Toward a global calibration for quantifying past oxygenation in oxygen minimum zones using benthic Foraminifera

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Abstract.

Oxygen Minimum Zones (OMZs) are oceanic areas largely depleted in dissolved oxygen, nowadays considered in expansion in the face of global warming. Their ecological and economic consequences are being debated. The investigation of past OMZ conditions allows us to better understand biological and physical mechanisms responsible for their variability with regards to climate change, carbon pump and carbonate system. To investigate the relationship between OMZ expansion and global climate changes during the late Quaternary, quantitative oxygen reconstructions are needed, but are still in their early development.

Here, past bottom water oxygenation (BWO) was quantitatively assessed through a new, fast, semi-automated, and taxon-free morphometric analysis of benthic foraminiferal tests, developed and calibrated using Eastern North Pacific (ENP) and the Eastern South Pacific (ESP) OMZs samples. This new approach is based on an average size and circularity index for each sample. This method, as well as two already published micropalaeontological approaches based on benthic foraminiferal assemblages variability and porosity investigation of a single species, were here calibrated based on availability of new data from 23 core tops recovered along an oxygen gradient (from 0.03 to 1.79 mL.L^{-1}) from the ENP, ESP, AS (Arabian Sea) and WNP (Western North Pacific, including its marginal seas) OMZs. Global calibrated transfer functions are thus herein proposed for each of these methods.

These micropalaeontological reconstruction approaches were then applied on a paleorecord from the ENP OMZ to examine the consistency and limits of these methods, as well as the relative influence of bottom and pore waters on these micropalaeontological tools. Both the assemblages and morphometric approaches (that is also ultimately based on the ecological response of the complete assemblage and faunal succession according to BWO) gave similar and consistent past BWO reconstructions, while the porosity approach (based on a single species and its unique response to a mixed signal of bottom and pore waters) shown ambiguous estimations.

1 Introduction

Oxygen Minimum Zones (OMZs) are defined by a dissolved oxygen content of water lower than 0.5 mL.L^{-1} (= 20 μmol.kg^{-1}) mainly due to combination of two factors: (1) a high oxygen consumption rate by biotic remineralisation of the organic matter originating from primary producers during its slow sedimentation in nutrient-rich environments; and (2) a limited physical

5 regeneration due to a slow oceanic circulation (Wyrtki, 1962; Paulmier and Ruiz-Pino, 2009; Gilly et al., 2013; Praetorius et al., 2015). These areas have expanded over the past 50 years (now represent about 10 % of the global oceans' volume), and a further deoxygenation is expected from now until the end of the century (Stramma et al., 2008, 2010; Gilly et al., 2013; Bopp et al., 2017)as a result of global warming (e.g., Moss et al., 2008). Due to their implication in structuring modern ecosystems, biodiversity, fisheries and their relationship with climate change, the investigation and quantification of past bottom water

10 oxygenation (BWO) are key to understanding their behaviour in a context of global warming and predict their future evolution (Paulmier and Ruiz-Pino, 2009; Gilly et al., 2013; Gilbert, 2017; Levin, 2018).

Fossil benthic foraminifera are considered to be sensitive tracers of temporal and spatial variations of OMZs' intensity (Bernhard and Reimers, 1991; Cannariato and Kennett, 1999) as oxygen is usually the main limiting factor in these areas (Jorissen et al., 1995). Whatever their investigation methods were, most of the studies concerned usually produced qualitative past OMZ

15 reconstructions and did not use the species specific preferences of benthic foraminifera with regards to oxygen concentration to produce quantitative reconstructions (e.g., den Dulk et al., 1998, 2000; Cannariato and Kennett, 1999; Cannariato et al., 1999; Ohkushi et al., 2013; Moffitt et al., 2014, 2015a, b). Regarding the dissolved oxygen preferences of benthic foraminiferal species usually found in OMZs, the scale historically used to define assemblages corresponds to oxic (> 1.5 mL.L^{-1}), suboxic or intermediate hypoxic (0.5 to 1.4 or 1.5 mL.L^{-1}) and dysoxic or severe hypoxic (< 0.5 mL.L^{-1}) (Kaiho, 1994; Cannariato

20 and Kennett, 1999; Cannariato et al., 1999; Jorissen et al., 2007; Ohkushi et al., 2013; Palmer et al., 2020), and we decided to follow the terminology recently used by Palmer et al. (2020). Our previous investigation focused on two methods based on assemblages composition (Tetard et al., 2017a) and porosity measurements (Tetard et al., 2017b) to quantitatively reconstruct variations in past BWO in the largest worldwide OMZ, the Eastern North Pacific (ENP) OMZ. However, both methods still required substantial taxonomical knowledge, and are time-consuming. A modern calibration is also still needed.

25 Several studies already reported morphological (size and shape of tests) responses of benthic foraminifera according to environmental gradients such as oxygenation (Corliss, 1991; Kaiho, 1994; Kaiho et al., 2006). Indeed, the principal idea behind the use of morphometry for paleo-environmental reconstructions is that benthic foraminiferal shell morphology usually depends on the micro-habitat preference of each species (Corliss, 1991). Palmer et al. (2020) reminds that in poorly oxygenated environment, benthic foraminiferal faunas are usually dominated by infaunal and elongate species with high porosity while

30 porcelaneous and epifaunal taxa are more abundant in well oxygenated conditions (Kaiho, 1994; Jorissen et al., 1995, 2007). Indeed, on the one hand, epibenthic species (surface dwellers living in oxic waters) are usually more circular (trochospiral and planospiral tests). Perfect examples are *Cibicides and Planulina* species that are completely rounded and usually lay flat on the sediment or attached to a substrate in oxygenated conditions. On the other hand, endobenthic species such as *Bolivina and Buliminella* thrive under oxygen-depleted conditions and tend to display more elongated (serial) tests (shallow

to deep infaunal), allowing them to burry themselves several centimetre-deep into the sediment. When oxic conditions prevail, the benthic fauna is dominated by epibenthic species. A decrease in bottom water oxygenation is usually associated with a replacement of the epibenthic fauna by deep and shallow endobenthic species moved up to the water / sediment interface following the redox front (Jorissen et al., 1995, 2007). Such changes were reported by the serial/spiral forms ratio in Core

5   MD02-2508 from the ENP OMZ. An increase in the average circularity of the assemblage is thus likely to indicate more oxic conditions while bottom water conditions progressively depleted in oxygen will show a decrease in circularity (Tetard et al., 2017a). The roundness factor is thus prone to inter-specific, but also to intra-specific (lengthening or widening of individual species in their respective oxygen range, due to an actual widening of chambers or due to a shortening of shells) influences.
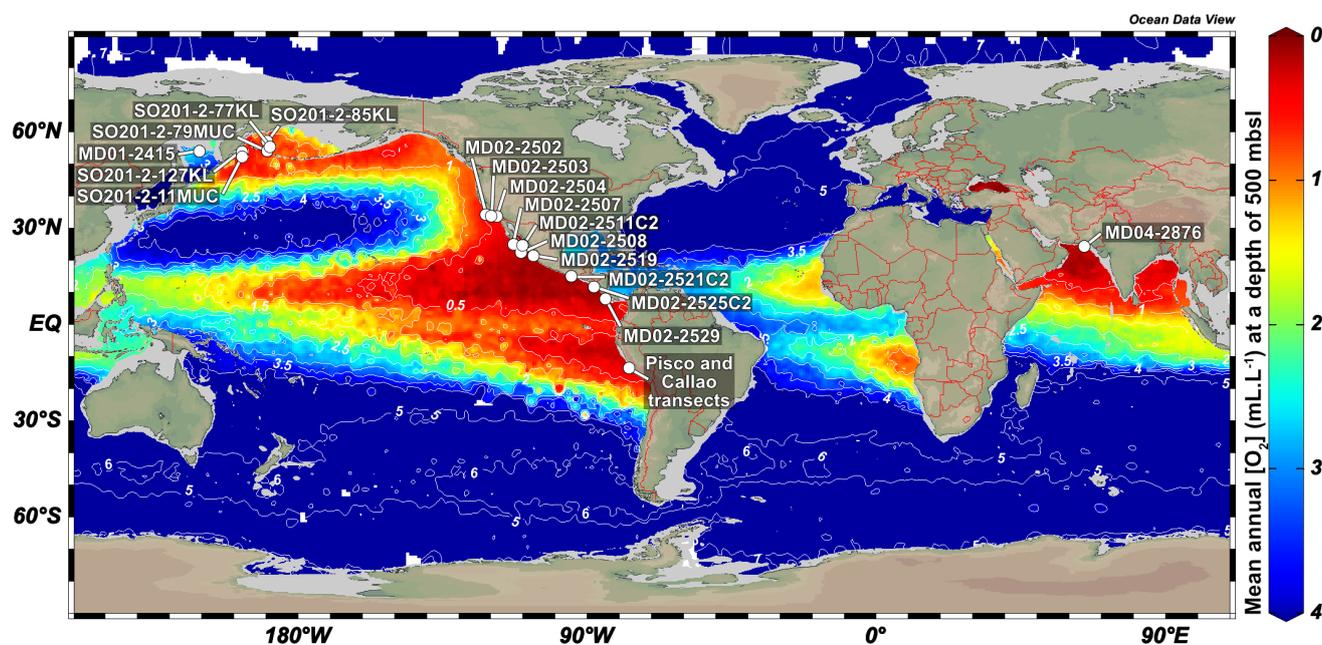
Figure 1. Location (white dot) of the different cores used in this study. Labels show core names. Depths and mean annual dissolved oxygen concentrations near core sites are available in Table 1. This figure was generated by using the Ocean Data View software (Schlitzer, Reiner, Ocean Data View, odv.awi.de, 2020) and the World Ocean Atlas 2013 data set (Garcia et al., 2014).

This led to the development of a new morphometric method, accessible and easy-to-perform for non-specialists, requiring
10   little equipment, and which is fast and relies on semi-automated size and shape measurements. However, relationships between benthic foraminifera (assemblages, measurements) and environmental parameters are usually region-based and difficult to be applied globally (Palmer et al., 2020). To this aim, twenty-three core tops recovered worldwide along oxygen gradients from several oxygen deficient areas such as the ENP, the ESP (Eastern South Pacific) the AS (Arabian Sea) and the WNP (Western North Pacific, including its marginal seas) OMZs, of which the modern values are known, were used for the global calibration
15   of each of the three past BWO estimation methods (based on assemblages, porosity, and morphometry).

2   Material and methods

2.1   Core materials

Core MD02-2508, the main core investigated in this study was retrieved $\sim$ 90 km off Baja California coast (latitude: 23°27.91'N;
longitude: 111°35.74'W) during the R.V. *Marion-Dufresne* MD126 MONA (IMAGES VII) campaign in 2002 (Fig.1a). This

5 40.42 m core was piston-cored (giant corer Calypso) at a depth of 606 mbsl and covers the last 80 kyr (Blanchet et al., 2007).
At this location and depth, the coring site lays in margin of the ENP OMZ core, where the current mean annual $[O_2]$ is about
0.13 mL.L^{-1} according to the World Ocean Atlas 2013 dataset (Garcia et al., 2014, http://www.nodc.noaa.gov/OC5/woa13/).

Several core tops, recovered along transects through the ENP, ESP, AS and WNP OMZs were also investigated, thus allow-
ing sampling throughout an oxygenation gradient (0.03 to 1.79 mL.L^{-1}) where bottom water concentrations were estimated

10 using the World Ocean Atlas 2013 (Garcia et al., 2014) regarding the ENP, AS and WNP core sites, and CTD measurements
concerning the ESP core sites. Core tops location, water depth, and modern $[O_2]$ values are detailed in Table 1. Only the first
cm (0-1 centimetre deep sections) that usually corresponding to less than a few hundreds of years was investigated. These cores
are thus suitable for faunal comparison and calibration purposes.

The ENP core tops (See Table 1) were carried out at CEREGE (preparation, census counting of benthic foraminifera and

15 morphometric measurements), except for cores MD02-2503 and MD02-2504 (Ohkushi et al., 2013) and Core MD02-2529
(Ovsepyan and Ivanova., 2009). The ESP Peruvian margin OMZ core tops (ST1 to ST13) were recovered during the April
2015 CRIO campaign where sediment sampling and CTD BWO measurements were carried out on five sites along the Callao
transect (ST1 to ST5), and three sites along the Pisco transect (ST12 to ST13) and also prepared and processed at CEREGE.
All the investigation on the core tops recovered from the WNP were carried out by Ekaterina Ovsepyan (regarding SO201-

20 2-11MUC, SO201-2-77KL, SO201-2-79MUC, SO201-2-127KL) and Bubenshchikova et al. (2015, regarding MD01-2415,
dataset of benthic foraminiferal counts is available their supplementary material). These samples were collected during the
R/V Sonne cruise Leg SO201-2 in 2009. Finally, Core MD04-2876 recovered from the AS OMZ was investigated by Laetitia
Licari.

2.2   Benthic foraminiferal assemblages study

25 Regarding the preparation of the 14 core top samples available at CEREGE for calibration purposes (seven from the ENP
(MD02-2502, MD02-2507, MD02-2508, MD02-2511C2, MD02-2519, MD02-2521C2, MD02-2525C2) and seven from the
ESP (ST1, ST2, ST3, ST4, ST5, ST12, ST13) transects), these samples usually contained benthic foraminifera often encrusted
in organic matter-rich clays. To extract benthic foraminiferal tests the following procedure was adapted from Bairbakish et al.
(1999):

30 (1) A 1 cm-thick slice is sampled and weighed.

(2) The sample is oven-dried during 48 hours and weighed again as a routine laboratory procedure to get estimate of wet
and dry weights of bulk sediment.

Table 1. Core station location, depth and modern dissolved oxygen level for each investigated core top sample.

Core top station	OMZ	Site location (latitude)	Site location (longitude)	Water depth (mbsl)	[O$_2$] measurement method	Modern [O$_2$] mL.L^{-1}
MD02-2502	ENP	34°39.94'N	120°58.03'W	404	WOA2013	0.83
MD02-2503	ENP	34°17.17'N	120°02.19'W	569	WOA2013	0.33
MD02-2504	ENP	34°13.99'N	119°52.08W	481	WOA2013	0.44
MD02-2507	ENP	25°08.00'N	112°42.09'W	495	WOA2013	0.25
MD02-2508	ENP	23°27.91'N	111°35.74'W	606	WOA2013	0.13
MD02-2511C2	ENP	24°38.74'N	110°36.12'W	417	WOA2013	0.16
MD02-2519	ENP	22°30.89'N	106°39.00'W	955	WOA2013	0.21
MD02-2521C2	ENP	15°40.25'N	95°18.00'W	718	WOA2013	0.09
MD02-2525C2	ENP	12°00.47'N	87°54.44'W	877	WOA2013	0.28
MD02-2529	ENP	8°12.33'N	84°07.32'W	1661	WOA2013	1.65
ST1	ESP	12°01.77'S	77°12.86'W	44	CTD	0.03
ST2	ESP	12°02.48'S	77°17.29'W	90	CTD	0.04
ST3	ESP	12°02.41'S	77°22.58'W	110	CTD	0.03
ST4	ESP	12°02.92'S	77°29.12'W	140	CTD	0.09
ST5	ESP	12°02.60'S	77°39.34'W	165	CTD	0.08
ST12	ESP	14°05.04'S	76°26.79'W	175	CTD	0.04
ST13	ESP	14°02.46'S	76°22.02'W	67	CTD	0.05
MD01-2415	WNP	53°57.09'N	149°57.52'E	822	WOA2013	1.03
SO201-2-11MUC	WNP	53°59.47'N	162°22.53'E	2169	WOA2013	1.79
SO201-2-77KL	WNP	56°19.90'N	170°41.97'E	2163	WOA2013	1.65
SO201-2-79MUC	WNP	56°42.99'N	170°29.78'E	1161	WOA2013	0.83
SO201-2-127KL	WNP	54°23.66'N	162°13.34'E	1440	WOA2013	1.14
MD04-2876	AS	24°50'57N	064°00'49E	828	WOA2013	0.17

(3) The sample is gently re-wet to disaggregate sediment mass using a water-spray over 63 and 150 μm sized meshes without damaging the foraminiferal tests.

(4) If the sediments do not diseggregate, >63 μm residues are placed into a 25 mL beaker where 6 mL of $\sim$ 3 % diluted NaClO (Sodium Hypochlorite solution) and 3 mL of $\sim$ 35 % diluted H$_2$O$_2$ (Hydrogen Peroxide solution) are added during 10 min to disaggregate organic clots. Residues are then rinsed with tap water and sieved over 63 and 150 μm sized meshes.

(5) The content of each sieve is rinsed with distilled water and filtered before being oven-dried and stored in vials.

(6) Fine (63-150 μm) and coarse (>150 μm) fractions are weighed. Only the coarse fraction was investigated herein.

The nine other core tops used for the calibration of the assemblages methods were previously counted for benthic foraminifera by E. Ovsepyan (MD02-2529, SO201-2-11MUC, SO201-2-77KL, SO201-2-79MUC, SO201-2-127KL), Bubenshchikova et al. (2015, MD01-2415), K. Ohkushi (MD02-2503 and MD02-2504), and L. Licari (MD04-2876). The benthic foraminiferal specimens used in this study for Core MD02-2508 were already picked for assemblage investigation in Tetard et al. (2017a). The reader is referred to this publication for more details.

2.3   Pore density analysis

Regarding the Pacific basin, *Bolivina seminuda* from the ENP was previously investigated for its porosity (Tetard et al., 2017b). This species was very abundant along Core MD02-2508, and is also present in two other ENP core tops (MD02-2519 and MD02-2525C2) and its ecological preferences are well documented in the literature (e.g. Glock et al., 2013). As a consequence, it was selected in order to associate porosity values to oxygenation. The original procedure consists in picking 30 specimens which are then gently crushed between two microscope glass slides. The test fragments are then dropped along with ethanol

into a compartmented decanter for a uniform and random settling of particles on a microscope glass slide. After drying, cover glasses are placed along with optical adhesive on each sample, and an automated image acquisition and image processing is performed for investigating porosity (see detailed procedure in Tetard et al. (2017b)).

2.4   Morphometric analysis procedure

5   As no tests were altered or broken (only some moderate in-situ dissolution was observed in a few samples; absolute preservation score of 6 to 8 on Nguyen et al. (2009)'s preservation scale), we were able to observe and measure several size and shape indices. Indeed, as the environmental conditions in OMZ usually correspond to oxygen-depleted clays with very limited bioturbation, shells are most of the time very well preserved. Although the delicate shell of typical OMZ species such as *Bolivina* and *Eubulimina* species might appear fragile and delicate, these tests are quite tough and we are confident that our cleaning

10   procedure did not affect their preservation, assemblage composition overall, and morphology of the shells. The taxon-free semi-automated morphometric analysis was performed on 13 samples available at CEREGE (seven from the ENP (MD02-2502, MD02-2507, MD02-2508, MD02-2511C2, MD02-2519, MD02-2521C2, MD02-2525C2) and six from the ESP (ST1, ST2, ST3, ST4, ST5, ST12) transects). In order to measure several morphometric parameters for the complete assemblage of each sample, every specimen picked in Tetard et al. (2017a) study (around 300 specimens per sample, corresponding to the

15   number of specimens needed for representing a complete assemblage; Buzas (1990); Fatela and Taborda (2002)) was dropped on a 20×20 mm black square and a single picture per sample was acquired with a 8.5 times magnification under a *Leica MZ16A* stereoscopic microscope equipped with a SPOT Flex 64 Mp digital camera (*Diagnostic Instruments*). These settings are the best compromise between resolution and spacing between every test for preventing contact. Images were acquired by using the *SPOT Imaging* image acquisition software (*SPOT v.5.1 Basic* available online at http://www.spotimaging.com/software/).

20   The following procedure was used for the automated morphometric processing of every sample image on the ImageJ image analysis software (v.1.52e Schneider et al., 2012, http://imagej.nih.gov/ij/), and automatically performed by using the MorFo_.ijm (**Mor**phometrics on **Fo**raminifera) java macro developed for this study (available at: https://github.com/ microfossil/ImageJ-LabView-Scripts). Once installed (simply put the MorFo_.ijm file into the plugin directory of your ImageJ software) and selected, the MorFo plugin will automatically:

25   (1) Ask the user for the input folder where original images are located and create three output subfolders for resized images, processed images, and results, respectively, into the designated input folder.

(2) Open each image individually, reduce its size to 1000×1000 pixels, and convert it into an 8-bit image for binarisation in order to obtain a black and white only image (Fig. 2).

(3) Separate the specimens in contact with each other using a "Watershed Irregular Features", performed by using the

30   BioVoxxel plugin (available online at http://fiji.sc/BioVoxxel_Toolbox).

(4) Select "Area", "Shape descriptors", and "Fit ellipse" within the "Set measurements" panel in order to measure a size and a shape parameter for every specimen.

(5) Run an "Analyze particles" operation ("Size" and "Circularity" are adjusted, here 40-infinity and 0.30-1.00 respectively, so as to exclude small and elongated particles such as dust) to count and measure each specimen.
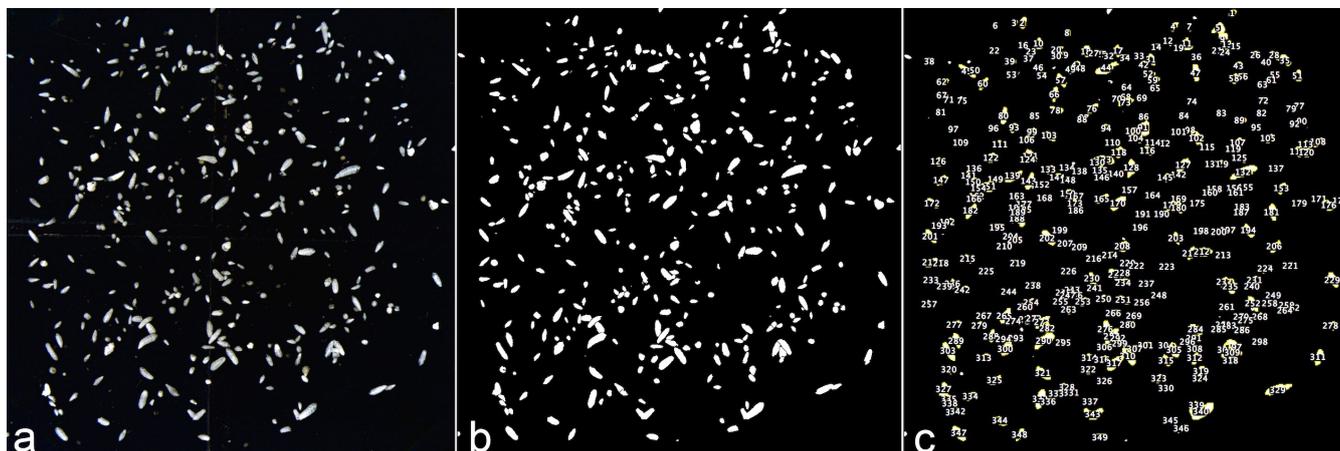
Figure 2. Principal steps of the automated image analysis within the *MorFo* macro. a. Original stereoscopic microscope image. b. Binarised image and watershed. c. Automated counting and measurements.

(6) Save the resized image, processed image, average results for each sample and detail results for each specimen, and delete the full size original image.

(7) Display a success message and automatically close the ImageJ distribution.

The shape descriptor retained in this study is the *Roundness index*, defined as: *Roundness index = (4 × Area) / (Pi × Major axis²)*

This *Roundness index* should then be corrected for size due to the presence of round species occurring in dysoxic conditions (e.g. *Takayanagia delicata* in the ENP samples). As these species are relatively small by comparison with large and round epibenthic species characteristic of well oxygenated environments (such as *Cibicides*-like species, or *Hoeglandina elegans*), more or less oxygenated periods can thus be distinguished by taking the size of species into account. The retained size descrip-

10 tor, here "Major", corresponds to the primary axis of the best fitting ellipse to each specimen. A correction factor (17.54) was applied to the size parameter to calibrate it from pixel to micrometre, according to stereoscopic microscope magnification and image size reduction.

Other size descriptors (e.g. *Feret's diameter* or *Area*) and shape descriptors (e.g. *Circularity* or *Length-to-width ratio*) can also be used (see the *ImageJ User Guide, IJ 1.46r* by Tiago Ferreira and and Wayne Rasband). In order to take simultaneously

15 both the size and shape descriptors into account into the Pacific OMZs, the morphometric index *MARIN* (**M**ajor **A**xis and **R**oundness **IN**dex) is then calculated: *MARIN (µm) = Major axis × Roundness*

This morphometric approach is particularly worthy of consideration for non-specialists as no taxonomic knowledge is required. Benthic foraminifera only need to be picked and imaged under a stereoscopic microscope (a single picture per sample). Images are then automatically processed and no identification is necessary. Approximately 10 min are needed for the process-

20 ing (picking and imaging) of each sample, while at least 1 hour is usually required for picking and identifying every specimen of each sample with a standard approach.

3 Results

3.1 Re-calibration of the [O$_2$] estimation by the assemblages method

A method to quantify past oxygenation within the ENP OMZ, based on the relative abundance and succession of three benthic foraminifera assemblages and the oxygenation preferences of their affiliated species (indicatives of dysoxic, suboxic, and oxic conditions) was developed by Tetard et al. (2017a). This method was originally calibrated using the theoretical [O$_2$] threshold between a 100 % dysoxic assemblage (0.1 mL.L^{-1}), 50 % dysoxic and 50 % suboxic (0.5 mL.L^{-1}) and 50 % suboxic and 50 % oxic (1.4 mL.L^{-1}). However, estimated [O$_2$] values tested on seven Pacific core tops using the assemblages method from Tetard et al. (2017a) show that this original approach seems to be slightly over-estimating oxygenation by comparison with the average oxygen concentration near each site (Garcia et al., 2014).

Table 2. Benthic foraminiferal assemblage composition, morphometry porosity, and their respective [O$_2$] estimation for each investigated core top sample.

Core top station	Dysoxic assemblages (%)	Suboxic assemblages (%)	Oxic assemblages (%)	Estimated [O$_2$] mL.L^{-1} (calibrated assemblages method)	Average size (major axis in μm)	Average roundness	MARIN	Estimated [O$_2$] mL.L^{-1} (calibrated morphometry method)	PSA (*B. seminuda*)	Estimated [O$_2$] mL.L^{-1} (calibrated porosity method)
MD02-2502	0.64	87.86	11.50	0.41	421.61	0.67	282.56	0.65	Not enough material	Not enough material
MD02-2503	0.00	99.29	0.71	0.33	/	/	/	/	/	/
MD02-2504	0.00	97.73	2.27	0.34	/	/	/	/	/	/
MD02-2507	41.45	41.82	16.73	0.19	310.36	0.70	217.34	0.06	Not enough material	Not enough material
MD02-2508	80.91	6.15	12.94	0.08	464.59	0.51	237.12	0.13	0.019	0.16
MD02-2511C2	44.90	48.48	6.61	0.15	368.29	0.63	233.18	0.11	Not enough material	Not enough material
MD02-2519	24.85	53.85	21.30	0.30	366.30	0.69	253.45	0.23	0.019	0.17
MD02-2521C2	56.55	9.23	34.23	0.20	356.30	0.61	217.64	0.07	Not enough material	Not enough material
MD02-2525C2	29.70	46.67	23.64	0.29	352.29	0.70	248.11	0.19	0.016	0.29
MD02-2529	0.74	22.06	77.21	1.61	/	/	/	/	/	/
ST1	96.54	2.30	1.15	0.04	306.88	0.69	212.14	0.05	/	/
ST2	99.88	0.12	0.00	0.04	324.14	0.69	224.15	0.08	/	/
ST3	99.81	0.00	0.19	0.04	307.34	0.67	204.87	0.04	/	/
ST4	91.75	7.28	0.97	0.05	369.82	0.57	210.24	0.05	/	/
ST5	63.88	25.50	10.62	0.11	437.17	0.56	246.31	0.18	/	/
ST12	75.46	22.69	1.85	0.07	361.82	0.62	224.86	0.08	/	/
ST13	97.65	0.00	2.35	0.04	/	/	/	/	/	/
MD01-2415	8.74	23.06	68.20	1.13	/	/	/	/	/	/
SO201-2-11MUC	1.50	1.50	97.01	2.40	/	/	/	/	/	/
SO201-2-77KL	8.19	4.09	87.72	1.72	/	/	/	/	/	/
SO201-2-79MUC	37.50	2.08	60.42	0.53	/	/	/	/	/	/
SO201-2-127KL	8.60	19.35	72.04	1.23	/	/	/	/	/	/
MD04-2876	47.42	49.24	3.34	0.13	/	/	/	/	/	/

As a consequence, we decided to use all the available census data from the 23 core tops (11 from the ENP, seven from the ESP, five from the WNP, and one from the AS; see Table 2) of which the modern [O$_2$] values are known (from Garcia et al., 2014, and CTD measurements) to propose a global calibration for the assemblages [O$_2$] estimation method based on actual [O$_2$] and not theoretical thresholds. The oxygen measurements available for calibration range from 0.03 to 1.79 mL.L^{-1} (see Table 1) and is compared with a term defined by the Equation 1 and referred to as the benthic foraminiferal assemblage index. This equation consists in assigning a number to each sample based on its dysoxic, suboxic, and oxic benthic foraminiferal

composition (from 100 if the sample is 100 % composed of dysoxic specimens, to 0 if the sample is 100 % composed of suboxic specimens, to -100 if the sample is composed of 100 % of oxic specimens; see Fig. 3a).

$$Benthic\ foraminiferal\ assemblage\ index = \%\ dysoxic - \%\ oxic \tag{1}$$

5   The original extrapolation method was refined and now consists in the Equation 2 where the relative abundance of the dysoxic and oxic assemblages (through the use of the benthic foraminiferal assemblage index) can directly be used to determine past oxygenation:

$$[O_2]_{(assemblages\ method)} = 0.326 \times \exp^{-0.0209 \times benthic\ foraminiferal\ assemblage\ index} \tag{2}$$

This equation is based on the consistent relationship (R^2 = 0.92, see Fig. 3a) between the benthic foraminiferal assemblage index and extrapolated and measured [O_2] values (from Garcia et al., 2014, and CTD measurements). Overall, poorly oxy-

10 genated samples are associated with high benthic foraminiferal assemblage index values (thus composed of dysoxic species) while well oxygenated core tops are associated with negative benthic foraminiferal assemblage index values (thus showing oxic species). To make these oxygen reconstructions more user-friendly, an excel spreadsheet is provided in supplement (Table S1) to automatically compute past oxygenation by filling at least two of the three columns corresponding to the relative abundance of the dysoxic, suboxic and oxic assemblages.

15 This approach produces accurate core top samples [O_2] estimates that are very close to the modern mean annual [O_2] values (Fig. 3d, regression line very close to the 1:1 line; R^2 = 0.92) for the ENP, ESP, AS and WNP OMZs altogether. It is thus likely to be used as a global index in oxygen-deficient areas from different OMZs.

3.2   Calibration of the porosity indices

In order to calibrate the procedure described in Tetard et al. (2017b), a microscope slide containing *B. seminuda* fragments

20 was prepared for the three Pacific core tops where this species was present in the first centimetre (MD02-2508, MD02-2519, MD02-2525C2). Considering the limited number of samples, the *PSA* (pore surface area) for these core tops shows a good correlation (R^2 = 0.75; Fig. 3c) to the [O_2] values near these stations (Garcia et al., 2014). Higher values of BWO is associated with a lower PSA of *B. seminuda* while a higher porosity index is observed together with lower BWO values. The following Equation 2 is then used to extrapolate [O_2] for Core MD02-2508 based on its *PSA* values downcore (Fig. 3f):

25   $$[O_2]_{(porosity\ method)} = 11.5 \times \exp^{-226 \times PSA_{(B.\ seminuda)}} \tag{3}$$

3.3   Calibration of the morphometric indices

In order to associate morphometric measurements to BWO concentrations, seven core tops available at CEREGE from the ENP transect, of which the modern annual mean [O_2] are known (Garcia et al., 2014), as well as six core tops from the ESP
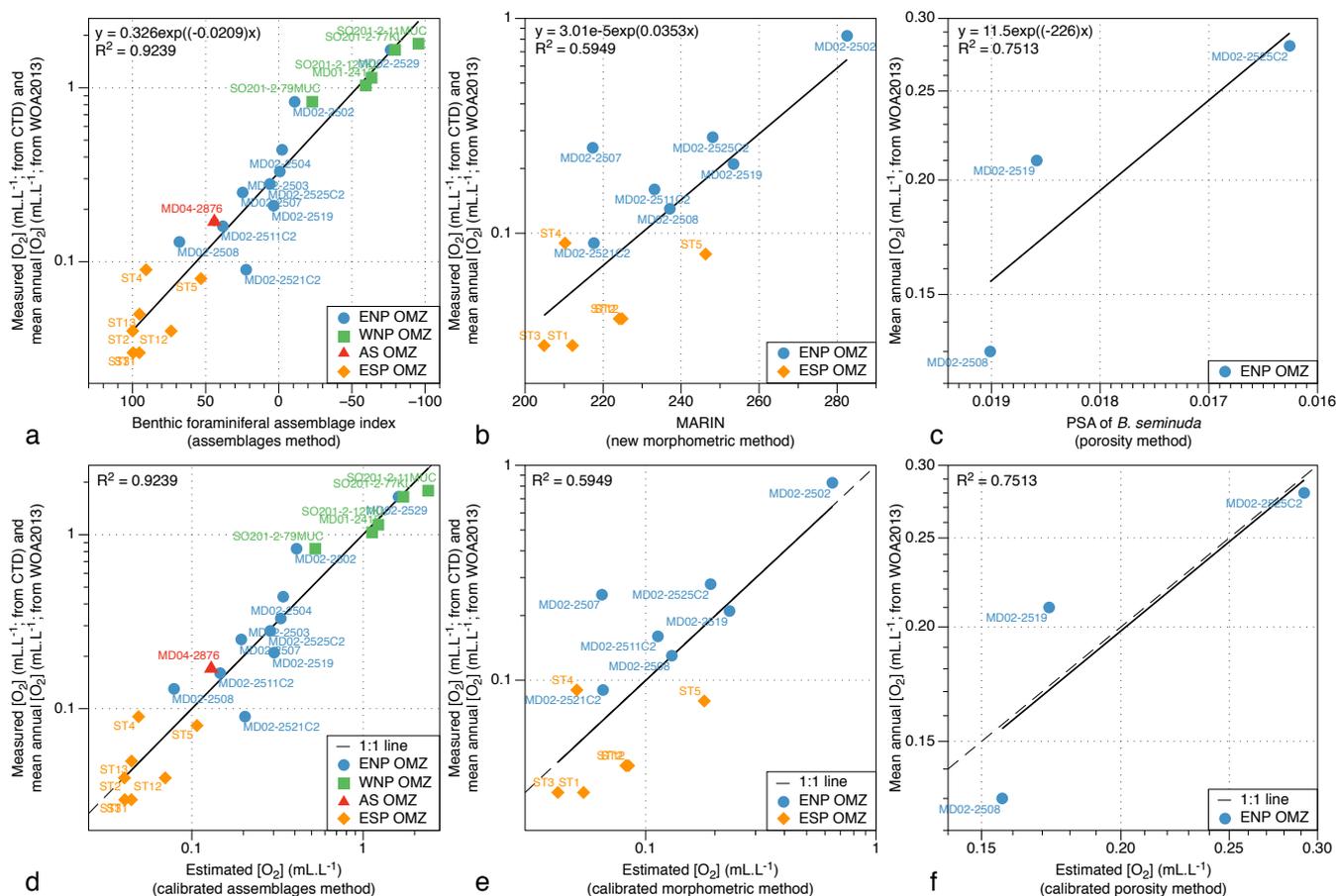
Figure 3. a, b, c: Relationship between the bottom water oxygenation and the benthic foraminiferal index, the new morphometric index (*MARIN*) and the porosity of *B. seminuda*. d, e, f: Relationship between the bottom water oxygenation and the calibrated assemblages method estimation, taxon-free morphometric method estimation, and porosity method estimation.

transects (when enough material was available, and not coloured by rose bengal) of which the modern [O_2] are known (CTD measurements) were used for calibration purposes. These samples show lower *MARIN* values during dysoxic conditions and higher values during oxic conditions. The significant correlation ($R^2 = 0.59$) between the estimated [O_2] (Garcia et al., 2014) and the corresponding *MARIN* values (Fig. 3b) can then be used to extrapolate past BWO concentrations based on the *MARIN*

5   values for each sample (Fig. 3e), according to the Equation 4:

$$[O_2]_{(morphometric\ method\ for\ the\ ENP\ OMZ)} = 0.0000301 \times \exp^{0.0353 \times MARIN} \tag{4}$$
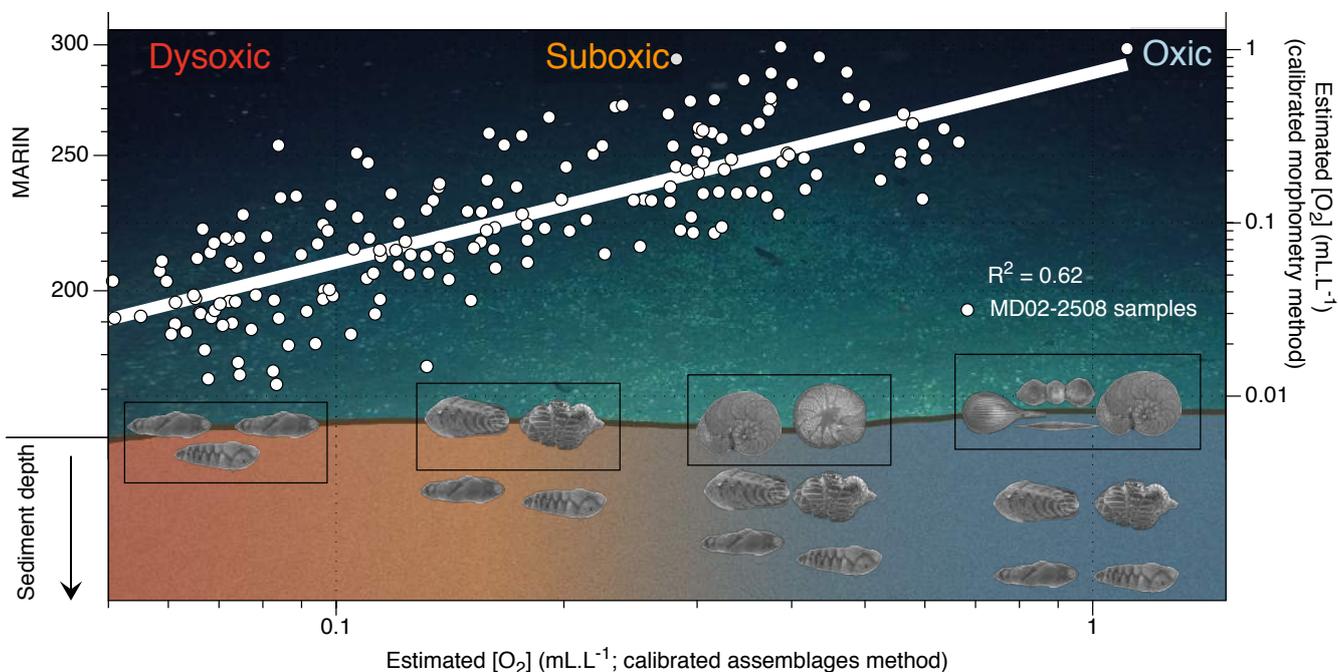
Figure 4. Conceptual graphic of the MARIN response of the top centimetres benthic foraminiferal assemblage to [O$_2$] variations (background image modified from Woods Hole Oceanographic Institution, courtesy of DEEP SEARCH 2018 - BOEM, USGS, NOAA).

4 Discussion

4.1 Understanding and advantages of the oxygen estimation methods

Some technical issues, specific to the morphometric analysis, are likely to induce biases during the data acquisition and processing that might result in inconsistencies in the [O$_2$] reconstruction. Broken shells, or shells that do not lay flat, might appear

5 distorted on images, leading to inaccurate size and shape measurements. The *watershed* step used to dissociate specimens in contact with each other during the image analysis on *ImageJ*, might occasionally be incorrect, resulting in inaccurately-cut specimens and measurements. Considering these potential biases that might affect morphometric measurements, we remain highly confident with this approach given that this only happens to very few specimens over usually more than 300 per sample.

Concerning the faunistic aspect behind the methods discussed herein, the assemblages and morphometric methods are based

10 on the whole benthic foraminiferal fauna and its variability and species succession through time according to their ecological preferences for dissolved oxygen. As both these approaches rely on numerous species and specimens, succeeding each other (Fig. 4), according to their [O$_2$] preferences, they are likely to record and operate on a relatively large oxygen gradient, from its nearly complete depletion (as some species can survive temporarily in anoxic conditions) until it cannot be considered as a limiting factor anymore (well oxygenated conditions, usually more than about 2 mL.L^{-1}). However, the indices defined in the

15 present study cannot exceed a certain threshold (e.g. the oxic assemblage cannot exceed 100 %).

Regarding the morphometry-based approach, even though a link has been shown between BWO and the average size and roundness for each sample, from elongated species in dysoxic conditions (e.g. *Bolivina, Buliminella* species) to rounded species in oxic conditions (e.g. *Cibicides, Planulina* species). This relationship is however likely to reverse after a certain BWO threshold (Fig. 4), where rarer and elongated oxic species will start to appear (e.g. *Lagena, Dentalina* species) As the later

5 species are usually longer than the elongated dysoxic species, a size factor can thus be used to distinguish between an overall dysoxic and elongated assemblage and an overall oxic and also elongated assemblage.

Concerning the porosity approach, previous studies already showed that some species react to bottom water oxygenation decrease (increase) by increasing (decreasing) the pore density (Kuhnt et al., 2013) and pore surface area of their shells (Fig. 5). A closer look at the correlation between [O$_2$] and *Bolivina pacifica*'s pore density from Kuhnt et al. (2013), for example,

10 indicates that within the estimated [O$_2$] range of Core MD02-2508 (from <0.1 to >1 mL.L^{-1}), pore density shows a limited variability. Thus, a complex response should occur on a relatively restricted oxygen gradient, where porosity probably responds to several factors at once, and therefore represents a mixed environmental signal (Glock et al., 2011). However, when the gradient is larger, significant porosity changes might occur (Kuhnt et al., 2013) while faunal turnovers are expected to happen and the species of interest may not be found anymore. This method should thus be used for past oxygen estimation comprised

15 within the oxygen range of predilection of the species of interest. The three methods discussed herein are then likely to be reliable in poorly oxygenated environments, but cannot ensure a consistent estimation in oxygenated environment (more than about 2 mL.L^{-1}), or when dissolved oxygen is not the principal ecological parameter responsible for observed faunal changes .

Regarding the recorded oxygen signal investigated with these three methods, one may question its water / sediment interface vs pore water origin. When oxic conditions prevail, the presence of potentially epibenthic species (recorded by the relative

20 abundance of the oxic assemblage and rounded shells through the assemblages and morphometry methods, respectively) at the sediment surface is considered to be representative of bottom water oxygenation. In time of oxygen depletion, these species are replaced by endobenthic (usually elongated) species migrating up to the water / sediment interface, which also become representative of bottom water conditions (Fig. 4). Conversely, during well oxygenated conditions the endobenthic species are likely to move deeper into the sediment while the epibenthic species colonise the water / sediment interface again. In

25 this way, the interface is always occupied by an assemblage or a morphometry characteristic of a specific oxygen level. The assemblages and morphometric methods are thus likely to be characteristic of bottom water and interface conditions (Fig. 4, black boxes). The endobenthic specimens (*B. seminuda* species) used for the porosity-based method, however, might migrate into their micro-habitat according to the redox front, and thus record either bottom water or pore water conditions depending on the level of oxygen and penetration of the front into sediment depth (Fig. 5). In addition, pore water oxygenation largely

30 depends on surrounding bottom water oxygenation. The porosity method is thus likely to represent a mixed signal between bottom and pore water conditions.

4.2 Comparison of oxygenation tracers

The reliability and consistency of the three assemblages, morphometric, and porosity-based methods used for past oxygenation reconstructions in this study, and based on benthic foraminifera, were investigated on Core MD02-2508 (ENP OMZ) as this
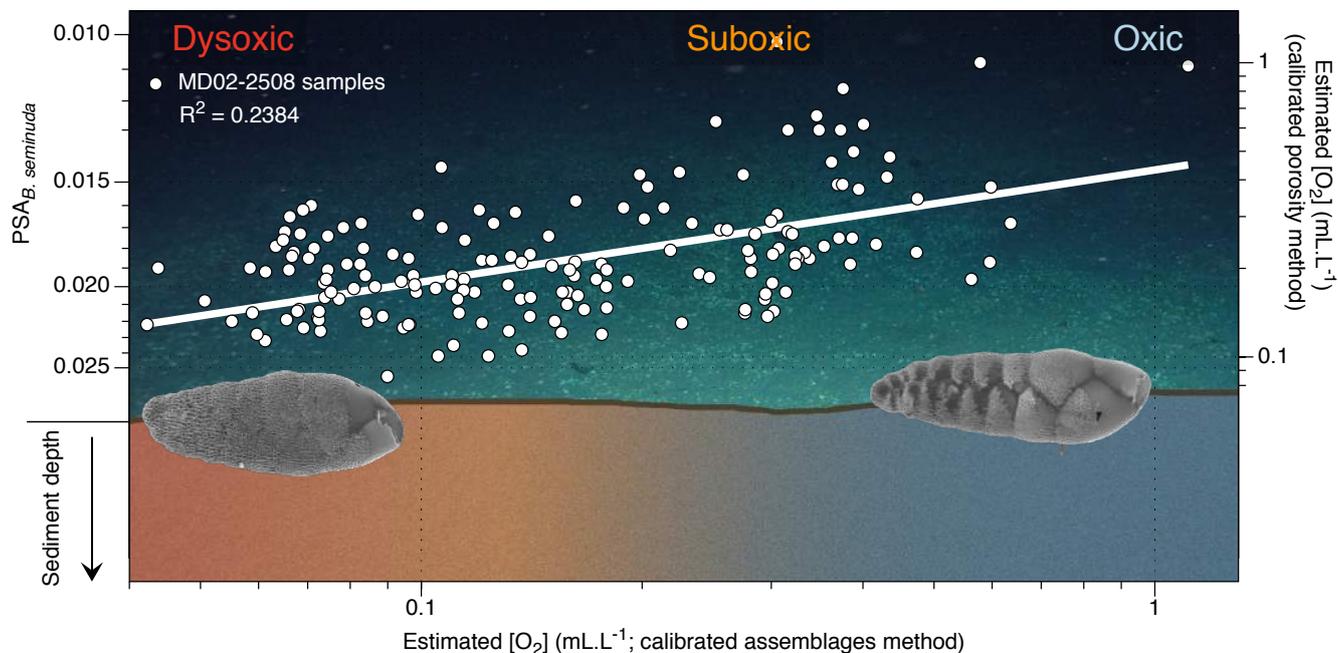
Figure 5. Conceptual graphic of the porosity response of benthic foraminifera (*B. seminuda* for the ENP OMZ) to [O$_2$] variations (background image modified from Woods Hole Oceanographic Institution, courtesy of DEEP SEARCH 2018 - BOEM, USGS, NOAA).

core was investigated using the three approaches at a high resolution (188 samples covering the last 80 kyr). The three methods provide similar [O$_2$] estimations for the modern investigated core tops (Figs. 3d, 3e and 3f). First, the modern [O$_2$] estimations based on the assemblages, morphometric, and porosity approaches (about 0.08 mL.L^{-1}, 0.13 mL.L^{-1} and 0.16 mL.L^{-1}, respectively, 0.12 mL.L^{-1} in average for the ENP OMZ) are very consistent with the modern mean annual dissolved [O$_2$] value of

5   0.13 mL.L^{-1} (Garcia et al., 2014) measured at 600 mbsl near the core site.

     Along Core MD02-2508, these three independent approaches also exhibit similar average values (0.21 mL.L^{-1}, 0.15 mL.L^{-1}, and 0.22 mL.L^{-1}, respectively for the assemblages, morphometric and porosity methods). These approaches also cover similar [O$_2$] gradients of 1.07 mL.L^{-1} (from 0.04 mL.L^{-1} to 1.11 mL.L^{-1}), 1.14 mL.L^{-1} (from 0.01 mL.L^{-1} to 1.15 mL.L^{-1}), and 1.10 mL.L^{-1} (from 0.04 mL.L^{-1} to 1.14 mL.L^{-1}), respectively. As the assemblage method was calibrated based on numerous core top

10   samples, we choose to use it as a reference for comparison with the other methods. Overall, the assemblages and morphometric approaches show similar and consistent estimated [O$_2$] values downcore ($R^2 = 0.62$, Fig. 4) which was expected as both methods rely on the complete assemblages (census data or morphometric measurements) of each sample. The assemblages and porosity approaches exhibit a less clear but still existing relationship ($R^2 = 0.24$, Fig. 5), which can be explained by the fact the the assemblage method is based on the whole assemblage, and is likely to reflect bottom water conditions, while the porosity

15   approach is based on porosity measurements of a single species and probably reflects mixed conditions between bottom and pore waters.

5 Conclusions

We conclude that the present study demonstrates the reliability of a new, fast and semi-automated morphometric analysis in OMZs, performed on benthic foraminifera for estimating past [O$_2$], with an overall higher MARIN morphometric index (higher circularity and larger specimens) in samples characteristic of oxic conditions, while poorly oxygenated samples are associated

5   with a lower MARIN (lower circularity and smaller size). Since no taxonomical knowledge is required for this new method, its main advantages are its user-friendliness to non-specialists besides its ease and speed of image acquisition and automated processing.

A calibration based on several modern core tops (compilation of 23 cores from oxygen deficient areas recovered from all over the world) located along several oxygen gradients for this new approach, as well as for the assemblages-based method

10 from Tetard et al. (2017a) and the porosity-based method from Tetard et al. (2017b) shows similar and consistent estimations, again proving the reliability of these approaches as global past [O$_2$] tracers. However, as these methods are prone to potential specific biases, we highly encourage their combination, whenever possible, for better reliability.

Competing interests. The authors declare that they have no conflict of interest.

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