1 Calcification response of planktic foraminifera to environmental change in the
2 Western Mediterranean Sea during the industrial era
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21 # Abstract

22
23 The Mediterranean Sea sustains a rich and fragile ecosystem currently threatened
24 by multiple anthropogenic impacts that include, among others, warming, pollution
25 and changes in seawater carbonate speciation associated to increasing uptake of
26 atmospheric CO_2. This environmental change represents a major risk for marine
27 calcifiers such as planktonic foraminifera, key components of pelagic Mediterranean
28 ecosystems and major exporters of calcium carbonate to the sea floor, thereby
29 playing a major role in the marine carbon cycle. In this study, we investigate the
30 response of planktic foraminifera calcification in the northwestern Mediterranean
31 Sea on different time scales across the industrial era. This study is based on data
32 from a 12-year-long sediment trap record retrieved in the in the Gulf of Lions and
33 seabed sediment samples from the Gulf of Lions and the promontory of Menorca.
34 Three different planktic foraminifera species were selected based on their different
35 ecology and abundance: *Globigerina bulloides*, *Neogloboquadrina incompta,* and
36 *Globorotalia truncatulinoides*. A total of 273 samples were weighted in both sediment
37 trap and seabed samples.

38 The results of our study suggest substantial different seasonal calcification patterns
39 across species: *G. bulloides* shows a slight calcification increase during the high
40 productivity period, while both *N. incompta* and *G. truncatulinoides* display a higher
41 calcification during the low productivity period. The comparison of these patterns
42 with environmental parameters indicate that controls on seasonal calcification are
43 species-specific. Interannual analysis suggest that both *G. bulloides* and *N.
44 incompta* did not significantly reduce their calcification between 1994 and 2005,
45 while *G. truncatulinoides* exhibited a constant and pronounced increase in its
46 calcification that translated in an increase of 20% of its shell weight. The comparison
47 of these patterns with environmental data reveals that Optimum Growth Conditions
48 affect positively and negatively *G. bulloides* and *G. truncatulinoides* calcification,
49 respectively. Sea Surface Temperatures have a positive influence on *N. incompta*
50 and *G. truncatulinoides* calcification, while carbonate system parameters appear to
51 affect positively the calcification of three species in the Gulf of Lions throughout the
52 12-year time series.
53 Finally, comparison between sediment trap data and seabed sediments allowed us
54 to assess the changes of planktic foraminifera calcification during the late Holocene,
55 including the preindustrial era. Several lines of evidence ~~strongly~~ indicate that
56 selective dissolution did not bias the results in any of our data sets. Our results
57 showed a ~~clear calcification~~ weight reduction between pre-industrial and post-
58 industrial Holocene and recent data, with *G. truncatulinoides* experiencing the
59 largest ~~calcification decrease~~ weight loss (32-40%) followed by *N. incompta* (20-
60 27%) and *G. bulloides* (18-24%). Overall, our results provide evidence of ~~clear~~ a
61 decrease in planktic foraminifera calcification in the western Mediterranean, most
62 likely associated with ongoing ocean acidification and regional SST trends, a feature
63 consistent with previous observations in other settings of the world's oceans.
64
65 **Key words:** Planktic foraminifera, foraminifera calcification, biogeochemical cycles,
66 Ocean Acidification, Mediterranean Sea.

67 ## 1. Introduction

68
69 Growing population and its linked human activity since the industrial period (defined
70 according to Sabine et al., (2004) from 1800 and therein) has caused an increase in
71 carbon dioxide, which ecological and economic consequences are considered a
72 major threat (Ipcc, 2022). Atmospheric CO_2 concentrations during the Pleistocene
73 and Holocene ranged from 200 to 280 parts per million (ppm) (Loulergue et al., 2007;
74 Lüthi et al., 2008; Parrenin et al., 2007), but these values have increased
75 dramatically since the onset of the industrial period, exceeding the threshold of 400

ppm in 2015 for the first time for at least the last 800.000 years (Lüthi et al., 2008). This increase is significantly more important since the 1950s, when rapid atmospheric changes due to human activity took place, a process referred as "Great Acceleration" (Head et al., 2022a). Since then, between, 25 and 30% of anthropogenic CO_2 has been absorbed by the world's ocean (Sabine et al., 2004). The ocean uptake of atmospheric CO_2 causes a drop in both pH and carbonate ion concentration (Barker et al., 2012), lowering seawater alkalinity; this process is commonly known as Ocean Acidification (OA), and it is expected to affect all areas of the ocean and to have a wide impact on marine life (Davis et al., 2017; Figuerola et al., 2021; Orr et al., 2005). One of the main questions about recent environmental change is how different ecosystems and regions in global ocean are going to react to the ongoing increase of anthropogenic atmospheric carbon dioxide.

A large body of evidence indicates that ocean acidification has substantial and diverse effects on the distribution and fitness of a wide range of marine organisms (Kroeker et al., 2013; Meier et al., 2014; Moy et al., 2009). For example, some fleshy algae and diatom species have been shown to increase their growth and photosynthetic activity at enhanced CO_2 concentrations (Kroeker et al., 2013). In turn, most calcifying organisms such as calcifying algae, corals, pteropods, coccolithophores and foraminifera are negatively affected by this process often showing a reduction in their abundance, calcification and growth rates (Kroeker et al., 2013; Orr et al., 2005).

Planktic foraminifera are a group of marine single-celled protozoans that produce calcareous shells. Their distribution across the water column is conditioned by factors that include, but are not limited to, food availability, temperature, salinity and sunlight (Schiebel and Hemleben, 2005). These organisms are considered to play a key role in marine carbon cycle and carbonate production, accounting for between 32 and 80% of the deep ocean calcite fluxes (Schiebel, 2002). Depending on their ecology and feeding strategies, these organisms can be algal (dinoflagellates) symbiont bearing or not symbiont bearing and be spinose or non-spinose. Planktic foraminifera represent a useful tool for palaeoecological and palaeoceanographic studies, as the abundances of different species and their geochemical signature allow reconstructing sea surface temperatures and water column physical and chemical properties (Lirer et al., 2014; Margaritelli, 2020; Schiebel and Hemleben, 2017).

Previous studies suggest that planktic foraminifera are sensitive to ocean acidification (OA). Laboratory experiments indicate that when carbonate ion concentration decreases, shell weight and calcification decrease too in a variety of species (Bijma et al., 2002; Lombard et al., 2011). Species that host symbionts have been described showing a higher tolerance to dissolution due to the capacity of algal

symbionts to alter immediate seawater chemistry (Lombard et al., 2009). Moy et al. (2009) documented a decrease of 30-35% shell weight in the planktic foraminifera *G. bulloides* during the industrial era in the subantarctic Southern Ocean, most likely induced by anthropogenic-driven ocean acidification. A recent study by Fox et al. (2020) showed that non-spinose (*N. dutertrei*) foraminifera species exhibit a more pronounced calcification reduction than the spinose (*G. ruber*) species in response to increasing CO_2. The main difficulty for studying the impact of OA on foraminifera (and any calcifying organisms) resides in finding long-term continuous records in order to be able to evaluate possible changes in shell calcification (Fox et al., 2020). In order to assess the impact of recent environmental change on planktic foraminifera, in this work we present data from Planier sediment trap (data from 1993 to 2006) (Rigual-Hernández et al., 2012) and from seabed sediments from three different sites located in both the Gulf of Lions and the promontory of Menorca. The Mediterranean Sea is a semi-enclosed sea with a high saturation state for calcite (Álvarez et al., 2014). It is often considered as a "miniature ocean" and a "laboratory basin" (Bergamasco and Malanotte-Rizzoli, 2010) which makes it a valuable zone to study the response of marine calcifying organisms to environmental change.

The advantage of sediment traps is that they can provide data coming from annual fluxes, avoiding the effects of seasonal abundance and ontogeny and making interannual comparisons more reliable (Jonkers et al., 2019). Three different planktic foraminifera species, each of which characterized by contrastingly different depth habitats and ecologies, were selected for our analysis: *G. bulloides,* a spinose opportunist surface dweller that lies above the thermocline (Schiebel and Hemleben, 2014); *N. incompta,* a non-spinose temperate surface dweller; and *G. truncatulinoides,* a non-spinose deep dwelling species which migrates through the water column with a complex life cycle. Our aims for this study are: (i) to compare two widely used foraminifera weighing and size-normalization techniques and provide a baseline of modern foraminifera weight data and calcification in the Western Mediterranean against which future changes in foraminifera calcification can be assessed (ii) document seasonal and interannual trends in the planktic foraminifera calcification of the three planktic foraminifera species, and (iii) evaluate possible changes in shell calcification through the Holocene to the present day by comparing shell weights of the foraminifera collected by the traps with those of the seafloor sediments.

2. Study area

The Mediterranean is a semi-enclosed sea and it is considered a concentration basin (Bethoux et al., 1999) with a negative hydrological budget: fresh water inputs do not

compensate the overall basin evaporation. The surface oceanic waters that enter the Mediterranean through the Strait of Gibraltar and spread towards the eastern basin compensate this negative balance. The waters of Atlantic origin (AW) circulate according to a cyclonic circuit (counterclockwise) along the Mediterranean rim (Fig. 1a). In the northwestern basin, this along-slope current, called the northern current (NC), is formed by the convergence at the level of the Ligurian Sea (LS) of the waters flowing on both sides of Corsica. The general circulation in this sub-basin forms a cyclonic pattern, flowing westward along the Gulf of Lions, bypassing the Balearic Sea and finally closing its circuit eastward along the North Balearic Front (NBF) (Fig. 1b).
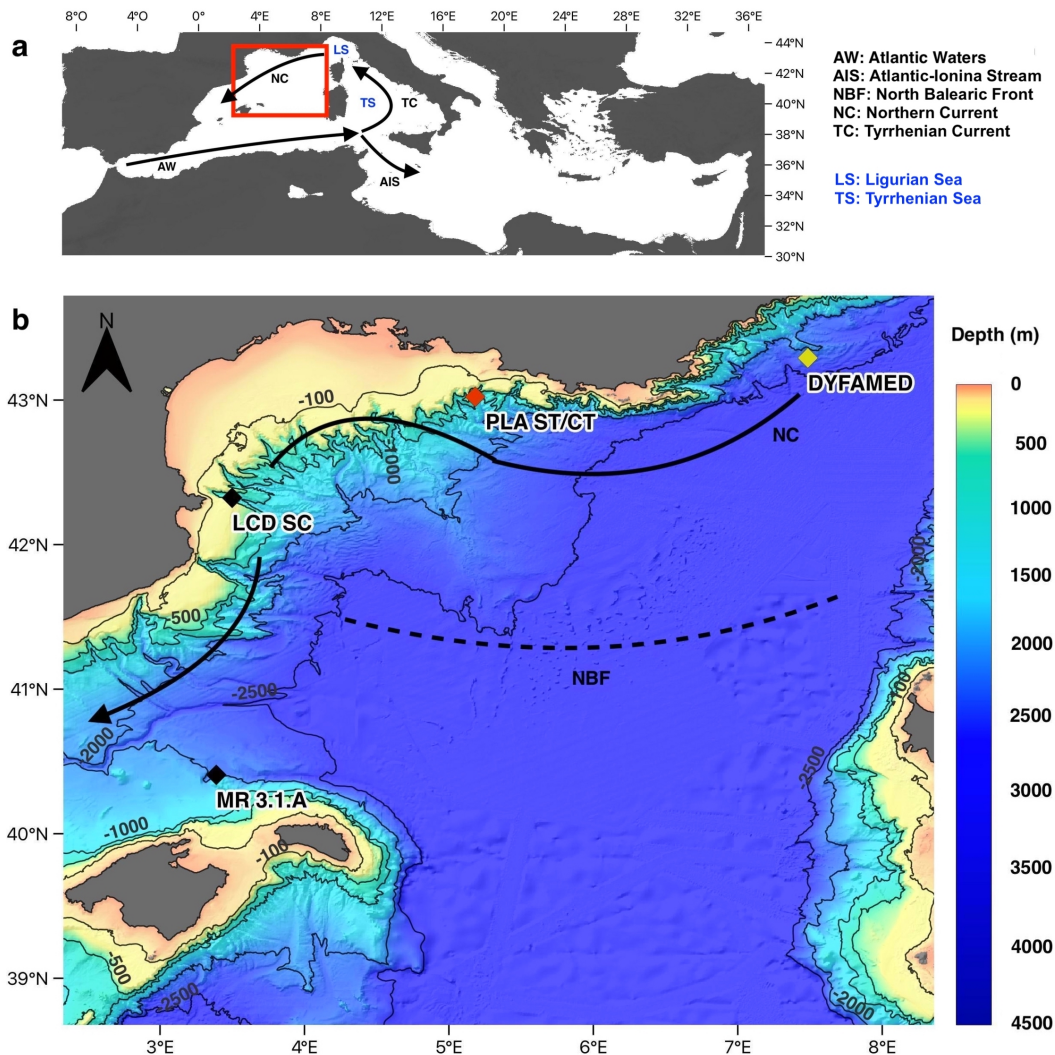

Figure 1. a. Study area location in the Mediterranean Sea and general surface circulation **b.** geographic setting of the Gulf of Lions and location of studied sites. Red diamond shows the position of the Planier site sediment trap and core-top (PLA ST/CT). Black diamonds represent the location of the

seabed sediments samples analyzed from Lacaze Duthiers canyon (LCD SC) and Menorca promontory (MR 3.1A). Yellow diamond represents the location of the Dynamics of Atmospheric Fluxes in the MEDiterranean Sea (DYFAMED) site, located 200 km upstream Planier station position. Arrows represent the surface circulation (Millot, 1999). The topographic model was downloaded from the GEBCO database.

Moreover, the Mediterranean is recognized as a sensitive region to increasing atmospheric CO_2 (Ziveri, 2012) due to the fast turnover time of its waters (Béthoux et al., 2005) and the fast penetration of anthropogenic CO_2 (Schneider et al., 2007). Sea surface temperatures are predicted to increase by 1.5-2°C by the end of the century, a faster rate than the global average (Lazzari et al., 2014). pH is expected to decrease according to the global average (0.3-0.4 units by 2100) or even exceed the global trend (Hassoun et al., 2015). The Mediterranean Sea is also affected by other stressors, which impact marine organisms in many ways (Lejeusne et al., 2009). Finally, it is also a region shaped by human development and its associated activities interact with environmental changes (Mediterranean Experts on Climate Change, MedECC, 2019).

The Gulf of Lions is located in the northwestern part of the Mediterranean Sea, and its morphology presents a continental slope with an array of complex submarine canyons (Rigual-Hernández et al., 2012) (Fig. 1b). Vertical mixing, generated by intense surface cooling and evaporation, occurs in winter in the Gulf of Lions driven by cold, dry northern winds, resulting in dense water on the shelf and offshore (Durrieu de Madron et al., 2005; Houpert et al., 2016; Millot, 1990). This winter mixing recharges surface waters with nutrients. This enrichment with increased solar radiation stimulates primary production in spring. Increasing heat fluxes during spring and summer cause water mass stratification and nutrient depletion, which lasts until late summer, until fall cooling breaks the stratification of the water column and causes a fall bloom (Heussner et al., 2006; Monaco et al., 1999; Rigual-Hernández et al., 2012). River inputs are the main source of suspended particles in the Gulf of Lions, and the Rhone river represents the most important river in the northwestern Mediterranean; however, other sources include Saharan dust deposits and biological production (Heussner et al., 2006; Monaco et al., 1999). Overall, the oceanographic setting of the Gulf of Lions is an exception to the general oligotrophy of the Mediterranean Sea.

3. Material and methods

3.1. Sediment traps, core-tops and sediment cores.

A series of deployments of sediment traps mooring lines in the Gulf of Lions continental margin was initiated in 1993 within the framework of several French and European projects (PNEC, Euromarge-NB, MTP II-MATER, EUROSTRATAFORM) and the monitoring of two sites, Planier and Lacaze-Duthiers stations (Fig. 1), continues as a component of the MOOSE program (Mediterranean Ocean Observing System for the Environment) (Coppola et al., 2019). Planier station (43°02'N, 5°18'E) is located at the northeastern end of the Gulf of Lions, in the axis of the Planier Canyon. The sediment trap used for this work was located at around 530 m water depth in a water column of ~1000m. Further details of the mooring design can be found in Heussner et al., (2006). Planktic foraminifera fluxes for the 1993 to 2006 period were documented by Rigual-Hernández et al., (2012). Here, we used the samples from the latter study for our weight and calcification analysis. This sediment trap is used here as a baseline of the planktic foraminifera dwelling in the modern Mediterranean Sea. Moreover, we analyzed a set of core top and sediment cores collected from several locations of the Northwestern Mediterranean that are considered to represent foraminifera assemblages sedimented during the Holocene era (Table 1).

Table 1. Description of the core tops used in this study. Data for Planier core-top (PLA CT) and Lacaze-Duthiers sediment core (LCD SC) are available in Heussner et al., (2006), and data concerning Menorca sediment core (MR 3.1.A) can be found in Cisneros et al., (2016). Conventional ^{14}C ages, 1-sigma uncertainties, local reservoir and the calibrated age have been rounded according to convention. See section 3.7 for details concerning "Bomb ^{14}C".

Site	Location	Water depth (m)	Sediment Samples	Samples Depth (cm)	Sample dated	Species dated	Radiocarbon age (^{14}C years BP)	1-sigma error (^{14}C years)	Local reservoir (^{14}C years BP)	Calibrated age (cal. years BP)
PLA CT	42.989° N 5.121° E	1095	2	0-1	0.5-1 cm	*G. bulloides*	490	60	165 ± 95	Bomb ^{14}C
LCD SC	42.265°N 3.54°E	990	7	0-5	0.5-1 cm	*G. bulloides*	460	60	165 ± 95	Bomb ^{14}C
MR 3.1.A	40.29°N 3.37° E	2117	40	0-27	14-14.5 cm	*G. bulloides*	1980	65	165 ± 95	1560

3.2. Sediment core samples processing

A total of 2 sediment samples from Planier core top, 7 from Lacaze-Duthiers sediment core and 40 from Minorca sediment core were weighed (Table 1). Dry bulk sediment samples from all sites was weighed using a Sartorius CP124S balance (precision= 0.1mg).

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234 The samples were then wet-sieved in order to separate the <63 *μ*m fraction and dry
235 sieved to separate the bigger fractions (>150 *μ*m and >300 *μ*m). The sediment
236 washing was carried out with potassium phosphate-buffered solution (pH= 7.5) in
237 order to optimize foraminifera preservation. Each fraction was oven dried at a
238 constant temperature (50°C) and then weighed. The >150 *μ*m fraction was used for
239 identification, counting and shell morphometric and weight analyses.
240
241 **3.3. Ecology and life cycle of *Globigerina bulloides*, *Neogloboquadrina***
242 ***incompta* and *Globorotalia truncatulinoides***
243 *G. bulloides* is a spinose surface to sub-surface dweller (Schiebel and Hemleben,
244 2017a), found in the upper 60 m of the water column. This species has affinity for
245 temperate to sub-polar waters and upwelling systems in lower to mid latitudes
246 (Azibeiro et al., 2023; Bé et al., 1977). In terms of its seasonal distribution, it has
247 been documented to be associated to enhanced productivity periods in mid to high
248 latitudes (Chapman, 2010; Schiebel and Hemleben, 2005). No symbiont algae are
249 hosted by this species and, contrary to most spinose species, its diet is mainly algae
250 based (Schiebel et al., 2001). *G. bulloides* shows an opportunistic feeding and
251 strategy, leading to a high abundance in the foraminifera assemblages preserved in
252 the sedimentary record. This is despite its tests have been documented to be more
253 susceptible to dissolution than the average of the planktic foraminifera species
254 (Dittert et al., 1999).
255 *N. incompta* is a surface dweller abundant in subpolar to temperate water masses
256 across all the ocean basins (Kuroyanagi and Kawahata, 2004). This is a non-spinose
257 species and does not carry symbiont algae. In North-Atlantic waters, *N. incompta* is
258 a major component of foraminifera assemblages from late spring to late fall, and
259 generally, is the dominant foraminifera species during late summer when maximum
260 shoaling of mixed layer depths occur (Schiebel and Hemleben, 2000). It shows a
261 minor presence in low latitudes and during periods of enhanced nutrient supply, *N.*
262 *incompta* is outnumbered by other more opportunistic species, (Schiebel et al.,
263 2002).
264 *G. truncatulinoides* is considered the deepest dweller among the extant planktic
265 foraminifera, with living specimens documented below 2000 m (Schiebel and
266 Hemleben, 2005). Considered a widespread species, it can be found from subpolar
267 to subtropical water masses (Schiebel and Hemleben, 2017). It is a non-spinose
268 species (Margaritelli, 2020), and it does not carry any symbiont algae (Takagi et al.,
269 2019). An important aspect to highlight about this species is its complex life cycle
270 (Margaritelli et al., 2022). It reproduces once a year in the upper water column during
271 late winter, when mixing of the water column allowed the migration of juveniles to
272 the surface waters (Lohmann and Schweitzer, 1990; Schiebel et al., 2002). The

former authors speculated that nutrient availability and the avoidance strategies to predation could explain this its life cycle. Then, the adult migrate downward the water column (Rebotim et al., 2017) and spend the rest of their life cycle developing an additional calcite layer in cooler waters below the thermocline (Lohmann and Schweitzer, 1990; Wilke et al., 2009). Around 70% of *G. truncatulinoides* calcification has been estimated to take place around the thermocline, while the remaining 30% take place in surface waters (LeGrande et al., 2004).

The abundance of these three species has been previously studied in the Gulf of Lions by Rigual-Hernández et al., (2012). The latter study showed that both *G. bulloides* and *N. incompta* displayed their maximum abundances during the spring bloom, while *G. truncatulinoides* abundance was maximum during early winter. On the other hand, minimum abundances were reached during late spring and summer for *G. bulloides* and *N. incompta* respectively, and *G. truncatulinoides* displayed a minimum abundance during fall.

3.4. Foraminifera picking and mass and size estimations

Different sizes were selected depending on the maximum availability of each species: 250-300, 200-250 and 400-500 *µm* for *G. bulloides, N. incompta* and *G. truncatulinoides*, respectively. For the latter species, both coiling morphotypes were selected although the right coiling was substantially less abundant representing less than 3% in our counts, a feature consistent with the literature that indicates a low presence of right coiled specimens (Margaritelli et al., 2020; 2022).

A total of 273 foraminifera samples were picked for this study, 126 coming from the sediment trap and 147 from the three sediment cores and core tops (Table 2). However, these numbers represent the total of samples analyzed but unique samples number is lower, as not all the sediment trap samples presented the three species in high enough numbers to perform the picking. The species were analyzed in size fractions in order to estimate the efficiency of sieve fractions and the impact of size and morphometric parameters on the foraminifera weight and calcification.

The mean weight of each available sediment trap sample was obtained by weighting between 15 to 45 specimens of *G. bulloides* (mean N= 27), 5 to 25 *N. incompta* (mean N= 15) and 5 to 25 *G. truncatulinoides* (mean N= 13). Concerning the analyses of the core top and sediment core samples, between 15 and 25 *G. bulloides* and *N. incompta* (mean N= 20 for both) and between 9 and 25 *G. truncatulinoides* (mean N= 18) were picked.

Each foraminifera sample was then cleaned by gentle ultrasonication (50 Hz) for 5 to 75 seconds (depending on the species and the degree of visual uncleanliness) in methanol in order to clean the shells. The samples were then left to dry in a temperature-controlled oven at 50°C. One out of three analyzed samples were

weighted before and after cleaning in order to assess potential shell mass losses and shell preservation due to ultrasonication. Our results indicate that this method has little impact on shell preservation with around 95% of the total foraminifera conserved in good conditions. Weight loss between non-cleaned samples and cleaned samples is a mean 0.5 to 3 μg (between 6 and 32% of the sample total measured weight) depending on the species, mainly due to the presence of clay and non-calcite material in the shells, which justifies this cleaning process (see Supplementary fig. 6).

The weightings were carried in the micropaleontology laboratory of the Geology Department at University of Salamanca using a Sartorius ME5 balance (precision= 0.001 mg). This method allowed us to obtain foraminifera Sieve Based Weight (SBW) by dividing the average shell weight per sample (5-45 tests) by the total number of foraminifera within each sample. The lowest number of individuals selected per sample was five in order to maximize the number of samples available for our study. According to Beer et al., (2010), the higher the number of individuals, the more reliable SBWs are. Here we aim to compare SBW results with a measured weight technique. Measured techniques are acknowledged to be reliable with a lower number of individuals, therefore a minimum of five individuals were selected in order to compare the two techniques.

However, it has been described that traditionally used sieve fractions method is considered unreliable because of the effect of morphometric parameters on the foraminifera weight (Beer et al., 2010). In order to remove the size effect on the weight, the mean SBW was normalized to the mean diameter and area of the planktic foraminifera to obtain Measurement Based Weights (MBW). Morphometric parameters were measured using a Nikon SMZ18 stereomicroscope equipped with a Nikon DS-Fi3 camera and NISElements software. These measurements were carried out on the same shells that were weighted. Foraminifera shells were positioned in order to obtain the maximum area of each individual, in this case, the umbilical side (aperture facing upwards) was measured for the three species.

MBW_{area} and $MBW_{diameter}$ were calculated according to the following formula (Aldridge et al., 2012; Beer et al., 2010), where "parameter" accounts for "area" or "diameter":

$$MBW\,sample = \frac{mean\ SBW_{sample} \times mean\ parameter_{size\ fraction}}{mean\ parameter_{sample}}$$

"Size fraction" accounts for the mean of the parameter (area or diameter) measured in all the sites studied, while "sample" accounts for the mean of the parameter in the particular sample being measured. The advantage of these measurements is that

10

350   the resulting MBW is being given with a weight unity (*μ*g), thereby allowing direct
351   comparison with other studies (Beer et al., 2010) and useful for estimating their
352   contributions to marine biogeochemical cycles.
353   Correlations between SBW and MBW$_{area}$ against area are displayed in Fig. 2. The
354   reason for this comparison is to show the relation between size and weight. ~~In order~~
355   and to avoid the effect of having the bigger specimens displaying the heaviest weight
356   and impacting the mean weight (therefore calcification indicator) of the sample.
357   Finally, in order to compare weights patterns from the sediment trap with weights
358   from core tops and sediment cores and overcome the seasonality effect, MBWs were
359   flux-weighted. Mean monthly MBWs values from each species were multiplied by
360   the corresponding mean monthly flux and then divided by the total annual flux of the
361   corresponding species. For these calculations, the flux data from each species
362   estimated for the >150 μm fraction from Rigual-Hernández et al., (2012) was
363   employed.
364

365   **3.5.   Environmental data**
366   Foraminifera fluxes and abundances together with chlorophyll-a were taken from
367   Rigual-Hernández et al., (2012) for the entire time span of the analyzed samples.
368   Both fluxes and abundance come from direct sediment observation from the Planier
369   site, while chlorophyll-*a* data was obtained from SeaWiFS monthly measurements
370   through NASA's Giovanni program on a 0.2 x 0.2° area around the mooring location.
371   SeaWiFS measurements started in 1997 and were used due to the lack of direct
372   chlorophyll measurements in our samples. Sea Surface Temperature (SST) was
373   recovered from the NOAA database with the same gridding as the data from the
374   NASA's Giovanni program.
375   Salinity, nutrient concentrations (nitrates and phosphates) and carbonate system
376   parameters data were collected from the DYFAMED database (http://www.obs-
377   vlfr.fr/dyfBase/index.php) (Coppola et al., 2008; 2021). DYFAMED site is located
378   around 200-220 km (Fig. 1b) east of the sediment trap location (43°25´N, 7°52´E), in
379   the Ligurian Sea. From an oceanographic view, its situation is upstream of the NC
380   circulation and can be considered representative of seasonal and interannual
381   variability of biological and water column properties of the open-ocean waters in the
382   northwestern Mediterranean (Heussner et al., 2006; Meier et al., 2014). Alkalinity
383   and total carbon measurements were available for years 1998 to 2000 and mid 2003
384   to 2005. Missing values comprised in these years were replaced with values
385   obtained from linear regression of the measurements from above and below. The
386   CO2SYS macro has been used to reconstruct the $[CO_2]$, $[CO_3^{2-}]$, $[HCO_3^-]$ and pH
387   values from the measured total alkalinity and dissolved inorganic carbon. The
388   constants used were the CO_2 dissociation constant by Mehrbach et al., (1973) refit

389 by Dickson and Millero, (1987); the KHSO$_4$ by Dickson, (1990); and the seawater
390 scale for pH.
391

3.6. Statistical analysis

393 In order to have uninterrupted monthly environmental values from the DYFAMED
394 site during available measurements, a resampling every 10 days has been carried
395 out with the QAnalySeries program.
396 Independence and correlation between the area the different species SBWs and
397 MBW$_{area}$ was tested using a Pearson linear correlation test with an R script (see
398 Supplementary material).
399 Seasonal correlation analyses were carried out with the Statistica program. A $p<0.05$
400 was used in order to consider a correlation as significant. The number (N) of
401 correlations depended on data availability and was 10 for *G. bulloides*, 9 for *N.*
402 *incompta* and 12 for *G. truncatulinoides*.
403 It should be noted that the analysis of interannual trends was hindered by gaps in
404 the sediment trap record and by the low number of specimens during some sampling
405 intervals. Therefore, interannual trends in planktonic foraminifera calcification should
406 be interpreted with caution.
407 The influence of environmental variables upon MBW$_{area}$ was assessed using
408 General Additive Models (GAM) (fitted using the *gam* function from the *mgcv* R
409 package). Due to data limitation, the GAMs could not be fitted to multiple
410 independent variables, so potential effects of interacting environmental variables
411 were could not be assessed. Each model tested the dependence of the different
412 MBW upon a single independent variable: month or year, to evaluate seasonal and
413 interannual trends; the flux of each species, to test effects of ecological variability;
414 and a suite of environmental variables to determine impacts of various aspects of
415 ocean chemistry on the calcification. Smooth functions of these measured quantities
416 were used as the single independent variable within the GAMs, which were fitted
417 using the default settings of the *gam* function: a Gaussian family and identity link
418 function; and the GCV.cp smoothing method. GAM results quantified the
419 significance of the effect of each independent variable upon MBW.
420 In order to investigate the difference between the MBW data from the sediment trap
421 and the core-top /sediment cores, a non-parametric two-way Mann-Whitney test has
422 been performed. This test determines if there are significant differences in the
423 medians of data sets without making assumptions about the data distributions. A p-
424 value <0.05 has been used to consider the median of two datasets different.
425

3.7. Radiocarbon dating

427 Between 50-100 individuals of well-preserved *G. bulloides* shells (>150 μm) were
428 picked for radiocarbon analyses. Radiocarbon ($^{14}C/^{12}C$) was measured as CO_2 with
429 a gas ion source in a Mini Carbon Dating System (MICADAS) at the Laboratory of
430 Ion Beam Physics from ETH Zürich. The employed automated method consists of
431 initial leaching of the outer shell to remove surface material with 100 μl of ultrapure
432 HCl (0.02M) and the subsequent acid digestion of the remaining carbonates with
433 100 μl of ultrapure H_3PO_4 (85%) (Wacker et al., 2013). Therefore, no cleaning was
434 applied after the picking contrary to the samples used for mass and size
435 measurements. Marble (IAEA-C1) was used for blank correction and results were
436 corrected for isotopic fractionation via $^{13}C/^{12}C$ isotopic ratios.
437 Conventional radiocarbon age for sample 14-14.5cm from MR 3.1.A site was
438 calibrated with the on-line calibration program CALIB (Stuiver and Reimer, 1993)
439 using the Marine20 curve, which applied a marine reservoir correction of 550 ^{14}C
440 years (Heaton et al., 2020) to the corresponding ^{14}C age and error. Additionally, a
441 local reservoir effect (Stuiver and Braziunas, 1993) of -165 ± 95 ^{14}C years was
442 considered. This local reservoir was calculated as the average of the 8 nearest
443 points to the sample location from the Marine Reservoir Correction database
444 (Reimer and Reimer, 2001), whose values have already been corrected for the
445 Marine20 curve. ^{14}C ages from samples 0.5-1cm from both PLA CT and LCD SC
446 lied out of the range for calendar calibration, implying these samples contain some
447 bomb ^{14}C and cannot be considered pre-industrial (Table 1, see "bomb ^{14}C"). In order
448 to have an estimation of the time span that could be covered by these dates, the
449 same marine and local reservoir corrections were applied to the most recent ^{14}C date
450 that could be corrected (i.e. 603 ^{14}C years BP). As the $F^{14}C$ for this sample was <1
451 (see Supplementary table 1), this means that the ^{14}C found in these samples is not
452 dominated by the bomb carbon. Here we propose a 110-50 cal. years BP age for
453 these samples. Then, these samples could be considered post-industrial. The
454 detailed results of the calibration and the ^{14}C dating can be found in the
455 Supplementary figs. 1 and 2.
456 Finally, it is important to consider that these ^{14}C ages represent mean average
457 values. Therefore, time integration within each sample and the effects of bioturbation
458 could cause a variation on the foraminifera real ages (Dolman et al., 2021).
459 Both the samples and dates obtained are detailed in Table 1. Planktic foraminifera
460 present in the dated samples that were not selected for radiocarbon dating were also
461 analyzed following the methodology described previously.

462 ## 4. Results
463
464 **4.1. Shell morphometric parameters and shell-weight normalization**

468   **Table 2**. Minimum, mean, maximum and standard deviation values of shell
469   area, diameter and SBW for *G. bulloides, N. incompta* and *G. truncatulinoides*
470   at all studied sites. The last 3 columns show the number of samples, the mean
471   number (N) of individuals analyzed per sample and the total number of
472   individuals measured for each site.

	Area (µm²)				Diameter (µm)				Sieve Based Weight (SBW, µg)				Total	N per	total
PLA Sediment Trap	Min	Mean	Max	Std.Dev	Min	Mean	Max	Std.Dev	Min	Mean	Max	Std.Dev	samples	sample	N
G. bulloides	16978	57353	168492	17261	147.0	267.5	463.2	38.6	3.21	4.43	5.60	0.66	35	27.2	893
N. incompta	26234	42821	135422	8934	182.8	232.4	415.2	22.6	3.17	4.45	5.40	0.59	32	15.0	455
G. truncatulinoides	70712	178952	527622	63572	291.9	468.5	819.6	81.9	10.67	23.11	39.57	7.79	59	13.0	729
PLA Core-Top															
G. bulloides	37163	55395	87894	12302	217.5	264.0	334.5	28.8	5.00	5.22	5.43	0.30	2	17.3	39
N. incompta	27635	36927	49619	5447	187.6	216.3	251.4	15.9	4.46	4.46	4.46	0.00	2	19.7	41
G. truncatulinoides	89778	174748	233229	44313	338.1	467.7	544.9	61.9	34.80	35.40	35.90	0.70	2	14.7	34
MIN Sediment core															
G. bulloides	20895	52132	138424	8722	163.1	256.8	419.8	20.5	4.00	5.07	6.57	0.46	40	19.6	761
N. incompta	24003	35098	57264	4658	174.8	211.0	270.0	13.7	3.45	4.11	5.00	0.34	40	20.3	791
G. truncatulinoides	116686	166318	365851	23262	385.4	459.1	682.5	30.8	28.33	34.99	42.60	3.25	40	14.4	576
LCD Sediment core															
G. bulloides	27624	52472	116605	8793	187.5	257.7	385.3	20.4	4.35	4.73	5.19	0.31	7	20.1	136
N. incompta	28089	37789	51284	4972	189.1	218.9	255.5	14.4	3.68	4.12	4.50	0.26	7	19.8	134
G. truncatulinoides	82534	143138	393754	41620	324.2	423.3	708.1	55.9	25.27	26.68	30.66	1.94	7	15.3	105

473

474 Overall, the mean values for both diameter and area correspond to the mean
475 narrowed size fraction used during the picking, but morphometric parameters show
476 some variability between the studied sites. Standard deviation of both area and
477 diameter values for the three species are higher in the sediment trap record than in
478 seafloor sediments, with mean values (of all three species) of 82% higher for area
479 and 69% higher for diameter. SBW exhibits the same pattern as both area and
480 diameter standard deviation is a mean 130% higher in the Planier sediment trap.
481 Regarding the variability across the seafloor samples, Planier core-top exhibits a
482 greater area and diameter values (about 40 to 50% increase for the three species)
483 compared to those of the other two sediment cores, probably due to the fewer
484 samples analyzed (Table 2).
485 The Planier sediment trap results (Table 2) show a higher standard deviation for both
486 area and diameter for the three species, i.e. 76 % and 68% higher for *G. bulloides*

487 compared to the data from core tops, 78% and 54% for *N. incompta* and 81% and
488 73% for *G. truncatulinoides*.
489 Because of the lack of precision of the initial individuals picking, carried out with a
490 micrometer installed in the microscope, the selection is not totally accurate. Due to
491 this issue, one third of the of the total measured foraminifera (i.e. 1645 of 4694) were
492 out of the desired size fraction, of which 12% were bigger (580/4694) and 23% were
493 smaller (1065/4694). Nonetheless, only 0.02% were more than 20% out of the
494 selected size range (64/4694 more than 20% bigger and 29/4694 more than 20%
495 smaller). Mean size difference for the foraminifera out of the size fraction is around
496 7%. Results vary according to the site and the species. 50% of the individuals from
497 the Planier sediment trap (1046/2077) and 26% of the individuals coming from the
498 core tops (692/2617) were out of range. *G. bulloides* showed a 45.5% (53.2% in the
499 sediment trap and 39.3% in the core-tops samples) of individuals out of selected size
500 fraction, while this value was 21.5% (22.2% in sediment trap, 21.1% in sediment
501 cores) for *N. incompta* and 35% for *G. truncatulinoides* (53.4% in sediment trap,
502 16.7% in sediment cores).
503 Even though a narrow size class was selected for each species (see section 3.4), a
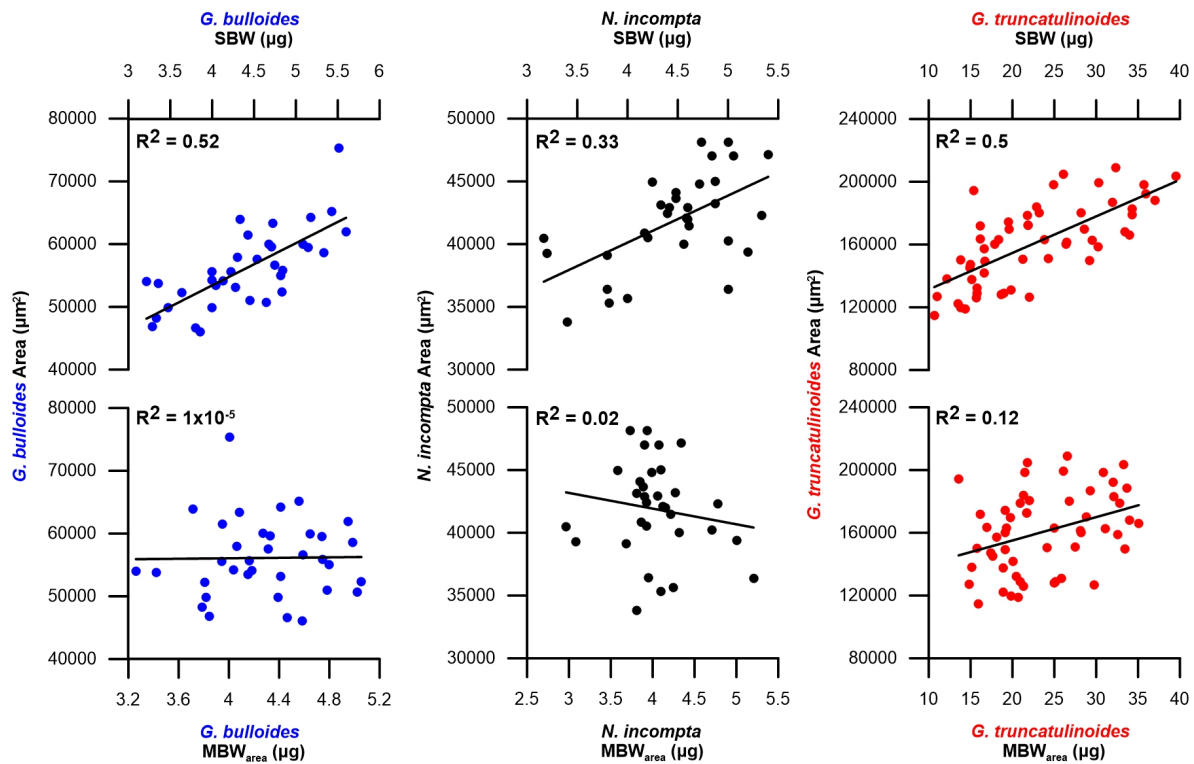504 clear influence of the area on the SBW was found in our data set (Fig. 2).
505

506

507 **Figure 2**. SBW in μg and MBW$_{area}$ in μg against the mean test area in μm^2 for
508 foraminifera samples in the Planier sediment trap. Dark blue dots correspond
509 to *G. bulloides*, black dots to *N. incompta* and red dots to *G. truncatulinoides*.

510 ~~In Fig. 2, we show the values for the Planier sediment trap record for both SBW and~~
511 ~~MBW$_{area}$ for all three species considered in this study, and their r^2 with the measured~~
512 ~~area.~~ In particular, SBW shows a positive correlation with area: $0.33 < r^2 < 0.53$ (Fig.
513 2). This indicates that the SBW is dependent on the size of the specimens within the
514 selected size range. Thus, to isolate the component of variation in foraminifera shell
515 thickness that represents a change in calcification and does not occur as a direct
516 result of changes in shell size, normalization of the shell weight was performed
517 following the formula detailed in section 3.3. (Beer et al., 2010). After normalization
518 MBW$_{area}$ shows no correlations with area: $1 \times 10^{-5} < r^2 < 0.12$ (Fig. 2). Note that the
519 weight variations in our dataset are quite considerable, especially for *G.*
520 *truncatulinoides*, probably due to the wider size fraction. Diameter does show
521 correlation with SBW: $0.33 < r^2 < 0.5$; and shows a non-negligible correlation with
522 MBW$_{diam}$: $0.2 < r^2 < 033$. Our data demonstrates that SBW correlates more strongly
523 with MBW$_{diam}$ than with MBW$_{area}$ for the 3 species: $0.9 > 0.48$ for *G. bulloides*,
524 $0.89 > 0.52$ for *N. incompta* and $0.97 > 0.81$ for *G. truncatulinoides*. These values are
525 consistent with previous studies (Beer et al., 2010).

526 **Table 3.** Pearson correlation test results for the three species correlation
527 between area (μm^2) and both SBW (μg) and MBW$_{area}$ (μg). Here c.i. stands
528 for "confidence interval". Significant r values ($0 < c.i. < 1$) are set in bold.

| | Area (μm^2) | | | | | |
| | G. bulloides | | N. incompta | | G. truncatulinoides | |
	r	c.i.	r	c.i.	r	c.i.
SBW (μg)	**0.72**	0.52, 0.85	**0.57**	0.28, 0.77	**0.62**	0.41, 0.76
MBW$_{area}$ (μg)	0.014	-0.32, 0.35	-0.15	-0.47, 0.21	0.21	-0.09, 0.44

529
530 Furthermore, a Pearson correlation test (see section 3.6) has been carried out in
531 order to assess the influence of area on SBW and MBW$_{area}$ (Table 3). Results
532 showed that the SBWs from the three species correlated positively and significantly
533 ($0 < c.i < 1$). With their corresponding areas ($0.57 < r < 0.72$). Concerning the MBWs,
534 no significant ($0 > c.i. > 1$) correlations with the area are observed ($-0.15 < r < 0.2$).
535 Therefore, these correlations further highlight the fact that SBW values are
536 significantly influenced by shell area, while MBW$_{area}$ values appeared to be
537 independent of the area.
538 Differences between SBW and both MBW$_{area}$ vary depending on the species: SBW
539 is slightly heavier for *G. bulloides*, heavier for *N. incompta* and lighter for *G.*

540   *truncatulinoides*. The mean standard deviation for all 3 species is around 8%: 7.8%
541   for *G. bulloides*, 6.4% for *N. incompta* and 13% for *G. truncatulinoides*. We take
542   these values as the error adjustment for SBW in the different size fractions (250-300
543   *µ*m, 200-250 *µ*m and 400-500 *µ*m respectively). It is difficult to compare these results
544   with other studies as size fractions and species are often different, but this error
545   estimates are in the same order of magnitude as some other MBW published in core-
546   tops records and sediment traps (de Moel et al., 2009; Moy et al., 2009).
547   These findings highlight the fact that the use of sieve fractions does not provide
548   enough control on the influence of morphometric parameters in test weight.
549   Morphometric variations described in Table 1 indicate that the typically used sieve
550   fractions may be unreliable due to the number of individuals out of the desired
551   fractions and the variability within the size range. The correlations between SBW
552   and shell area are consistent with previous studies (Aldridge et al., 2012; Beer et al.,
553   2010) and underscore the importance of isolating the component of variation in
554   foraminifera shell thickness that represents a change in calcification and does not
555   occur as a direct result of change in shell size. Thus, the shell weight was size-
556   normalized after Beer et al., (2010) by isolating the influence of isometric scaling on
557   wall thickness and calcification density.
558   Moreover, both MBW_{area} (Fig. 2) and MBW_{diam}, in either the sediment trap data and
559   core-top data, do not correlate with area and diameter ($1x10^{-5} < r^2 < 0.33$ and 0.001
560    $< r^2 < 0.2$ respectively) indicating that size does not have an influence on these
561   values. This suggests that our size-normalization procedure adequately removes the
562   size influence (Fig. 2) and therefore, our MBW data represents a robust parameter
563   reflecting test wall thickness and calcification intensity not influenced by test size
564   (Table 3). Therefore, MBWs can be considered as a reliable calcification intensity
565   proxy.
566   Based on all the above, from this point we'll focus our discussion on the MBW_{area} to
567   discuss the foraminifera shell weight variability on seasonal, interannual and pre to
568   post-industrial Holocene time scales.
569
570   **4.2. Seasonal variations of foraminifera calcification in the NW Mediterranean**
571   MBW_{area} values were calculated for the three species to illustrate the seasonal
572   variability of these parameters (Figs. 3 and 4). Samples have been assigned to their
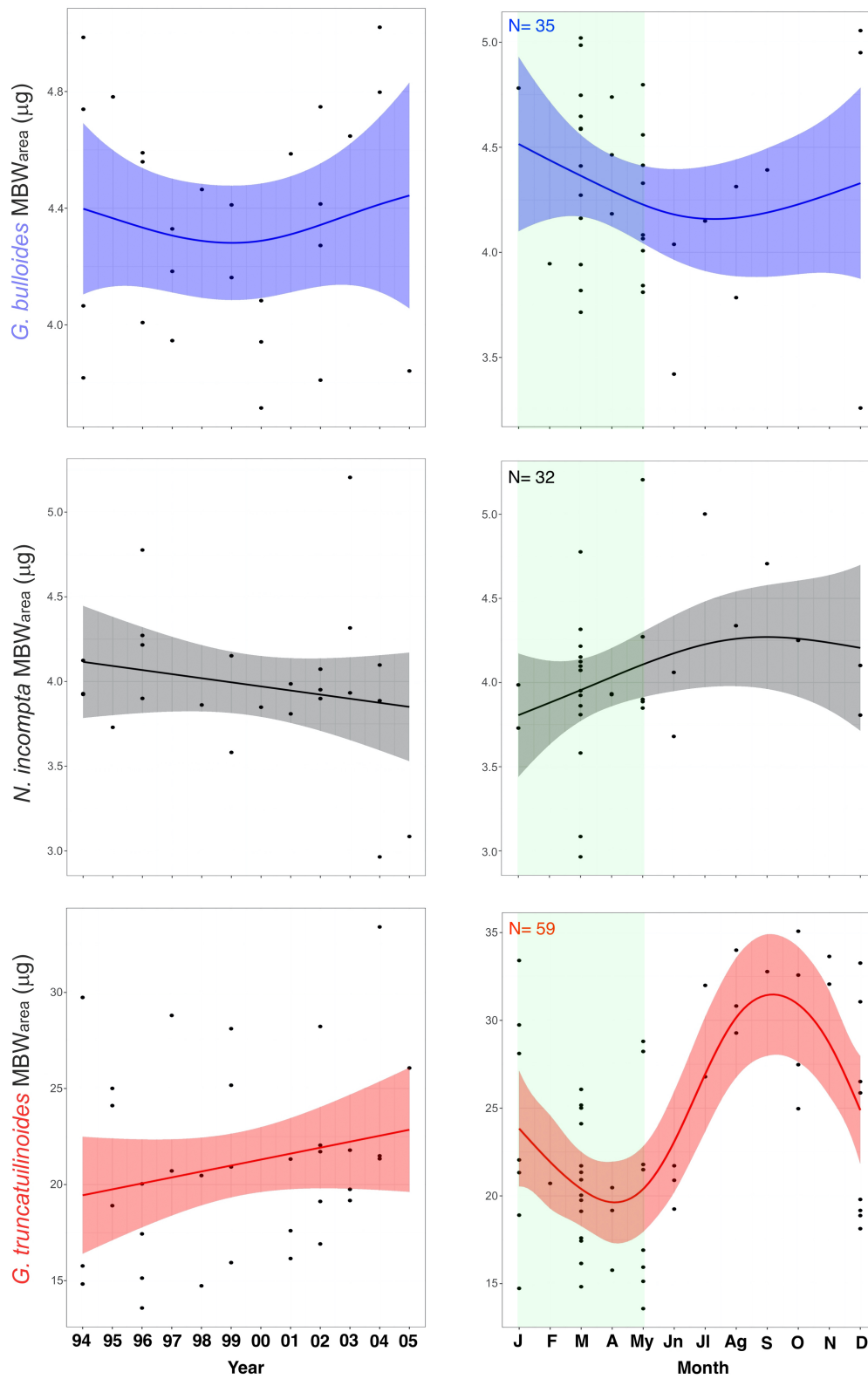573   corresponding month according to the mean cup sampling date.

574

Figure 3. Mean MBW$_{area}$ (µg) values across the years and for a composite
year for *G. bulloides, N. incompta* and *G. truncatulinoides* in the Planier

577   sediment trap. Light-green shaded area represents the high productivity
578   period in the study zone (Rigual-Hernández et al., 2012).

579   The mean MBW$_{area}$ for the three species in the Planier sediment trap are 4.29 μg ($\pm$

580   0.45 μg for *G. bulloides*, 4.04 μg ($\pm$ 0.4 μg) for *N. incompta* and 23.25 μg ($\pm$ 6.2 μg)

581   for *G. truncatulinoides*. The seasonal variations in shell calcification differ according

582   to the species.

583   In the case of *G. bulloides*, maximum annual calcification values are reached during

584   winter and early spring: 5.05 in December and 5.02 μg in March. January displays

585   the highest mean value: 4.78 μg. Minimum values are reached during summer: 3.72

586   μg in June, which is also the month that exhibits the lowest mean MBW$_{area}$. Overall,

587   there is a 1 μg seasonal difference in calcification between maximum and minimum

588   values, which corresponds to a 24.5% change in the mean MBW$_{area}$ value. Mean

589   seasonal standard deviation is $\pm$ 0.47 μg.

590   *N. incompta* shows a maximum in calcification in late spring to mid-summer: a

591   maximum value of 5 μg is reached in May, while July is the month that displays the

592   highest mean value (5 μg). Lowest values are reached in early spring: 2.96 μg in

593   March, while January displays the lowest mean value (3.85 μg). Thus, the annual

594   mean seasonal amplitude is 1.15 μg which translates into a 28% seasonal MBW$_{area}$

595   variability. Standard deviation is $\pm$ 0.28 μg.

596   Finally, *G. truncatulinoides* displays a seasonal maximum MBW$_{area}$ value in late

597   summer-autumn, with a maximum reached in October: 35.07 μg, while November;

598   is the month that shows the highest mean MBW$_{area}$ value (32.85 μg). The lowest

599   value is reached in March: 13.57 μg, and April is the month that shows the lowest

600   mean value: 18.45 μg. Seasonal MBW$_{area}$ difference is 14.3 μg: a 60% variability.

601   Mean typical seasonal deviation is $\pm$ 3.7 μg.

602

603   **4.3. Interannual MBW$_{area}$ trends**

604   Trends throughout the 12-year record are represented in Figs. 3 and 5. In order to

605   obtain representative data for each year, maximize data availability of each species

606   and avoid the impact of months with insufficient specimens on the interannual trends,

607   only MBWs from the productive period (January to May) of each year analyzed were

608   included.

609   *G. bulloides* MBW$_{area}$ showed a slight decrease from 1994 to 2000 and a slight

610   increase from 2000 to 2006. Over the studied interval, the lowest value is reached

611   in the year 2000 and the highest in 2004. Lowest mean annual values were reached

612   during years 2000 and 2005 (3.9 and 3.85 μg, respectively).

613   On the other hand, *N. incompta* MBW$_{area}$ showed a slight calcification reduction with

614   the highest variability in recent years. Both maximum and minimum values are

615 displayed in recent years: 2004 and 2005 respectively. Mean yearly MBW$_{area}$ values
616 reach a maximum in 2003 (4.4 μg) and a minimum in 2005 (3.2 μg).
617 Finally, *G. truncatulinoides* MBW$_{area}$ displayed a different pattern, with an overall
618 steep calcification increase throughout the record. Minimum calcification values are
619 observed in 1996, which is also the year with the lowest mean MBW$_{area}$ (16.5 μg)
620 observed. Maximum value is displayed in 2003, and its mean value is also the
621 highest of the record (26.1 μg).
622 All environmental parameters showed variations across the years. Sea Surface
623 Temperatures (SSTs) displayed a slight but constant decrease over the years, while
624 salinity showed a slight increase, mainly since 2002. From late 2000 until late 2002,
625 phosphate and nitrate concentrations were exceptionally low (Fig. 5). This feature
626 has already been described in the Gulf of Lions (Meier et al., 2014). Between the 2
627 periods for which direct *in situ* carbonate system parameters measurements were
628 available, 1998 to 2000 and 2003 to 2005 (Fig. 5), CO_3^{2-} dropped by 10-15 μmol/kg,
629 DIC increased by 40 to 60 μmol/kg, leading to a pH decrease of 0.02 to 0.025.
630
631 **4.4. Sediment trap, core tops and sediment cores MBW patterns**
632 Foraminifera weights analyzed in core tops and sediment cores from the NW part of
633 the Mediterranean (Fig. 6) and radiocarbon dating allowed a further insight on
634 foraminifera calcification during the Holocene.
635 Flux-weighted MBWs (see section 3.4) from Planier sediment trap for the three
636 planktic species were 4.1 μg for *G. bulloides*, 3.3 μg for *N. incompta* and 22.3 μg for
637 *G. truncatulinoides* (Fig. 6).
638 Data from Planier core-top showed higher mean MBW$_{area}$ values: 5.3 μg, 4.65 μg
639 and 35.4 μg. ^{14}C dating carried out in this core-top was out of the calibration range
640 (see section 3.7 for more details), implying that this sample could be considered
641 post-industrial. Compared to the flux-weighted MBWs from the sediment trap, *G.*
642 *bulloides* weight has been reduced by 1.2 μg, *N. incompta* by 1.3 μg and *G.*
643 *truncatulinoides* by 12-13 μg.
644 Located west of Planier site, Lacaze Duthiers sediment core mean MBWs were:
645 4.99 μg for *G. bulloides*, 4.14 μg for *N. incompta*, and 32.9 μg for *G. truncatulinoides*.
646 ^{14}C analysis displayed a post-industrial age (see section 3.7) for this sample and
647 corresponding MBWs from this sample for *G. bulloides*, *N. incompta* and *G.*
648 *truncatulinoides* respectively were: 4.7 μg, 4.2 μg and 34 μg. Overall, compared to
649 the data from the sediment trap, this corresponds to a 0.6 μg weight loss for *G.*
650 *bulloides*, 0.9 μg for *N. incompta* and 12.2 μg for *G. truncatulinoides* in.
651 Finally, in the Gulf of Minorca, northwest of Planier site, Minorca sediment core mean
652 MBWs were: 5.4 μg for *G. bulloides*, 4.5 μg for *N. incompta* and 36.3 μg for *G.*

653 *truncatulinoides* (Fig. 6). ^{14}C dating on this core top was carried out on an
654 intermediate depth (see section 3.7) due to the lack of availability of enough
655 specimens in the core-top and displayed a date of 1560 calendar years BP (Table
656 1). Corresponding MBWs for this sample were 5.4 µg, 4.9 µg, 38.2 µg for the three
657 species. Therefore, the weight reduction compared to the sediment trap flux-
658 weighted MBWs are: 1.3 µg for *G. bulloides*, 1.6 µg for *N. incompta* and finally, 16 µg
659 for *G. truncatulinoides.*

660 **Table 4.** Mann-Whitney variance test results between the MBW$_{area}$ of the
661 different sites for the three species. Significant values (p<0.05) are set in bold.

	PLA ST	PLA CT	LCD SC	MR 3.1.A
		MBW$_{area}$		
G. bulloides				
PLA ST		0.110	**0.003**	**7.86e^{-13}**
PLA CT	0.110		1	1
LCD SC	**0.003**	1		0.114
MIN SC	**7.86e^{-14}**	1	0.114	
N. incompta				
PLA ST		0.438	0.890	**2.59e^{-5}**
PLA CT	0.438		0.342	1
LCD SC	0.890	0.342		**0.034**
MIN SC	**2.59e^{-5}**	1	**0.03**	
G. truncatulinoides				
PLA ST		0.120	**0.003**	**3.13e^{-15}**
PLA CT	0.120		0.644	1
LCD SC	**0.003**	0.644		**0.01316**
MIN SC	**3.13e^{-15}**	1	**0.013**	

662
663 A Mann-Whitney variance test (see section 3.6) was carried out in order to analyze
664 the variance between the different MBW$_{area}$ datasets (Table 4) from the different
665 sites. MBW$_{area}$ data from the sediment trap appeared to have a significantly different
666 variance compared to the MBW$_{area}$ from Menorca sediment core for the three
667 species (3.13e^{-15}<p<2.59e^{-5}), however, differences between the sediment trap data
668 and the with Lacaze-Duthiers sediment core were only significant for *G. bulloides*
669 and *G. truncatulinoides* (p=0.003). Concerning differences between the Planier
670 sediment trap and the underlying core-top, no significant differences were observed
671 for any of the species (0.11<p<0.438), most likely due to the small number of

672 samples from the latter site: only 2 samples were available. Note that the differences
673 between the sediment cores MBW$_{area}$ datasets differed according to the site and
674 species. In the case of *G. bulloides*, no significant differences were observed
675 between Planier core-top, Lacaze-Duthiers sediment core and Menorca sediment
676 core. In the case of *N. incompta* and *G. truncatulinoides*, differences between
677 Lacaze-Duthiers and Menorca sediment core were significant (0.013<p<0.03),
678 although on lower orders of magnitude compared to the differences between the
679 sediment trap and sediment cores datasets (Table 4). This demonstrates that the
680 difference between the sediment trap MBW$_{area}$ dataset and the seabed sediments
681 MBW$_{area}$ datasets was greater than the difference between the different seabed
682 MBW$_{area}$ datasets.

683 ## 5. Discussion

684

685 **5.1. Seasonal controls on planktic foraminifera shell calcification in the NW**
686 **Mediterranean**

687 As described in section 4.2, the seasonal variability of MBW$_{area}$ displays important
688 differences across the three species analyzed. The different seasonal pattern in
689 MBW$_{area}$ is reflected by the lack of correlation between the seasonal patterns of
690 MBW$_{area}$ of the different species, i.e., r= -0.23 (p>0.05) between *G. bulloides* and *N.*
691 *incompta* and r= 0.16 (p>0.05) between *G. bulloides* and *G. truncatulinoides*. Only
692 the seasonality of *N. incompta* MBW$_{area}$ and *G. truncatulinoides* MBW$_{area}$ share some
693 similarities, as reflected in the significant and positive correlation (r= 0.66; p<0.05).
694 In order to examine the main controls on foraminifera seasonal calcification in the
695 Gulf of Lions, here we compare the seasonal variability of planktic foraminifera
696 calcification with foraminifera fluxes previously estimated for the Planier sediment
697 trap (Rigual-Hernández et al., 2012) satellite data for the studied site and a suite of
698 environmental parameters measured at the DYFAMED site (see section 3.4).
699 Furthermore, GAM have been generated for all three species (see Supplementary
700 figs. 3,4 and 5) and the environmental parameters considered here in order to give
701 a further insight on the potential factors controlling the MBW$_{area}$. These models
702 showed that *G. bulloides* and *G. truncatulinoides* seasonal calcification trends are
703 significant (p=0.05 and p=2.4e-5 respectively). On the other hand, *N. incompta*
704 seasonal trend does not appear to be significant (p=0.14).

705 **Table 5**. Correlation matrix of seasonal (monthly) test weights and the
706 environmental parameters from Planier (sediment trap and satellite data) and
707 DYFAMED site (see section 3.4). Significant correlations (p<0.05) are set in
708 bold.

Parameters	Planier site data								DYFAMED site data					
	G. bull.	*N. inc.*	*G. truncat.*	*G. bull.*	*N. inc.*	*G. truncat.*	Chl-a	SST	Salinity	$[NO_3]$	$[PO_4]$	pH	$[CO_3]$	$[CO_2]$
		MBW$_{area}$			Fluxes									
G. bull.	1	0.232	0.167	0.012	0.027	0.152	0.318	-0.32	-0.163	0.292	0.33	0.096	0.189	0.243
N. inc.	-0.232	1	**0.667**	**-0.582**	-0.407	-0.405	-0.484	**0.688**	0.368	0.272	0.235	-0.35	0.474	-0.28
G. truncat.	0.167	**0.667**	1	**-0.905**	**-0.725**	**-0.666**	**-0.585**	**0.672**	-0.299	0.258	0.512	0.113	**0.732**	0.541

(MBW$_{area}$ label applies to the left row block)

Here, we first approach seasonal shell calcification by considering the Optimum Growth Conditions (OGC). Previous studied have defined these conditions on a wide variety of ways: abundance of foraminifera, the chlorophyll-a concentration and even nutrients concentration (de Villiers, 2004; Schiebel et al., 2001; Schiebel and Hemleben, 2017). Therefore, we aim to explore the impact of these parameters as OGC on the shell calcification.

Among all the environmental parameters, de Villiers; (2004) suggested that shell calcification, and therefore MBWs, is primarily controlled by the OGC that can be defined as the most suitable environmental conditions for the development of a given planktic foraminifera species. Based on the latter study, it could be expected that favorable environmental conditions for foraminifera growth would lead to both greater shell fluxes and enhanced shell calcification. Our correlation analysis shows ~~different relationships between foraminifera abundance (as inferred from foraminifera shell fluxes) and shell weight. In particular, *G. bulloides* MBW$_{area}$ shows no correlation with its fluxes (Table 5), while both *N. incompta* and *G. truncatulinoides* exhibit a negative correlation between MBW$_{area}$ and their species fluxes although only significant for the latter species (r= -0.4, p>0.05 and -0.66, p<0.05 respectively)~~ that only *G. truncatulinoides* displays a significant (and negative) correlation with it's flux (r= -0.66, p>0.05). GAM results (see Supplementary figs. 3, 4 and 5) support these observations, with shell flux showing a stronger effect on the calcification for *G. truncatulinoides* compared to the other two species fluxes.

According to the OGC theory, species calcification patterns vary according to the species and their fluxes. Interestingly, *G. truncatulinoides* calcification correlates negatively and significantly with all three species fluxes, a pattern opposite to what the OGC theory predicts (de Villiers, 2004), i.e., optimum ecological niche is associated with enhanced calcification. Thus, a possible explanation reconciling our observations with the OGC theory may be that *G. truncatulinoides* tends to prioritize energy allocation toward growth and reproduction at the price of a reduced calcification. ~~As described previously (see section 3.3), this species life cycle is~~

741 ~~complex as it migrates through different depth levels of the water column throughout~~
742 ~~the year.~~ It is thought to reproduce once a year in winter in subtropical waters and it
743 has been speculated that nutrient availability and the lack of predation could explain
744 this strategy. ~~Therefore, the observation of peak calcification in autumn/winter (Figs.~~
745 ~~3 and 4) may reflect the migration of adults – that have spent time in deeper waters~~
746 ~~developing a thick calcite crust – to shallower waters in late autumn to winter to~~
747 ~~undergo reproduction~~. During this interval, the other major species display low
748 abundances in the water column, which could allow *G. truncatulinoides* to reproduce
749 due to the lack of competition. *N. incompta* calcification displays a similar pattern, a
750 negative correlation with all three species, but with a lower level of significance. It's
751 MBW_{area} correlates negatively and significantly ($p<0.05$) with *G. bulloides* flux, but
752 its fluxes correlate positively and significantly with the latter species fluxes (see
753 Supplementary table 2). This is interesting, as it may highlight interspecific relations.
754 First, this could lead to the assumption that when *G. bulloides* dominates the
755 assemblages, *N. incompta* also displays a high abundance (Rigual-Hernández et
756 al., 2012). Then, it could show that when conditions are favorable, *N. incompta*
757 reproduces at a higher rate at the price of thinner shells (Table 1). This agrees with
758 *N. incompta* life cycle, which is known to be outnumbered by opportunistic species
759 when nutrients supply is high (Schiebel et al., 2002), but dominate the assemblages
760 when stratified waters are set, therefore, when conditions are favorable or when in
761 cohabitation with opportunistic species, it could focus on its reproduction. Note that
762 *G. truncatulinoides* and *N. incompta* MBW_{area} correlate positively and significantly
763 ($p<0.05$), showing a similar calcification pattern on a seasonal scale.
764 An alternative proxy for OGC that may be considered is chlorophyll-*a* concentration.
765 Chlorophyll is considered an indicator of the algal biomass concentration, which is
766 known to represent a large part of some foraminifera species diet (Schiebel and
767 Hemleben, 2017)~~. Specially for *G. bulloides* (Schiebel and Hemleben, 2017a). Our~~
768 ~~data shows a positive but not significant correlation between chlorophyll~~
769 ~~concentration and *G. bulloides* MBW (r= 0.32, p>0.05), suggesting a negligible~~
770 ~~influence of phytoplankton concentration on *G. bulloides* calcification.~~ However, our
771 data only showed a significant correlation of chlorophyll-a with *G. truncatulinoides*
772 calcification. A stronger trend would be expected under the OGC theory for *G.*
773 *bulloides* as algae are a vital part of its diet (Hemleben et al., 1989; Schiebel and
774 Hemleben, 2017). This lack of correlation between *G. bulloides* and chlorophyll-*a*
775 has already been described (Weinkauf et al., 2016). We speculate that *G. bulloides*
776 may preferentially feed on certain groups of phytoplankton which changes in
777 seasonal abundance in the photic zone do not necessarily follow the seasonal
778 pattern of total chlorophyll concentration (Marty et al., 2002). Also, note that the
779 chlorophyll-a data presented here only represents the conditions in the surface layer.

780 ~~In the case of *N. incompta* and *G. truncatulinoides*, correlations between MBW~~$_{area}$
781 ~~and chlorophyll-*a* are negative and stronger although only significant for the latter~~
782 ~~species (r= -0.58, p<0.05).~~ GAM results further support these observations (see
783 Supplementary fig. 5), with chlorophyll-a showing a significant impact on *G.*
784 *truncatulinoides* calcification. This observation indicates that optimum calcification
785 conditions for *G. truncatulinoides* are reached at times of minimum annual algal
786 biomass concentration in the photic zone. It is possible that, due to its deeper habitat
787 (Schiebel and Hemleben, 2017), *G. truncatulinoides* feeds on phytoplankton
788 dwelling in subsurface levels of the water column. In fact, a deep chlorophyll
789 maximum is known to develop during large part of the year in the Northwestern
790 Mediterranean (Estrada et al., 1993) but its presence is not detected by satellites.
791 This interpretation is in agreement with earlier work by Pujol and Vergnaud Grazzini,
792 (1995) who found peak abundances of this species during the summer below the
793 thermocline.
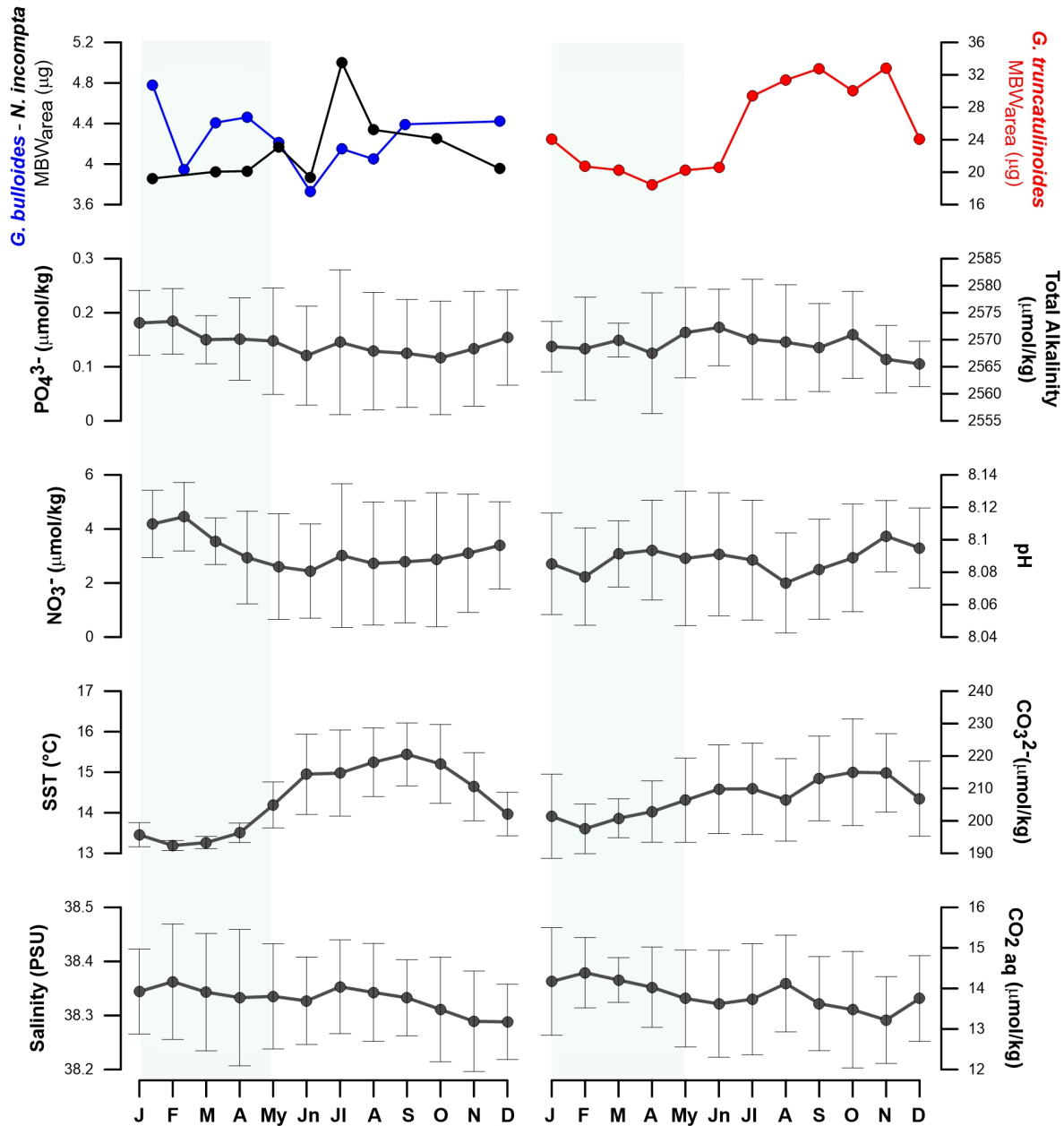
Figure 4. *G. bulloides*, *N. incompta* and *G. truncatulinoides* seasonal mean monthly MBW$_{area}$ variations compared with Planier environmental data and the resampled seasonal signal of environmental parameters from the DYFAMED site across a composite year.

Something to consider when using chlorophyll as an OGC proxy is that it can be confounded with the nutrient concentrations. Previous studies have described that, in those settings where foraminifera abundance covaries with nutrient concentrations, then nutrients are probably a better OGC proxy than chlorophyll concentrations (Schiebel et al., 2001). In turn, the correlation of nutrients (nitrates and phosphates) with fluxes were positive for all three species, although only

805 significative (p<0.05) for *G. truncatulinoides* abundance (r= 0.58 and 0.59 for nitrates

806 and phosphates respectively). Although here we have first described the OGC as

807 species fluxes and then as the chlorophyll-*a* concentration, it is important to

808 remember that the niche and favorable conditions meant to be described by the OGC

809 for each species are multi-dimensional.

810 Note that nitrate and phosphate concentration variations were closely linked to each

811 other (r= 0.876, p<0.05), making it difficult to determine if the resulting effect on

812 foraminifera calcification is due to the effect of a single driver or to the combination

813 of both. ~~High phosphate concentrations are generally considered an inhibitor for~~

814 ~~foraminifera calcification (Zeppenfeld, 2019). Evidences show that calcite formation~~

815 ~~is inhibited by PO_4^{3-} due to its adsorption on the calcite surface, impeding its~~

816 ~~precipitation by blocking the crystal growth. Aldridge et al., (2012) showed a negative~~

817 ~~effect of phosphate concentration on *G. bulloides* with PO_4^{3-} concentrations of 0.1-~~

818 ~~0.4 µM. This feature has been shown in other calcareous organisms such as~~

819 ~~coccolithophores (Paasche and Brubank, 1994) and calcifying algae (Demes et al.,~~

820 ~~2009), resulting in a higher growth and calcification under controlled PO_4^{3-}. On the~~

821 ~~other hand, no studies show a reduced calcification in marine organisms under high~~

822 ~~NO_3^- values (Fig. 4).~~ Our work shows that nutrient concentrations (both nitrates and

823 phosphates) do not correlate significantly with any of the three species MBW studied,

824 and this observation is supported by the GAM results which do not show any

825 significant effect of nutrients concentrations on the calcification.

826 Previous studies have suggested that salinity may have an influence on foraminifera

827 calcification (Zarkogiannis et al., 2022). ~~Found that salinity may control calcification~~

828 ~~of certain foraminifera species in the central Atlantic region.~~ However, our data

829 suggest that the role of salinity on calcification in our study region is unlikely since

830 its seasonal amplitude is tiny (0.1 PSU; Fig. 4). This idea is supported by the lack of

831 correlation between salinity and MBW$_{area}$ for the three species studied (Table 5) and

832 the GAM results ~~In which salinity was the parameter that displayed the lowest effect~~

833 ~~on calcification.~~

834 Temperature (Sea Surface Temperature) has been described as a major factor that

835 controls the size (Schmidt et al., 2004) and porosity (Burke et al., 2018) of planktic

836 foraminifera, therefore it could represent a major control factor on shell calcification

837 in the NW Mediterranean. In particular, calcification could be positively linked to

838 temperature through different mechanisms: (i) warmer temperatures have been

839 shown to increase enzymatic activity and therefore enhanced growth and

840 calcification rates (Spero et al., 1991); (ii) Lombard et al., (2011) stated that higher

841 temperatures could also increase feeding and ingestion rates, but it remains unclear

842 if this could result in a calcification rate increase. Our data revealed that SST

843 correlates ~~negatively, but without significance with *G. bulloides* calcification, while~~

844 ~~correlations between SST and~~ positively and significantly with *N. incompta* and *G.*
845 *truncatulinoides* calcification ~~were both positive and significant~~ (r= 0.69 and 0.67
846 respectively, p<0.05). GAM results also displayed a positive and the most
847 significative effect of the SST on these two species. These findings highlight that
848 SSTs are one of the main factors affecting *N. incompta* and *G. truncatulinoides*
849 calcification among the parameters considered here. Finally, in addition to having an
850 impact on the size and calcification of the planktic foraminifera, temperature is well
851 known as a major control of the carbonate system, due to the increased solubility of
852 atmospheric CO_2 at lower temperatures, and therefore it could have an indirect effect
853 on foraminifera calcification by affecting the carbonate system.
854 Data for the carbonate system were only available for years 1998 to 2000 and 2003
855 to 2005 and, therefore gaps comprised in these years were filled with estimates
856 using the CO2sys macro (see section 3.6 for more details). However, note that the
857 data available for these parameters was relatively smaller compared to the other
858 parameters and may have prevented detection of other significant relationships. The
859 relationship between CO_3^{2-} and MBW has been described in previous studies
860 (Barker and Elderfield, 2002; Marshall et al., 2013) and the bulk of evidence indicates
861 that foraminifera MBWs to be positively linked with CO_3^{2-} concentrations (Aldridge et
862 al., 2012; Osborne et al., 2016). However, it appeared that planktic foraminifera
863 response to CO_3^{2-} concentration was not uniform and varied across species (Beer
864 et al., 2010; Lombard et al., 2010). The trends between carbonate system
865 parameters and MBWs were similar to those observed when comparing MBWs with
866 temperature, highlighting the covariations between these two parameters (Fig. 4).
867 Our data showed that CO_3^{2-} concentrations were only significantly correlated with ~~G.~~
868 ~~bulloides MBW_{area} nor with *N. incompta*. Only~~ *G. truncatulinoides* MBW_{area} ~~displayed~~
869 ~~a clear significant correlation with CO_3^{2-} concentration~~ (r= 0.73, p<0.05), implying
870 that carbonate availability may represent a key control on this species in the
871 Northwestern Mediterranean. ~~On the other hand, CO_2 concentrations, excepting a~~
872 ~~negative and almost significant relationship with *G. truncatulinoides* MBW_{area} (r= -~~
873 ~~0.54, p= 0.06), showed no correlation with the other 2 species MBWs. None of the~~
874 ~~remaining carbonate system parameters (pH, alkalinity and calcite saturation),~~
875 ~~exhibited a significant seasonal correlation with the MBWs.~~ On the other hand, GAM
876 result (see Supplementary figs. 3, 4 and 5) did not show a significant impact of any
877 carbonate system parameters for any of the three species calcification. As stated
878 previously, the lack of data could have prevented the detection of further trends, but
879 considering the seasonal patterns of carbonate system parameters, a potential role
880 of the CO_3^{2-} concentration could be expected.
881 In summary, seasonal correlations, trends and GAM showed that the environmental
882 parameters that displayed the highest correlation with MBW_{area} vary according to the

species. *G. bulloides* calcification appeared to be affected mainly by the OGC and interspecific relations. *N. incompta* calcification showed to be mainly positively linked to the SST. Finally, *G. truncatulinoides* calcification was positively linked with the SST and potentially CO_3^{2-} concentration, while OGC displayed a negative effect on its MBW_{area}. ~~OGC (considered as fluxes and chlorophyll-a concentration), SST and potentially CO_3^{2-} are the most likely parameters that control the seasonal changes in calcification of the planktic foraminifera species studied here.~~ The combined effect of these parameters seems to control foraminifera calcification in the Gulf of Lions; however, it should be considered that covariation between these parameters is strong, and therefore it is difficult to isolate the effect of a single parameter. Moreover, it is likely that the ecology and life cycle of the species could also be a major factor affecting the response of the species calcification to the environmental parameters variations. Our results are in agreement with earlier studies that stated that OGC (de Villiers, 2004), SST and CO_3^{2-} (de Villiers, 2004; Marshall et al., 2013; Osborne et al., 2016) concentrations are the main factors that impact calcification in planktic foraminifera, while the calcification response to those parameters is species-specific, which is in agreement with the work of Weinkauf et al, (2016).

5.2. Interannual trends in planktic foraminifera calcification

As stated previously, the Mediterranean Sea is a sensitive zone to atmospheric CO_2 accumulation (Ziveri, 2012) and is experiencing ongoing ocean acidification. On an interannual time scale, different studies (Beer et al., 2010; Osborne et al., 2016) have shown that sea surface warming and carbonate system parameters are the most likely parameters to control calcification on key calcifying phytoplankton species such as the coccolithophore *Emiliania huxleyi* organisms (Meier et al., 2014). However, datasets from sediment traps that cover a wide span of years and in which foraminifera weights have been analyzed are rare (Kiss et al., 2021), therefore it is difficult to place our results in a more global context. Our GAM results (see Supplementary figs. 3 and 4) showed that both *G. bulloides* and *N. incompta* interannual patterns were non-significant. This is not surprising as the calcification trends for these two species did not display a clear and marked variation over the years, excepting a small mean calcification reduction (Fig. 3) and minimum calcification values in 2004 and 2005 (Fig. 3 and Supplementary figs. 3 and 4).
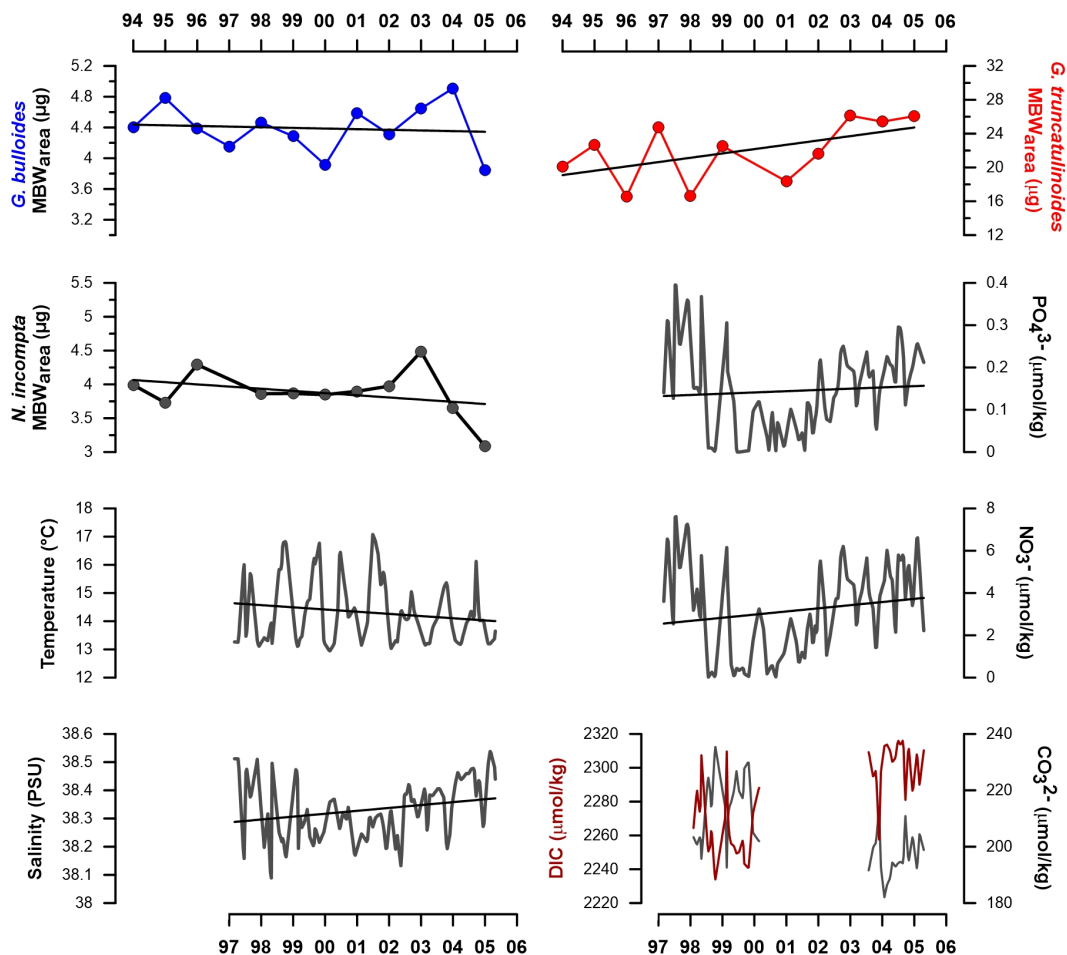
Figure 5. Interannual mean MBW$_{area}$ (μg) values for *G. bulloides*, *N. incompta* and *G. truncatulinoides* from the high productivity period (see section 2) and Planier and DYFAMED environmental data variations across the record. Black lines represent the trends from the MBW$_{area}$ and resampled data. DIC represents "Dissolved Inorganic Carbon".

Notably, the trend in *G. truncatulinoides* is opposed to the previous two species and shows a steady and steep increase throughout our record. Over the analyzed time span, its MBW increased around 20% (equivalent to an increase of ~5 μg). According to the GAM results, the interannual calcification trend for this species is significant (see Supplementary fig. 5). If this calcification increase continues on current trends, then the average MBW of *G. truncatulinoides* will double by 2024. Analysis of present *G. truncatulinoides* populations is urgently needed to assess if the observed trend held true during the last two decades. It is important to note that while *G. truncatulinoides* seems to exhibit a positive correlation with CO_3^{2-} concentration on a seasonal scale, no clear correlation was found with the interannual changes of CO_3^{2-} concentration. This feature is also supported by the GAM results. A similar enhancement in shell calcification has been described in the

934 Balearic Sea for *G. truncatulinoides* in high-resolution sediment cores (Pallacks et
935 al., 2020), but also in *Globorotalia inflata*. Taken together, our observations and the
936 study mentioned above, suggest that deep dwellers are unaffected by the recent
937 ocean acidification and changes in the carbonate system and that the recent change
938 in one or several environmental drivers may be stimulating the calcification of these
939 species.
940 Here, we theorize that the interannual patterns presented in Figs. 3 and 5 mainly
941 reflect the seasonal changes in the regional oceanographic setting. As described
942 previously (see section 2 for more details), the Gulf of Lions is influenced by a strong
943 seasonality. The recent SST decrease could be linked to an enhancement in water
944 mixing, as cold and deep salty water reach up to the surface. This mechanism would
945 be less intense during years 2000 to 2002, corresponding to a SST increase along
946 with a salinity decrease and absolute minimums in nutrients concentrations (Fig. 5),
947 as water stratificates, these are consumed by primary production. Finally, in recent
948 years, water mixing seems to be reactivated, as SST keeps decreasing and nutrients
949 concentrations increase again. This mechanism also affects the carbonate system
950 parameters, as water mixing brings to surface deeper DIC enriched waters to the
951 surface, coupled with a $[CO_3^{2-}]$ reduction. Our data shows that alkalinity patterns
952 display similar tendencies to DIC, however, until the second time span covered by
953 carbonate system data, alkalinity variations are proportionally higher than DIC
954 variations (see Supplementary material), suggesting a water mixing phenomenon.
955 On the other hand, DIC variations turn to be higher than alkalinity variations from
956 2003 to 2005, suggesting an additional effect of carbon inputs on the carbonate
957 system not reflected in the alkalinity data.
958 Note that SSTs, despite showing a positive and significant correlation with *N.*
959 *incompta* and *G. truncatulinoides* on a seasonal scale and the GAM showing a
960 positive and significant effect on the calcification, did not follow the same pattern as
961 the latter species. This observation implies that other mechanisms or parameters
962 than the ones considered here may be affecting the MBW_area on recent years.
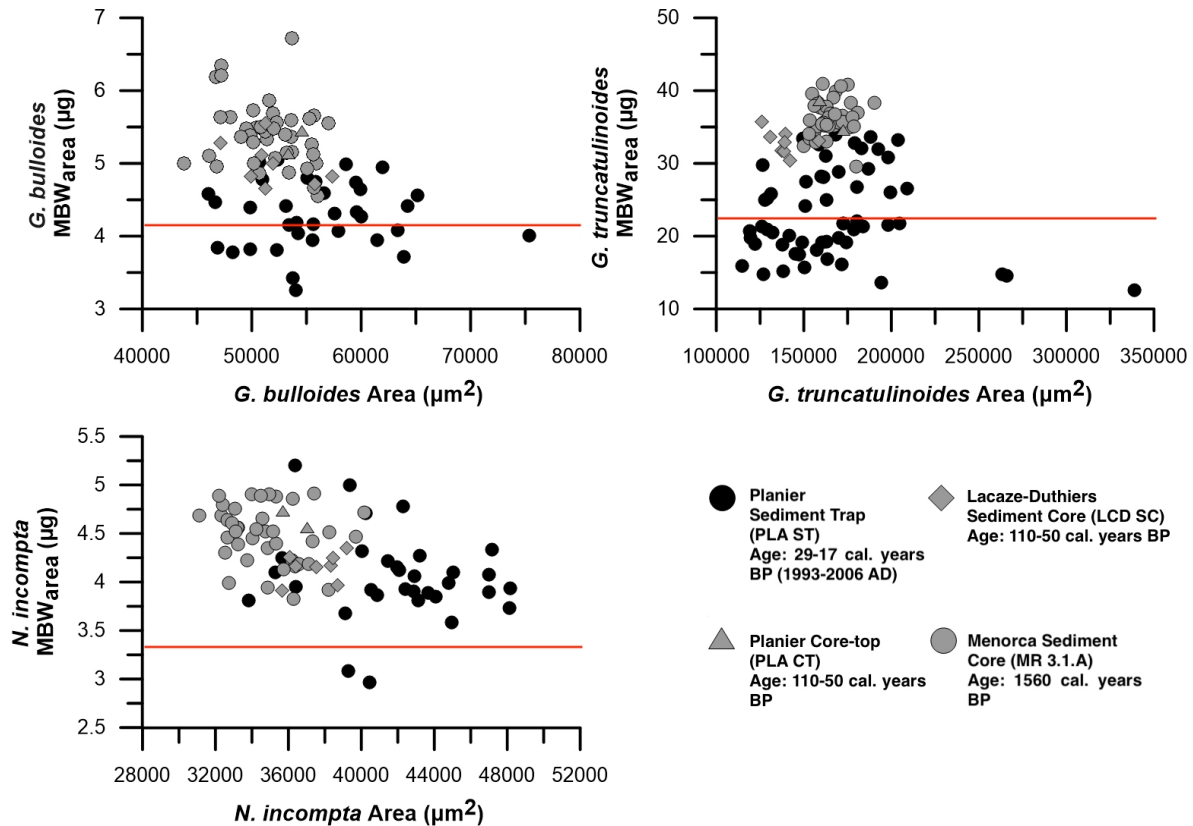963
964 **5.3. Holocene core-top data comparison**
965

Figure 6. MBW$_{area}$ in μg and area in μm^2 comparison in the sediment trap (PLA ST), Planier core-top (PLA CT), and both Lacaze-Duthiers (LCD SC) and Minorca sediment core (MR 3.1.A). Black dots represent data from the sediment trap, while lighter colors represent data from the different seabed sediments. Red lines represent the flux-weighted values from the sediment trap.

The comparison of the well-preserved assemblages of planktic foraminifera in the pre-industrial and industrial Holocene-aged surface sediments with those collected by a long-sediment trap record offers a unique opportunity to assess the impact of recent environmental change on the calcification of calcareous zooplankton in the Mediterranean Sea (Fig. 6). However, when comparing data from sediment traps and seabed sediments, the possible role of calcite dissolution must be taken into account.

Calcite dissolution in the water column and/or on the sea floor could be invoked as a source of variability between the sediment trap and surface sediment data sets (e.g., Dittert et al., 1999). Therefore, in order to obtain meaningful interpretations from our data sets it is important to assess the possible role of dissolution in the preservation of planktic foraminifera shells. Several lines of evidence suggest, however, that calcite preservation does not represent an important source of bias in our study area. Firstly, the Mediterranean Sea is supersaturated with respect to calcite (Millero et al., 1979) and the location of all the analyzed samples is much

988   shallower than the location of the calcite saturation horizon (Álvarez et al., 2014),
989   therefore, calcite dissolution seems unlikely (Schneider et al., 2007). Secondly,
990   several sediment trap studies have documented that calcareous plankton
991   experience negligible dissolution in their transit from the surface ocean to the sea
992   floor (Beaufort et al., 2007; Moy et al., 2009; Rigual-Hernández et al., 2020). Thirdly,
993   SEM and microscopic observations of all 3 species in samples from both the
994   sediment traps and sediment cores showed no sign of dissolution and foraminifera
995   were well preserved (see Supplementary fig. 6). These arguments suggest that
996   calcite dissolution does not represent an important control in the weight of the
997   planktic foraminifer shells in the analyzed samples. However, it has been
998   documented that when dissolution takes place, the thinnest shells are affected first
999   (Berger, 1970) while the heaviest and more calcified specimens remain. In our study,
1000 the specimens from the sediment trap were lighter that the ones from the sediment
1001 cores, which corresponds to the previous statement. This is important to
1002 acknowledge as the individuals from the seabed sediment could only represent more
1003 calcified and solid individuals, while the most fragile and less calcified individuals
1004 may not have been preserved. Therefore dissolution cannot be completely ruled out
1005 here as a possible source of variability between the surface sediment and sediment
1006 trap data sets.
1007 Overall, the lower shell weights of the foraminifera collected by the traps ~~strongly~~
1008 suggests that the three planktic foraminifera species may have experienced a
1009 reduction in their calcification since pre-industrial times to post-industrial and recent
1010 Holocene. While the shell weight of each species measured in the sediments show
1011 some variability across seabed sediments (Fig. 6), our data suggest an overall
1012 reduction of 18-24% for *G. bulloides*, 20-27% for *N. incompta*, and 32-40% for *G.*
1013 *truncatulinoides.* It is important to note that the range of shell weight variability across
1014 core-tops and sediment cores (4.5-6.7 μg and 0.37 μg typical deviation for *G.*
1015 *bulloides*, 3.8-4.9 μg and 0.23 μg typical deviation for *N.incompta*, and 29.5-40.9 μg
1016 and 2.6 μg typical deviation for *G. truncatulinoides*) is substantially lower than the
1017 difference with the sediment trap data (3-5 μg and 0.5 μg typical deviation for *G.*
1018 *bulloides*, 2.9-5.2 μg and 0.5 μg typical deviation for *N. incompta* and 12-35 μg and
1019 6 μg typical deviation for *G. truncatulinoides*), implying that the shell weight of recent
1020 foraminifera populations for the three species is lower than anywhere in the NW
1021 Mediterranean in the pre-industrial and post-industrial times. The source of the
1022 variability across core tops and sediment cores is most likely caused by the different
1023 age of the samples, ranging from 1560 cal. years BP at Minorca mid-depth (Table
1024 1) sample to post-industrial at Planier and Lacaze-Duthiers core-tops, and the
1025 different environments associated to the location of each core top.

1026 A non-parametric two-way Mann-Whitney test (see sections 3.6 and 4.3) showed
1027 that the sediment trap MBW$_{area}$ dataset was significantly different (p<0.05) from MR
1028 3.1.A and non-different from PLA CT for all three species studied here (Table 5).
1029 Something to consider when comparing recent sediment trap data with pre-industrial
1030 Holocene data is the life cycle of the species. As all the species analyzed presented
1031 a lighter weight in the sediment traps, the degree to which the different specimens
1032 responded varied. The greatest weight reductions were observed for *G.*
1033 *truncatulinoides* populations, while *G. bulloides* populations exhibited the lowest
1034 weight loss.
1035 Previous work stated that those species hosting photosynthetic algal symbionts
1036 exhibit a higher tolerance to environmental changes that may affect their calcification
1037 (Lombard et al., 2009). This is due to the fact that these symbionts can modify the
1038 sea water chemistry that is in a close range to the shell, allowing a calcification
1039 enhancement. Of the species studied here, none are known, with the possible
1040 exception of *G. bulloides*, to be symbiont bearing species, therefore, they are among
1041 the most vulnerable foraminifera species to any sea water chemistry change.
1042 It has been described that some morphotypes of *G. bulloides* do actually host
1043 bacterial endobionts in their cytoplasm (Bird et al., 2017). The later work showed
1044 that high amounts of *Synechococcus*, a cyanobacteria, were found in morphotype Id
1045 specimens of *G. bulloides* from the California coast. Although no such observations
1046 have been reported on morphotype Ib, the dominant *G. bulloides* morphotype in the
1047 Mediterranean sea (Schiebel and Hemleben, 2017), this could be relevant as
1048 bacterial photosynthetic activity would interact on the close range seawater
1049 chemistry by removing $^{12}CO_2$ and therefore impacting the $^{13}C/^{12}C$ ratios in the
1050 surrounding dissolved CO_2. Moy et al., (2009) work in the Southern Ocean, showed
1051 a 30-35% calcification reduction for *G. bulloides* during the industrial era. Our study
1052 shows that such a similar reduction in *G. bulloides* MBW$_{area}$ (i.e., a mean 20% taking
1053 into account the 3 sites studied) has also taken placed in the Mediterranean Sea.
1054 Even though the species studied were different in Fox et al., (2020), and that shell
1055 thickness was analyzed, that work showed a massive shell reduction for *N. dutertrei*
1056 (around 75%) and a smaller reduction for *G. ruber* (around 20%). *N. incompta* weight
1057 reduction in this study is around 25%, despite that life cycles are different between
1058 these species, our results come in the same line.
1059 Data for *G. truncatulinoides* calcification comparison between pre-industrial
1060 Holocene and post-industrial Holocene is scarce. One of the few available studies is
1061 the one of Pallacks et al., (2020) in the western Mediterranean sea using pre-
1062 industrial data and recent foraminifera weight data obtained from high resolution
1063 core-tops. Size-normalized weights showed that all the species calcification
1064 decreased since the onset of the industrial revolution, an observation that is

1065 ~~supported by our data (Fig. 6).~~ *G. truncatulinoides* showed a 24% weight reduction,
1066 which is a lower reduction than what is shown in our study (around 35% MBW_{area}
1067 decrease), but shows a similar trend. Taken together, all these observations suggest
1068 that a decrease in major planktic foraminifera calcification is not only a regional
1069 feature but a global scale process.

1070 On a more regional scale, Hassoun et al., (2015) documented the ongoing changes
1071 in seawater carbonate speciation in the Mediterranean waters. In the latter work, the
1072 distributions of anthropogenic CO_2 showed that all Mediterranean water masses
1073 have already experienced ocean acidification. This effect was more pronounced in
1074 the intermediate to deep masses (300-500m and >500m respectively) in the western
1075 basin, which translated into a minimum pH reduction of 0.1 in this part of the
1076 Mediterranean. As stated previously, over the years in which carbonate parameters
1077 were retrieved from the DYFAMED database, pH was reduced, DIC showed a
1078 marked increase and $[CO_3^{2-}]$ displayed a decrease. Taken together these
1079 observations and our data, it is possible that the observed changes in foraminifera
1080 calcification could have been ~~totally or~~ partially driven by the ongoing ocean
1081 acidification in the Mediterranean.

1082 Moreover, the largest calcification reduction is observed between the seabed
1083 sediments and the sediment trap, this means that the highest calcification reduction
1084 has taken place between post-industrial Holocene and recent Holocene (i.e. the
1085 reduction between LCD SC/PLA CT and PLA ST) (Fig. 6). This could be explained
1086 with the "Great Acceleration theory". The Great Acceleration is a term used to
1087 describe the trends in CO_2 emissions and the associated temperature changes as
1088 consequences of the human impacts on the atmosphere since the 1950s (Head et
1089 al., 2022a, 2022b).

1090 However, other important changes in physical and chemical parameters co-occur
1091 with ocean acidification, and therefore should be also considered. Based on the
1092 seasonal and interannual patterns of the SST in the Gulf of Lions (Figs. 4 and 5),
1093 temperature trends could also be invoked as a likely parameter to affect calcification
1094 here. As shown by the correlations (Table 5) and the GAM results, SSTs are one of
1095 the most likely parameters to affect calcification on different timescales. However,
1096 on a pre-industrial to post-industrial timescale, the effect of the SST on the
1097 foraminifera calcification on longer time scales may be hard to evaluate due to the
1098 effect of the latter on the carbonate system parameters such as CO_2 and CO_3^{2-}
1099 concentration in the water. But note that the Mediterranean is considered to be
1100 warming at a faster rate than the global average (Hassoun et al., 2015; Lazzari et
1101 al., 2014).

1102 Calcification data from the sediment trap has been flux-weighted (see section 3.4) in
1103 order to be compared with the sedimentary calcification data, therefore, this data

1104 could be affected by a change in the incoming foraminifera flux (de Moel et al., 2009).
1105 In this line, the Gulf of Lions, presents a marked seasonality (see section 2) and the
1106 both the mass fluxes (Heussner et al., 2006) and foraminifera fluxes present strong
1107 seasonal variations. Parameters such as the North Atlantic Oscillation index, the
1108 river runoff and the intensity of the seasonal water cascading process have been
1109 suggested to play a role on planktic foraminifera production and export (Rigual-
1110 Hernández et al., 2012). The later study shows that most of the species flux showed
1111 a yearly uni-modal distribution, but the flux values and distribution remained fairly
1112 constant over the years. This highlights that, in our study zone, a major change in
1113 the foraminifera flux affecting the flux-weighted calcification value is unlikely.

1114 In summary, our results suggest that the interactive effect of rising ocean acidity,
1115 and enhanced SST (regionally amplified in the NW Mediterranean, (Hassoun et al.,
1116 2022, 2015)) represent the most likely responsible factors for the MBW differences
1117 between the pre-industrial and post-industrial to recent Holocene. However, the
1118 analysis of seasonal and interannual trends indicates that the influence of these
1119 parameters is species-specific and varies across the studied time scales. This
1120 implies that the controls of planktonic foraminifera are complex and that factors other
1121 than ocean acidification and warming are likely to also account for part of the
1122 variability observed between sediment trap and seabed sediments.

1123

1124 **5.4. Influence of environmental variability on MBW$_{area}$ across different time**
1125 **scales**

1126 Our results show that the influence of environmental parameters over the different
1127 time scales studied is not constant and depends on the species, the environmental
1128 driver and timescale.

1129 In the case of *G. bulloides*, our data suggest that OGC and inter-specific
1130 relationships seem to affect its MBW on a seasonal scale, carbonate system seems
1131 to play a major role while on an interannual and on a pre/post-industrial time scales.
1132 *N. incompta* calcification seems affected by OGC, inter-specific relationships and
1133 SST on a seasonal scale, while on longer time-scales carbonate system appears to
1134 play preponderant role. Finally, *G. truncatulinoides* calcification seems positively
1135 correlated to carbonate system and SSTs and negatively with the OGC on a
1136 seasonal scale. However, these patterns seem to have an opposite effect on an
1137 interannual scale, as *G. truncatulinoides* calcification shows a clear increase while
1138 carbonate system parameters become less and less favorable for calcification. In
1139 turn, on a pre/post-industrial Holocene time scale, its MBW$_{area}$ seem to be affected
1140 by regional processes such as OA and warming.

1141 Factors such as changes in the regional oceanographic processes (Cisneros et al.,
1142 2019; Durrieu de Madron et al., 2017) affect the physical and chemical properties of

1143 the water column and hence, could impact the life cycle of the species studied here.
1144 Also, while *G. bulloides* can either present regular or encrusted forms; *N. incompta*
1145 and *G. truncatulinoides* are crust forming species. In our study, *G. bulloides*
1146 individuals are mainly regular forms, but encrusted individuals were identified in both
1147 the sediment trap and seabed sediments. It is out of the scope of this work to focus
1148 on the effect of the crust on the species MBW, however, Osborne et al., (2016) study
1149 showed that encrusted *G. bulloides* individuals are around 20-30% heavier than the
1150 regular ones. ~~Finally, reproductive strategy could be invoked as a factor affecting~~
1151 ~~calcification. Planktic foraminifera mainly reproduce by gametogenesis, however,~~
1152 ~~asexual reproduction has been documented to happen on a rare but constant rate~~
1153 ~~(Meilland et al., 2021; Takagi et al., 2020). It has been theorized with overwintering~~
1154 ~~the polar species *N. pachyderma* that if all of the individuals reproduce with an~~
1155 ~~asexual strategy, they would double their size populations in 2 generations, with~~
1156 ~~observations reporting the growth of extra chambers (Meilland et al., 2022).~~
1157 ~~However, it remains to be shown if this phenomenon only affects polar species in~~
1158 ~~such proportions and if other species show similar patterns.~~

1159 ## 6. Conclusions
1160
1161 The variability in shell calcification of three planktic foraminifera species (*G.*
1162 *bulloides*, *N. incompta* and *G. truncatulinoides*) was studied in the northwestern
1163 Mediterranean Sea at different time scales using sediment trap and seabed samples.
1164 The analysis of 273 samples and more than 4000 individuals revealed that:

1165   i.   The Sieve Based Weight (SBW) method is not a reliable tool as
1166   calcification indicator due to the influence of morphometric parameters on
1167   foraminifera weight. The Measured Based Weight (MBW) technique, on
1168   the other hand, shows little to negligible influence of the morphometric
1169   parameters, and therefore, can be considered a reliable calcification
1170   proxy.

1171   ii.   Analysis of the seasonal variability of planktic foraminifera calcification
1172   revealed important differences between species. *G. bulloides* exhibited
1173   peak calcification during winter, *N. incompta* during mid-summer and *G.*
1174   *truncatulinoides* during late summer to autumn.

1175   iii.   Interannual analysis suggest that *G. bulloides* and *N. incompta* did not
1176   display any significant pattern between 1994 and 2005, on the other hand,
1177   *G. truncatulinoides* displays a constant and steady calcification increase
1178   over recent years.

1179   iv.   Sediment trap and seabed sediment data comparisons between pre-
1180   industrial, post-industrial and recent Holocene assemblages shows that

1181   all three species experienced ~~a clear and conspicuous~~, calcification

1182   reduction. Modern *G. bulloides*, *N. incompta* and *G. truncatulinoides*

1183   individuals were 18-24%, 20-27% and 32-40% less calcified respectively.

1184   v.   Finally, correlations with environmental parameters and GAM indicate that

1185   Optimum Growth Conditions affect positively *G. bulloides* and negatively

1186   *G. truncatulinoides* calcification respectively. Sea Surface Temperatures

1187   affect positively both *N. incompta* and *G. truncatulinoides* calcification.

1188   Finally, CO_3^{2-} concentration is also a likely parameter to influence

1189   positively planktic foraminifera calcification in the Northwestern

1190   Mediterranean. However, calcification appeared to be species-specific

1191   and vary depending on the time scale studied. This may suggest that other

1192   parameters than the ones studied here may play a role in foraminifera

1193   calcification.

1194 As planktic foraminifera represent roughly about 50% of pelagic calcite production

1195 (Schiebel, 2002) in the world's oceans, and therefore, an important component of

1196 the marine carbon cycle, a reduction in the calcification of their shell could induce

1197 important changes in the future carbon cycle with feed-backs on climate. Our results

1198 call for increasing efforts in monitoring planktic foraminifera calcification the

1199 Mediterranean in order to determine if the trends suggested by our data will be

1200 sustained over time.

1201

1202 The Supplement related to this article is available at DOI: 10.17632/4t9x554dwz.1

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