Biological Invasions

The Chronicles of a small invader: the Canal, the Core and the Tsunami

--Manuscript Draft--

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Abstract:	Information on early invasion stages, whether successful or not, is often lacking because most invaders are only discovered once they have become abundant enough to be casually detected or have caused appreciable changes to the recipient environment. Moreover, when newcomers fail to establish self-sustaining populations, they are often not even documented; likewise the cause(s) of the failure remains unknown in most cases. Here we report for the first time a probable failed early invasion, caused by an unpredictable geological event, that was detected from two sediment records radiometrically dated through 210Pb chronology. The cores, collected from Marsamxett Harbour in Malta (Central Mediterranean), reveal a continuous record for at least the last 110 years. Both cores contain towards the bottom (dated to the beginning of the 20th century) the highly invasive Lessepsian

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	immigrant benthic foraminifer Amphistegina lobifera Larsen 1976, demonstrating that it was present in this region long before it was first recognized in the Mediterranean. It then abruptly disappeared from the cores. We document that the disappearance may have been triggered by the 1908 Messina earthquake, with a resulting tsunami wave that reached Marsamxett Harbour and deposited over 20 cm of sediment. This event suddenly buried the sea-bottom, destroying the existing benthic community and damaging the seagrass Posidonia oceanica meadow. Today, A. lobifera is abundant along the Maltese coast, likely as a result of re-invasion in the 1940s, yet followed by a long detection lag time until it was first found in 2006.
Response to Reviewers:	Reviewer #1: BINV-D-22-00247 The Chronicles of a small invader: the Canal, the Core and the Tsunami Recommendation: Minor revisions Mancin et al. provide a most interesting case of the apparent failed early invasion of a marine foraminifer from Malta. Using paired sediment cores from relatively shallow depths, they have reconstructed the timeline of invasion of A. lobifera and suggest that the species could have been introduced in the Mediterranean long before it was detected. First of all, this is way cool. What an inventive way to look at biological invasions! The manuscript is well written, and I only have a few comments related to editing/grammar (see below). I do have two larger suggestions/questions, however. REPLY: thank you for your appreciation to our multidisciplinary approach, and for the careful linguistic check. (1) The flow of the manuscript is disrupted, in my opinion, by making 1.1 its own section. It may read better by having this section before Line 20 on Page 4? Otherwise, it just ends on Line 1 on page 6 and I've forgotten what you were doing. REPLY: We agree with this comment and moved the entire section at the beginning of Discussion. (2) Figure 4, first graph of A. lobifera. I feel like this is THE graph for this paper, but it is really hard to see the lines for the cores at the deeper depths. I wonder if it would be a better idea to pull this one graph out and make it large, like you did for figure 3 (which in my opinion, it not THE graph). In particular, I was confused by these sections in the paper: "The non-indigenous species Amphistegina lobifera showed the same distribution pattern in both cores, thus indicating that the collected data are well replicated (Fig. 4, Table S4 supplementary data). The species was sporadically present with very low abundances (< 1 specimen per gram of dry sediment - Ng-1) in the lower part of both cores, from cm 40-39 up to cm 30-29 bsf, then it abruptly disappeared (Fig. 4)." In the graph I am viewing, I do not see anything at the lower depths, from cm 40-39 up to cm 30-29 bsf, for CORE19. "The highest occurrence was recorded in CORE19, at cm 29-28bsf." In the graph I am viewing, I do not see any data for CORE19 at cm 29-28bsf. Could this be confused with CORE18? "After an interval of over 10 cm where the species was missing, A. lobifera occurred again in the studied records, respectively, in CORE19 at cm 16-17bsf and in CORE18 at cm 15-14bsf." In the graph I am viewing, it is again very hard to see anything for CORE19 below 15. REPLY: thank you for the suggestion. We have prepared a larger and better defined version of figure 4 (now labelled as Fig. 4-new) reporting the single curve of absolute abundance of A. lobifera down core. We have added some graphic details that make it easier for the reader to observe. Then, we have partially modified old fig. 4 (now fig. 5-modified), removing the curve of A. lobifera and slightly enlarging the other ones. Finally we have renumbered all the other figures. Minor comments Abstract: Line 4 "invaders are only discovered once"; Line 13: "invasion, caused by an…" REPLY: done Introduction: Page 3 line 56: "low probability of having a successful invasion"; Page 4 line 20-30: this sentence is very long and should be divided; Page 4 line 52: "reach the coast,"; Page 5 line 45: remove comma after boulders; Page 5 line 52: add comma after moorings

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REPLY: done

Materials and Methods: Page 6 line 36: respectively in May 2018; Page 7 line 1: sediment cores using the following methodology
REPLY: done

Results: Page 9 Line 5: add comma after core; Page 10 line 18: remove "upwards"; Page 10 line 42: add comma after records; Page 10 line 45: remove comma after abundance; Page 10 line 54: remove comma after occurred; Page 10 line 54: remove parentheses; Page 11 line 23: change was to were
REPLY: done

Discussion: Page 15 line 30: change to accumulated and buried the sea bed; Page 15 line 45: possibility of carrying out further; Page 15 Line 50: However, the current 14C; Page 15 line 52: add comma after 6ky); Page 16 line 1: application of the 14C method is more than unreliable; Page 17 Line 6: environmental mismatches, while others could be due to habitat changes; Page 17 line 16: note that Oahu is in Hawaii; Page 17 Line 25: played a role in its invasion success as well; Page 17 line 32: remove "the case history of"; Page 17 line 42: change "of which" to "that"; Page 17 line 47: Similarly, tsunamis play
REPLY: done

Reviewer #2: The manuscript is a valuable contribution dealing with the invasive historical record of the foraminifer Amphistegina lobifera. In this sense, the manuscript entitled "The chronicles of a small invader: the Canal, the Core and the Tsunami provide novel and valuable information, demonstrating that A. lobifera has been present in the region for a longer period that initially reported. Although this is an interesting finding, the most valuable contribution of the article is related with the invasion failure of the species at an early stage of the colonization process. As the authors highlighted along the manuscript, invasion failure can hypothetically occur for many different reasons, but these events are frequently overlooked. The relevance of identifying failed invasions and their causes, as well as the contribution of this article on this field are exhaustively and accurately discussed by the authors. Therefore, I think that the manuscript deserves to be published in Biological Invasions.
My only major concern about the article is related with some of the highlighted patterns concerning big differences about the upper and lower part of the cores. For example: "In both cores, significant changes in sediment grain-size, porosity and micropaleontological content occurred at around cm 25-24 bsf, dividing the studied records into two distinct parts, a lower and an upper part". These differences are frequently stated along the article and referred to Figure 2, Figure 4 and Figure 7, but patterns are not always clear and such differences (as well as the starting point of such differences) could be subjective. I would suggest the authors to include some additional data in the manuscript to support these statements. Below I provide some specific comments on this matter:
REPLY: Thank you for the comment. To make the sediment patterns clearer we modified figures and text to facilitate pattern recognition by readers.

- Granulometry: It is stated that the lower part mainly consisted of mud and very fine sands and with a coarsening trend in the upper part. Some broad percentages intervals are provided but, due to the high variability, along the COREs. I would suggest adding a simple comparison of the mean data above and below this 25 cm to support your statement.
REPLY: We added the requested data in the text and in a new table showing statistical comparisons between lower and upper core (Table 1). In Fig. 2 (sedimentological data), we also added a grey strip that marks the stratigraphical level where major sedimentological changes occurred. It divides the studied cores in two portions: lower and upper, respectively, and corresponds to the probable top of tsunamiite. The same grey strip has been added in figures reporting micropaleontological data, namely Figs. 4, 5 and 8.

- The similar applied to the abundance of epiphytic foraminifera (both total abundance, different groups according to their motility and some species such as S. orbiculus). In the discussion section it is suggested that abundance of M. miniacea, P. mediterranea and S. orbiculus increased along the rapid burial event but that can not

	be inferred from the data provided in figure 4B. REPLY: In the text we added some quantitative data that can help the reader and a table with statistical comparisons (Table 1). Moreover, as previously anticipated, in Fig. 4 (now Fig. 5) we added a grey strip that marks the stratigraphical level where major micropaleontological changes occurred, along with other details. - Although some patterns of the abundances of mollusc shells along core portions are highlighted, no data are provided. REPLY: Indeed we did not measured molluscs in terms of abundance, but limited our observations to the preservation status of the shells. - Regarding calcareous nannoplankton, a lower total abundance up to cm 27-26 is also highligted, followed by a marked increase (e.g. "The marked and sudden increase of coccolith abundance in the upper portions of both cores, starting from cm 25-26 bsf up to the core top (Fig. 7)… "). Minimum and maximum data are provided but, again, some additional data would be helpful since the high variability observed in Figure 7 makes harder to identify clear patterns. REPLY: Thank you for this suggestion, we modified the text and the figure (now Fig. 8) to make patterns clearer. Title of the article is not much informative. I would suggest highlighting the fact that this article provides evidence of an invasion failure. REPLY: we definitely considered mentioning the 'failed invasion' concept in the title, but since our evidence is limited to Marsamxett harbour and cannot be extended to neighbouring areas, we preferred to provide a more general overview of the manuscript contents in the title, and opted for the current version, in reference of course to "The chronicles of Narnia: The Lion, the Witch and the Wardrobe". Results: "The highest occurrence [of Amphistegina] was recorded in CORE19 AT CM 29-28 bsf". Figure 4A suggests a depper depth (around 30-40). REPLY: The historical records are commonly described by micropaleontologists from bottom to top, following the stratigraphic order. With this purpose, Highest Occurrence (HO) is used to indicate the uppermost level where the species occurs in the record (in this specific case, within the lower portion of the studied cores, it corresponds to cm 29-28 bsf); by contrast Lowest Occurrence (LO) is used to indicate the lowest level where the species occurs in the record, that also corresponds to the deepest level in the core (in this specific case, within the lower portion of the studied cores, it corresponds to cm 39-40 bsf). To avoid confusion, the sentence was deleted. Material and methods last paragraph: "Coccoliths were counted on that area within a number of randomly selected fields of view". Could the authors be more specific about the number of replicates considered. REPLY: we added the number (300) Concerning the characterization of biotic assemblages, I consider that the study design, samples collection and data analysis are correct and, thus the objective of the article are successfully fulfilled. On the other hand, isotope chronology is far away from my area of expertise, so I'm not able to evaluate properly the accuracy of the results obtained and the conclusions derived from them. This is, however, an important aspect of the article, so I expect additional reviewers could check on this topic. REPLY: the same radiometric dating approach has been employed and described more in details in another manuscript already published after peer-review (Guastella et al., 2021). I hope that my comments will be helpful. REPLY: Thank you very much, we think that the manuscript has been much improved after providing quantitative evidence of the differences between upper and lower cores.

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The Chronicles of a small invader: the Canal, the Core and the Tsunami

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Abstract

Information on early invasion stages, whether successful or not, is often lacking because most invaders are only discovered once they have become abundant enough to be casually detected or have caused appreciable changes to the recipient environment. Moreover, when newcomers fail to establish self-sustaining populations, they are often not even documented; likewise the cause(s) of the failure remains unknown in most cases.

Here we report for the first time a probable failed early invasion, caused by an unpredictable geological event, that was detected from two sediment records radiometrically dated through ^{210}Pb chronology. The cores, collected from Marsamxett Harbour in Malta (Central Mediterranean), reveal a continuous record for at least the last 110 years. Both cores contain towards the bottom (dated to the beginning of the 20th century) the highly invasive Lessepsian immigrant benthic foraminifer *Amphistegina lobifera* Larsen 1976, demonstrating that it was present in this region long before it was first recognized in the Mediterranean. It then abruptly disappeared from the cores. We document that the disappearance may have been triggered by the 1908 Messina earthquake, with a resulting tsunami wave that reached Marsamxett Harbour and deposited over 20 cm of sediment. This event suddenly buried the sea-bottom, destroying the existing benthic community and damaging the seagrass *Posidonia oceanica* meadow. Today, *A. lobifera* is abundant along the Maltese coast, likely as a result of re-invasion in the 1940s, yet followed by a long detection lag time until it was first found in 2006.

Keywords

Lag time, alien species, benthic foraminifera, tsunami deposit, 1908 Messina Earthquake, Central Mediterranean

1 INTRODUCTION

During the last several decades, biological invasions have been largely investigated because they represent a serious global environmental problem leading to significant impacts on ecosystem services and the economy (Jeschke & Heger, 2018). Bioinvasions have also attracted the attention of community and ecosystem ecologists relative to how the addition of novel species may alter trophodynamics and resident species' abundances and diversity. Because of this, invasion ecologists have mainly focused on the study of species that have successfully invaded new areas, while relatively less attention has been given to failed invasions and to the causes that determine invasion failure (Miller and Ruiz, 2009; Ings et al., 2010; Zenni & Nuñez, 2013). Invasion failure can occur during any stage of the colonization process (Blackburn et al., 2011), if alien species are not able to survive, reproduce or maintain a sustainable population in the new recipient environment (Zenni & Nuñez, 2013). Many factors have been suggested to drive the success or failure of biological invasions (Zenni & Nuñez, 2013; Jeschke & Heger, 2018). Propagule pressure could be insufficient for a species to survive demographic stochasticity and maintain a population (Simberloff, 2009). Habitat match between source and recipient regions could be inadequate and, consequently, the introduced organisms could find unfavourable environmental conditions for their establishment and reproduction, a concept known as 'abiotic resistance' (Fenoglio et al., 2016; Zhang et al., 2020). Interspecific interactions may also play a role in this phenomenon; introduced organisms may face novel microbial, herbivore or predator communities, competitive regimes or prey species, a concept known as 'biotic resistance' (Levine, 2004; Colautti & Lau, 2015). Opportunistic traits that increase survival and reproduction in the novel environments may promote establishment and proliferation (Garcìa-Ramos & Rodrìguez, 2002; Miller et al., 2007). As a consequence, if the newcomers are either not pre-adapted or not able to adjust to new environmental conditions, they may have a low

probability of having a successful invasion. Genetic bottleneck effects may also play a role in this process (Zenni & Nuñez, 2013). In addition, invasions may fail due to stochastic events, such as volcanic eruptions, fires, freezes, and hurricanes and typhoons that can abruptly change environmental conditions, triggering population extinction.

In most cases, early failed invasions remain unknown, especially when unintentional introductions are concerned (Phillips et al., 2010). However, the identification of failed invasions, as well as the causes that determine failure of an invasion, are fundamental to advance the general understanding of invasion ecology and to potentially support management actions (Carlton, 1996; Zenni & Nuñez, 2013). Similarly, early stages of invasions are often very poorly known, because species receive researchers' attention only after having successfully established in a new area (Mancin et al. 2022). This situation may prevent understanding of the fine-grained timing of initial introduction events and the subsequent early stages of invasion. We report here the discovery of the unexpected early occurrence, in sediment cores dated to the beginning of the 20th century, of a Lessepsian invader, the foraminifer *Amphistegina lobifera* Larsen, 1976, in Malta, Central Mediterranean Sea. This species was previously thought to have first arrived in this region in the mid-1940s (Guastella et al., 2021), albeit not documented as present until 2006 (Yokeş et al., 2007). This benthic foraminifer is a large symbiont-bearing Indo-Pacific species, which entered the eastern Mediterranean after the 1869 opening of the Suez Canal (Prazeres et al. 2020). The bottom of the cores bearing *Amphistegina* specimens correlated with a horizon of the 1908 Messina earthquake and tsunami. Our work provides insights into the invasion history of this species in the Central Mediterranean, driving hypotheses on the possible role of catastrophic geological events in interrupting what eventually may be successful species invasions.

2 MATERIALS AND METHODS

The Sicily Channel, located in the Central Mediterranean basin between Italy and North Africa, is a natural biogeographical corridor for both Lessepsian invaders originating from the Red Sea and warm-water colonizers coming from the Atlantic (Azzurro et al., 2014 and references therein). The channel is characterised by a complex topography formed by several islands (e.g. the Maltese and Pelagie archipelagos and Pantelleria island) and elevated ridges which alternate with deep submarine canyons; this topography controls the modern oceanography and sedimentation (Hassen et al. 2019).

The Maltese islands are centrally located within the Sicily Channel, about 90 km south of Sicily and about 290 km north of the North African coast (Fig. 1a-b). Malta is the largest island of the archipelago covering a surface of about 250 km^2 and with a perimeter of about 197 km mainly formed by rocky shores incised by few natural bays. Two sediment cores (CORE18 and CORE19) were collected, respectively in May 2018 and September 2019, at 16 m and 17 m water depth, close to Manoel island, an islet located within Marsamxett Harbour of Malta (Fig. 1c-d). Thanks to its peculiar location within a narrow creek (Fig. 1d), the sampling site was partly sheltered from the probable direction of the tsunami waves that moved from NE to SW and mostly impacted on the northeastern Maltese coast in 1908.

Criteria adopted for the sampling site selection and methods for grain-size, micropaleontological and radiometric analyses are the same as described in Guastella et al. (2021). Here we describe only the methodologies of the additional investigations performed in the present study. Analyses were carried out on subsamples of the same core level (a total of 91 subsamples, spacing 1 cm).

Porosity was calculated for both sediment cores using the same methodology samples were weighed, oven-dried at 55 °C, and then re-weighed to determine water content. Porosity was calculated from the loss of water between wet and dry sediments according to equations suggested by Berner (1971), assuming a sediment density of 2.6 g cm^{-3} and a water density of 1.034 g cm^{-3}. Grain-size analysis was carried out on samples from CORE19 not previously studied in Guastella et al. (2021).

The foraminiferal content was quantified in 91 samples, also including samples from the lower part of both cores, not previously analysed for the study of Guastella et al. (2021). Foraminiferal specimens (including the target species *A. lobifera*) were determined under a stereomicroscope on the > 63 μm size washed fraction. Quantitative data were collected as number of individuals per gram of dry sediment (N g^{-1}). Epiphitic foraminifera were grouped into four categories (A – D) following Langer (1993): A- sessile (including both encrusting and permanently attached by glycosaminoglycans taxa), B- temporary motile (by swimming on pseudopodial network), C- motile (by using pseudopodia extruded from canal system and multiple apertures), and D- permanently motile (by striding on the apertural face in an upright position). Unpaired *t*-tests were conducted to verify differences between lower core and upper core in terms of sediment composition and foraminiferal abundance.

The calcareous nannoplankton content was analysed using a polarizing light microscope at 1250X magnification on smear slides prepared according to the “drop technique” proposed by Bordiga et al. (2015). This preparation technique is based on the assumption that a known concentration volume of suspension (bulk sediment weigh/mL, 0,005 g/20 mL) is evenly distributed on a known area (corresponding to the cover slip area: 768 mm^2). Coccoliths were counted on that area within 300 randomly selected fields of view (FOV); their absolute abundance was expressed as total number of specimens recorded per mm^2 (N mm^{-2}).

3 RESULTS

3.1 Sedimentological features and porosity

Both cores showed similar sedimentological signatures, thus indicating a good replicability of the collected records (Fig. 2; Tables S1-S2 available on-line as supplementary data). They were characterised by a gradual coarsening upwards trend, starting from about cm 25-24 below sea floor (bsf) up to top (Fig. 2a).

In both records, the lower part (from the bottom up to ~25-24 cm bsf) mainly consisted of fine and very fine sands and mud. Percentages of the fine-grained fractions varied from 53% to 69%, with an average of 63.1% ± 2.7% in CORE18 and from 52% to 74% with an average of 64.9% ± 3.1% in CORE19 (Table 1; for full data see also Table S1, supplementary data). Sediments from this portion were characterised by a grey colour, probably due to the high concentration of reduced organic matter (Fig. 2a). This was inferred from both the smell of hydrogen sulphide present during the core sectioning and sampling and the very high abundance of undecomposed *Posidonia oceanica* remains, mainly rhizoids, well visible to the naked eye (see detail in Fig. 2b). These sediments were also homogeneous, without any evident lamination and gradation and characterised by abundant mollusc shells (often fragmented) and large benthic foraminifera incorporated in the mud.

In the upper parts of both records, from cm 24 bsf up to top, the fine-grained fractions (fine sand + very fine sand + mud) gradually decreased, reaching average percentages of 49.7% ± 8.1% in CORE18 and of 50.6% ± 5.3% in CORE19 (Table 1; for full data see also Table S1, supplementary data). According to the unpaired *t*-test, differences between lower and upper core in terms of fine fraction percentage were statistically significant in both cores; the same

could be observed when considering mud fraction alone (Table 1). In the same core interval, remains of *P. oceanica* rapidly disappeared and mollusc shells became rarer. This core portion also contained abundant iron Fe-oxides, as well shown by both the rust-coloured tube of CORE19 and by the light brown to yellow colour of sediments towards the core top (Fig. 2c).

Porosity curves mirrored sediment grain size curves but with an opposite trend (Fig. 2a; Tab S2 supplementary data): the highest values (0.6 - 0.8) were registered in the lower fine-grained part of both cores, from the bottom up to cm ~25-24 bsf, then porosity progressively decreased upwards.

3.2 ^{210}Pb and ^{137}Cs chronologies

^{210}Pb curves showed the typical activity-depth profile, with higher activities at the core top that rapidly decreased down core, halving within the first 25 cm bfs of the studied records (Fig. 3, Table S3 supplementary data). In this interval, the reconstructed Sediment Accumulation Rate (SAR) was constant, respectively of ~0.20 cm yr^{-1} in CORE18 and 0.22 cm yr^{-1}in CORE19 (scatter plots A and B) indicating a good replicability and reliability of the collected data (Table S3 supplementary data). The derived age model furnished an estimated time interval of ~4.5 years for each centimetre of sediment; thus the collected cores probably recorded at least the last 150 years (Table S3, supplementary data). Unfortunately, no ^{137}Cs was recorded in either core, thus an independent validation through this method was not possible. While the absence of the Chernobyl peak of ^{137}Cs is common in sediments collected in the southern part of the Mediterranean Sea, due to the dispersion pattern of ^{137}Cs fallout that followed the accident, it is surprising to have no signal of nuclear bomb experiments. Nevertheless, the absence of ^{137}Cs in both cores supports the finding that in this area of the

Sicily Channel the ^{137}Cs supply is negligible as also reported by other works (e.g. Hassen et al. 2019).

3.3 Foraminiferal content

The non-indigenous species *Amphistegina lobifera* showed the same distribution pattern in both cores, thus indicating that the collected data are well replicated (Fig. 4, Table S4 supplementary data). Starting from the core bottom, the species was sporadically present with very low abundances (< 1 specimen per gram of dry sediment - Ng^{-1}) in the lower part of both cores, from cm 40-39 up to cm 29-28 bsf, then it abruptly disappeared (Fig. 4). After an interval of over 10 cm where the species was missing, *A. lobifera* occurred again in the studied records, respectively, in CORE19 at cm 17-16bsf and in CORE18 at cm 15-14bsf. In the upper part of both cores, *A. lobifera* was continuously present with an increasing trend of abundance, that became more accentuated from cm 7-6 bsf up to the core top (Fig. 4).

Along both records, the benthic foraminiferal assemblage was abundant, well diversified and preserved (Fig. 5), with a peak of ~2000N g^{-1} at cm 48-47bsf in CORE19 (Fig. 5; for full data see also Table S4, supplementary data). The benthic foraminiferal assemblage was dominated by epiphytic taxa (average values of 1000 Ng^{-1}), that continuously and abundantly occurred along both cores. Other benthic foraminifera, such as the agglutinated species *Textularia pseudorugosa* and *T. pala* and the genus *Ammonia*, were always subordinated (40-70 Ng^{-1}) and did not show any particular distribution patterns along the cores (Fig. 5). Epiphytic foraminifera mainly consisted of permanently motile miliolids (group D of Langer, 1993), with total abundances varying between 250 and 1000 Ng^{-1} in CORE18 and 200 and 800 Ng^{-1}

in CORE19; other epiphytic groups (A-C) had lower abundances, usually < 400 Ng^{-1}. Group A (sessile taxa) was characterised by a decreasing trend of abundance from cm 25-24 bsf up to top. Average absolute abundances changed dramatically from the lower to the upper core, from 141.6 ± 33.5 Ng^{-1} to 85.2 ± 29.3 Ng^{-1} in CORE18, and from 301.5 ± 69.4 Ng^{-1} to 96.2 ± 30.9 Ng^{-1} in CORE19. According to the unpaired *t*-test, between upper and lower core in terms of Group A abundance were statistically significant in both cores (Table 1; for full data see also Table S4, supplementary data). By observing, in fact, the abundance curves of the species belonging to this group (Fig. 5b, Table S4, supplementary data), both *Miniacina miniacea* and *Planorbulina mediterranensis* significantly decreased in abundance (Table 1). *Sorites orbiculus* showed a decreasing abundance trend in the lower part of both records up to cm 25-24 bsf, then, after an interval where abundance was constant (average values around 10 N g^{-1}), it markedly increased (30-40 Ng^{-1}) from cm 7-6 bsf up to top.

Planktonic foraminifera (e.g. *Globigerinoides* spp.) only occurred as very few specimens in some samples in the lower part of the studied cores (Fig. 5). They occurred together with scarce benthic foraminifera, such *as Uvigerina peregrina*, *Reusella spinulosa*, *Bulimina marginata*, *Bolivina variabilis* and *Buccella granulata* (Fig. 6), typical of deeper environments in the Mediterranean Sea (Murray, 2006; Milker et al., 2009) and whose presence is quite unusual at littoral depths (16 and 17 m depth for the studied cores). Reworked foraminifera were sporadically present along the records and consisted exclusively of few Miocene planktonic specimens belonging to the genera *Globigerinoides* (*G. immaturus* and *G. trilobus*) and *Globigerina* supplied by the homonym formation around Marsamxett Harbour.

From the core bottom up to cm 25-24 bsf, the washed residues also contained very abundant remains of *P. oceanica* (Fig. 2b), sometimes with epiphytic specimens still attached to the largest fragments, together with gastropod and fewer bivalve shells, and echinoid plates and

spines. Noteworthy is that most of the mollusc shells were still perfectly coloured and some of them were broken with sharp edge fractures (Fig. 7, images 6-9). On the contrary, the shells from the upper core interval were not commonly well preserved: the external shell surface was opaque, sometimes abraded and often bio-perforated (Fig. 7, image 15).

3.4 Calcareous nannoplankton content

Since in shallow waters (shallower than 12 m depth) the wave motion can prevent the deposition of the smallest-sized sediment particles (<20 μm), such as nannoplankton remains ("high energy gap" by Ferreira & Cachão; 2005), the analysis of calcareous nannoplankton content was used to investigate the hydrodynamic conditions of the sampling site.

The continuous occurrence of nannoplankton down core in both records (Fig. 8), collected at 16 m and 17 m depth respectively, indicated that the energy conditions were suitable for nannoplankton deposition. In the lower part of both records, total abundance was characterised by a decreasing trend: starting from cm 41-40, abundances progressively decreased, changing from maximum values of about 26 Nmm^{-2} in CORE18 and of 20 Nmm^{-2} in CORE19 to minimum values of 4-7 N mm^{-2} in the stratigraphic interval from cm 30-29 to 27-26 bsf of both records.. Moving upwards, from cm 26-25 up to top, absolute abundances markedly increased, recording average values of about 16 Nmm^{-2} in both cores, with peaks of 29 Nmm^{-2} in CORE18 and of 28 Nmm^{-2} in CORE19 (Fig. 8; Table S5, supplementary data). The identified assemblages were dominated by reworked taxa, late Oligocene to early Miocene in age, supplied from the active erosion of rocks cropping out all around Marsamxett Harbour (*Globigerina* Limestone Formation). Modern species were always rare to very rare and mainly consisted of the long-ranging *Coccolithus pelagicus* and *Gephyrocapsa oceanica* and *Emiliana huxleyi*. The K-strategist *Florisphaera profunda,* a species living in the deep

photic zone (100-200 m depth) in the open sea, sporadically occurred at cm 36-35 and 31-30 bsf, in the same samples where deep-sea benthic foraminifera and planktonics were also found (Fig. 5). The studied smear slides also contained very abundant spicules of ascidians (Chordata: Ascidacea). In both records, ascidian spicules were more abundant in the lower part of the cores then they rapidly decreased upwards (Table S5, supplementary data).

4 DISCUSSION

4.1 The 1908 Messina tsunami and its effects on the Maltese archipelago

Tsunamis are among the most catastrophic events on Earth. When tsunami waves reach the coast, they flood wide areas damaging cultivated lands and buildings and causing loss of human life (e.g. Gusiakov et al. 2019 and references therein). Due to its high seismicity and the presence of active volcanoes, the Central Mediterranean basin is one of the main tsunami risk areas in the World (e.g. Papadopoulos et al. 2014). One of the most destructive examples associated with an intense earthquake was the 1908 Messina tsunami; such combined events caused over 80,000 deaths and are considered the worst disaster in modern history in the Mediterranean region (Guidoboni et al. 2007).

On 28 December 1908, a severe earthquake (Mw 7.1) destroyed major towns in eastern Sicily and Calabria, including Messina and Reggio Calabria, and caused a violent tsunami consisting of at least three major waves (Guidoboni et al. 2007). The waves, over 10 m high in the Messina Strait, propagated in all directions reaching the coasts of Maltese islands, Albania, Montenegro and the Greek Ionian islands (e.g. Guidoboni et al. 2007; Pino et al. 2009). Over 100 years after this catastrophic event, the exact cause of the 1908 Messina tsunami remains unresolved (e.g. Billi et al., 2008); nonetheless recent works have proposed

a dual earthquake/submarine landslide mechanism (Schambach et al., 2020 and references therein).

In the Maltese islands, about 250 km south of the epicentre (Fig. 1), the tsunami waves arrived about one hour after the earthquake, causing damages mostly along the eastern, more exposed coasts, as documented by both historical chronicles and field evidence (e.g. Galea, 1909; Borg et al., 2016; Mottershead et al., 2017). The peculiar topography of the eastern coast, characterised by shore platforms due to the general tilting of sedimentary strata towards the northeast, amplified the impact of tsunami waves: the shores were flooded causing massive landslides and the formation of several boulders that accumulated at the top of the submerged escarpment (Mottershead et al., 2017; Biolchi et al., 2016). Along the eastern coasts, fisherman boats were crushed and pushed adrift on the shore inducing a general panic among people; in the Grand Harbour (La Valletta), boats broke their moorings, and the houses at Msida, Sliema and Pieta were inundated (Malta Herald 1908; Borg et al. 2016 and references therein). On the contrary, Marsamxett Harbour, located in a lateral creek, was naturally sheltered from the tsunami waves; in fact no significant damages to buildings and boats were reported, but only a going and coming of the sea several times during the day (Borg et al., 2016).

4.2 Combined evidences for a sudden high energy depositional event

It appears clear from the core records described here that *A. lobifera* arrived very early in time in Marsamxett Harbour, Malta island, but the species disappeared soon thereafter. It took several decades before the species re-appeared in the records, starting the current colonization as described in Guastella et al. (2021). If the age model derived from radiometric analyses (~4.5 years for each centimetre of sediment; Table S3 supplementary data) is regularly applied along the whole cores, it would appear as if the onset of the early invasion recorded at

cm 39-40 bsf happened around 1840. However, this is clearly an unrealistic conclusion because the Suez Canal, through which *A. lobifera* passed to enter the Mediterraean (Prazeres et al. 2020) opened in 1869. Therefore, in order to explain the presence of *A. lobifera* in the core bottom we formulated two alternative interpretations of the age model: I) altered patterns of ^{210}Pb decay, but this seems highly improbable since ^{210}Pb activity curves show otherwise; and II) occurrence of a rapid depositional event, which could have altered the sedimentation rate and caused the sudden accumulation of a thick layer of sediments in the lower portion of both records. This second hypothesis is supported by the data that yield several lines of evidence for a sudden high-energy depositional event. In both cores, changes in sediment grain-size, porosity and micropaleontological content occurred at around cm 25-24 bsf (Figs. 2, 5, 8), dividing the studied records into two distinct parts, a lower and an upper part. The lower part mainly consisted of grey mud and very fine sands with a higher porosity (reasonably due to the high content of water contained in the *P. oceanica* remains) and a higher content of undecomposed organic matter with symptoms of anoxic conditions, which are compatible with a sudden burial of live organisms. Sediments also contained abundant mollusc shells perfectly preserved, still coloured and, sometimes, as noted above, broken with sharp edge fractures (Fig. 7), distinctly different from the depigmented, eroded and bio-perforated shells of the upper layers (Fig. 7, image 15), which likely remained for a long time on the sea-floor before burial. Moreover, very abundant epiphytic foraminifera (e.g. *M. miniacea*, *P. mediterranensis* and *S. orbiculus*), sometimes still attached to the largest leaves of *P. oceanica*, were incorporated in the mud (Fig. 2b). All of this evidence suggests a very rapid burial of molluscs, foraminiferal shells and *P. oceanica* remains, probably caused by a high-energy depositional event that, at the same time, uprooted *P. oceanica* from the sea floor, broke mollusc shells and prevented the deposition of coccoliths (nannoplankton remains). The marked and sudden increase of coccolith abundance in the upper portion of

both cores, starting from cm 26-25 bsf up to the core top (Fig. 8), suggests a consequent rapid decrease in depositional energy, that allowed the accumulation of the finest sediment particles, as coccoliths. Additionally, the upper portion of both cores was characterised by a decrease of porosity, related to the absence of *P. oceanica* remains (Fig. 2a).

4.3 The tsunamiite deposited in Malta after the 1908 Messina earthquake

Considering the lower part of both cores (from 25-24 cm bsf down core) as the sedimentary product of a rapid high-energy depositional event and applying the current age model of 4.5 years per each centimetre of sediment (Table S3 supplementary data) limitedly to the upper part of both cores (from the top down to cm 25 bsf), we could infer that the upper core records correspond to a time interval spanning from 2019 (the date of collection) to about 1905. In particular, sediments from cm 25-24 bsf have accumulated from 1905 to 1910, and thus they could represent the top of a high-energy depositional event of 1908, the year of the catastrophic earthquake occurred off the coast of Messina (Sicily). This abrupt geological event generated, as noted earlier, a violent tsunami, that quickly reached the Maltese coasts (Galea, 1909; Borg et al., 2016; Mottershead et al., 2017). We suggest that the lower muddy part of both cores, from the base up to ~ cm 24 bsf, could represent the tsunamiite deposited by the tsunami waves within Marsamxett Harbour, Malta.

Tsunami deposits recorded in sediment cores from deep-water settings (e.g. off Augusta Bay, eastern Sicily; Smedile et al., 2012) are easily recognised, thanks to their peculiar sedimentary signatures, such as the distinct erosional base, coarse-grained and gradated layers and a high content of shallow-water taxa, *P. oceanica* remains and beach debris displaced from the shore by the backwash wave. On the contrary, tsunamiites recorded in historical records from coastal areas are more rare and difficult to be recognised, mainly because transitional environments are subjected to continuous current reworking and human disturbance activities,

and because tsunami waves can leave little or no sedimentary record (Dawson and Stewart, 2007; Noda et al. 2007; Judd et al. 2017). Nonetheless, in coastal areas, tsunami deposits can mimic other high-energy depositional events, such as storm waves, and thus they can be frequently confused with tempestite layers (Nanayama et al., 2000). In shallow-water contexts, tsunami deposits usually do not exceed a few tens of centimetres in thickness and do not display peculiar sedimentary signatures apart from a higher content of mud, sometimes characterised by rare laminae, and an abrupt erosional basal surface that is cut when seabed sediments are suspended (Dawson and Stewart, 2007; Papadopoulus et al., 2014; Biguenet et al., 2021). These features depend on the hydrodynamic conditions during transport and sedimentation and on the coastal topography (Dawson and Stewart, 2007; Papadopoulus et al., 2014). Shallow-water tsunamiites are also characterised by abundant biogenic remains (mollusc shells, marine plants, ostracods and foraminifera), which are commonly incorporated in the mud and can display broken shells due to the turbulent water movement (Dawson and Stewart, 2007 and references therein). Some of them could have originated in deeper environments followed by landward transport by the tsunami wave (Nanayama and Shigeno, 2006).

Our sedimentological and micropaleontological results described above agree with the typical depositions triggered by a tsunami in coastal settings (Dawson and Stewart, 2007; Noda et al. 2007; Judd et al. 2017; Biguenet et al., 2021). As reported in historical newspapers, in the naturally sheltered bay of Marsamxett Harbour in Malta the tsunami waves caused only a going and coming of the sea several times during the day (Borg et al., 2016 and references). The oscillatory wave movement probably reworked sea bottom sediments, keeping the fine-grained particles suspended, perhaps for days before settling out, depending on the scale of residual turbulence, but without any significant transport landwards or seawards. As a result, a tsunamiite (about 25 cm thick) accumulated and buried the sea bed in Marsamxett Harbour.

Unfortunately, both cores failed to record the tsunamiite base, since the basal erosional surface and the abrupt change in sediment grain-size are missing. Therefore, it is impossible to determine when after 1869 *A. lobifera* really arrived in Marsamxett Harbour. Yet, we can document the presence of its remains within sediments deposited before 1908 and, then, remobilised by the tsunami waves, which is a surprising and significant backdating of *A. lobifera*'s first arrival in the Central Mediterranean Sea (Guastella et al., 2021). We also explored the possibility of carrying out further radiometric analyses (e.g. radiocarbon dating) directly on *A. lobifera* tests picked from the tsunamiite interval (e.g. Gottschalk et al. 2018; Guerra et al. 2019). However, the current ^{14}C method works poorly for such recent records (since this isotope has a half-life of about 6 ky), and the error that usually derives from the different measurements (~ 20-30 years) is comparable to the resolution interval, thus preventing a precise age determination. Furthermore, since the nuclear tests carried out since the 1950s have altered the natural signal of this radiogenic isotope (the so called "bomb effect", Nydal and Lövseth 1983), application of the ^{14}C method is more then unreliable for records younger than 150 yr.

We are aware that there can be other causes of population extinction within a sedimentary record that could be invoked, but the correlation in time and space with the Messina's tsunami event recorded in both cores appears rather persuasive.

4.1 Triggering mechanisms for the early failed invasion

The 1908 tsunami may hence have caused the failure of the early invasion of *A. lobifera* in Marsamxett Harbour through a cascade of events. First, the rapid deposition of the tsunamiite buried the seagrass meadow under over 25 cm of muddy sediments, damaging and causing a drastic change of habitat for most benthic foraminiferal species, including the target taxon. In

fact, the *P. oceanica* meadow existing in the harbour was probably unable to recover and develop new patches, as documented by the absence in both cores of *P. oceanica* remains above the tsunamiite. Since this plant has very low growth rates (Cabaço et al., 2008; Noè et al., 2020), its recovery after a destructive event is highly unlikely in the human time scale. Therefore, the sea bottom of Marsamxett Harbour in Malta appears to have irreversibly changed after the 1908 tsunami. All of the benthic community was directly impacted by this sudden depositional event, as supported by the decreasing trend in abundance of sessile epiphytic foraminifera (Fig. 5), which suffered a rapid decline and never fully recovered in subsequent years, as documented by the marked reduction of *Miniacina miniacea*. Ascidians also likely reduced their abundance as a probable consequence of the habitat damage (Table S6, supplementary data). This response has been observed for some Mediterranean ascidian populations, known as "regressive species" (Naranjo et al., 1996), which disappear or reduce their populations when the habitat conditions become stressful. The invasive species *A. lobifera*, which abruptly disappeared from Marsamxett Harbour, may have experienced a similar fate. As we noted in the Introduction, failed invasions are by their very nature difficult to detect and, likely, overlooked the vast majority of the time. Similarly, we do not know how many successful invasions were preceded by either failures or by very long lag times in developing robust populations to the point where they may be detected in random sampling. Some failures are due (as we also noted earlier) to environmental mismatches, while others could be due to habitat changes. Thus, while the well-known European shore crab *Carcinus maenas* has been found alive in tropical environments around the world, no populations of this colder-water crab became established in lower latitudes (Carlton & Cohen, 2003). A non-native cephalaspidean "bubble snail," *Bulla* sp. (identified at the time as *B. adamsi*; see Malaquias & Reid, 2008) became established on Oahu (Hawaii) in the 1940s, but it is believed that habitat destruction destroyed the populations (Carlton & Eldredge, 2009). The

European shore snail *Truncatella subcylindrica* was found living abundantly intertidally in Newport, Rhode Island, USA in 1880 (Verrill, 1880), but no vestiges of the original shoreline remain today (JTC, personal observations), suggesting habitat destruction may have played a role in its invasion success as well. The European ascidian *Ascidiella scabra* was collected in the 1860s in Japan, but disappeared for unknown reasons (Nishikawa & Otani, 2004). A more recent example of the failure of a marine invader is the European sea anemone *Sagartia elegans*, which thrived for nearly a decade under the influence of a powerplant thermal discharge in New England before becoming extinct (Wells & Harris, 2019). Perhaps more similar to the present case of natural disaster-induced population obliteration is the history of the Indo-Pacific soft coral *Dendronephthya* sp. in the Hawaiian Islands, a growing colony that had been established for at least 7 years, but which then abruptly disappeared coincident with the passage of Hurricane Iniki over the exact site where it occurred (Carlton & Eldredge, 2009). Similarly, tsunamis play a significant role in impacting and shaping populations of intertidal and shallow water marine species (e.g. Kanaya et al. 2012; Miura et al. 2012; 2017; Urabe and Nakashizuka, 2016).To our knowledge, *A. lobifera* is the first modern-day invasion that was apparently rendered extinct by a tsunami.

5 CONCLUDING REMARKS

The non-indigenous foraminiferan *Amphistegina lobifera* has a curious and complex history in Malta, as now more fully revealed by sedimentary cores and radiometric analyses. We here suggest a three-phase invasion model leading to the current presence of this Indo-Pacific species in the Maltese archipelagos.

In Phase I, *A. lobifera* invaded the Mediterranean reaching the Maltese coast sometime before 1908. The 1908 Messina earthquake and tsunami then destroyed these early populations. In

Phase II, *A. lobifera* re-invaded the island of Malta in the mid-1940s (Guastella et al. 2021). It then remained in relatively low numbers over the next six decades. In Phase III, *A. lobifera* became abundant enough to be discovered alive in the Maltese archipelago in 2006 (Yokeş et al. 2007), perhaps due to ocean warming leading to population surges (Guastella et al. 2021). Thus, there was a significant lag time after 1908 before *A. lobifera* reappeared and became re-established, and another significant lag time after the mid-1940s before it became sufficiently abundant to be detected. While it is not impossible that residual populations remained after the 1908 tsunami, we are not at this time aware of a mechanism which would have led earlier remnant populations (if indeed they existed) to undergo a population expansion in the 1940s, parallel to the probable warming trigger of the early 21st century, leading us to conclude that the 1908 event did in fact render *A. lobifera* extinct in the Mediterranean in the early 1900s.

Finally, the revelation that this non-indigenous foraminiferan has a much deeper history than that reported by conventional sampling of living populations suggests that the invasion of the Mediterranean Sea after 1869 may have commenced far earlier than suspected for many species. Put another way, it would appear unlikely that this small shelled protist is the only Lessepsian invader to have entered the Mediterranean long before it was first detected.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Author Contributions

NM and AM developed the idea; AC and JE collected and sampled the cores; NM, RG and MC performed micropaleontological analyses; LL carried out radiometric dating; MC and LC interpreted sedimentological data. All authors contributed to interpretation of results and discussions and wrote the manuscript, with relevant contributions from JTC.

Data availability statement

All data generated or analysed during this study are included in this published article [and its supplementary online material].

Conflict of interest statement

The authors have no competing interests to declare that are relevant to the content of this article.

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TABLES

Table 1: Differences in sediment composition between lower and upper core portions (threshold corresponds to 25-24 cm bsf; see also Figg. 2, 4, 5, and 8). Sediment composition is represented by: percentage of fine sediments (fine sand + very fine sand + mud), percentage of mud, and abundance of selected foraminifera (Group A = sessile species, *M. miniacea* and *P. mediterranensis*). All variables are shown as average values ± SD. Results of unpaired *t*-tests (lower-core *vs* upper-core) are also reported.

		Sediment fraction (%)		Foraminifera abundance (N g^{-1})		
		Fine fraction	*Mud*	Group A	*Miniacina miniacea*	*Planorbulina mediterranensis*
CORE18	Lower-core	63.1%± 2.7%	33.4%± 4.8%	141.6 ± 33.5	8.7 ± 6.1	119.9 ± 28.6
	Upper-core	49.7%± 8.1%	22.1%± 5.8%	85.2 ± 29.3	1.6 ± 2.3	67.7 ± 28.5
	t-value	*5.2754*	*5.0242*	*4.4820*	*4.0330*	*4.5731*
	p-value	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
CORE19	Lower-core	64.9%± 3.1%	29.7%± 1.9%	301.5 ± 69.4	20.4 ± 10.5	229.6 ± 58.3
	Upper-core	50.6%± 5.3%	19.8%± 3.9%	96.2 ± 30.9	2.51 ± 3.4	65.0 ± 21.9
	t-value	*8.9344*	*8.9777*	*9.5124*	*5.9661*	*9.5334*
	p-value	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*

FIGURE CAPTIONS

Figure 1: a-b) The Mediterranean basin and the Sicily Channel with the probable epicentre of the tsunami generated by the 1908 Messina earthquake (Billi et al. 2008). **c-d)** Location of the sampled site in Marsamxett Harbour (Malta island); note the sheltered position within the natural bay with respect to the probable direction of tsunami waves.

Figure 2: a) Images of the sectioned cores and sediment grain-size and porosity curves of the studied records; b) detail of CORE19 showing abundant rhizoids of *Posidonia oceanica* and macroscopic mollusc shells often fragmented; c) the sectioned CORE19 and its containing tube: note the rust-coloured portion from cm 25-24 up to top. The grey strip marks the

stratigraphic level where major sedimentological changes occurred. The level has been used to subdivide the cores in two portions (lower and upper) and corresponds to the probable top of tsunamiite.

Figure 3: ^{210}Pb curves showing the typical activity profile decreasing with depth and scatter-plots reporting a constant SAR, respectively of 0.20 cm yr-1 for CORE18 (in red) and 0.22 cm yr-1 for CORE19 (in blue); this last value was utilised in the applied age model, which leads to an estimated time interval of about 4.5 years for each cm of sediment.

Figure 4: Total abundance (N g^{-1}) of *Amphistegina lobifera*. The grey strip marks the stratigraphic level where major sedimentological changes occurred.

Figure 5: Total abundance (N g^{-1}) of benthic foraminiferal assemblage along the studied records: a) total benthic foraminifera, total epiphytic foraminifera (Groups A to D); b) the most abundant species of Group A (*Miniacina miniacea*, *Planorbulina mediterranensis*, *Sorites orbiculus*) and other components of the assemblage. The grey strip marks the stratigraphic level where major sedimentological and micropaleontological changes occurred.

Figure 6: SEM images in secondary electrons of deep-sea benthic foraminifera from the tsunamiite interval of both records. Scale bars are 100 μm. 1:*Siphonina reticulata* cm 31-32bsf. 2: *Angulogerina angulosa* cm 31-32bsf. 3a,b: *Uvigerina peregrina*; a specimen from cm 31-32bsf, b specimen from cm 29-30bsf. 4: *Siphouvigerina* sp. cm 27-28bsf. 5: *Reussella spinulosa* cm 24-25bsf. 6: *Bulimina aculeata* cm 30-31bsf. 7: *Bolivina variabilis* cm 31-32bsf. 8: *Brizalina* sp. cm 27-28bsf. 9: *Fissurina* sp. cm 27-28bsf. 10a,b *Buccella granulata* cm 31-32bsf. 11: *Lenticulina cultrata* cm 24-25bsf.

Figure 7: Photos at the stereomicroscope of gastropod and bivalve shells from the tsunamiite interval of both cores. Note the specimens characterized by shells perfectly preserved and still coloured, but mechanically broken (images 6-9) indicative of a very rapid burial. For

comparison is reported a gastropod specimen badly preserved from the upper core record, indicative of its staying on the sea-floor for long time before burial. Scale bars are 1mm.

1a,b: *Rissoa* sp. (Rissoidae) cm 33-34 bsf. **2:** *Turbonilla* sp. (Pyramidellidae) cm 32-33 bsf. **3:** Triphorid specimen not identified cm 32-33 bsf. **4:** *Parvioris ibizenca* (Eulimidae) cm 29-30 bsf. **5:** *Gibberula* sp. (Cysticidae) cm 35-36 bsf. **6:** Fragmented shell of *Smaragdia viridis* (Neritidae) cm 32-33 bsf. **7:** Fragmented shell of *Gibbula ardens* (Trochidae) cm 30-31 bsf. **8:** Fragmented shell of *Alvania* sp. (Rissoidae) cm 31-32 bsf. **9a,b:** *Tricolia pullus* ((Phasianellidae) cm 31-32 bsf. **10a,b** *Pusillina radiata* (Rissoidae) cm 32-33 bsf. **11a,b:** *Rissoella* sp. (Rissoellidae) cm 20-30 bsf. **12:** *Parvicardium* sp. (Cardiidae) cm 27-28 bsf. **13a,b:** *Tricolia pullus* ((Phasianellidae) cm 53-36 bsf. **14a,b:** *Asperarca* sp. 20-30 bsf. **15:** *Alvania* sp. specimen with the shell surface opaque and bio-perforated, cm 10-9 bsf.

Figure 8: Total abundance (N mm^{-2}) of calcareous nannoplankton along the studied records (from the left): total abundance, *Gephyrocapsa oceanica*, *Emiliania huxleyi*, strategist-species, long-ranging species (e.g. *Coccolithus pelagicus*) and reworked taxa. The grey strip marks the stratigraphic level where major sedimentological and micropaleontological changes occurred.

SUPPLEMENTARY MATERIAL AVAILABLE ONLINE

Table S1: granulometric data recorded along the studied records (CORE18 and CORE19)

Table S2: porosity data recorded along the studied records (CORE18 and CORE19)

Table S3: radiometric data and chronological constrain based on ^{210}Pb decay (CORE18 and CORE19).

Table S4: Absolute abundance of benthic foraminifera, including the target species *A. lobifera*, recorded along the studied records (CORE18 and CORE19).

Table S5: absolute abundance of calcareous nannoplankton and ascidian remains along the studied records (CORE18 and CORE19).

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The Chronicles of a small invader: the Canal, the Core and the Tsunami

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Abstract

Information on early invasion stages, whether successful or not, is often lacking because most invaders are only discovered ~~only~~ once they have become abundant enough to be casually detected or have caused appreciable changes to the recipient environment. Moreover, when newcomers fail to establish self-sustaining populations, they are often not even documented; likewise the cause(s) of the failure remains unknown in most cases.

Here we report for the first time a probable failed early invasion, caused by an unpredictable geological event, that was detected from two sediment records radiometrically dated through ^{210}Pb chronology. The cores, collected from Marsamxett Harbour in Malta (Central Mediterranean), reveal a continuous record for at least the last 110 years. Both cores contain towards the bottom (dated to the beginning of the 20th century) the highly invasive Lessepsian immigrant benthic foraminifer *Amphistegina lobifera* Larsen 1976, demonstrating that it was present in this region long before it was first recognized in the Mediterranean. It then abruptly disappeared from the cores. We document that the disappearance may have been triggered by the 1908 Messina earthquake, with a resulting tsunami wave that reached Marsamxett Harbour and deposited over 20 cm of sediment. This event suddenly buried the sea-bottom, destroying the existing benthic community and damaging the seagrass *Posidonia oceanica* meadow. Today, *A. lobifera* is abundant along the Maltese coast, likely as a result of re-invasion in the 1940s, yet followed by a long detection lag time until it was first found in 2006.

Keywords

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Lag time, alien species, benthic foraminifera, tsunami deposit, 1908 Messina Earthquake, Central Mediterranean

1 INTRODUCTION

During the last several decades, biological invasions have been largely investigated because they represent a serious global environmental problem leading to significant impacts on ecosystem services and the economy (Jeschke & Heger, 2018). Bioinvasions have also attracted the attention of community and ecosystem ecologists relative to how the addition of novel species may alter trophodynamics and resident species' abundances and diversity. Because of this, invasion ecologists have mainly focused on the study of species that have successfully invaded new areas, while relatively less attention has been given to failed invasions and to the causes that determine invasion failure (Miller and Ruiz, 2009; Ings et al., 2010; Zenni & Nuñez, 2013). Invasion failure can occur during any stage of the colonization process (Blackburn et al., 2011), if alien species are not able to survive, reproduce or maintain a sustainable population in the new recipient environment (Zenni & Nuñez, 2013). Many factors have been suggested to drive the success or failure of biological invasions (Zenni & Nuñez, 2013; Jeschke & Heger, 2018). Propagule pressure could be insufficient for a species to survive demographic stochasticity and maintain a population (Simberloff, 2009). Habitat match between source and recipient regions could be inadequate and, consequently, the introduced organisms could find unfavourable environmental conditions for their establishment and reproduction, a concept known as 'abiotic resistance' (Fenoglio et al., 2016; Zhang et al., 2020). Interspecific interactions may also play a role in this phenomenon; introduced organisms may face novel microbial, herbivore or predator communities, competitive regimes or prey species, a concept known as 'biotic resistance' (Levine, 2004; Colautti & Lau, 2015). Opportunistic traits that increase survival and reproduction in the novel environments may promote establishment and proliferation (Garcìa-Ramos & Rodrìguez, 2002; Miller et al., 2007). As a consequence, if the newcomers are either not pre-adapted or not able to adjust to new environmental conditions, they may have a low

probability of ~~carrying out~~having a successful invasion. Genetic bottleneck effects may also play a role in this process (Zenni & Nuñez, 2013). In addition, invasions may fail due to stochastic events, such as volcanic eruptions, fires, freezes, and hurricanes and typhoons that can abruptly change environmental conditions, triggering population extinction.

In most cases, early failed invasions remain unknown, especially when unintentional introductions are concerned (Phillips et al., 2010). However, the identification of failed invasions, as well as the causes that determine failure of an invasion, are fundamental to advance the general understanding of invasion ecology and to potentially support management actions (Carlton, 1996; Zenni & Nuñez, 2013). Similarly, early stages of invasions are often very poorly known, because species receive researchers' attention only after having successfully established in a new area (Mancin et al. 2022). This situation may prevent understanding of the fine-grained timing of initial introduction events and the subsequent early stages of invasion. We report here the discovery of the unexpected early occurrence, in sediment cores dated to the beginning of the 20th century, of a Lessepsian invader, the foraminifer *Amphistegina lobifera* Larsen, 1976, in Malta, Central Mediterranean Sea. This~~, a~~ species was previously thought to have first arrived in this region in the mid-1940s (Guastella et al., 2021), albeit not documented as present until 2006 (Yokeş et al., 2007)~~, as we discuss further below~~. This benthic foraminifer is a large symbiont-bearing Indo-Pacific species, which entered the eastern Mediterranean after the 1869 opening of the Suez Canal (Prazeres et al. 2020). The bottom of the cores bearing *Amphistegina* specimens correlated with a horizon of the 1908 Messina earthquake and tsunami. Our work provides insights into the invasion history of this species in the Central Mediterranean, driving hypotheses on the possible role of catastrophic geological events in interrupting what eventually may be successful species invasions.

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1.1 The 1908 Messina tsunami and its effects on the Maltese archipelago

Tsunamis are among the most catastrophic events on Earth. When tsunami waves reach the coast amplifying their destructive force, they flood wide areas damaging cultivated lands and buildings and causing loss of human life (e.g. Gusiakov et al. 2019 and references therein). Due to its high seismicity and the presence of active volcanoes, the Central Mediterranean basin is one of the main tsunami risk areas in the World (e.g. Papadopoulos et al. 2014). One of the most destructive examples associated with an intense earthquake was the 1908 Messina tsunami; such combined events caused over 80,000 deaths and are considered the worst disaster in modern history in the Mediterranean region (Guidoboni et al. 2007).

On 28 December 1908, a severe earthquake (Mw 7.1) destroyed major towns in eastern Sicily and Calabria, including Messina and Reggio Calabria, and caused a violent tsunami consisting of at least three major waves (Guidoboni et al. 2007). The waves, over 10 m high in the Messina Strait, propagated in all directions reaching the coasts of Maltese islands, Albania, Montenegro and the Greek Ionian islands (e.g. Guidoboni et al. 2007; Pino et al. 2009). Over 100 years after this catastrophic event, the exact cause of the 1908 Messina tsunami remains unresolved (e.g. Billi et al., 2008); nonetheless recent works have proposed a dual earthquake/submarine landslide mechanism (Schambach et al., 2020 and references therein).

In the Maltese islands, about 250 km south of the epicentre (Fig. 1), the tsunami waves arrived about one hour after the earthquake, causing damages mostly along the eastern, more exposed coasts, as documented by both historical chronicles and field evidence (e.g. Galea, 1909; Borg et al., 2016; Mottershead et al., 2017). The peculiar topography of the eastern coast, characterised by shore platforms due to the general tilting of sedimentary strata towards the northeast, amplified the impact of tsunami waves: the shores were flooded causing massive landslides and the formation of several boulders, that accumulated at the top of the

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Reply: We agree with this comment and moved the entire section at the beginning of Discussions.

~~submerged escarpment (Mottershead et al., 2017; Biolchi et al., 2016). Along the eastern coasts, fisherman boats were crushed and pushed adrift on the shore inducing a general panic among people; in the Grand Harbour (La Valletta), boats broke their moorings and the houses at Msida, Sliema and Pieta were inundated (Malta Herald 1908; Borg et al. 2016 and references therein). On the contrary, Marsamxett Harbour, located in a lateral creek, was naturally sheltered from the tsunami waves; in fact no significant damages to buildings and boats were reported, but only a going and coming of the sea several times during the day (Borg et al., 2016).~~

2 MATERIALS AND METHODS

The Sicily Channel, located in the Central Mediterranean basin between Italy and North Africa, is a natural biogeographical corridor for both Lessepsian invaders originating from the Red Sea and warm-water colonizers coming from the Atlantic (Azzurro et al., 2014 and references therein). The channel is characterised by a complex topography formed by several islands (e.g. the Maltese and Pelagie archipelagos and Pantelleria island) and elevated ridges which alternate with deep submarine canyons; this topography controls the modern oceanography and sedimentation (Hassen et al. 2019).

The Maltese islands are centrally located within the Sicily Channel, about 90 km south of Sicily and about 290 km north of the North African coast (Fig. 1a-b). Malta is the largest island of the archipelago covering a surface of about 250 km^2 and with a perimeter of about 197 km mainly formed by rocky shores incised by few natural bays. Two sediment cores (CORE-18 and CORE-19) were collected, respectively ~~o~~in May 2018 and September 2019, at 16 m and 17 m water depth, close to Manoel island, an islet located within Marsamxett Harbour of Malta (Fig. 1c-d). Thanks to its peculiar location within a narrow creek (Fig. 1d),

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the sampling site was partly sheltered from the probable direction of the tsunami waves that moved from NE to SW and mostly impacted on the northeastern Maltese coast in 1908.

Criteria adopted for the sampling site selection and methods for grain-size, micropaleontological and radiometric analyses are the same as described in Guastella et al. (2021). Here we describe only the methodologies of the additional investigations performed in the present study. Analyses were carried out on subsamples of the same core level (a total of 91 subsamples, spacing 1 cm).

Porosity was calculated for both sediment cores using the same methodology~~:~~ samples were weighed, oven-dried at 55 °C, and then re-weighed to determine water content. Porosity was calculated from the loss of water between wet and dry sediments according to equations suggested by Berner (1971), assuming a sediment density of 2.6 g cm^{-3} and a water density of 1.034 g cm^{-3}. Grain-size analysis was carried out on samples from CORE ~~20~~19 not previously studied in Guastella et al. (2021).

The foraminiferal content was quantified in 91 samples, also including samples from the lower part of both cores, not previously analysed for the study of Guastella et al. (2021). Foraminiferal specimens (including the target species *A. lobifera*) were determined under a stereomicroscope on the > 63 µm size washed fraction. Quantitative data were collected as number of individuals per gram of dry sediment (N g^{-1}). Epiphitic foraminifera were grouped into four categories (A – D) following Langer (1993): A- sessile (including both encrusting and permanently attached by glycosaminoglycans taxa), B- temporary motile (by swimming on pseudopodial network), C- motile (by using pseudopodia extruded from canal system and multiple apertures), and D- permanently motile (by striding on the apertural face in an upright position~~-~~). Unpaired *t*-tests were conducted to verify differences between lower core and upper core in terms of sediment composition and foraminiferal abundance.

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The calcareous nannoplankton content was analysed using a polarizing light microscope at 1250X magnification on smear slides prepared according to the "drop technique" proposed by Bordiga et al. (2015). This preparation technique is based on the assumption that a known concentration volume of suspension (bulk sediment weigh/mL, 0,005 g/20 mL) is evenly distributed on a known area (corresponding to the cover slip area: 768 mm^2). Coccoliths were counted on that area within ~~a number of~~300 randomly selected fields of view (FOV); their absolute abundance was expressed as total number of specimens recorded per mm^2 (N mm^{-2}).

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Reply: we added the number (300)

3 RESULTS

3.1 Sedimentological features and porosity

Both cores showed similar sedimentological signatures, thus indicating a good replicability of the collected records (Fig. 2; Tables S1-S2 available on-line as supplementary data). They were characterised by a gradual coarsening upwards trend, starting from about cm 25-24 below sea floor (bsf) up to top (Fig. 2a).

In both records, the lower part (from the bottom up to ~25-24 cm bsf) mainly consisted of fine and very fine sands and mud. ~~(p~~Percentages of ~~60-70~~the fine-grained fractions varied from 53% to 69%, with an average of 63.1% ± 2.7% in CORE18 and from 52% to 74% with an average of 64.9% ± 3.1% in CORE19 (Table 1; for full data see also Table S1, supplementary data). Sediments from this portion were characterised by a grey colour, probably due to the high concentration of reduced organic matter (Fig. 2a). This was inferred from both the smell of hydrogen sulphide present during the core sectioning and sampling and the very high abundance of undecomposed *Posidonia oceanica* remains, mainly rhizoids, well visible to the naked eye (see detail in Fig. 2b). These s~~S~~ediments ~~from this interval~~ were also

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Reply: We added the requested data in the text and in a new table showing statistical comparisons between lower and upper core (Table 1). In fig. 2 (sedimentological data), we also added a grey strip that marks the stratigraphical level where major sedimentological changes occurred. It divides the studied cores in two portions: lower and upper, respectively, and corresponds to the probable top of tsunamiite.

homogeneous, without any evident lamination and gradation and characterised by abundant mollusc shells (often fragmented) and large benthic foraminifera incorporated in the mud.

In the upper parts of both records, from cm 24 bsf up to top, the ~~coarse~~fine-grained fractions (~~very coarse and coarse sands~~fine sand + very fine sand + mud) gradually ~~in~~decreased~~, in percentage, with values passing from 25-30% to over 60% in CORE18 at cm 6-5 bsf (Fig. 2a)~~reaching average percentages of 49.7% ± 8.1% in CORE18 and of 50.6% ± 5.3% in CORE19 (Table 1; for full data see also Table S1, supplementary data). According to the unpaired *t*-test, differences between lower and upper core in terms of fine fraction percentage were statistically significant in both cores; the same could be observed when considering mud fraction alone (Table 1).~~Sediments from this interval mainly consisted of very coarse sands and, in equal proportion, by coarse and medium sands (together the coarse-grained fractions made up 60-70% of the whole sediment); fine and very fine sands and mud were subordinated, particularly the mud fraction had percentages between 18% and 5%.~~ In the same core interval, remains of *P. oceanica* rapidly disappeared and mollusc shells became rarer. This core portion also contained abundant iron Fe-oxides, as well shown by both the rust-coloured tube of CORE19 and by the light brown to yellow colour of sediments towards the core top (Fig. 2c).

Porosity curves mirrored sediment grain size curves but with an opposite trend (Fig. 2a; Tab S2 supplementary data): the highest values (0.6 - 0.8) were registered in the lower fine-grained part of both cores, from the bottom up to cm ~25-24 bsf, then porosity progressively decreased upwards.

3.2 ^{210}Pb and ^{137}Cs chronologies

^{210}Pb curves showed the typical activity-depth profile, with higher activities at the core top that rapidly decreased down core, halving within the first 25 cm bfs of the studied records (Fig. 3, Table ~~.~~ S3 supplementary data). In this interval, the reconstructed Sediment Accumulation Rate (SAR) was constant, respectively of ~0.20 cm yr^{-1} in CORE18 and 0.22 cm yr^{-1}in CORE19 (scatter plots A and B) indicating a good replicability and reliability of the collected data (Table ~~.~~ S3 supplementary data). The derived age model furnished an estimated time interval of ~4.5 years for each centimetre of sediment; thus the collected cores probably recorded at least the last 150 years (Table S3, supplementary data). Unfortunately, no ^{137}Cs was recorded in either core, thus an independent validation through this method was not possible. While the absence of the Chernobyl peak of ^{137}Cs is common in sediments collected in the southern part of the Mediterranean Sea, due to the dispersion pattern of ^{137}Cs fallout that followed the accident, it is surprising to have no signal of nuclear bomb experiments. Nevertheless, the absence of ^{137}Cs in both cores supports the finding that in this area of the Sicily Channel the ^{137}Cs supply is negligible as also reported by other works (e.g. Hassen et al. 2019).

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3.3 Foraminiferal content

~~Along both records, the benthic foraminiferal assemblage was abundant, well diversified and preserved. The highest total abundance was recorded in the lower part of both cores from the base up to cm 25-24bsf (average values of ~1000-1200 Ng^{-1} in both cores, with an abundance peak of ~2000N g^{-1} at cm 48-47bsf in CORE19), then abundance gradually decreased (respectively up to cm 8-7 in CORE19 and 6-5 bsf in CORE18, ~400 Ng^{-1}). In the uppermost centimetres of both cores, total abundance rapidly increased again (~1700 Ng^{-1} at the top of CORE18) (Fig. 4, Tab. S4 supplementary data).~~

The non-indigenous species *Amphistegina lobifera* showed the same distribution pattern in both cores, thus indicating that the collected data are well replicated (Fig. 4, Table S4 supplementary data). ~~T~~Starting from the core bottom, the species was sporadically present with very low abundances (< 1 specimen per gram of dry sediment - Ng^{-1}) in the lower part of both cores, from cm 40-39 up to cm ~~30-29~~ 29-28 bsf, then it abruptly disappeared (Fig. 4). ~~The highest occurrence was recorded in CORE19, at cm 29-28bsf.~~ After an interval of over 10 cm where the species was missing, *A. lobifera* occurred again in the studied records, respectively, in CORE19 at cm 17~~6~~-16~~7~~bsf and in CORE18 at cm 15-14bsf. In the upper part of both cores, *A. lobifera* was continuously present with an increasing trend of abundance ~~upwards,~~ that became more accentuated from cm 7-6 bsf up to the core top (Fig. 4).

Along both records, the benthic foraminiferal assemblage was abundant, well diversified and preserved (Fig. 5), with a peak of ~2000N g^{-1} at cm 48-47bsf in CORE19 (Fig. 5; for full data see also Table S4, supplementary data). The benthic foraminiferal assemblage was dominated by epiphytic taxa (average values of 1000 Ng^{-1}), that continuously and abundantly occurred along both cores. Other benthic foraminifera, such as the agglutinated species *Textularia pseudorugosa* and *T. pala* and the genus *Ammonia*, were always subordinated (40-70 Ng^{-1}) and did not show any particular distribution patterns along the cores (Fig. ~~4~~5). Epiphytic foraminifera mainly consisted of permanently motile miliolids (group D of Langer, 1993), with total abundances varying between 250 and 1000 Ng^{-1} in CORE18 and 200 and 800 Ng^{-1} in CORE19; other epiphytic groups (A-C) had lower abundances, usually < 400 Ng^{-1}. Group A (sessile taxa) was characterised by a decreasing trend of abundance from cm 25-24 bsf up to top. Average absolute abundances changed dramatically from the lower to the upper core, from 141.6 ± 33.5 Ng^{-1} to 85.2 ± 29.3 Ng^{-1} in CORE18, and from 301.5 ± 69.4 Ng^{-1} to 96.2 ± 30.9 Ng^{-1} in CORE19. According to the unpaired *t*-test, between upper and lower core in terms of Group A abundance were statistically significant in both cores (Table 1; for full data

Commented [R111]: Figure 4, first graph of A. lobifera. I feel like this is THE graph for this paper, but it is really hard to see the lines for the cores at the deeper depths. I wonder if it would be a better idea to pull this one graph out and make it large, like you did for figure 3 (which in my opinion, it not THE graph)

Reply: thank you for the suggestion. We have prepared a larger and better defined version of figure 4 reporting the single curve of absolute abundance of *A. lobifera* down core. We have added some graphic details that make it easier for the reader to observe. Then, we have moved information on other species to a new Figure 5. Finally we have renumbered all the other figures.

Commented [R12]: Results: "The highest occurrence [of Amphistegina] was recorded in CORE19 AT CM 29-28 bsf". Figure 4A suggests a depper depth (around 30-40).
Reply: The historical records are commonly described by micropaleontologists from bottom to top, following the stratigraphic order. With this purpose, Higest Occurrence (HO) is used to indicate the uppermost level where the species occurs in the record (in this specific case, within the lower portion of the studied cores, it corresponds to cm 29-28 bsf); by contrast Lowest Occurrence (LO) is used to indicate the lowest level where the species occurs in the record, that also corresponds to the deepest level in the core (in this specific case, within the lower portion of the studied cores, it corresponds to cm 39-40 bsf). To avoid confusion, the sentence was deleted.

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Commented [R14]: - The similar applied to the abundance of epiphytic foraminifera (both total abundance, different groups according to their motility and some species such as S. orbiculus). In the discussion section it is suggested that abundance of M. miniacea, P. mediterranea and S. orbiculus increased along the rapid burial event but that can not be inferred from the data provided in figure 4B.
Reply: In the text we added some quantitative data that can help the reader and a table with statistical comparisons (Table 1). Moreover, as previously anticipated, in Fig. 4 (now Fig. 5) we added a grey strip that marks the stratigraphical level where major micropaleontological changes occurred, along with other details.

see also Table S4, supplementary data). By observing, in fact, the abundance curves of the species belonging to this group (Fig. 45b, Table. S4, supplementary data), both *Miniacina miniacea* ~~disappeared in the upper part of both~~ records and *Planorbulina mediterranensis* significantly decreased in abundance (Table 1)~~markedly reduced its abundance, from 440 Ng^{-1} at cm 48-47bsf to ~7 Ng^{-1} at cm 17-16 bsf in CORE19~~. *Sorites orbiculus* showed a decreasing abundance trend in the lower part of both records up to cm 25-24 bsf, then, after an interval where abundance was constant (average values around 10 N g^{-1}), it markedly increased (30-40 Ng^{-1}) from cm 7-6 bsf up to top.

Planktonic foraminifera (e.g. *Globigerinoides* spp.) only occurred~~,~~ as very few specimens~~)~~ in some samples in the lower part of the studied cores (Fig. 45). They occurred together with scarce benthic foraminifera, such *as Uvigerina peregrina*, *Reusella spinulosa*, *Bulimina marginata*, *Bolivina variabilis* and *Buccella granulata* (Fig. ~~5~~6), typical of deeper environments in the Mediterranean Sea (Murray, 2006; Milker et al., 2009) and whose presence is quite unusual at littoral depths (16 and 17 m depth for the studied cores). Reworked foraminifera were sporadically present along the records and consisted exclusively of few Miocene planktonic specimens belonging to the genera *Globigerinoides* (*G. immaturus* and *G. trilobus*) and *Globigerina* supplied by the homonym formation around Marsamxett Harbour.

From the core bottom up to cm 245-24 bsf, the washed residues also contained very abundant remains of *P. oceanica* (Fig. 2b), sometimes with epiphytic specimens still attached to the largest fragments, together with gastropod and fewer bivalve shells, and echinoid plates and spines. Noteworthy is that most of the mollusc shells were~~as~~ still perfectly coloured and some of them were broken with sharp edge fractures (Fig. 7~~6~~, images 6-9). On the contrary, the shells from the upper core interval were not commonly well preserved: the external shell surface was opaque, sometimes abraded and often bio-perforated (Fig. 7~~6~~, image 15).

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Reply: the sentence has changed

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Commented [R117]: Page 10 line 54: remove parentheses
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Commented [R18]: - Although some patterns of the abundances of mollusc shells along core portions are highlighted, no data are provided.
Reply: Indeed we did not measured molluscs in terms of abundance, but limited our observations to the preservation status of the shells.

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3.4 Calcareous nannoplankton content

Since in shallow waters (shallower than 12 m depth) the wave motion can prevent the deposition of the smallest-sized sediment particles (<20 µm), such as nannoplankton remains ("high energy gap" by Ferreira & Cachão; 2005), the analysis of calcareous nannoplankton content was used to investigate the hydrodynamic conditions of the sampling site.

The continuous occurrence of nannoplankton down core in both records (Fig. ~~7~~8), collected at 16 m and 17 m depth respectively, indicated that the energy conditions were suitable for nannoplankton deposition. In the lower part of both records, total abundance was characterised by a decreasing trend ~~up to cm 27-26 bsf~~ : starting from cm 41-40, abundances progressively decreased, changing from maximum values of about 26 Nmm^{-2} in CORE18 and of 20 Nmm^{-2} in CORE19 to (minimum values of 4-7 N mm^{-2} in the ~~core interval 30-26 cm bsf~~stratigraphic interval from cm 30-29 to 27-26 bsf of both records.~~) followed by a marked increase from cm 26-25 bsf upwards (Fig. 7)~~. Moving upwards, from cm 26-25 up to top, absolute abundances markedly increased, recording average values of about 16 Nmm^{-2} in both cores, with peaks of 29 Nmm^{-2} in CORE18 and of 28 Nmm^{-2} in CORE19 (Fig. 8; Table S5, supplementary data). The identified assemblages were dominated by reworked taxa, late Oligocene to early Miocene in age, supplied from the active erosion of rocks cropping out all around Marsamxett Harbour (*Globigerina* Limestone Formation). Modern species were always rare to very rare and mainly consisted of the long-ranging *Coccolithus pelagicus* and *Gephyrocapsa oceanica* and *Emiliana huxleyi*. The K-strategist *Florisphaera profunda*, a species living in the deep photic zone (100-200 m depth) in the open sea, sporadically occurred at cm 36-35 and 31-30 bsf, in the same samples where deep-sea benthic foraminifera and planktonics were also found (Fig. ~~4~~5). The studied smear slides also contained very

Commented [R20]: - Regarding calcareous nannoplankton, a lower total abundance up to cm 27-26 is also highligted, followed by a marked increase (e.g. "The marked and sudden increase of coccolith abundance in the upper portions of both cores, starting from cm 25-26 bsf up to the core top (Fig. 7)... "). Minimum and maximum data are provided but, again, some additional data would be helpful since the high variability observed in Figure 7 makes harder to identify clear patterns.
Reply: Thank you for this suggestion, we modified the text and the figure (now Fig. 8) to make patterns more clear.

abundant spicules of ascidians (Chordata: Ascidacea). In both records, ascidian spicules were more abundant in the lower part of the cores then they rapidly decreased upwards (Table S5, supplementary data).

4 DISCUSSION

4.1 The 1908 Messina tsunami and its effects on the Maltese archipelago

Tsunamis are among the most catastrophic events on Earth. When tsunami waves reach the coast, they flood wide areas damaging cultivated lands and buildings and causing loss of human life (e.g. Gusiakov et al. 2019 and references therein). Due to its high seismicity and the presence of active volcanoes, the Central Mediterranean basin is one of the main tsunami risk areas in the World (e.g. Papadopoulos et al. 2014). One of the most destructive examples associated with an intense earthquake was the 1908 Messina tsunami; such combined events caused over 80,000 deaths and are considered the worst disaster in modern history in the Mediterranean region (Guidoboni et al. 2007).

On 28 December 1908, a severe earthquake (Mw 7.1) destroyed major towns in eastern Sicily and Calabria, including Messina and Reggio Calabria, and caused a violent tsunami consisting of at least three major waves (Guidoboni et al. 2007). The waves, over 10 m high in the Messina Strait, propagated in all directions reaching the coasts of Maltese islands, Albania, Montenegro and the Greek Ionian islands (e.g. Guidoboni et al. 2007; Pino et al. 2009). Over 100 years after this catastrophic event, the exact cause of the 1908 Messina tsunami remains unresolved (e.g. Billi et al., 2008); nonetheless recent works have proposed a dual earthquake/submarine landslide mechanism (Schambach et al., 2020 and references therein).

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In the Maltese islands, about 250 km south of the epicentre (Fig. 1), the tsunami waves arrived about one hour after the earthquake, causing damages mostly along the eastern, more exposed coasts, as documented by both historical chronicles and field evidence (e.g. Galea, 1909; Borg et al., 2016; Mottershead et al., 2017). The peculiar topography of the eastern coast, characterised by shore platforms due to the general tilting of sedimentary strata towards the northeast, amplified the impact of tsunami waves: the shores were flooded causing massive landslides and the formation of several boulders that accumulated at the top of the submerged escarpment (Mottershead et al., 2017; Biolchi et al., 2016). Along the eastern coasts, fisherman boats were crushed and pushed adrift on the shore inducing a general panic among people; in the Grand Harbour (La Valletta), boats broke their moorings, and the houses at Msida, Sliema and Pieta were inundated (Malta Herald 1908; Borg et al. 2016 and references therein). On the contrary, Marsamxett Harbour, located in a lateral creek, was naturally sheltered from the tsunami waves; in fact no significant damages to buildings and boats were reported, but only a going and coming of the sea several times during the day (Borg et al., 2016).

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4.2 Combined evidences for a sudden high energy depositional event

It appears clear from the core records described here that *A. lobifera* arrived very early in time in Marsamxett Harbour, Malta island, but the species disappeared soon thereafter. It took several decades before the species re-appeared in the records, starting the current colonization as described in Guastella et al. (2021). If the age model derived from radiometric analyses (~4.5 years for each centimetre of sediment; Table~~.~~ S3 supplementary data) is regularly applied along the whole cores, it would appear as if the onset of the early invasion recorded at cm 39-40 bsf happened around 1840. However, this is clearly an unrealistic conclusion because the Suez Canal, through which *A. lobifera* passed to enter the Mediterraean (Prazeres

et al. 2020) opened in 1869. Therefore, in order to explain the presence of *A. lobifera* in the core bottom we formulated two alternative interpretations of the age model: I) altered patterns of ^{210}Pb decay, but this seems highly improbable since ^{210}Pb activity curves show otherwise; and II) occurrence of a rapid depositional event, which could have altered the sedimentation rate and caused the sudden accumulation of a thick layer of sediments in the lower portion of both records. This second hypothesis is supported by the data that yield several lines of evidence for a sudden high-energy depositional event. In both cores, ~~significant~~ changes in sediment grain-size, porosity and micropaleontological content occurred at around cm 25-24 bsf (Figs. 2, 5, 8), dividing the studied records into two distinct parts, a lower and an upper part. The lower part mainly consisted of grey mud and very fine sands with a higher porosity (reasonably due to the high content of water contained in the *P. oceanica* remains) and a higher content of undecomposed organic matter with symptoms of anoxic conditions, which are compatible with a sudden burial of live organisms. Sediments also contained abundant mollusc shells perfectly preserved, still coloured and, sometimes, as noted above, broken with sharp edge fractures (Fig. ~~6~~7), distinctly different from the depigmented, eroded and bio-perforated shells of the upper layers (Fig. ~~6~~7, image 15), which likely remained for a long time on the sea-floor before burial. Moreover, very abundant epiphytic foraminifera (e.g. *M. miniacea*, *P. mediterranensis* and *S. orbiculus*), sometimes still attached to the largest leaves of *P. oceanica*, were incorporated in the mud (Fig. 2b). All of this evidence suggests a very rapid burial of molluscs, foraminiferal shells and *P. oceanica* remains, probably caused by a high-energy depositional event that, at the same time, uprooted *P. oceanica* from the sea floor, broke mollusc shells and prevented the deposition of coccoliths (nannoplankton remains). The marked and sudden increase of coccolith abundance in the upper portion of both cores, starting from cm ~~25-26~~ 26-25 bsf up to the core top (Fig. ~~7~~8), suggests a consequent rapid decrease in depositional energy, that allowed the accumulation of the finest

sediment particles, as coccoliths. Additionally, the upper portion of both cores was characterised by a decrease of porosity, related to the absence of *P. oceanica* remains (Fig. 2a).

4.3 The tsunamiite deposited in Malta after the 1908 Messina earthquake

Considering the lower part of both cores (from 25-24 ~~25~~ cm bsf down core) as the sedimentary product of a rapid high-energy depositional event and applying the current age model of 4.5 years per each centimetre of sediment (Table S3 supplementary data) limitedly to the upper part of both cores (from the top down to cm 25 bsf), we could infer that the upper core records correspond to a time interval spanning from 2019 (the date of collection) to about 1905. In particular, sediments from cm 25-24 bsf have accumulated from 1905 to 1910, and thus they could represent the top of a high-energy depositional event of 1908, the year of the catastrophic earthquake occurred off the coast of Messina (Sicily). This abrupt geological event generated, as noted earlier, a violent tsunami, that quickly reached the Maltese coasts (Galea, 1909; Borg et al., 2016; Mottershead et al., 2017). We suggest that the lower muddy part of both cores, from the base up to ~ cm 24 bsf, could represent the tsunamiite deposited by the tsunami waves within Marsamxett Harbour, Malta.

Tsunami deposits recorded in sediment cores from deep-water settings (e.g. off Augusta Bay, eastern Sicily; Smedile et al., 2012) are easily recognised, thanks to their peculiar sedimentary signatures, such as the distinct erosional base, coarse-grained and gradated layers and a high content of shallow-water taxa, *P. oceanica* remains and beach debris displaced from the shore by the backwash wave. On the contrary, tsunamiites recorded in historical records from coastal areas are more rare and difficult to be recognised, mainly because transitional environments are subjected to continuous current reworking and human disturbance activities, and because tsunami waves can leave little or no sedimentary record (Dawson and Stewart,

2007; Noda et al. 2007; Judd et al. 2017). Nonetheless, in coastal areas, tsunami deposits can mimic other high-energy depositional events, such as storm waves, and thus they can be frequently confused with tempestite layers (Nanayama et al., 2000). In shallow-water contexts, tsunami deposits usually do not exceed a few tens of centimetres in thickness and do not display peculiar sedimentary signatures apart from a higher content of mud, sometimes characterised by rare laminae, and an abrupt erosional basal surface that is cut when seabed sediments are suspended (Dawson and Stewart, 2007; Papadopoulus et al., 2014; Biguenet et al., 2021). These features depend on the hydrodynamic conditions during transport and sedimentation and on the coastal topography (Dawson and Stewart, 2007; Papadopoulus et al., 2014). Shallow-water tsunamiites are also characterised by abundant biogenic remains (mollusc shells, marine plants, ostracods and foraminifera), which are commonly incorporated in the mud and can display broken shells due to the turbulent water movement (Dawson and Stewart, 2007 and references therein). Some of them could have originated in deeper environments followed by landward transport by the tsunami wave (Nanayama and Shigeno, 2006).

Our sedimentological and micropaleontological results described above agree with the typical depositions triggered by a tsunami in coastal settings (Dawson and Stewart, 2007; Noda et al. 2007; Judd et al. 2017; Biguenet et al., 2021). As reported in historical newspapers, in the naturally sheltered bay of Marsamxett Harbour in Malta the tsunami waves caused only a going and coming of the sea several times during the day (Borg et al., 2016 and references). The oscillatory wave movement probably reworked sea bottom sediments, keeping the fine-grained particles suspended, perhaps for days before settling out, depending on the scale of residual turbulence, but without any significant transport landwards or seawards. As a result, a tsunamiite (about 25 cm thick) accumulated ~~burying~~and buried the sea bed in Marsamxett Harbour. Unfortunately, both cores failed to record the tsunamiite base, since the basal

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erosional surface and the abrupt change in sediment grain-size are missing. Therefore, it is impossible to determine when after 1869 *A. lobifera* really arrived in Marsamxett Harbour. Yet, we can document the presence of its remains within sediments deposited before 1908 and, then, remobilised by the tsunami waves, which is a surprising and significant backdating of *A. lobifera*'s first arrival in the Central Mediterranean Sea (Guastella et al., 2021). We also explored the possibility ~~to~~ of carrying out further radiometric analyses (e.g. radiocarbon dating) directly on *A. lobifera* tests picked from the tsunamiite interval (e.g. Gottschalk et al. 2018; Guerra et al. 2019). However, the current ^{14}C method works poorly for such recent records (since this isotope has a half-life of about 6 ky), and the error that usually derives from the different measurements (~ 20-30 years) is comparable to the resolution interval, thus preventing a precise age determination. Furthermore, since the nuclear tests carried out since the 1950s have altered the natural signal of this radiogenic isotope (the so called "bomb effect", Nydal and Lövseth 1983), ~~the~~ application of the ^{14}C method is more then unreliable for records younger than 150 yr.

We are aware that there can be other causes of population extinction within a sedimentary record that could be invoked, but the correlation in time and space with the Messina's tsunami event recorded in both cores appears rather persuasive.

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4.1 Triggering mechanisms for the early failed invasion

The 1908 tsunami may hence have caused the failure of the early invasion of *A. lobifera* in Marsamxett Harbour through a cascade of events. First, the rapid deposition of the tsunamiite buried the seagrass meadow under over 25 cm of muddy sediments, damaging and causing a drastic change of habitat for most benthic foraminiferal species, including the target taxon. In fact, the *P. oceanica* meadow existing in the harbour was probably unable to recover and

develop new patches, as documented by the absence in both cores of *P. oceanica* remains above the tsunamiite. Since this plant has very low growth rates (Cabaço et al., 2008; Noè et al., 2020), its recovery after a destructive event is highly unlikely in the human time scale. Therefore, the sea bottom of Marsamxett Harbour in Malta appears to have irreversibly changed after the 1908 tsunami. All of the benthic community was directly impacted by this sudden depositional event, as supported by the decreasing trend in abundance of sessile epiphytic foraminifera (Fig. ~~4~~5), which suffered a rapid decline and never fully recovered in subsequent years, as documented by the ~~disappearance~~ marked reduction of *Miniacina miniacea*. Ascidians also likely reduced their abundance as a probable consequence of the habitat damage (Table S6, supplementary data). This response has been observed for some Mediterranean ascidian populations, known as "regressive species" (Naranjo et al., 1996), which disappear or reduce their populations when the habitat conditions become stressful. The invasive species *A. lobifera*, which abruptly disappeared from Marsamxett Harbour, may have experienced a similar fate. As we noted in the Introduction, failed invasions are by their very nature difficult to detect and, likely, overlooked the vast majority of the time. Similarly, we do not know how many successful invasions were preceded by either failures or by very long lag times in developing robust populations to the point where they may be detected in random sampling. Some failures are due (as we also noted earlier) to environmental mismatches, while others could be due to habitat changes. Thus, while the well-known European shore crab *Carcinus maenas* has been found alive in tropical environments around the world, no populations of this colder-water crab became established in lower latitudes (Carlton & Cohen, 2003). A non-native cephalaspidean "bubble snail," *Bulla* sp. (identified at the time as *B. adamsi*; see Malaquias & Reid, 2008) became established on Oahu (Hawaii) in the 1940s, but it is believed that habitat destruction destroyed the populations (Carlton & Eldredge, 2009). The European shore snail *Truncatella subcylindrica* was found living

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abundantly intertidally in Newport, Rhode Island, USA in 1880 (Verrill, 1880), but no vestiges of the original shoreline remain today (JTC, personal observations), suggesting habitat destruction may have played a role ~~here~~in its invasion success as well. The European ascidian *Ascidiella scabra* was collected in the 1860s in Japan, but disappeared for unknown reasons (Nishikawa & Otani, 2004). A more recent example of the failure of a marine invader is ~~the case history of~~ the European sea anemone *Sagartia elegans*, which thrived for nearly a decade under the influence of a powerplant thermal discharge in New England before becoming extinct (Wells & Harris, 2019). Perhaps more similar to the present case of natural disaster-induced population obliteration is the history of the Indo-Pacific soft coral *Dendronephthya* sp. in the Hawaiian Islands, a growing colony that~~of which~~ had been established for at least 7 years, but which then abruptly disappeared coincident with the passage of Hurricane Iniki over the exact site where it occurred (Carlton & Eldredge, 2009). Similarly, t~~T~~sunamis play a significant role in impacting and shaping populations of intertidal and shallow water marine species (e.g. Kanaya et al. 2012; Miura et al. 2012; 2017; Urabe and Nakashizuka, 2016).To our knowledge, *A. lobifera* is the first modern-day invasion that was apparently rendered extinct by a tsunami.

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5 CONCLUDING REMARKS

The non-indigenous foraminiferan *Amphistegina lobifera* has a curious and complex history in Malta, as now more fully revealed by sedimentary cores and radiometric analyses. We here suggest a three-phase invasion model leading to the current presence of this Indo-Pacific species in the Maltese archipelagos.

In Phase I, *A. lobifera* invaded the Mediterranean reaching the Maltese coast sometime before 1908. The 1908 Messina earthquake and tsunami then destroyed these early populations. In

Phase II, *A. lobifera* re-invaded the island of Malta in the mid-1940s (Guastella et al. 2021). It then remained in relatively low numbers over the next six decades. In Phase III, *A. lobifera* became abundant enough to be discovered alive in the Maltese archipelago in 2006 (Yokeş et al. 2007), perhaps due to ocean warming leading to population surges (Guastella et al. 2021). Thus, there was a significant lag time after 1908 before *A. lobifera* reappeared and became re-established, and another significant lag time after the mid-1940s before it became sufficiently abundant to be detected. While it is not impossible that residual populations remained after the 1908 tsunami, we are not at this time aware of a mechanism which would have led earlier remnant populations (if indeed they existed) to undergo a population expansion in the 1940s, parallel to the probable warming trigger of the early 21st century, leading us to conclude that the 1908 event did in fact render *A. lobifera* extinct in the Mediterranean in the early 1900s.

Finally, the revelation that this non-indigenous foraminiferan has a much deeper history than that reported by conventional sampling of living populations suggests that the invasion of the Mediterranean Sea after 1869 may have commenced far earlier than suspected for many species. Put another way, it would appear unlikely that this small shelled protist is the only Lessepsian invader to have entered the Mediterranean long before it was first detected.

Acknowledgements

Sonia Albertazzi (CNR-ISMAR) and M. P. Riccardi (university of Pavia) are thanked for radiometric analysis and SEM photos, respectively. We acknowledge two anonymous reviewers for their constructive comments.

Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Author Contributions

NM and AM developed the idea; AC and JE collected and sampled the cores; NM, RG and MC performed micropaleontological analyses; LL carried out radiometric dating; MC and LC interpreted sedimentological data. All authors contributed to interpretation of results and discussions and wrote the manuscript, with relevant contributions from JTC.

Data availability statement

All data generated or analysed during this study are included in this published article [and its supplementary online material].

Conflict of interest statement

The authors have no competing interests to declare that are relevant to the content of this article.

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TABLES

Table 1: Differences in sediment composition between lower and upper core portions (threshold corresponds to 25-24 cm bsf; see also Figg. 2, 4, 5, and 8). Sediment composition is represented by: percentage of fine sediments (fine sand + very fine sand + mud), percentage of mud, and abundance of selected foraminifera (Group A = sessile species, *M. miniacea* and *P. mediterranensis*). All variables are shown as average values ± SD. Results of unpaired *t*-tests (lower-core *vs* upper-core) are also reported.

		Sediment fraction (%)		Foraminifera abundance (N g^{-1})		
		Fine fraction	*Mud*	Group A	*Miniacina miniacea*	*Planorbulina mediterranensis*
CORE18	Lower-core	63.1%± 2.7%	33.4%± 4.8%	141.6 ± 33.5	8.7 ± 6.1	119.9 ± 28.6
	Upper-core	49.7%± 8.1%	22.1%± 5.8%	85.2 ± 29.3	1.6 ± 2.3	67.7 ± 28.5
	t-value	*5.2754*	*5.0242*	*4.4820*	*4.0330*	*4.5731*
	p-value	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*
CORE19	Lower-core	64.9%± 3.1%	29.7%± 1.9%	301.5 ± 69.4	20.4 ± 10.5	229.6 ± 58.3
	Upper-core	50.6%± 5.3%	19.8%± 3.9%	96.2 ± 30.9	2.51 ± 3.4	65.0 ± 21.9
	t-value	*8.9344*	*8.9777*	*9.5124*	*5.9661*	*9.5334*
	p-value	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*<0.001*

FIGURE CAPTIONS

Figure 1: a-b) The Mediterranean basin and the Sicily Channel with the probable epicentre of the tsunami generated by the 1908 Messina earthquake (Billi et al. 2008). **c-d)** Location of the sampled site in Marsamxett Harbour (Malta island); note the sheltered position within the natural bay with respect to the probable direction of tsunami waves.

Figure 2: a) Images of the sectioned cores and sediment grain-size and porosity curves of the studied records; b) detail of CORE19 showing abundant rhizoids of *Posidonia oceanica* and macroscopic mollusc shells often fragmented; c) the sectioned CORE-19 and its containing tube: note the rust-coloured portion from cm 25-24 up to top. The grey strip marks the

stratigraphic level where major sedimentological changes occurred. The level has been used to subdivide the cores in two portions (lower and upper) and corresponds to the probable top of tsunamiite.

Figure 3: ^{210}Pb curves showing the typical activity profile decreasing with depth and scatter-plots reporting a constant SAR, respectively of 0.20 cm yr-1 for CORE18 (in red) and 0.22 cm yr-1 for CORE19 (in blue); this last value was utilised in the applied age model, which leads to an estimated time interval of about 4.5 years for each cm of sediment.

Figure 4: Total abundance (N g^{-1}) of ~~benthic foraminiferal assemblage along the studied records: **a)** *Amphistegina*. *Lobifera*~~. The grey strip marks the stratigraphic level where major sedimentological changes occurred.~~, total benthic foraminifera, total epiphytic foraminifera (Groups A to D); **b)** the most abundant species of Group A (*Miniacina miniacea*, *Planorbulina mediterranensis*, *Sorites orbiculus*) and other components of the assemblage.~~

Figure 5: Total abundance (N g^{-1}) of benthic foraminiferal assemblage along the studied records: a) total benthic foraminifera, total epiphytic foraminifera (Groups A to D); b) the most abundant species of Group A (*Miniacina miniacea*, *Planorbulina mediterranensis*, *Sorites orbiculus*) and other components of the assemblage. The grey strip marks the stratigraphic level where major sedimentological and micropaleontological changes occurred.

Figure ~~5~~6: SEM images in secondary electrons of deep-sea benthic foraminifera from the tsunamiite interval of both records. Scale bars are 100 µm. 1:*Siphonina reticulata* cm 31-32bsf. 2: *Angulogerina angulosa* cm 31-32bsf. 3a,b: *Uvigerina peregrina*; a specimen from cm 31-32bsf, b specimen from cm 29-30bsf. 4: *Siphouvigerina* sp. cm 27-28bsf. 5: *Reussella spinulosa* cm 24-25bsf. 6: *Bulimina aculeata* cm 30-31bsf. 7: *Bolivina variabilis* cm 31-32bsf. 8: *Brizalina* sp. cm 27-28bsf. 9: *Fissurina* sp. cm 27-28bsf. 10a,b *Buccella granulata* cm 31-32bsf. 11: *Lenticulina cultrata* cm 24-25bsf.

Figure ~~6~~7: Photos at the stereomicroscope of gastropod and bivalve shells from the tsunamiite interval of both cores. Note the specimens characterized by shells perfectly preserved and still coloured, but mechanically broken (images 6-9) indicative of a very rapid burial. For comparison is reported a gastropod specimen badly preserved from the upper core record, indicative of its staying on the sea-floor for long time before burial. Scale bars are 1mm.

1a,b: *Rissoa* sp. (Rissoidae) cm 33-34 bsf. **2:** *Turbonilla* sp. (Pyramidellidae) cm 32-33 bsf. **3:** Triphorid specimen not identified cm 32-33 bsf. **4:** *Parvioris ibizenca* (Eulimidae) cm 29-30 bsf. **5:** *Gibberula* sp. (Cysticidae) cm 35-36 bsf. **6:** Fragmented shell of *Smaragdia viridis* (Neritidae) cm 32-33 bsf. **7:** Fragmented shell of *Gibbula ardens* (Trochidae) cm 30-31 bsf. **8:** Fragmented shell of *Alvania* sp. (Rissoidae) cm 31-32 bsf. **9a,b:** *Tricolia pullus* ((Phasianellidae) cm 31-32 bsf. **10a,b** *Pusillina radiata* (Rissoidae) cm 32-33 bsf. **11a,b:** *Rissoella* sp. (Rissoellidae) cm 20-30 bsf. **12:** *Parvicardium* sp. (Cardiidae) cm 27-28 bsf. **13a,b:** *Tricolia pullus* ((Phasianellidae) cm 53-36 bsf. **14a,b:** *Asperarca* sp. 20-30 bsf. **15:** *Alvania* sp. specimen with the shell surface opaque and bio-perforated, cm 10-9 bsf.

Figure ~~7~~8: Total abundance (N mm^{-2}) of calcareous nannoplankton along the studied records (from the left): total abundance, *Gephyrocapsa oceanica*, *Emiliania huxleyi*, strategist-species, long-ranging species (e.g. *Coccolithus pelagicus*) and reworked taxa. The grey strip marks the stratigraphic level where major sedimentological and micropaleontological changes occurred.

Commented [R35]: - Regarding calcareous nannoplankton, a lower total abundance up to cm 27-26 is also highligted, followed by a marked increase (e.g. "The marked and sudden increase of coccolith abundance in the upper portions of both cores, starting from cm 25-26 bsf up to the core top (Fig. 7)... "). Minimum and maximum data are provided but, again, some additional data would be helpful since the high variability observed in Figure 7 makes harder to identify clear patterns.
Reply: Thank you for this suggestion, we modified the figure (now fig. 8) to make patterns more clear.

SUPPLEMENTARY MATERIAL AVAILABLE ONLINE

Table S1: granulometric data recorded along the studied records (CORE-18 and CORE-19)

Table S2: porosity data recorded along the studied records (CORE-18 and CORE-19)

Table S3: radiometric data and chronological constrain based on ^{210}Pb decay (CORE-18 and CORE-19).

Table S4: Absolute abundance of benthic foraminifera, including the target species *A. lobifera*, recorded along the studied records (CORE-18 and CORE-19).

Table S5: absolute abundance of calcareous nannoplankton and ascidian remains along the studied records (CORE-18 and CORE-19).

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Figure 1

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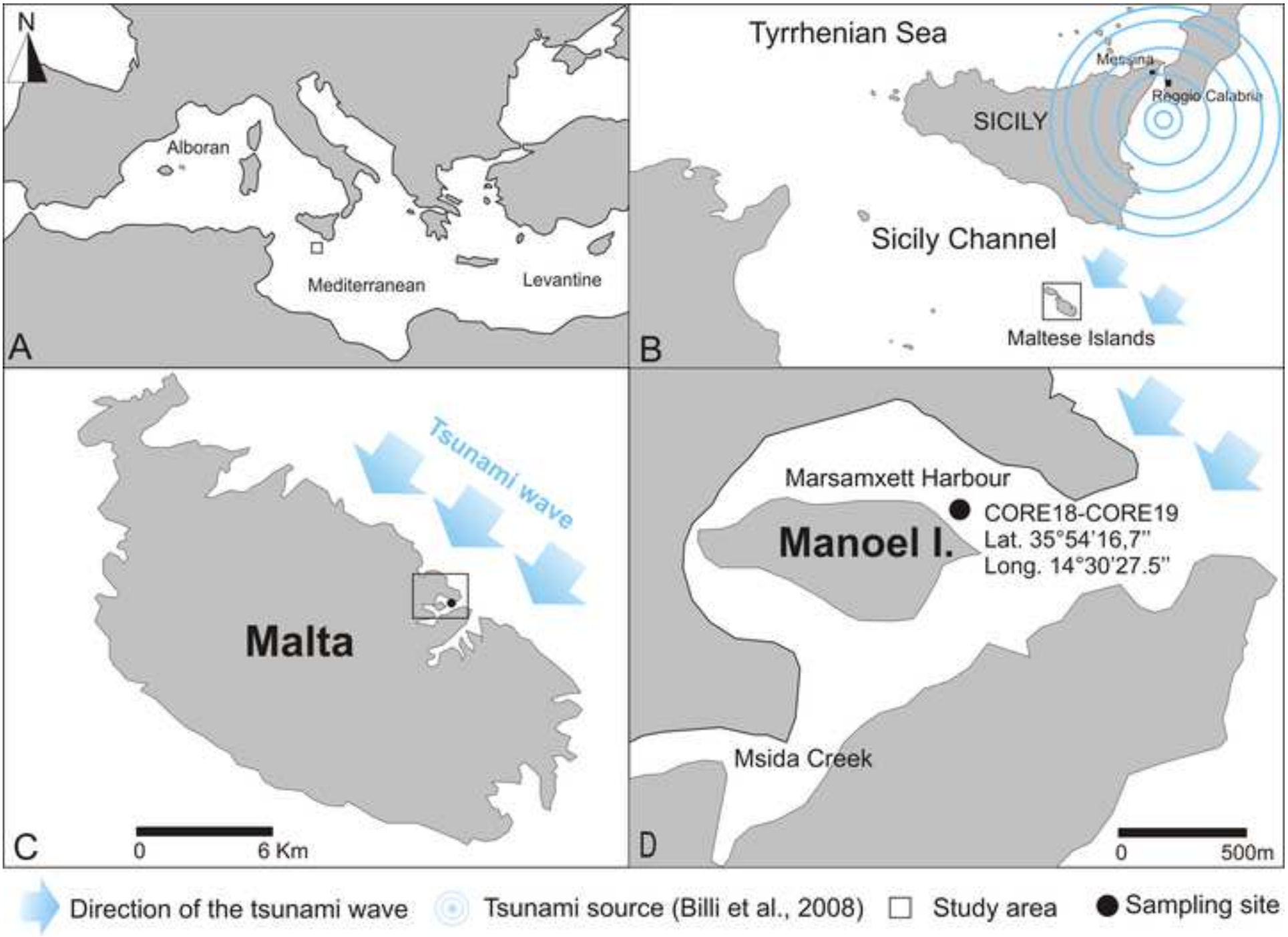

Figure 2

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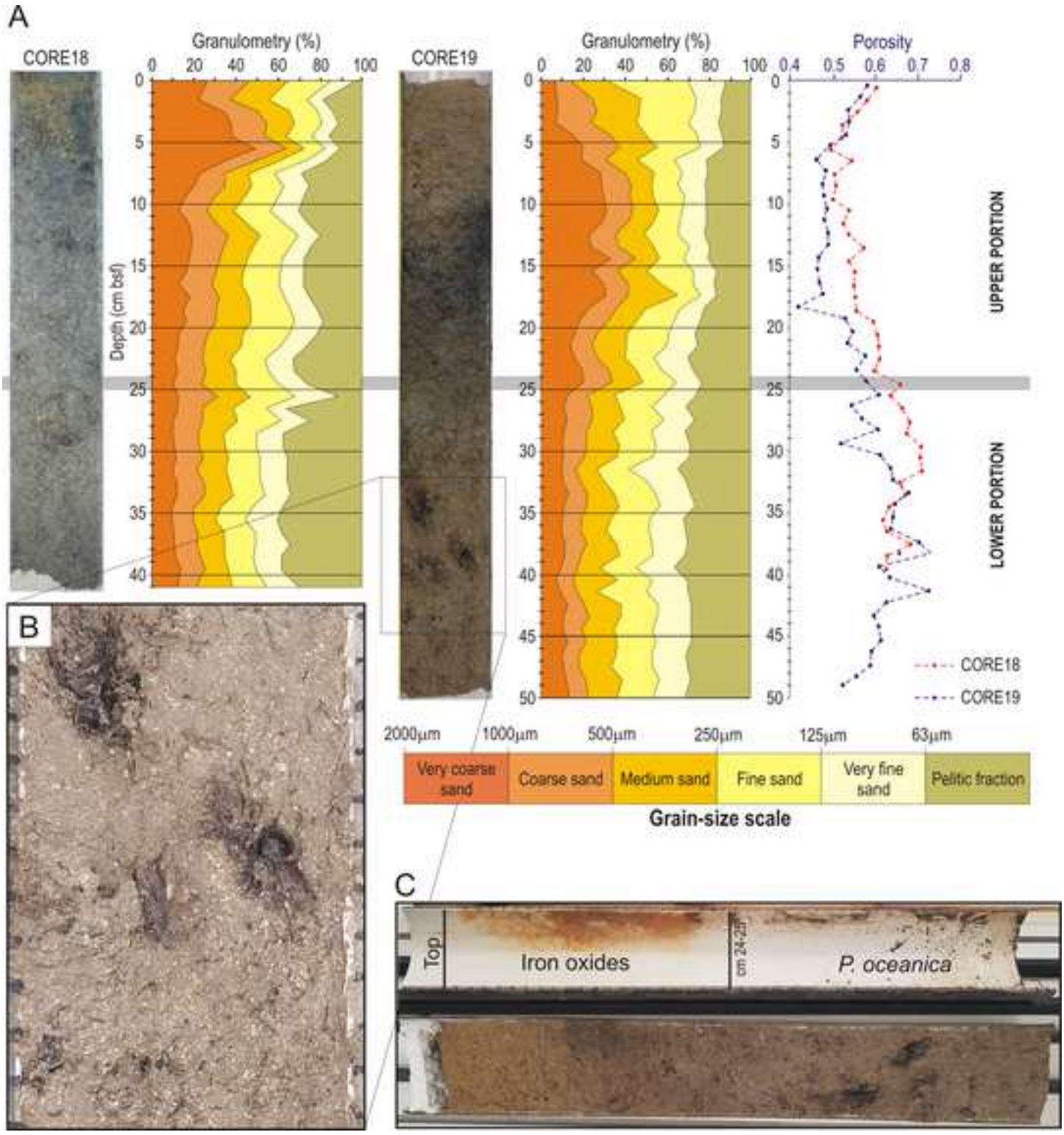

Figure 3

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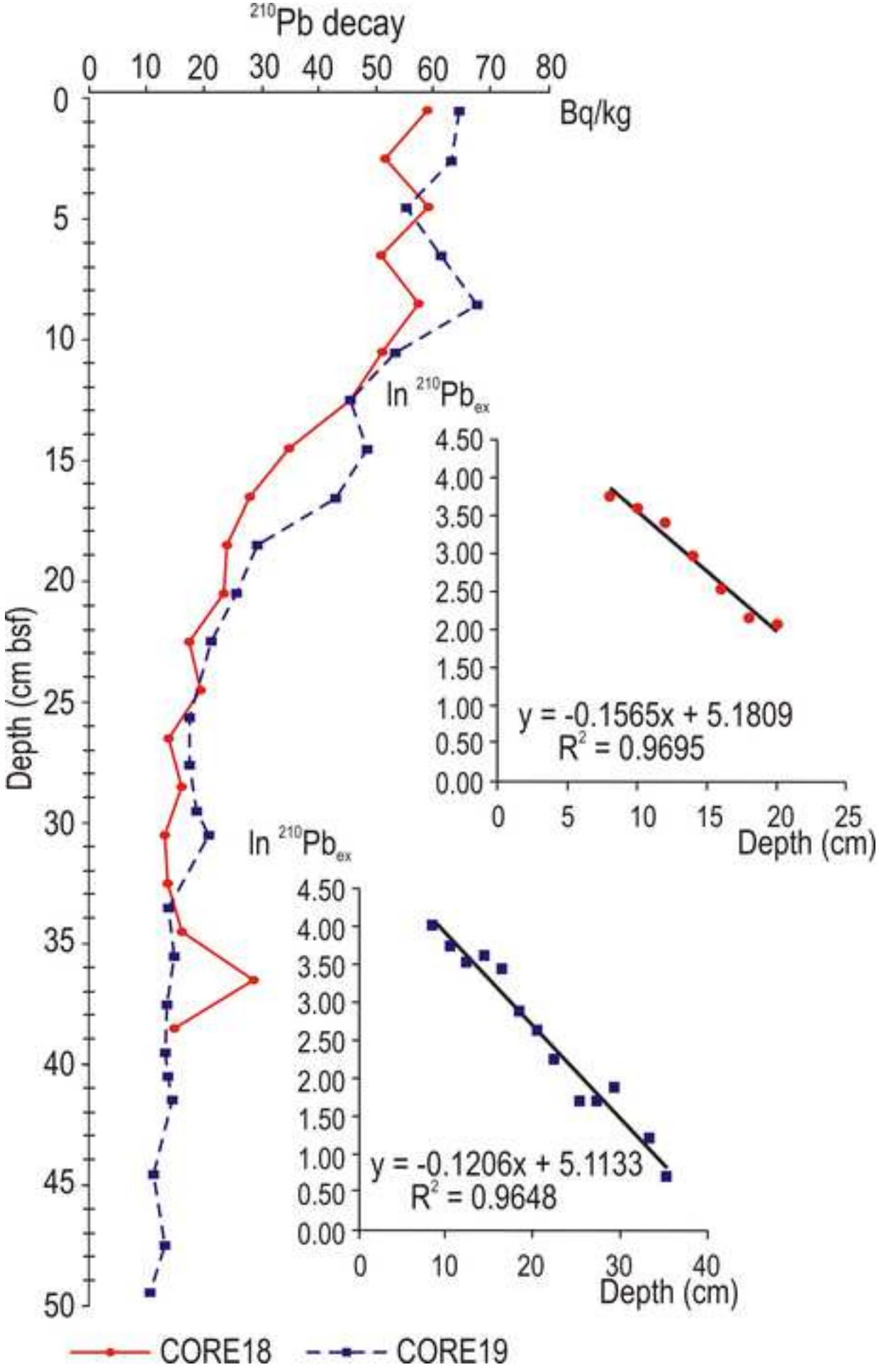

Figure 4

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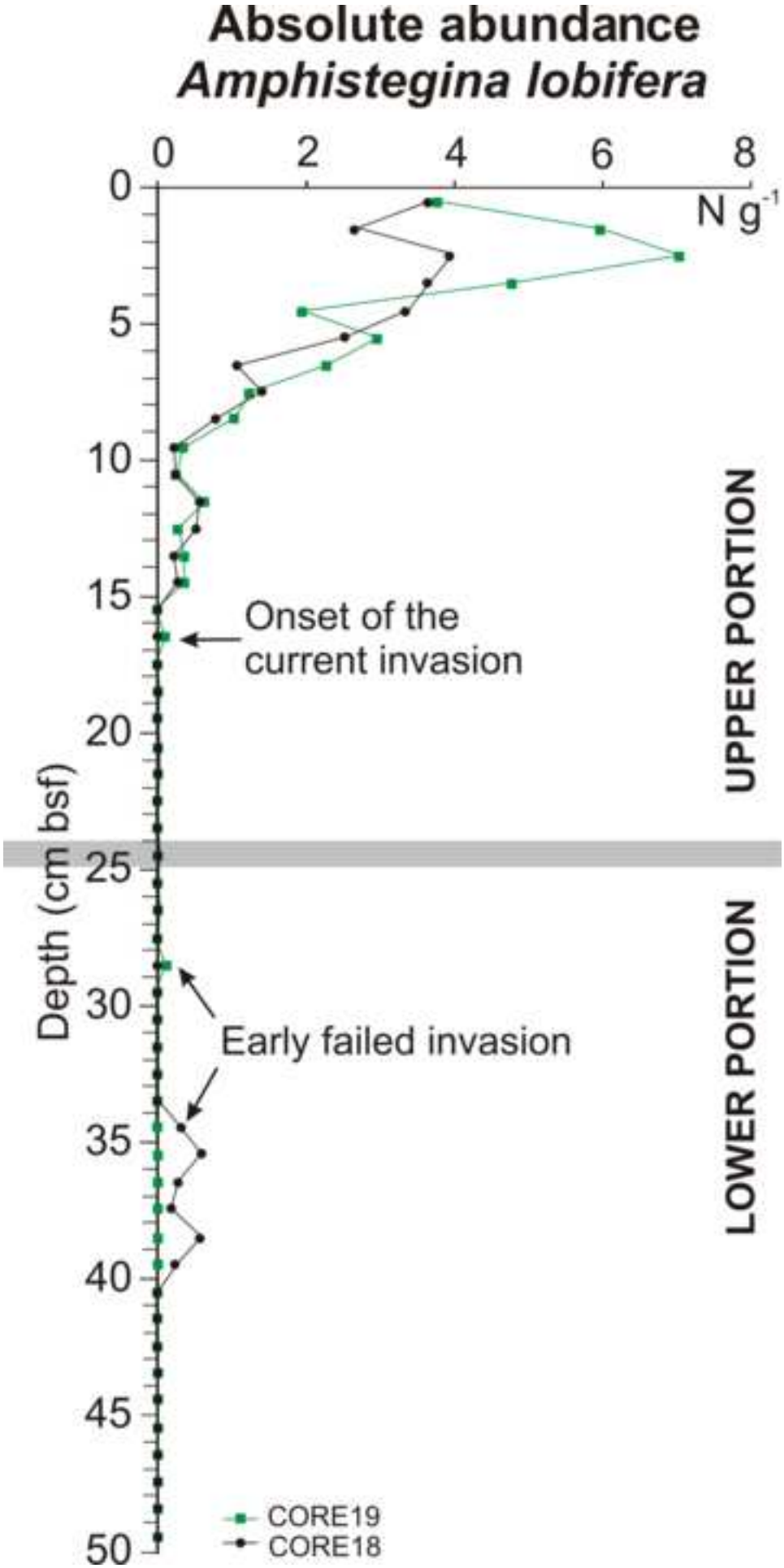

Figure 5

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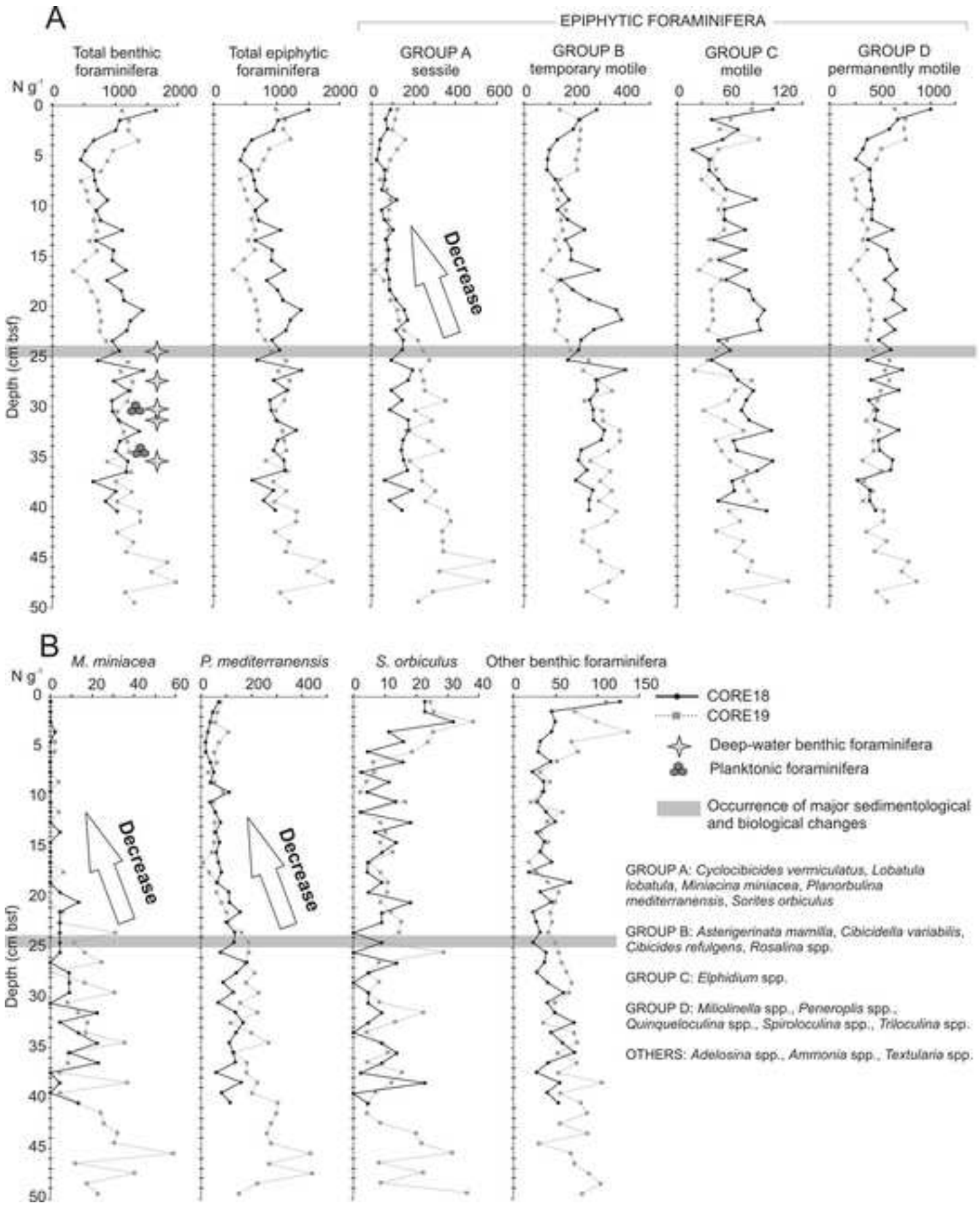

Figure 6

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Figure 7

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Figure 8

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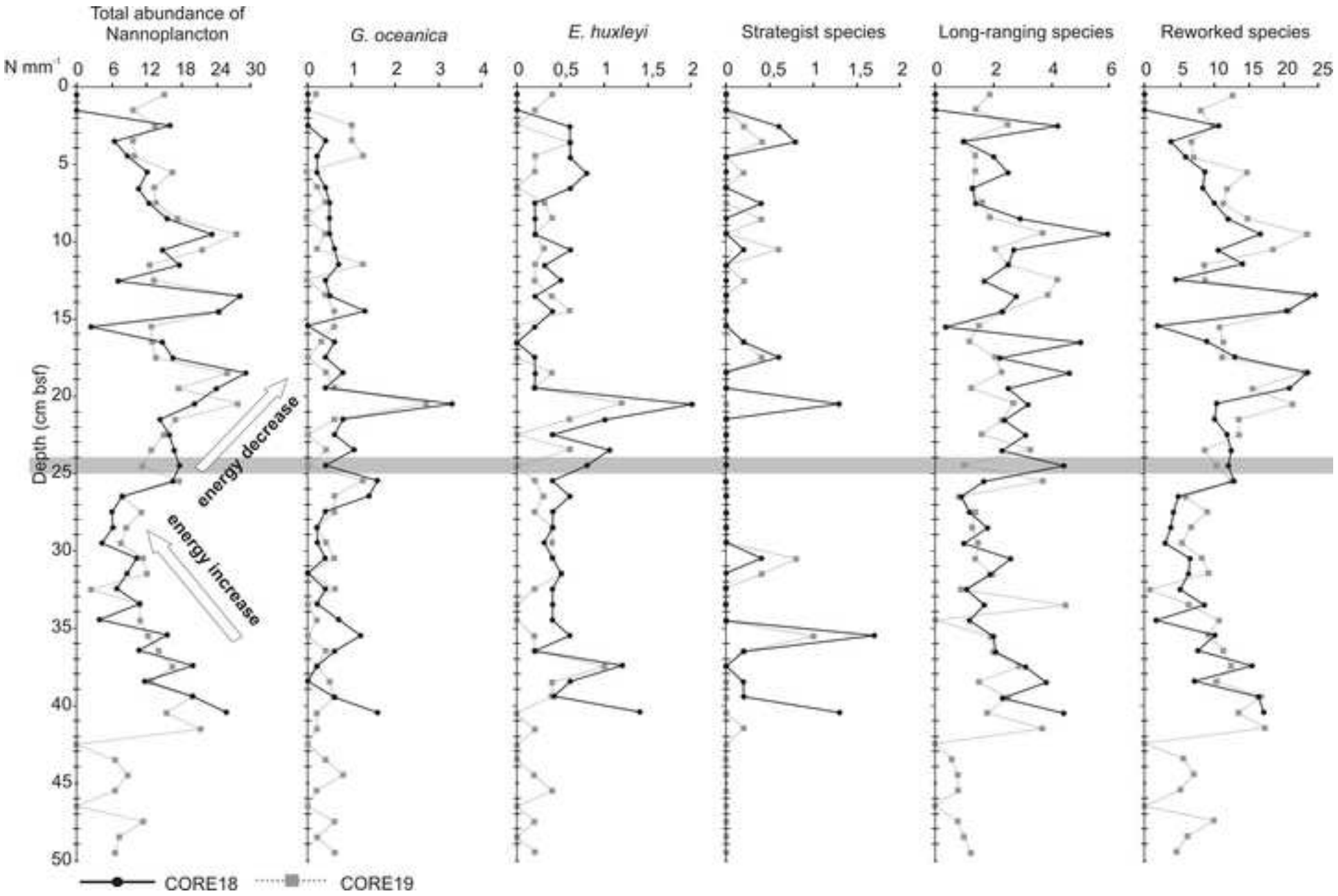

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