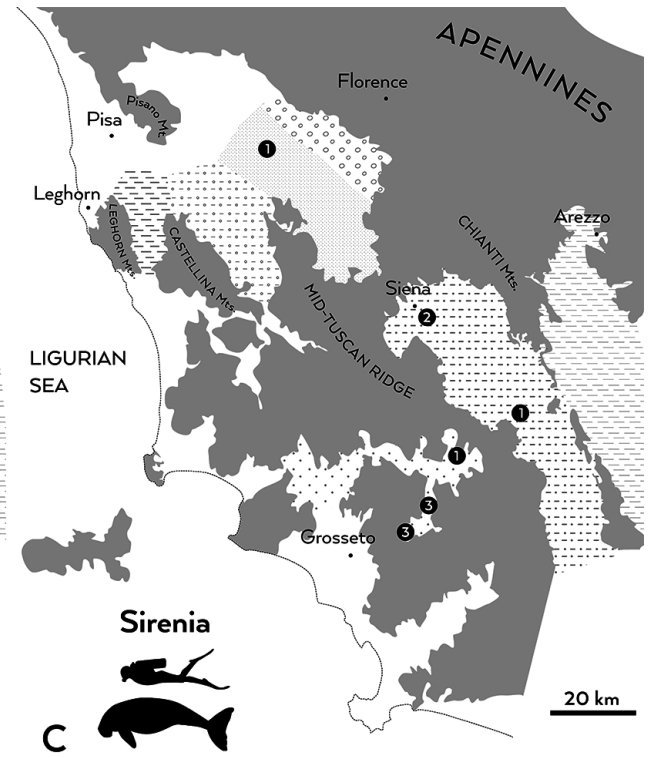
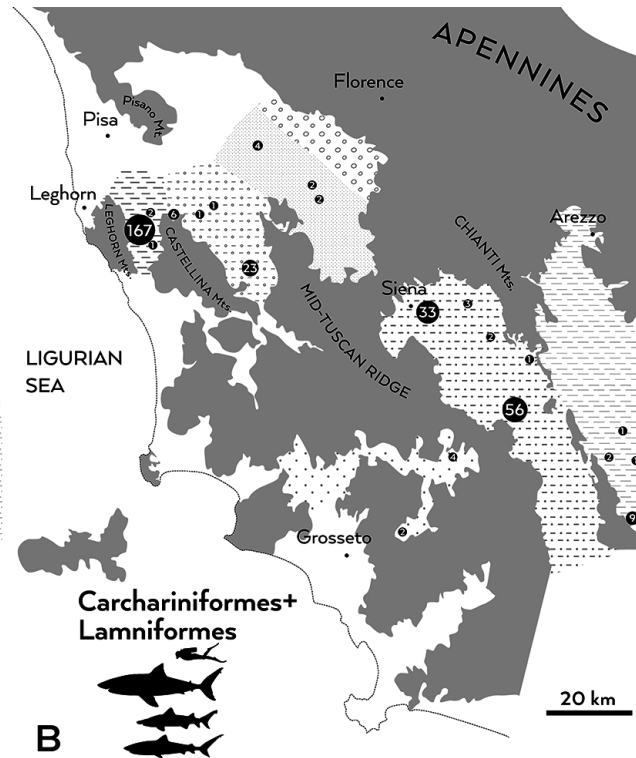
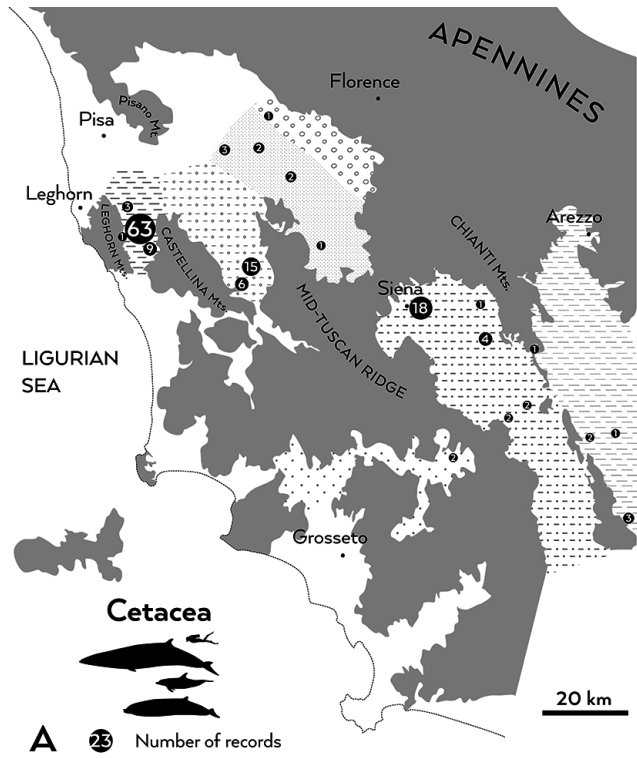


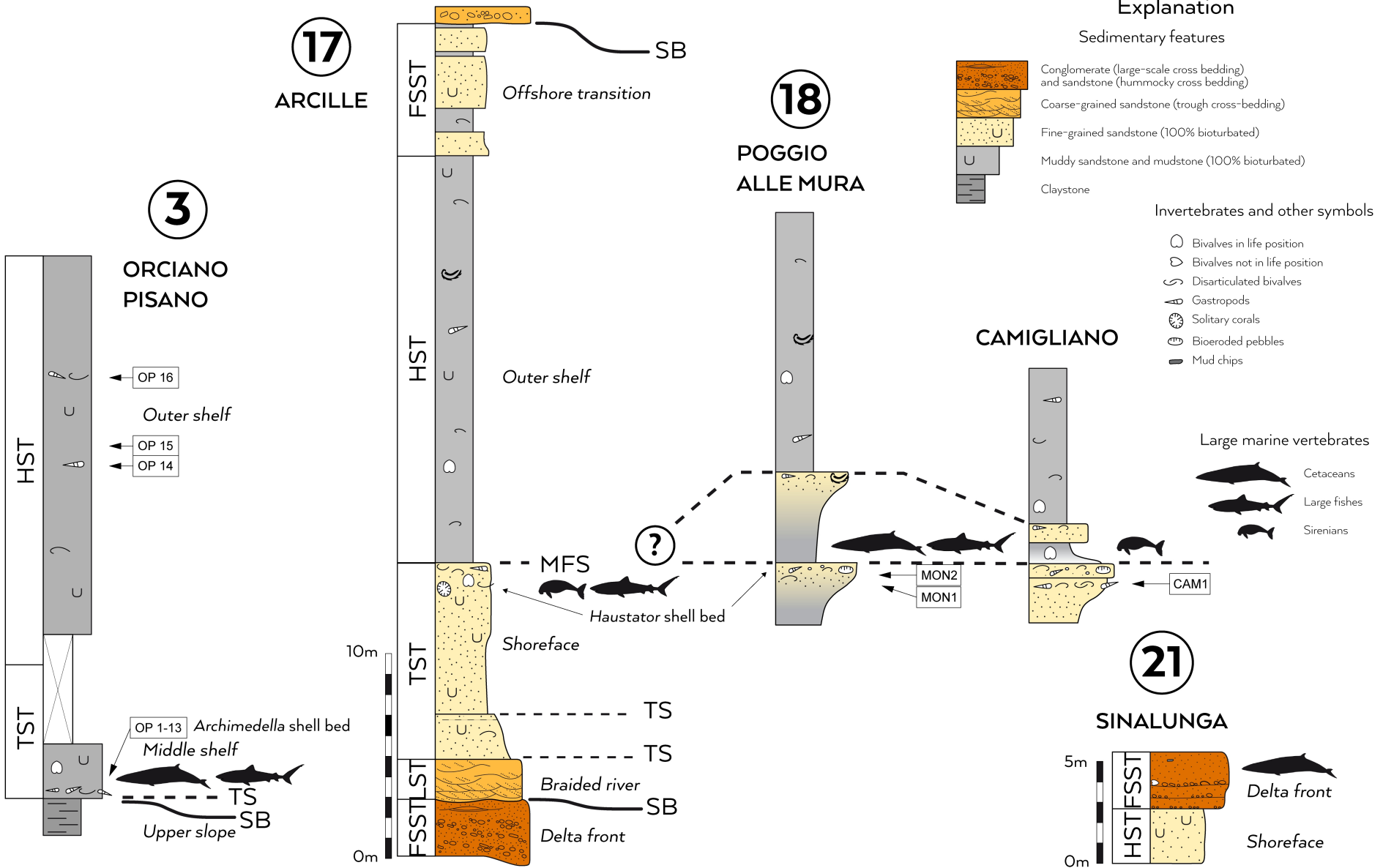
Chiana Basin

Explanation

- Outer shelf and epibathyal mudstone
 - Lower shoreface bioturbated sandstone
 - Fluvial sandstone and conglomerate
 - Inner- and outer shelf mudstone and siltstone
 - Upper shoreface and delta front sandstone
 - Alluvial mudstone and siltstone
 - Outer shelf sandstone and conglomerate
 - Intertidal and brackish-water mudstone and sandstone
 - Shelf biogenic carbonates
- Stage boundary
 Biozone boundary
CSLO Bulk sample







17
ARCILLE

3

ORCIANO PISANO

OP 16
OP 15
OP 14

Outer shelf

OP 1-13 Archimedeella shell bed
Middle shelf

Upper slope

SB
Offshore transition

18

POGGIO ALLE MURA

FSST
HST
Outer shelf

MFS
Haustator shell bed

10m
0m
TST
Shoreface
TS
Braided river
SB
Delta front

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

CAMIGLIANO

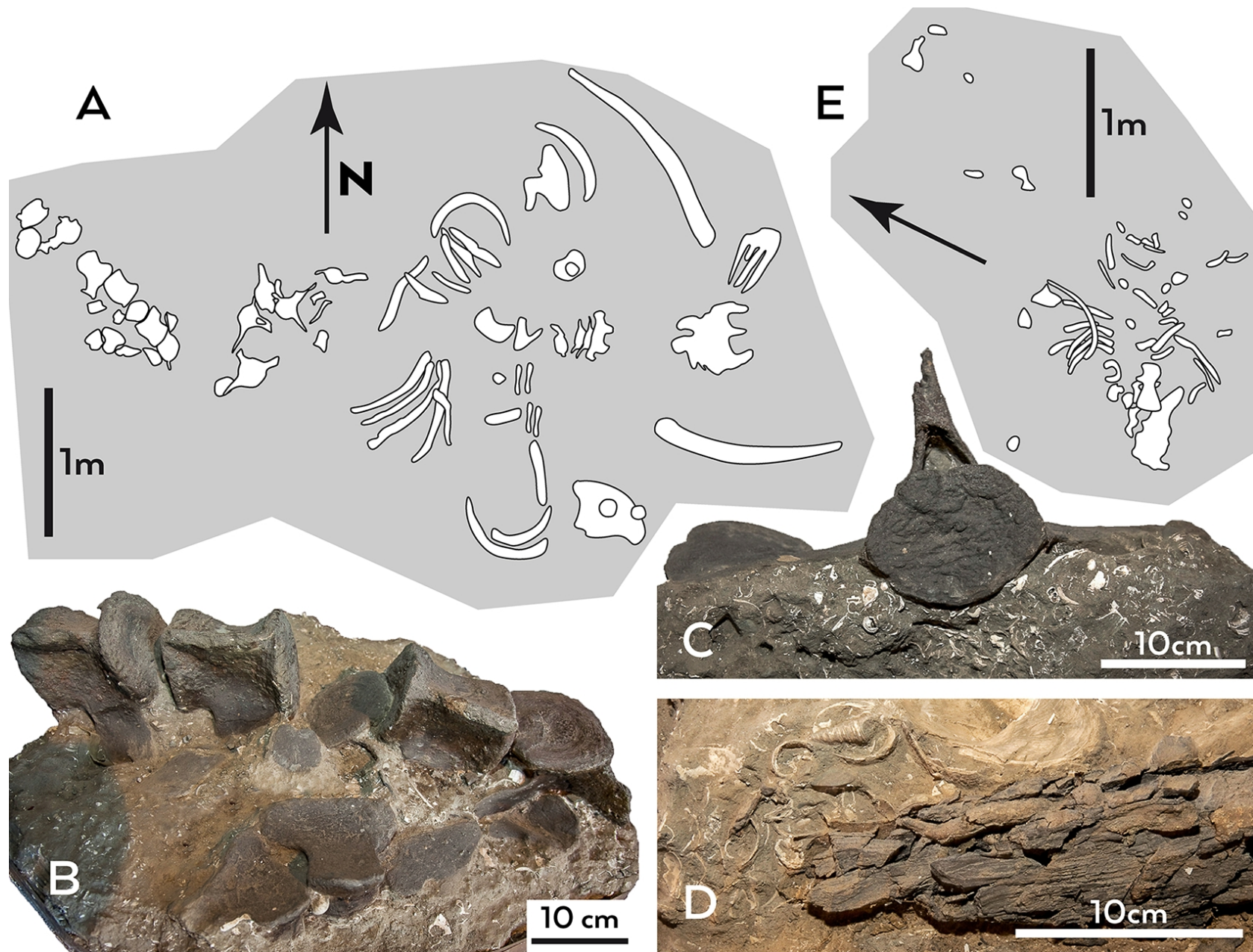
MON2
MON1

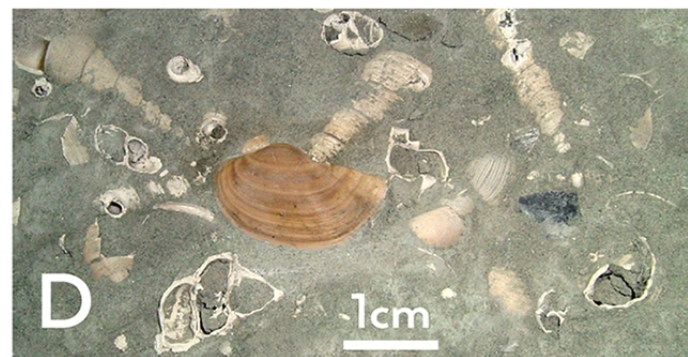
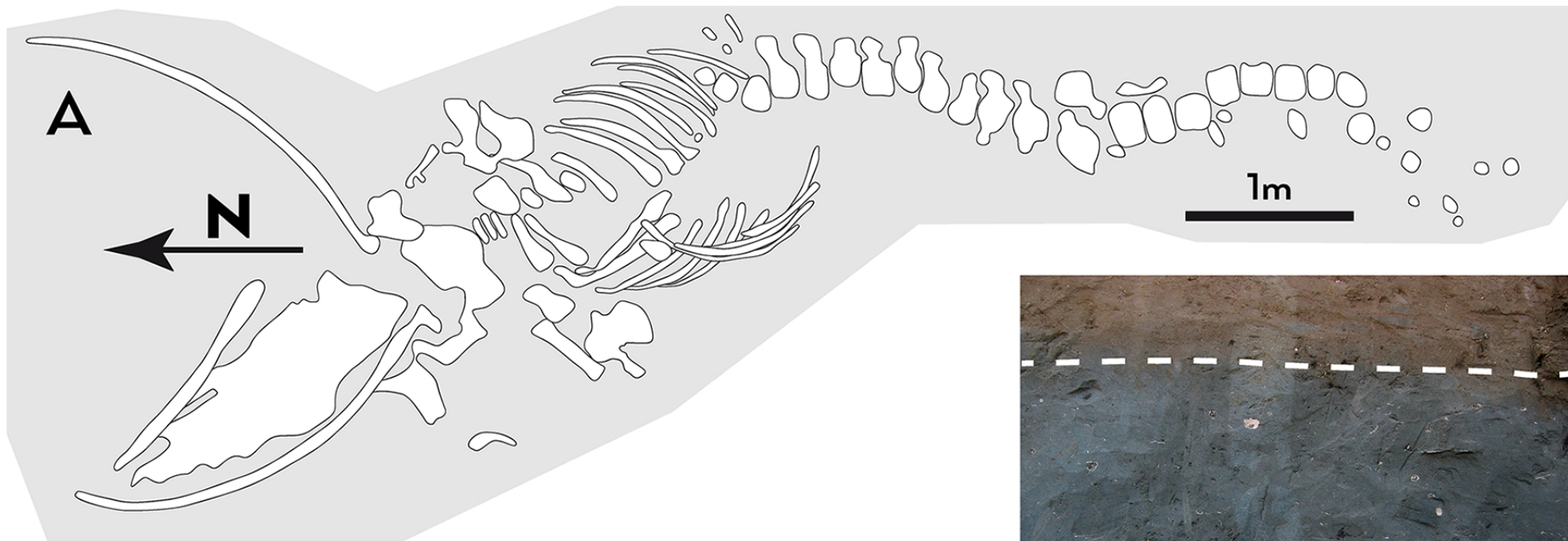
CAM1

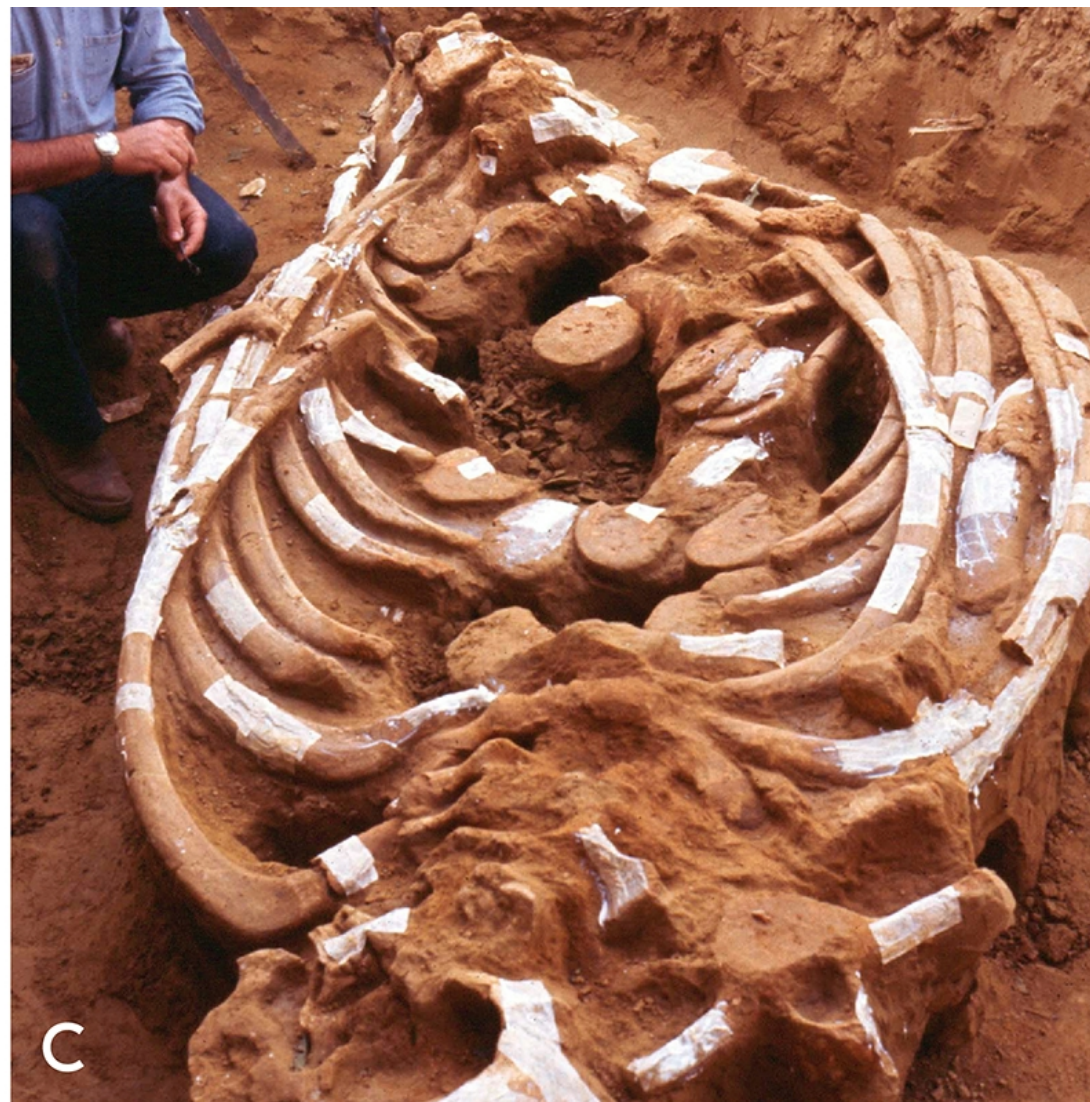
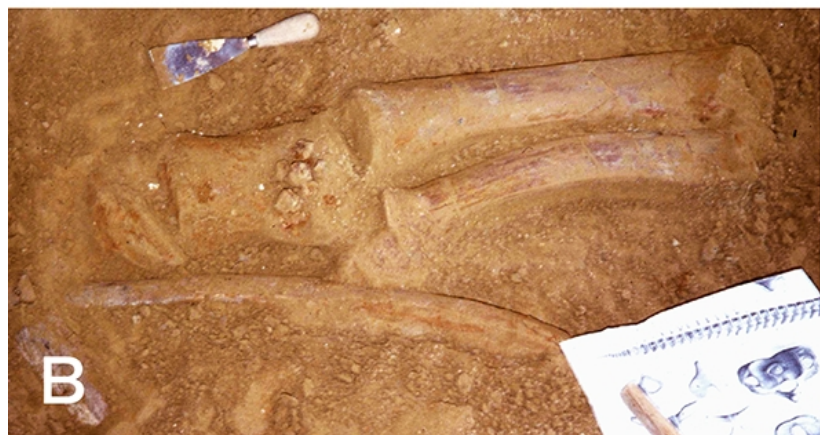
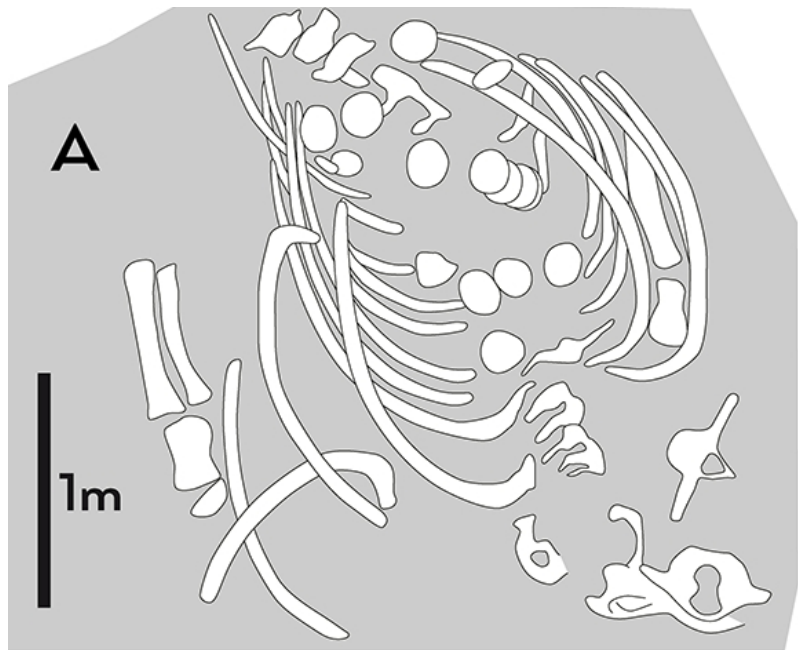
21

SINALUNGA

5m
0m
Delta front
Shoreface

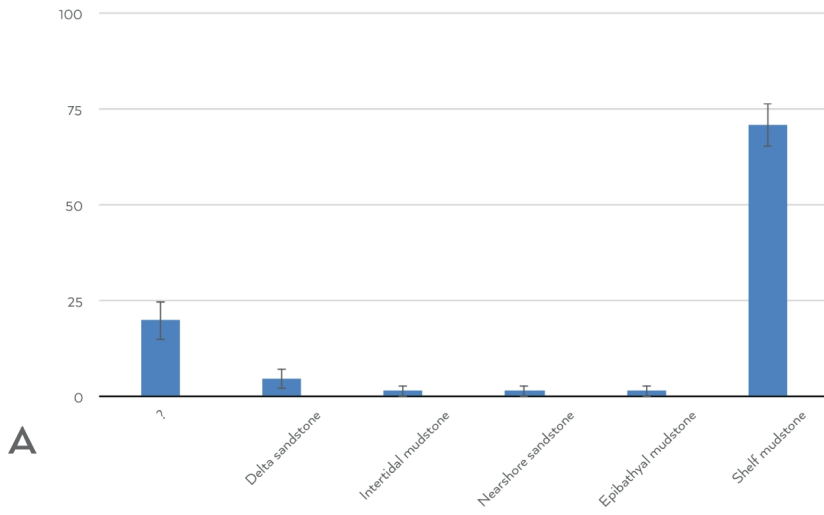




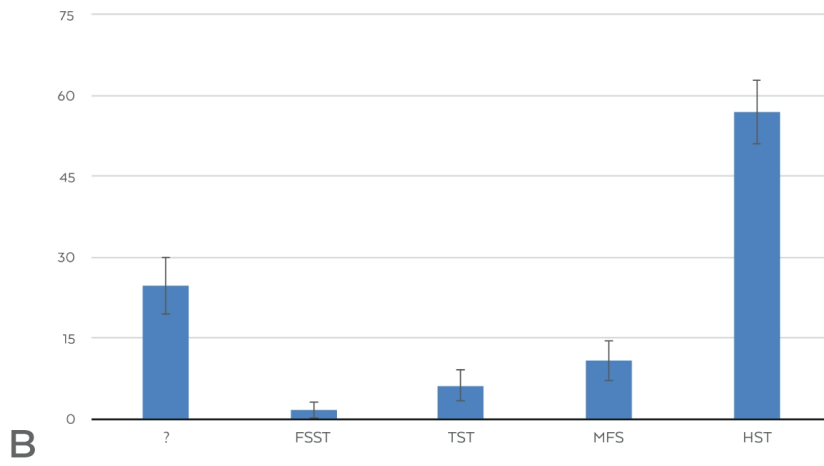




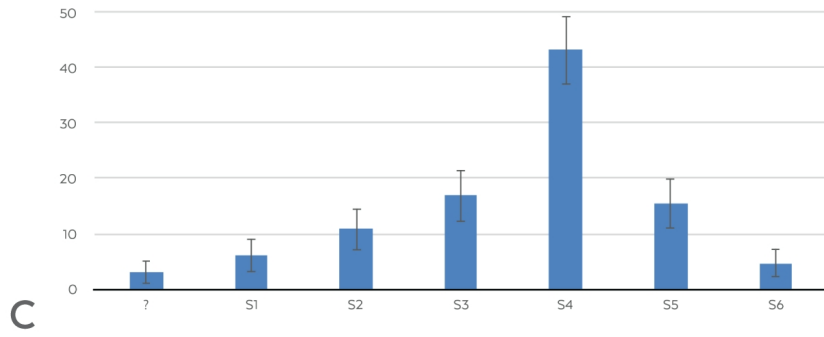
Marine mammal frequency per facies type (%)



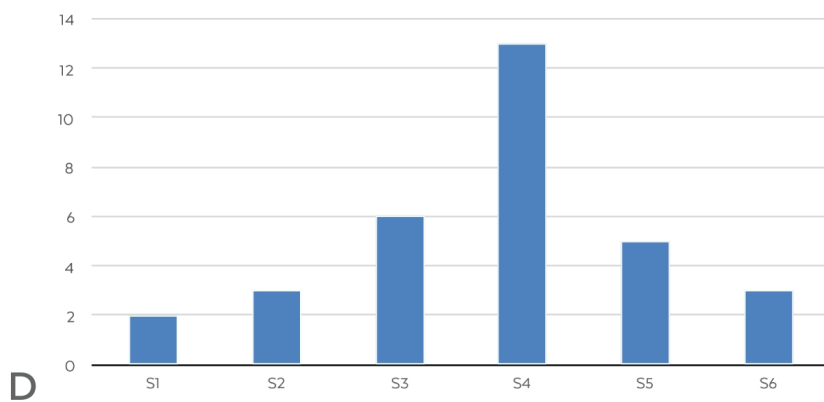
Marine mammal frequency per systems tract (%)



Marine mammal frequency per synthem (%)

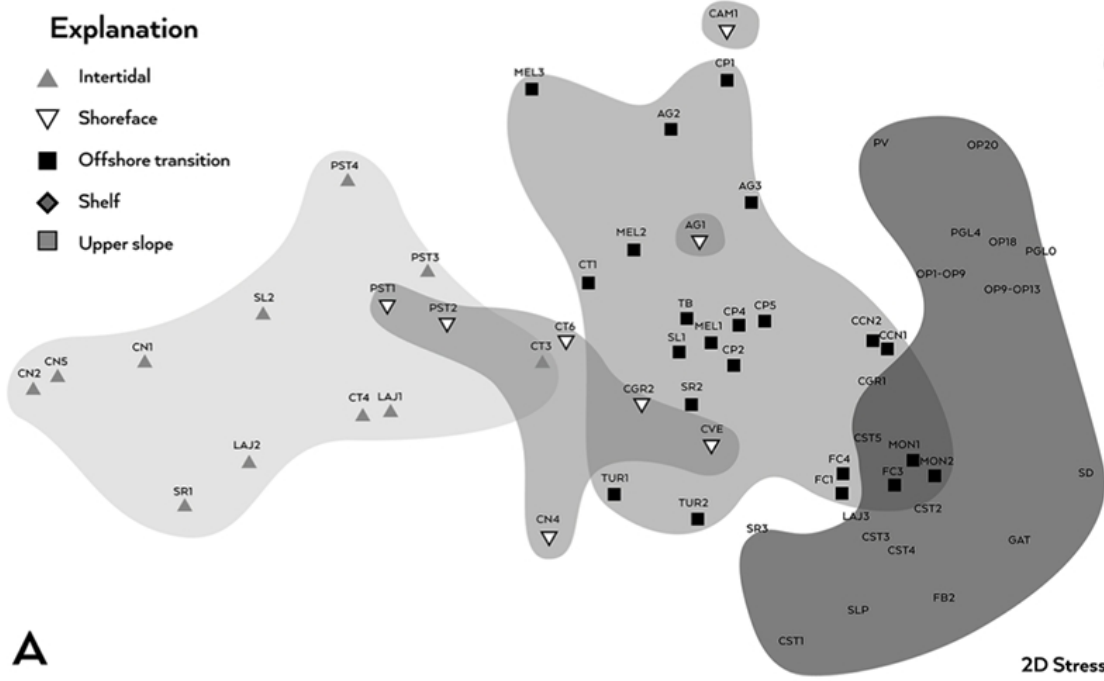


Marine mammal specie richness per synthem

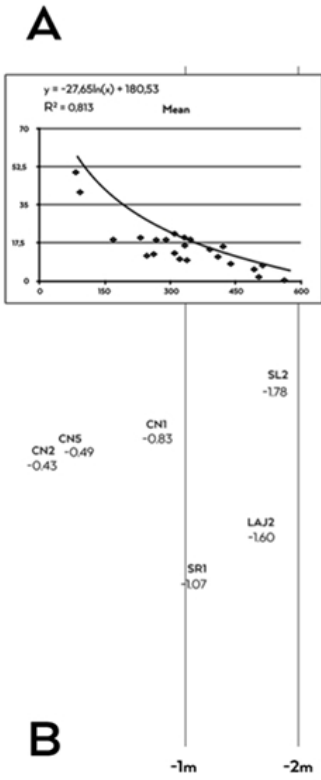


Explanation

- ▲ Intertidal
- ▽ Shoreface
- Offshore transition
- ◆ Shelf
- Upper slope

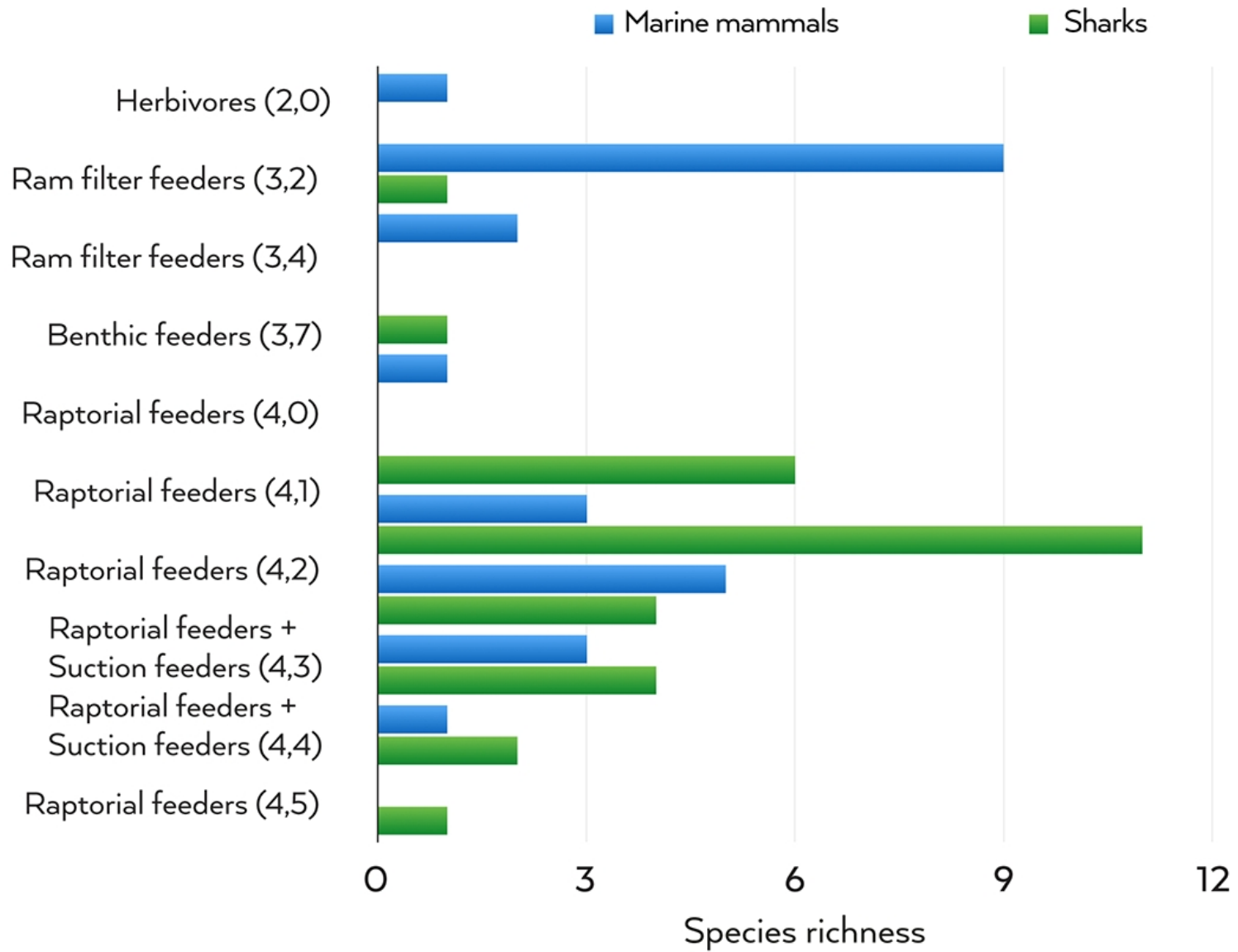


2D Stress: 0,17



B

-1m -2m -3m -10m -20m -30m -100m -200m -300m



Explanation

