REVIEWER 2

This is an original manuscript on a highly relevant topic. I am sure that we will soon witness an explosion in this style of papers. This study is definitely timely. My comments are all minor and aimed towards improving the clarity of the argument, pointing in places to additional background literature. The authors highlight the role of deltaic systems on sedimentary dynamics, noting the higher sedimentation rates in the prodelta in comparison with areas in the northwest Adriatic Sea. Some cores are coming from prodelta settings (Po and Isonzo) and others from areas off strandplains. Deltaic settings are characterized by a complex array of stressors. It is clear that sedimentation rate is a first-rate controlling factor in this area. However, what about other potential factors, such as freshwater discharge, hypoxia, or substrate consolidation in connection with a deltaic source? Some of these (e.g. hypoxia) are assessed through the text, but a better articulation with the deltaic context would be advisable.

Response: We thank the reviewer for all comments. Benthic communities in deltaic environments of the northern Adriatic Sea are affected by a combination of natural and anthropogenic impacts, although it seems that the present-day states are mainly determined by the effects of eutrophication, hypoxia and trawling, and tend to be dominated by species adapted to sediment disturbance (as *V. gibba*) or by mobile species. However, other limits on distribution – salinity, turbidity, and whether the location is below or above the thermocline – are also important. In the Discussion, we have expanded on the ecological (as opposed to the taphonomic) effect of sedimentation rate as follows: "*High sedimentation rates typical of deltaic environments can limit mixing and irrigation via high substrate instability (MacEachern et al., 2005; Bhattacharya et al., 2020), and benthic communities at Po Delta are affected by short-term seasonal variability in sediment input and reworking (Ambrogi et al., 1990; Paganelli et al., 2012). However, water depths at ~20 m at Po prodelta are probably largely beyond the reach of proximal deposition of thicker flood deposits (Tesi et al., 2012) and thus less affected by substrate instability, and tend to be mainly limited by the frequency of hypoxic events (Crema et al., 1991; Simonini et al., 2004; Tomašových et al., 2020).“*

A discussion on other influences on pyritization would be useful as well. For example, the higher abundance of pyritized shells is present in nearshore areas where restricted circulation may have been associated with lower oxygen content. Also, these are areas with higher amounts of organic carbon and iron in the fine-grained sediment. In particular, bioturbation is strongly affected by the interplay of these parameters.

Response: We have revised the manuscript so that it is clear that the focus is on linings formed by clustered pyrite framboids (rather than on pyritization in general). Although the oxygen depletion (owing to limited water circulation or other causes) is certainly one of the key factors in reducing bioirrigation and in fostering the preservation of pyrite linings by reducing its potential to re-oxidation, persistence of bio-mixing can induce the formation of suboxic zones with dissolved iron (especially in organic-rich muds) – this factor is probably necessary to avoid iron limitation and thus to ensure the confinement of H_2S produced during the decay of organic tissues. To clarify our reasoning, we have significantly expanded our Discussion of conditions that are needed for the formation and preservation of pyrite linings (persisting sediment mixing and the lack of intense and deep bioirrigation) as follows:

"*The preferential occurrence of pyrite linings in valves with periostracum and with higher concentrations of amino acids and the negative correlation of pyrite-lined valves with the frequencies of other types of alteration at the scale of increments indicate that pyrite framboids* *formed soon after, or concurrent with, the decay of tissues of V. gibba and associated microbes (framboids arranged in filaments or strings in Fig. 5L or 7F resemble bacterial relicts, Westall, 1999; Wilson and Taylor, 2017). Two steps are necessary for preservation of pyrite-linings in the subsurface stratigraphic record, including their initial formation in reduced microenvironments rich in dissolved iron and (2) the subsequent lack of their reoxidation.*

(1) The early formation of concentrations of pyrite framboids that cluster on valve surfaces requires that the organic tissues within shells do not decay or are not scavenged under aerobic conditions and that sediment is rich in iron so that sulfides produced bu sulfate reduction remain confined to the decay location (Fisher and Hudson, 1987; Raiswell et al., 1993; Farrell et al., 2009; Schiffbauer et al., 2014). Such conditions can occur under the decay of reactive organics in reducing (suboxic) conditions in non-sulfidic, iron-dominated pore-water zones (Berner, 1969; Briggs et al., 1996; Allen, 2002; Raiswell et al., 2008; Stockdale et al., 2010). These early-sequestration conditions can be attained (i) when freshly-dead shells are episodically buried under a deposition of new sediment (obrution, Brett et al., 1997) sourced by river floods or storms, and can decay in reducing conditions beyond the reach of burrowers; the thickness of the obrution deposits needs to be sufficiently high so that pyrite is not reoxidized by burrowing infauna later (Allison, 1988; Brett et al., 2012a, b; Schiffbauer et al., 2014) and/or (ii) when biomass of decaying infaunal organisms is tightly enclosed within shells or in intra-skeletal pores (as in V. gibba), generating reducing microenvironments even without the obrution (Jorgensen, 1977; Thomsen Vorren, 1984), and the oxygen penetration by bioirrigation is shallow or intermittent (as can be typical of poorly-permeable fine-grained sediments). Although these two pathways can be complementary, they may also act independently.

The first scenario with obrution is frequently invoked in the deep-time stratigraphic record because it explains the short exposure of organic remains to O_2 *and their rapid sequestration below the mixed layer (Brett et al., 2012a). Distinct layers deposited by major decadal floods preserved in cores at Po prodelta (Tesi et al., 2012; Tomašových et al., 2018) may have triggered episodic burial of benthic communities, but similar flood-event layers were not detected at Panzano. However, first, the major discharge events that lead to the deposition of flood deposits occur at decadal scales at Po prodelta (seven events during the 20th century, Zanchettin et al., 2008), whereas age distributions of pyrite-lined valves indicate that pyrite linings form almost every year. The frequency of flood events did not increase during the 20th century, in contrast to the increasing frequency of pyrite-lined valves. Second, pyrite-lined valves younger than 10 years old occur in the uppermost 5-10 cm of the mixed layer close to the sediment-water interface. Their high abundance in the uppermost zones indicates that they do not represent transient valves that were just recently exhumed from deeper zones. Although mixing after the deposition of thin flood layers can rework some subset of valves upward, exhumation of initially-buried valves to oxic conditions would lead to removal of pyrite linings. Third, equally-old valves with and without pyrite linings occur at similar depths and age distributions of pyrite-lined valves and valves without pyrite at Po and Panzano are similar (Fig. 9A-F), indicating that valves with and without pyrite were buried below the mixed layer at the similar rate. A single episodic burial pulse that mixes living or recently-dead shells (with decaying biomass and potential for framboid formation) with older shells (without biomass) will generate one age distribution of valves with pyrite linings dominated by younger cohorts and another age distribution of valves without pyrite linings dominated by older cohorts whereas Under mixing, age distributions will be smoothed by stochastic movement of valves, but age distributions of valves wit pyrite linings should be steeper and their median ages should be still lower, in contrast to our observations both at Po and Panzano. Although multimodal whole-core age distributions* *and stratigraphic changes in abundance indicate that input rates of V. gibba were not constant over the duration of core deposition at all sites (especially increasing in abundance after~1950 AD, Tomašových et al., 2018), the burial-rate parameter based on the exponential model (assuming the temporally-constant input of V. gibba) can be realistic when based on the topcore increments characterized by yearly to decadal time averaging at Po and Panzano (i.e., these increments were deposited after the mid-20th century increase in dominance by V. gibba). The pyrite framboids thus did not preferentially form within valves that were rapidly buried deeper in sediments (either by new sediment deposition or by burrowers) as predicted by the obrution scenario and rather precipitated in near-surface sediment levels naturally inhabited by V. gibba.*

In the second scenario, shells can be located in reducing microenvironments even without any fast episodic burial by obrution, close to the sediment-water interface, (i) when the oxic-anoxic interface redoxcline shallows seasonally owing to higher sediment oxygen demand driven by organic enrichment from phytoplankton blooms, mucilages or mass mortality (ii) irrigation is persistently patchy and limited and a large portion of dead shells is exposed to reducing conditions. Although organic enrichment with abundant disseminated organic matter can lead to porewater sulfidization and to exhaustion of highly reactive iron in porewaters, organic-rich sites at Po prodelta still show high concentrations of dissolved irons in the uppermost few cm (Barbanti et al., 1995). Sediment mixing by (weakly-irrigating) infauna can counteract the potential buildup of H_2S in porewaters because burrowers transfer particles with iron oxides from the sediment-water interface to reducing conditions in subsurface zones (Faganeli and Ogrinc, 2009). In contrast to bioirrigation, and mixing alone also contributes to higher oxygen consumption, thus further reducing the exposure of sedimentary particles to O_2; van de Velde and Meysman, 2016).

Several lines of evidence indicate that this second scenario, with the inherent potential of decaying tissues in articulated shells to generate reducing microenvironments coupled with the spatially and temporally-limited bioirrigation, is important: the initial phase of pyrite precipitation occurred in reduced microenvironments (within shells) in near-surface muddy sediments with iron-dominated pore waters and that the limited O_2 penetration (and temporary shallowing of the redoxcline under seasonally-higher oxygen demand of sediments) enhanced the formation of reducing microenvironments. First, qualitative observations indicate that pyrite linings are very rare in valves of Nucula that co-occur with pyrite-lined V. gibba valves, and pyrite linings occur rarely in apertures of gastropods. The tightly-articulated shells of V. gibba with the overlapping periostracum, the internal groove that can lock valves to some degree, and low opening moments of a small internal ligament that can be insufficient to open valves against the sediment pressure (as in other members of the superfamily Myoidea, Trueman, 1954; Yonge, 1982) can be intrinsically susceptible to the formation of reducing conditions. Second, muddy sediments are on average oxygenated to less than 1-2 cm in the northern Adriatic Sea (Epping and Helder, 1997; Moodley et al., 1998, 2000), and zones with high concentrations of dissolved iron tend be limited to the uppermost 5 cm in the NW Adriatic Sea (Hammond et al., 1999) and in the Gulf of Trieste (Faganeli and Ogrinc, 2009). In contrast, sandy sediments exhibit stronger bioirrigation and a thicker extent of ferruginous conditions in the upper 20 cm (Faganeli and Ogrinc, 2009). Third, the uppermost sediments become oxygen-depleted during late-summer mucilage, hypoxic and mass mortality events in the northern Adriatic Sea (Stachowitsch, 1984), and the pyrite formation and the initial formation of reduced microenvironments was thus probably further enhanced when the oxic-anoxic interface seasonally moved close to the sediment-water interface during late summer (Stachowitsch, 1984; Cermelj et al., 2001).

(2) Most of the sulfide is re-oxidized in marine environments with bioirrigation and sediment mixing (Canfield et al., 1993; Thamdrup et al., 1994a). Reduced conditions with pyrite linings within shells or burrows thus will be transient when sedimentation rate is low and/or when bioirrigation and sediment exhumation by burrowers oxidize such microenvironments (Bertics and Ziebis, 2010). The positive relation between pyrite and fine-scale dissolution, and transformation of some pyrite grains to iron oxides and gypsum indicates that some pyrite-lined valves at Po or Panzano were briefly exposed to oxygenated pore waters and were partly dissolved by sulfuric acid (Cai et al., 2006; Pirlet et al., 2010; Hu et al., 2011). However, this reoxygenation did not erase the pyrite linings, and many valves at Po and Panzano were still buried at sufficiently high rate relative to the time scale of pyrite oxidation and shell dissolution (ultimately driven by mixing and bioirrigation) so that a significant subset of pyrite-lined valves survived into the subsurface record. The conditions that ultimately allow the transit of reduced microenvironments formed by pyrite-lined shells at sites with high sedimentation rate into the subsurface stratigraphic record can occur when bioirrigation is spatially-patchy and temporally-impersistent. These conditions can occur when the frequency of hypoxic or mucilage events is high, leading to high oxygen demand of sediments, thus perpetually reducing the extent of O_2 *sediment penetration, and/or when recovery of infaunal communities in the wake of anoxic or hypoxic events in environments affected by eutrophication (as in the northern Adriatic Sea) is slow and in hysteresis (Elliott et al., 2007; Kemp et al., 2009; Borja et al., 2010; Duarte et al., 2015). To conclude, the presence of very young and well-preserved pyrite-lined valves in the uppermost 5-10 cm of the mixed layer suggests that, with the exception of burial of V. gibba to their position below the sediment-water interface during their life, postmortem obrution by episodic sediment deposition is not needed for preservation of pyrite linings when sediment irrigation is limited and background sedimentation rates are not low.*

Depending on the frequency and duration of hypoxic events or other disturbances limiting benthic fauna, two preservation scenarios can be envisioned (Fig. 16): (i) If the frequency of hypoxic events is low and infaunal organisms efficiently mixing and irrigating sediments rapidly recover, articulated shells will disarticulate and disintegrate when exposed to scavengers, borers and degradation of organics in TAZ. For example, maceration of the conchiolin layer triggers delamination of valves into inner and outer layers (Fig. 5E-H). In such conditions, the thickness of the aerobic zone within the mixed layer will increase (Fig. 16A). First, pyrite framboids will not nucleate on valves anymore if the labile biomass and microbes coating the decaying tissues were degraded during the earlier phase of decomposition. Second, bacterial sulfate reduction in microenvironments surrounded by iron-dominated pore waters triggers initial formation of pyrite linings, oxidation induced by bioirrigation will catch up with pyrite-lined shells prior to their deep burial and thus inhibit their subsurface sequestration. (ii) If the frequency of hypoxic events is high relative to the recovery time of the burrowing community with efficient bioirrigators, some subset of pyrite-lined shells can remain preserved if recovery of bioirrigation-inducing burrowers is slow or communities with infrequent bioirrigators are locked by hysteresis effects in an alternative stable state even when hypoxic conditions abated, and O_2 *penetration depths thus remain close to the sediment-water interface (Fig. 16B). However, the recovery of deposit and detritus feeders that still mix sediments support the formation of the ferruginous suboxic zone (van de Velde and Meysman, 2016), thus allowing the precipitation of pyrite framboids at location of decaying molluscs. These conditions with reduced bioirrigation and limited iron recycling are typical of eutrophied environments (Karlson et al., 2007; Lehtoranta et al., 2009). We suggest that such conditions with limited bioirrigation but persisting mixing characterize present-day benthic ecosystems inhabiting muddy sediments in the northern Adriatic Sea. If the* *nutrient-fueled eutrophication or other sources of sediment organic enrichment lead to permanent anoxia of bottom waters and high sulfate reduction, the concentrations of pyrite framboids within shells will be prohibited because sulfide production by bacterial sulfate reduction in organic-rich sediments can exceed in-situ availability of reactive iron oxides,* H_2S *diffuses and precipitates elsewhere (Raiswell and Berner, 1985; Schenau et al., 2002; Raiswell et al., 2008; Farrell et al., 2009). Iron limitation can be driven by iron bounded to framboids linked to disseminated organic matter under high sediment organic enrichment but also to release of ferrous iron from sediments to water column (if water column is not sulfidic, Pakhomova et al., 2007). In addition, as mentioned above, mixing of sediments by burrowers that underlies the iron-based redox shuttle is aborted under anoxic conditions, and iron-limitation in pore waters is thus further enhanced by the lack of bioturbation. The absence of pyrite linings in anoxic sediments documented in the deep-time stratigraphic record (e.g., Brett et al., 1997) indicates that in marine environments with persistent bottom-water anoxia, the window for the early and rapid formation of pyrite linings (e.g., within shells of nektonic groups as cephalopods that fell on the anoxic seafloor) will be closed when organic matter degradation in surface sediments leads to the excess of hydrogen sulfide."*

There are various papers published on this topic during the last fifteen years or so. I suggest, for example, to check MacEachern, J. A., Bann, K. L., Bhattacharya, J. P., 2005. Ichnology of deltas: Organisms' responses to the dynamic interplay of rivers, waves, storms and tides. In: Giosan, L., Bhattacharya, J. P. (Eds.), River Deltas: Concepts, Models, and Examples. SEPM Special Publication, 83, 49–85. Also of relevance is: Bhattacharya, J.P., Howell, C.D., MacEachern, J.A. and Walsh, J.P., 2020. Bioturbation, sedimentation rates, and preservation of flood events in deltas. Palaeogeography, Palaeoclimatology, Palaeoecology, 560, p.110049. In short, the proposed interpretation relies heavily on sedimentation rates, but bringing other parameters to the discussion would be important to reflect more adequately the complex dynamics of deltaic systems.

Response: As we have mentioned above, although the effect of sedimentation rate is important, it is probably not sufficient for formation of pyrite linings (i.e., clusters of framboids associated with the decay of larger organic tissues, as opposed to disseminated pyrite). We think that the condition of reduced bioirrigation is probably still needed for subsurface preservation of pyrite linings. It can be also argued that the condition of iron limitation is in fact best resolved when the sediment is just mixed but not intensely irrigated.
In the Discussion, we have added: "*However, although high background sedimentation rate (or rapid episodic burial) is to some degree a necessary condition for preservation of pyrite linings, we argue below that it is not a sufficient condition, and that potential for reoxidation must be also reduced by disturbances (such as hypoxia) limiting the functioning of irrigating infauna."*

In line 61, the classic paper in this regard is: Bromley, R.G. and Ekdale, A.A., 1986. Composite ichnofabrics and tiering of burrows. Geological magazine, 123(1), pp.59-65. **Thanks, we have added this reference.**