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ORIGINAL RESEARCH ARTICLE

Taphonomy of mass mollusc shell accumulation at Amvrakikos Gulf lagoon complex sandy barriers (NW Greece)

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Abstract The preservation status of the mollusc shell accumulation of sandy barriers at the Amvrakikos Gulf lagoon complex was studied. Taphonomic shell analysis of dead mollusc depositions was undertaken in the summer of 2016 at Amvrakikos lagoon complex within the Tsoukalio and Logarou sandy barriers, which showed significant differences among the major abundant bivalve species of *Cerastoderma glaucum* and *Polititapes aureus*. Both hydrodynamic transport and differential exposure to environmental conditions differ among the accumulated shells depositions of the lagoonal sandy barriers. The heavier and more durable shells of *C. glaucum* are frequently found concentrated at the Tsoukalio lagoon accumulations and show a higher intensity of fragmentation whereas at Logarou lagoon the bioerosion and abrasion is more intense. On the other hand, the lighter, thinner, and thus more fragile shells of *P. aureus* show higher concentration and intensity of fragmentation and bioerosion at Logarou lagoon sandy barriers. The continuous deposition of shells at Tsoukalio lagoonal sandy barriers, contrary to the long-term deposition at Logarou lagoon, explains the different types of accumulations among the lagoons which are attributed to the geomorphology of the sandy shores as well as the morphological characteristics of the different shells.

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1. Introduction

Coastal lagoons owe their existence to the seaward sandy barriers which act as natural dams. Coastal management plans should therefore take this into account as a prerequisite for the conservation and protection of these coastal lagoons (Avramidis et al., 2014; Christia and Papastergiadou, 2006; Christia et al., 2014). According to the European Directive 92/43 EEC, the lagoons represent priority habitats for their ecological importance of preserving biodiversity and for their economic contribution to coastal areas, respectively. They are extremely unstable ecosystems due to their limited interaction with the open sea, their shallow depths which are highly sensitive to climatic conditions, the role of the human factor itself by means of activities such as the hydroelectric power dams (Mertzanis et al., 2011) and finally for being characterized by low biodiversity and high productivity (Christia and Papastergiadou, 2006; Piroddi et al., 2016). An in-depth analysis of the status of deposited materials in sandy barriers is crucial for the recommendation of conservation measures preventing erosion (Gracia et al., 2018).

Mass mollusc shell accumulations have been found and thus examined in various types of wetlands such as delta rivers, lagoons and tidal shores, as a result of severe weather conditions, such as strong storms (Boyajian and Thayuer, 1995), hurricanes (Davies et al., 1989) or after intense natural phenomena such as a tsunami (Donato et al., 2008). Most research, however, refers to accumulation deposits that occur as a result of the tidal conditions (Kowalewski et al., 1994; Schneider-Storz et al., 2008; Weber and Zuschin, 2013). Since mollusc shell deposits are derived from living populations, it is clear that they reflect the relative abundance of living specimens and therefore can be used to compare the size and conservation status of existing populations (Cummins et al., 1986; Kidwell, 2001, 2002; Kidwell et al., 1991; Peterson, 1976; Warme, 1969; Weber and Zuschin, 2013).

Dead mollusc shell accumulations analysis through taphonomy studies can capture the past and the present ecological status of a region (i.e. biodiversity, carbon cycling), which can be a powerful guidance tool for conservation management plans, i.e. the Water Framework Directive and the Framework Directive for the Marine Strategy (Dietl et al., 2016; Kowalewski et al. 1994; Smith et al., 2016; Warwick and Light, 2002). Several palaeoecological studies of coastal lagoon systems in the Mediterranean demonstrate the evolutionary succession, as well as the prevailed environmental conditions, after analyzing the composition of deposited sediments where molluscs are involved (Avramidis et al., 2014, 2015a; Dimiza et al., 2016; Koukousioura et al., 2019; Panagiotaras et al., 2012). Furthermore, evaluation of the sediment studies shows that human interaction in modern times can have both a negative (increase of anoxia) and a positive (decrease of phosphates) impact on the environmental and ecological status of the lagoons as water influx plays the leading role (Avramidis et al., 2008, 2013, 2015b).

The Amvrakikos Gulf (Figure 1) is a hydrological regime (400 km^2) situated in northwest Greece, separated from the open Ionian Sea by a beach-barrier complex (Ferentinos et al., 2010). The maximum depth of

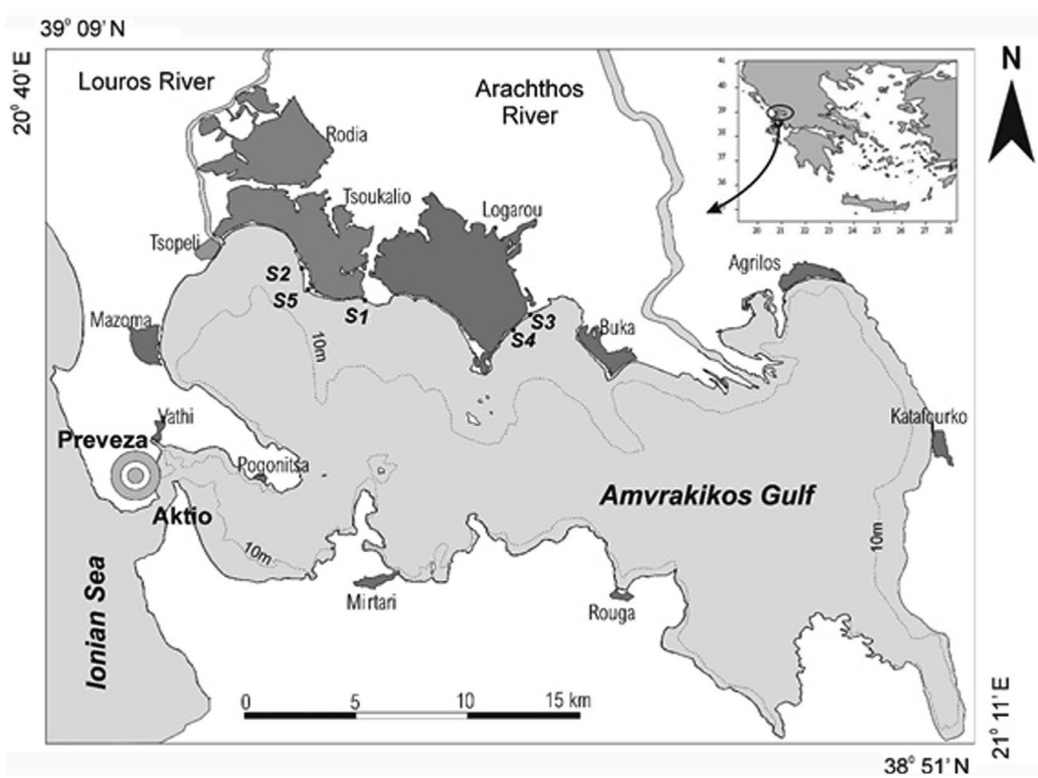

Figure 1 Location map of sampling stations (Si) at Tsoukalio (S1, S2 and S5) and Logarou (S3, S4) lagoons (L.) in the northern part of Amvrakikos Gulf, NW Greece (according to Table 1).

the gulf is 65 m with a seabed covered by mud or sand (Ferentinos et al., 2010; Piroddi et al., 2016), while two main rivers (Arachthos and Louros) flow into the gulf. The construction of three hydroelectric power dams at the rivers of Louros (1 dam) and Arachthos (2 dams) eliminated sediment supply to the gulf (Mertzanis et al., 2011). Surface salinity of the gulf remains low throughout the year (17—35 psu) and sea surface temperature ranges between 9.0°C and 30.6°C (Ferentinos et al., 2010; Piroddi et al., 2016). The gulf includes 14 enclosed lagoons covering an area of about 86 km^2 (about 20% of the total area of the Greek lagoons) (Katselis et al., 2013). The Amvrakikos Gulf wetland complex has been declared as a national park which is designated to be of international importance under the Ramsar Convention, listed in the Natura 2000 Europe Network and protected under the Habitats Directive (92/43/EEC). Tsoukalio (28.3 km^2) and Logarou (35.0 km^2) are the largest lagoons located in the northern part of the gulf. Historically, these were semi-open type lagoons separated from the gulf by a natural sandy barrier interrupted by natural outlets through which water was transported to and from the lagoons. Nowadays, they have been transformed into a closed-type lagoons, mainly due to human interventions. The sandy barriers were reinforced in the 1980s and covered with a gravel road and the outlets restructured and transformed into fixed channels (Katselis et al., 2013; Spyratos, 2008). Massive depositions of dead shell accumulations are observed in several places at the sandy barriers from the seaside.

Sandy barriers at the Amvrakikos Gulf lagoons are a key component of their structure, but current data available regarding shell accumulations and their species composition in the lagoons of the Amvrakikos Gulf is still limited (Fischer, 2005; Poulos et al., 2008; Tsolakos et al., 2019), resulting in a general lack of knowledge with regard to the conservation status of the deposited shells.

The aim of this study is to interpret the role of shells in the deposited accumulations in the complex of Amvrakikos lagoons. The shell depositions in the sandy barriers of the two major Amvrakikos lagoons, named here the Logarou and Tsoukalio lagoons, were examined as case studies. The effects of shell characteristics on the distribution and preservation of the accumulations in the sandy barriers and the role of bivalves in the conservation of the massive shell accumulations in these sandy barriers were analyzed using a taphonomic approach.

2. Material and methods

2.1. Mollusca macrofauna

Cerastoderma glaucum (Bruguière, 1789) and *Polititapes aureus* (Gmelin, 1791), which are described below, are the bivalve individuals which were found to dominate the accumulations of mollusca macrofauna at the sandy barriers of the Amvrakikos Gulf lagoons.

C. glaucum, commonly known as the lagoon cockle, is found in brackish waters throughout the Mediterranean, mostly in the upper infralittoral zone, on a soft substrate of sand and/or mud with a penetration depth as long as its shell's length (Gallinou-Mitsoudi et al., 2007; Leontarakis et al., 2008; Malham et al., 2012). It is one of the most ecologically resistant species, capable of surviving in a wide range of salinity (5—38 psu) and temperature (0—25°C) as a consequence of its natural strategy to protect itself from predators and lagoon's instability due to abrupt environmental conditions (Leontarakis et al., 2008). The bivalve shell (Figure 2) is solid, spherical to square in shape, having 17—28 ribs with deep channels on its outer surface, colored white, brown, greenish to the posterior, while the interior is brownish in color (Gallinou-Mitsoudi, 2010).

P. aureus, commonly known as the "golden carpet shell", is found throughout the Mediterranean in the infralittoral up to sublittoral zone (depth ranging: down to −65 meters), on a soft substrate biotope (sand, mud, gravel), buried in a few centimeters depth, while the maximum length of the shell is about 5 cm. The bivalve shell (Figure 3) is robust, oval, almost triangular in shape, elongated towards the posterior, thin as well as glossy (almost smooth surface with numerous

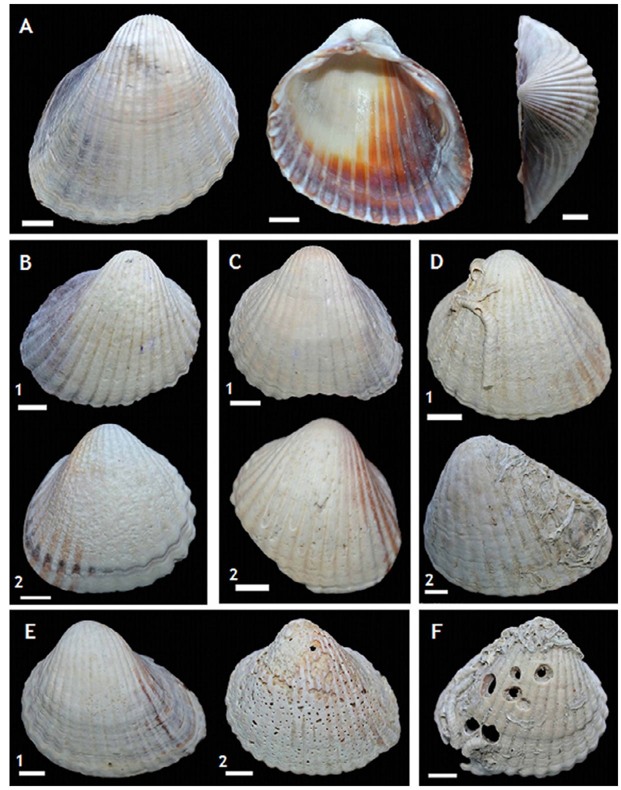

Figure 2 *Cerastoderma glaucum* (Bruguière, 1789) valves. A — right valve preserved in "good" condition (Abrasion = 0, Fragmentation = 0, Encrustation = 0, Bioerosion = 0), B — abrasion: taphonomic grade 1 = "fair" state of preservation, slightly affected as ribs are still visible, taphonomic grade 2 = "poor" state of preservation, heavy affected as ribs have been lost, C — fragmentation: taphonomic grade 1 = small part missing, taphonomic grade 2 = missing part larger than 10% of the valve, D — encrustation: taphonomic grade 1 = encrusted less than 10% of the shell surface, taphonomic grade 2 = surface encrusted more than 10%, E — bioerosion: taphonomic grade 1 = penetration less than 10% of the surface, taphonomic grade 2 = penetration more than 10% of the surface, F — holes from gastropod predators. Scale bars = 0.5 cm.

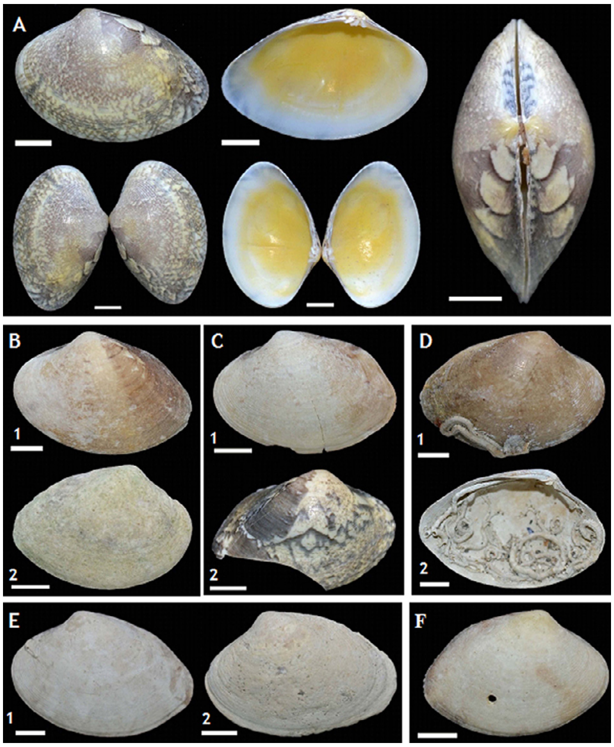

Figure 3 *Polititapes aureus* (Gmelin, 1791) valves. A — left valve preserved in "good" condition (abrasion = 0, fragmentation = 0, encrustation = 0, bioerosion = 0), B — abrasion: taphonomic grade 1 = "fair" state of preservation, slightly affected as loss of the surface less than 10%, taphonomic grade 2 = "poor" state of preservation, heavy affected as surface gloss has been lost, C — Fragmentation: taphonomic grade 1 = small part missing, taphonomic grade 2 = missing part larger than 10% of the valve, D — encrustation: taphonomic grade 1 = encrusted less than 10% of the shell surface, taphonomic grade 2 = surface encrusted more than 10%, E — bioerosion: taphonomic grade 1 = penetration less than 10% of the surface, taphonomic grade 2 = penetration more than 10% of the surface, F — hole from gastropod predator. Scale bars = 0.5 cm.

concentric ribs and crossed channels with thin radial lines that are barely visible), while its color is brown in a large variety with linear brownish-red angular designs (zig-zag), stains, etc. (Gallinou-Mitsoudi, 2010). *P. aureus* is a common bivalve species found in lagoon habitats and, generally, in coastal wetlands of the Mediterranean and has also been used as an ecological indicator for benthic ecosystems (Borja et al., 2000; Zenetos, 1997).

2.2. Study — sampling area

A sampling of dead mollusc shells was conducted during the summer of 2016 (June to August) along the coastal sandy barriers of Logarou and Tsoukalio lagoons located in the northern part of the Amvrakikos Gulf (Figure 1). Accumulations were observed in different types of sand dunes between the lagoons. At Tsoukalio lagoon, the accumulations appear at the beginning of the dune which was directly after the end of the incipient foredune, while in the Logarou lagoon the accumulations appeared at the beach berm/swash zone where waves break at the shore (terminology sensu Kidd, 2001; Muñoz-Vallés and Cambrollé, 2014).

Five sampling stations (Si) were selected, S1, S2 and S5 from the Tsoukalio lagoon and S3, S4 stations from the Logarou lagoon as shown in Figure 1 according to Table 1. Massive shell accumulations were located at different distances from the coastline and samplings were taken at the distances shown in Table 1.

2.3. Sampling and analysis techniques

Samples were taken using a 1 × 1 square meter frame placed at the sampling stations and the material collected at a sediment depth of approximately 10 cm. The collected samples were weighed and their volumes calculated. Then, in order to evaluate the samples, three sub-samples were randomly collected from each sample, with a total of fifteen sub-samples corresponding to the five samples. The total weight of all the collected samples was 10,122.83 g.

Sub-samples were taken with an equivalent volumetric unit and after being weighed at a tolerance of 0.01g, they were sieved with a 2 mm sieve. The remaining material was divided into bivalves, gastropods and various materials such as stones, woods, crabs, etc., and weighed by category. In the case of samples that contained adherent materials due to moisture (sand), the samples were washed and then dried and weighed. Complete valves were separated from those with unspecified length, as well as conjoined shells which were counted as two valves. They were all counted and weighed. Bivalve molluscs were identified according to their morphological characteristics (Poutiers, 1987). The complete shells were separated into a left and right valve and their length was measured while each valve was

Table 1 Coordinates of sampling stations and distance from the coastline as well as weight of sediment samples per sampling station.

Lagoon	Sampling station	Lat. (°N)	Long. (°E)	Distance from the coastline (m)	Weight of sediment sample (g)
Tsoukalio	S1	39.033414	20.858163	4.0	2,010.46
Tsoukalio	S2	39.050287	20.824250	2.0	2,148.05
Logarou	S3	39.032889	20.955775	29.0	1,920.48
Logarou	S4	39.031642	20.950878	25.0	2,502.99
Tsoukalio	S5	39.042358	20.827275	22.0	1,540.85

examined for its taphonomic features including abrasion, fragmentation, encrustation and bioerosion. Correlation analysis was applied in order to examine the relation between the taphonomic features (Zar, 1999). Finally, the linear relationship between the taphonomic values and the shell length was examined by correlation coefficient (r; t-test; $p = 0.05$) (Zar, 1999).

Abrasion is observed in the loss of shell surface characteristics such as growth lines, gloss, as well as in the appearance of spots (Figures 2B and 3B) (Schneider-Storz et al., 2008). Fragmentation is attributed to the loss of shell parts (Figures 2C and 3C), the encrustation of species deposited on the shell's surface such as polychaetes and/or bryozoans (Figures 2D and 3D) and bioerosion is observed as holes in the shell (Figures 2E and 3E) (Kowalewski et al., 1994).

Taphonomic features were calibrated into three grades: grade "0" referring to non-affected specimens preserved in "good" condition, grade "1" representing the slightly affected specimens (up to 10% of the shell surface) being in "fair" state of preservation, and grade "2" representing the heavily affected specimens that are in a poor state of preservation (Kowalewski et al., 1995; Schneider-Storz et al., 2008). Taphonomic features were then analyzed by using ternary diagrams (Kowalewski taphograms). The ternary diagram depicts the ratios of the three variables as positions in an equivalent triangle and thus allows the comparison of the samples in relation to their examined taphonomic features contributing to the interpretation of conservation characteristics (Kowalewski et al., 1995).

3. Results

3.1. Qualitative and quantitative identification

The majority of shells belongs to bivalves (62.59%) (complete bivalve shells and fragments of the shell) and gastropods (13.07%) while the rest of the deposited material consists of sieved material less than 2 mm (21.68%) and various inorganic materials (2.67%) such as stones and sand.

The composition of the massive shell accumulation differs between the lagoons. Shells of bivalves (whole shell and parts of the shell) reach 70.85% of the deposited material in the Tsoukalio lagoon, while in the Logarou lagoon it reaches up to 50.19%. Contrary to bivalve and gastropod shells, sieved material (<2 mm) was deposited in a higher percentage at Logarou lagoon's shell accumulations (39.40%), compared to Tsoukalio lagoon where it reached only 9.87% of the deposition. The gastropod weight percentage in the Tsoukalio lagoon (15.66%) is almost twice as high compared to that of the Logarou lagoon (9.17%).

Bivalve shells dominate over the deposited accumulations at Tsoukalio lagoon's sampling stations (S1, S2, S5), in particular, reaching 79.91% in the S1 station, unlike the Logarou lagoon's accumulations where bivalve species appear to be at lower rates such as in S4 station (40.65%). Furthermore, half of S4 station's deposition consists of sieved material (<2 mm: 50.03%), while in the Tsoukalio lagoon high rates are only present at sampling station S2 (23.24%). Logarou lagoon's sampling station S4 contains the largest diversity of bivalve species (36 species), while Tsoukalio lagoon's sampling station S1 shows the smallest (26 species); the remaining stations show the following values S2: 30, S3: 33, and S5: 32 species.

3.2. Quantitative analysis

3.2.1. *Cerastoderma glaucum* and *Polititapes aureus*

Forty-one (41) species of bivalve molluscs were identified in all, and 33,837 shells were counted in total (Tsolakos et al., 2019). The bivalve individuals with the major relative abundance in terms of weight are *C. glaucum* (38.29%) and *P. aureus* (19.39%).

Overall, 2579 whole shells and 12987 parts of *C. glaucum* and *P. aureus* were recorded in the sampling stations sub-samples. *P. aureus* is the major deposited accumulation species (whole shells and parts with 57.54% and 67.14% respectively) at Logarou lagoon, while *C. glaucum* (whole shells and parts, with 56.05% and 51.19%, respectively) is the major deposited accumulation species at Tsoukalio. The proportion of the whole shell to the shell's parts for both bivalve individuals differs between the lagoons as the two species have more intact shells at Tsoukalio lagoon, while at Logarou lagoon, broken shells of both species dominate over complete shells.

The major part of total shelly mass weight of *C. glaucum* (81.99%) is found at Tsoukalio, while *P. aureus* seems to have similar weight distribution to both lagoons (Tsoukalio 53.76% and Logarou 46.24%). Weight proportion of both species are present in an almost equal distribution at Logarou lagoon (*C. glaucum* 43.47% and *P. aureus* 56.53%), while at Tsoukalio lagoon the *C. glaucum* (75.06%) prevails over *P. aureus* (24.94%). This relationship is due to the major weight portion of *P. aureus* shell parts at Logarou (62.87%), and *C. glaucum* at Tsoukalio (whole and shell parts are 79.75% and 69.99%, respectively).

3.2.2. Length distribution

C. glaucum and *P. aureus* show a significant difference concerning shell's average length between the lagoons, as their shell length is 2 mm smaller at Logarou lagoon compared to that of the Tsoukalio lagoon. *C. glaucum* has a right asymmetric distribution at Logarou lagoon with an average shell length of 1.51 cm, but an almost normal distribution at Tsoukalio lagoon with an average shell length of 1.73 cm (Figure 4a). On the contrary, *P. aureus* has a normal distribution in both lagoons with an average shell length of 1.73 cm at Tsoukalio lagoon and 1.52 cm at Logarou lagoon (Figure 4b).

3.2.3. Left / right valves

The proportion of left and right valves differs slightly between the sampling stations. The right valves of *C. glaucum* are more abundant in the S2, S5 and S1 stations at Tsoukalio lagoon than in the S3 and S4 stations at Logarou lagoon. As far as *P. aureus* is concerned, the right valves are more abundant at the Logarou lagoon's sampling stations. On the contrary, left valves are more abundant in the Tsoukalio lagoon's sampling stations S2 and S1, with an exception of the appearance of more left valves in sampling station S5.

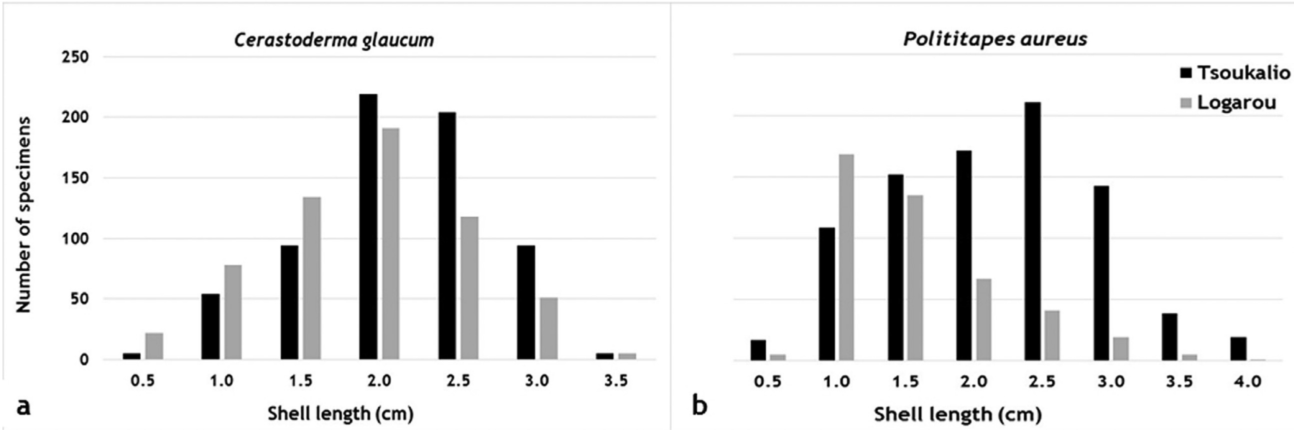

Figure 4 Length size distribution of (a) *Cerastoderma glaucum* and (b) *Polititapes aureus*, between the Tsoukalio and Logarou lagoons.

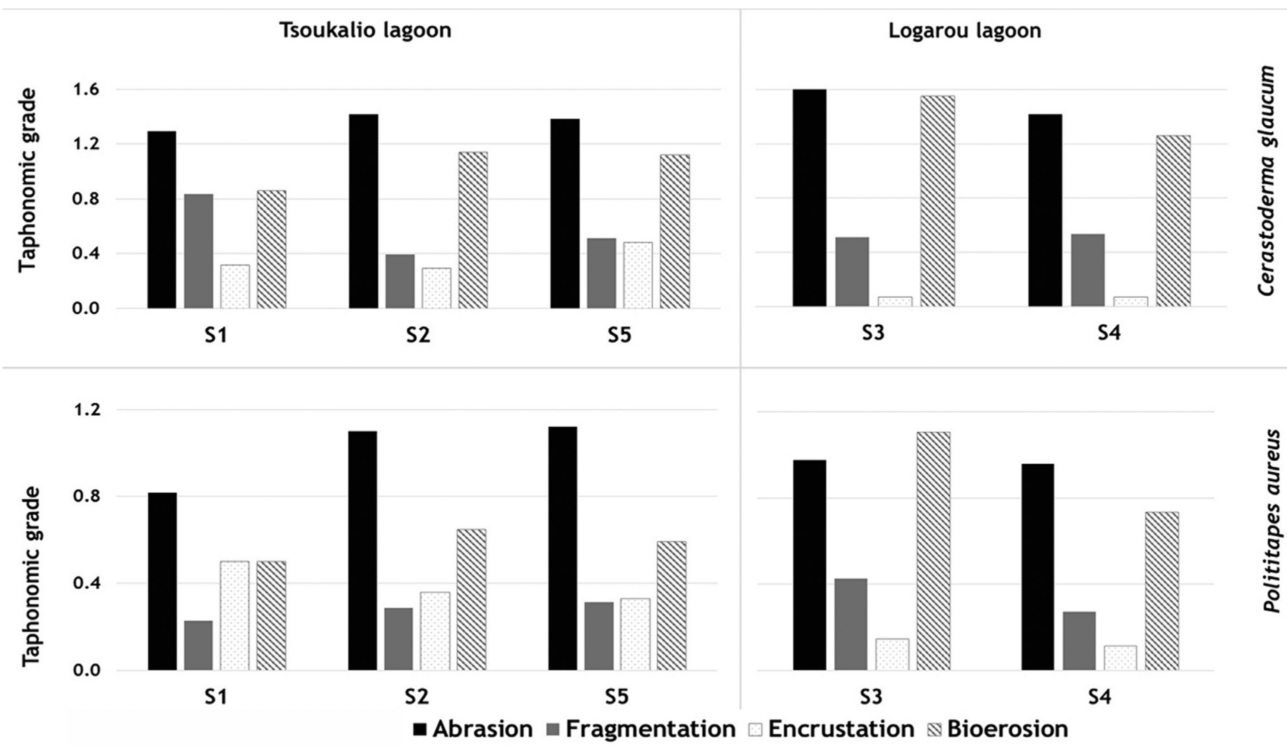

Figure 5 Distribution of average taphonomic values for abrasion, fragmentation, encrustation and bioerosion per bivalve individuals and lagoons.

3.3. Taphonomic analysis

3.3.1 Abrasion

Abrasion of *C. glaucum* shell results in the smoothing and loss of the ribs of the outer shell's surface (Figure 2B). Abrasion of *P. aureus* shell results in the loss of shell's surface gloss to both outer and inner surfaces including lack of smooth surface and loss of the numerous concentric sculpturing on the outer surface (Figure 3B).

Abrasion, among all other taphonomic features, occurs at a higher intensity for both species at Tsoukalio lagoon, and for *C. glaucum* at Logarou lagoon (Figure 5). The higher abrasion intensities are also found for the *P. aureus* individuals at Logarou lagoon, along with bioerosion (see below), especially at sampling station S3 (Figure 5).

The Kowalewski taphogram shows that abrasion is more intensive concerning *C. glaucum* individuals in both lagoons. Contrary to *P. aureus* shell abrasion, which is more intense at Tsoukalio lagoon, with the exception of sampling station S1. Furthermore, overall, abrasion is less intense in the Logarou lagoon samples (Figure 6). Concerning abrasion, the preservation status of *C. glaucum* shells is "uneven" at both lagoons approaching the poor state. The taphonomic values of abrasion for *P. aureus* shells show an uneven state of

Table 2 Correlation analysis of the taphonomic grades per bivalve species (*Cerastoderma glaucum* / *Polititapes aureus*).

Bivalve species	Abrasion	Fragmentation	Encrustation
Abrasion			
Fragmentation	0.205/0.208		
Encrustation	0.236/0.255	0.054/0.093	
Bioerosion	0.615/0.577	0.092/0.240	0.254/0.232

preservation at both lagoons. Abrasion tends to increase together with shell length in both lagoons for *C. glaucum* and *P. aureus*, respectively ($r > 0.66$; df = 6; $P < 0.05$) (Figures 7 and 8).

In both species, abrasion and bioerosion showed a statistically significant correlation ($r > 0.57$; $P < 0.05$) while the other taphonomic grades showed a non-statistically significant correlation ($r < 0.25$; $P > 0.05$) (Table 2).

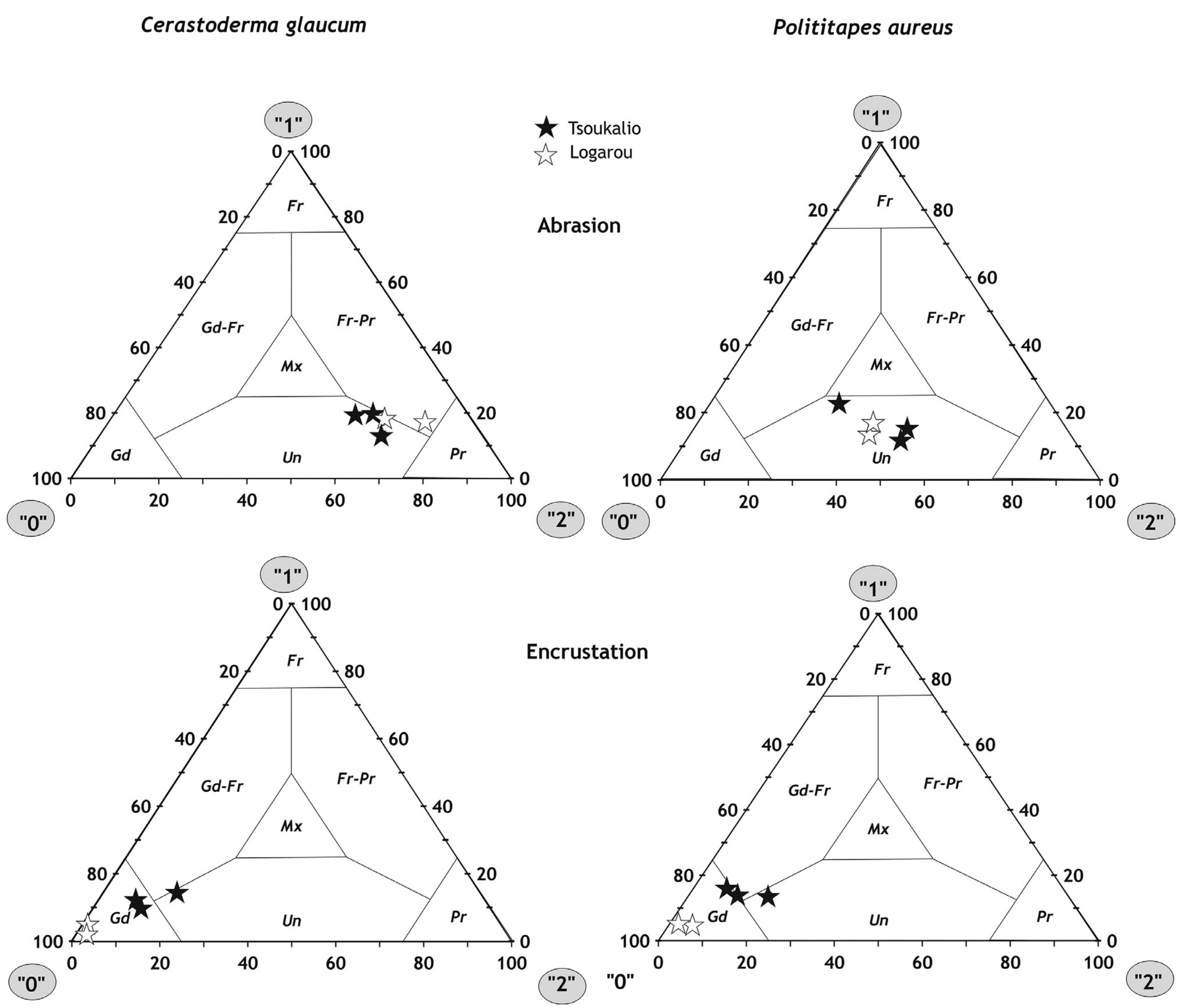

Figure 6 Kowalewski taphograms of abrasion, encrustation, fragmentation, and bioerosion, by bivalve individuals (*Cerastoderma glaucum* and *Polititapes aureus*) between the lagoons (Tsoukalio and Logarou) of Amvrakikos Gulf. Taphonomic grade "0" = good state of preservation, taphonomic grade "1" = fair state of preservation and taphonomic grade "2" = poor state of preservation. Variation of taphonomic grades in the ternary histogram illustrate the status of preservation: Gd-Fr = good-fair status of preservation, Fr-Pr = fair-poor status of preservation, Mx = mixed satus of preservation and Un = uneven status of preservation (Kowalewski et al., 1995).

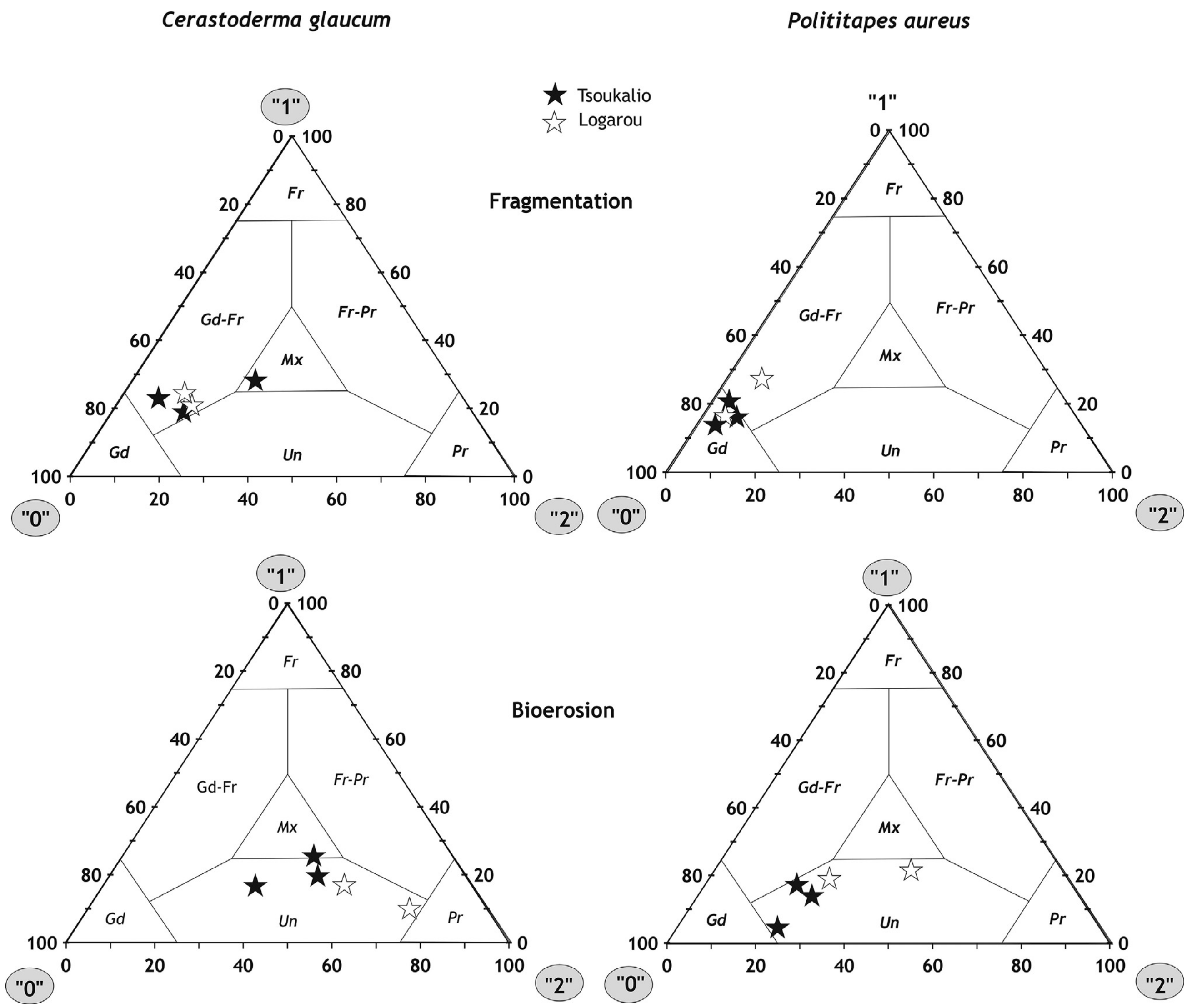

Figure 6 *Continued.*

3.3.2. Fragmentation

Fragmentation (Kidwell et al., 1991, 2001; Kowalewski et al., 1994) is visible on the outer sides of the *C. glaucum* shell (Figure 2C). Shell hardness contributes to the lack of the production of large segments, and therefore most of the *C. glaucum* shells consist of complete valves. On the contrary, the thinner and more fragile *P. aureus* shells are highly fragmented and are thus often excluded from the analysis as only complete valve lengths are taken into account.

Fragmentation of *C. glaucum* shells shows almost the same intensity at the lagoons, with the exception of sampling station S1 where it is almost twice as high as at the other stations (Figure 5). Similarly, Kowalewski taphograms present almost the same intensity of fragmentation for both bivalve individuals (Figure 6). The preservation status of *C. glaucum* shells is "good-fair" at both lagoons as depicted from fragmentation whereas, the taphonomic values of fragmentation for *P. aureus* shells show a "good" state of preservation. Moreover, as noted, the number of broken shells recorded for the two species is higher for *P. aureus* at Logarou lagoon. *C. glaucum* and *P. aureus* shell length at both lagoons, was not related with shell fragmentation ($r < 0.66$; $df = 6$; $P > 0.05$).

3.3.3. Encrustation

Encrustation observed on both *C. glaucum* and *P. aureus* (Figures 2D and 3D) was mostly by calcareous tube-forming worms (*Serpulidae* spp.). The Tsoukalio lagoon has the greatest tendency for shell encrustation, with *P. aureus* showing the highest values, compared to encrustation figures at Logarou lagoon (Figure 5). Similar results are presented by the Kowalewski taphograms (Figure 6). The preservation status of *C. glaucum* and *P. aureus* shells is similarly characterized as "good" at the lagoons concerning the taphonomic values of encrustation. Furthermore, the intensity of encrustation increases with shell length for both of the lagoons for the two species, the same can be said of the taphonomic feature of abrasion ($r > 0.66$; $df = 6$; $P < 0.05$) (Figures 7 and 8).

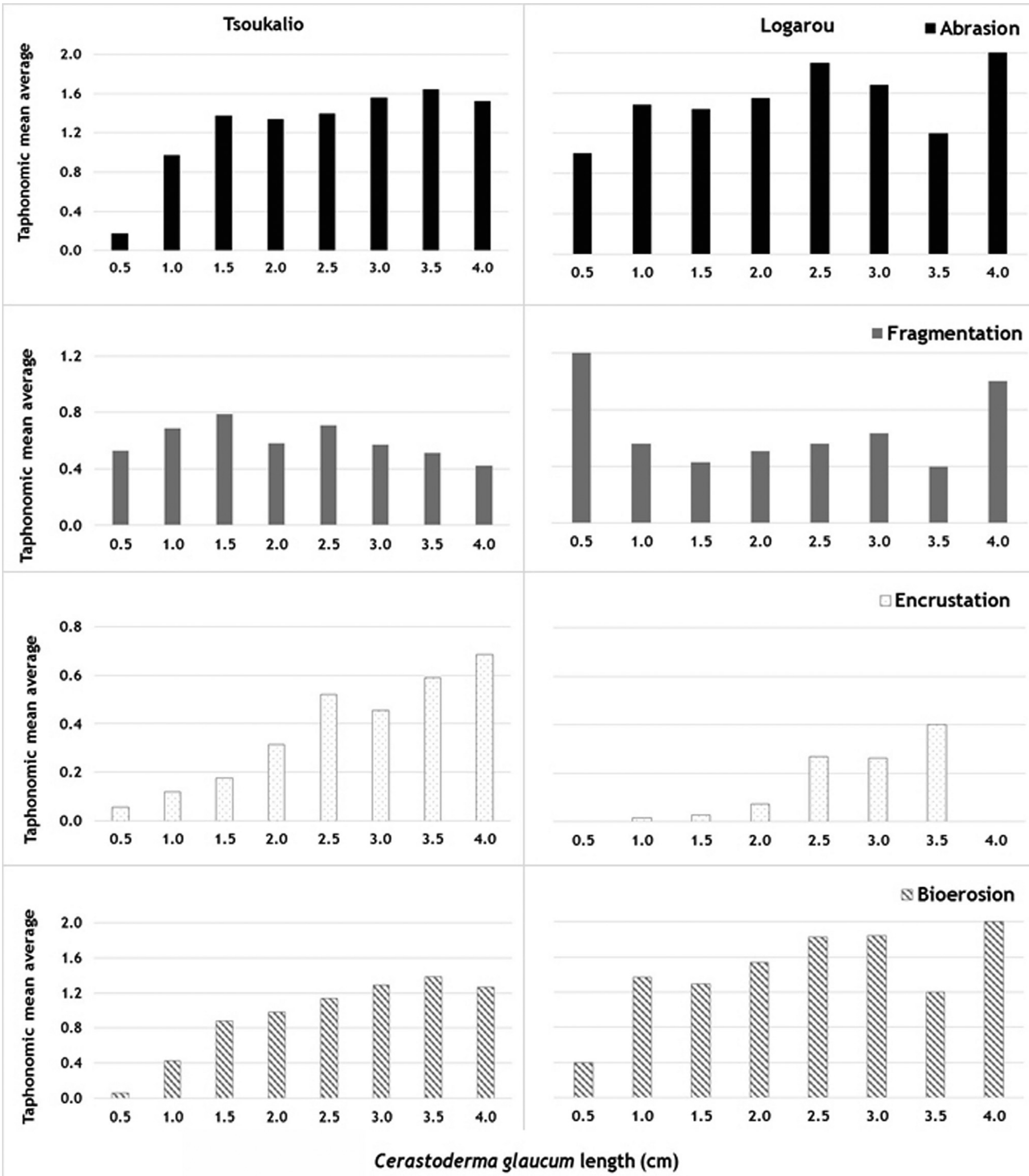

Figure 7 Taphonomic grades of *Cerastoderma glaucum* in relation to the shell length classes for each lagoon (Tsoukalio, Logarou) and for each taphonomic feature (abrasion, fragmentation, encrustation, bioerosion).

3.3.4. Bioerosion

Bioerosion intensity is the highest, after abrasion, for both species at both lagoons. The Logarou lagoon has the highest value of bioerosion for *P. aureus* compared to other taphonomic features (Figure 5). It also shows the highest value of shell bioerosion for both bivalves, especially for *C. glaucum* (Figure 5).

The analysis of the Kowalewski taphograms shows the "poor" state of preservation for *C. glaucum* shells at Logarou lagoon, while *P. aureus* has a medium bioerosion intensity, with the exception of the S3 sampling station (Figure 6). The preservation status of *C. glaucum* and *P. aureus* shells is "uneven" at both lagoons concerning the taphonomic values of bioerosion. The intensity of bioero-

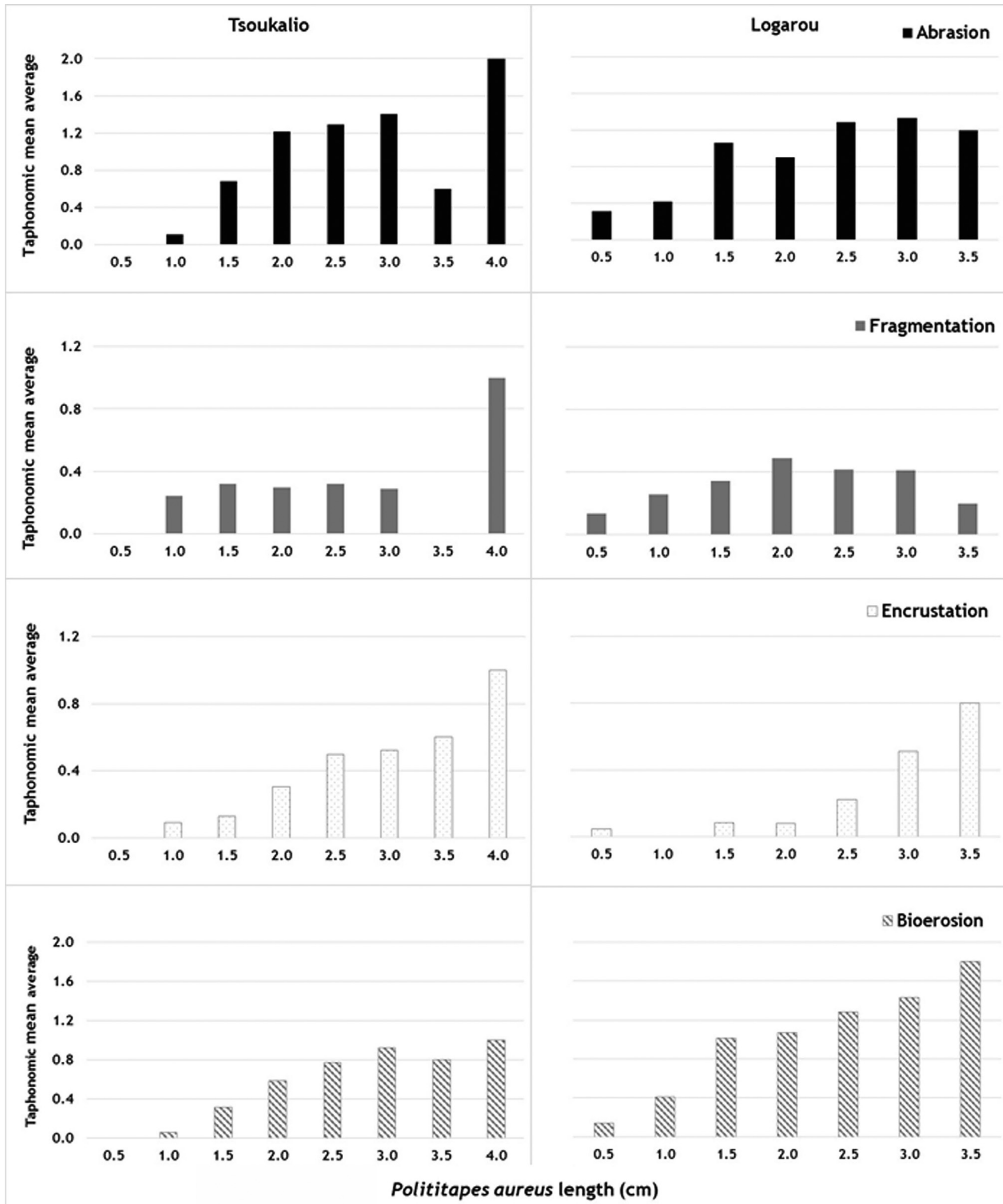

Figure 8 Taphonomic grades of *Polititapes aureus* in relation to the shell length classes for each lagoon (Tsoukalio, Logarou) and for each taphonomic feature (abrasion, fragmentation, encrustation, bioerosion).

sion, as was the case for the taphonomic features of abrasion and encrustation, increases along with shell length at the lagoons for both bivalve individuals ($r > 0.66$; $df = 6$; $P < 0.05$) (Figures 7 and 8).

4. Discussion

4.1. Distribution of deposited accumulations between lagoons

The compositions of the accumulated material depositions in the sandy barriers of the two main lagoons (Tsoukalio and Logarou) at the Amvrakikos Gulf present a different spatial distribution concerning the proportion of organic and inorganic materials as well as the composition of shell materials. The shell accumulations at the eastern sampling stations (Logarou lagoon) contain higher proportions of shells and shell parts than the western sampling stations (Tsoukalio lagoon). This is attributed to the fact that the two groups of sampling stations show different conditions of water and wind dynamics (Stamou et al., 2012).

At sampling stations S3 and S4 at Logarou lagoon, incipient dunes that support the growth of vegetation contribute to the low impact from the wave and wind, while sampling stations S1, S2 and S5 are at the swash zone of the dune with high impacts from the waves and wind (Kidd, 2001). It is clear that the higher concentration of sieved material at sampling station S2 compared to the rest of the sampling stations at Tsoukalio lagoon is due to the protected position of the station. Therefore, the different composition of the deposited materials, with respect to sampling stations S1 and S2, can be attributed to the higher rate of transfer of the lighter grains (e.g., sand, shell fragments) by water movement. On the contrary, the rest of the sampling stations which are outside the effect of the waves, support dune vegetation and enhance the retention of lighter components (Kidd, 2001).

The different spatial distribution of the major bivalve shells in the coastal zone of the Amvrakikos Gulf can be attributed to the shell's particular morphological characteristics (heavier shell of *C. glaucum* compared to that of *P. aureus*), that are affected accordingly by water and wind dynamics respectively. The coastline is particularly affected by the water inflow of the Arachtos river's outflow in the NE part of the gulf which is four times larger than that of the Louros river in the NW part of the gulf (Katselis et al., 2013). This results in the observed different spatial distributions of the deposited bivalves composition in the lagoons' sandy barriers.

Bivalves recorded at the 5 sampling stations are mainly found at low water depths. The depth zone from 0—10 meters in front of the study area (Figure 1) extends from 1 to 3 kilometers covering about 20% of the Gulf's surface. Therefore, it seems that the fauna of bivalve molluscs originating from the midlittoral up to infralittoral/sublittoral zone supplies the shells accumulations that occur on the northern coastline of the Gulf.

4.2. Distribution of *Cerastoderma glaucum* and *Polititapes aureus*

4.2.1. Quantitative valves distribution

Both bivalve individuals inhabit the infralittoral zone up to midlittoral zone, preferring soft substrates. Their common feature is their shallow burial depth which is up to as much as the shell length in the case of *C. glaucum* or a few centimeters depth in the case of *P. aureus*. The difference between the two bivalve molluscs lies mainly in their shells, as *C. glaucum* is spherical to square in shape, robust and heavy, whereas *P. aureus* is oval, almost triangular in shape and rather thin and light.

The transport and distribution of the two examined species between the lagoons is thus directly dependent on these particular features of their shell and not on their habitat or any other features such as depth of burial into the substrate. Bivalve species usually do not show significant differences in the distribution of left and right valves in accumulated depositions unless there is a special feature in the shell shape, such as the extended chondrophore in the left valve of *Mya areanaria*, that acts as an anchor during shell's transportation (e.g. Angseesing, 2018; Schneider-Storz et al., 2008). The Logarou and Tsoukalio lagoons have the same distribution of left and right valves for both species, with a slight difference of more right valves in Tsoukalio lagoon accumulations. In those cases, where there is no distinct separation between the left-right valves depositions, the most likely cause of transport is due to the prevailing currents rather than the waves (Angseesing, 2018).

4.2.2. Shell length distribution

Fossil size distribution frequency has been widely used to study population dynamics and species survival over time, as well as to distinguish between the deposits of fossil communities with respect to transported and non-transported accumulations (Bitner, 2002; Cadée, 1988; Fagerstrom, 1964). The right-skewed distribution of *C. glaucum* shell's length at Logarou lagoon is referred to as "Type III" survivorship curve of invertebrate species, where, according to Pianka (2011) sudden abrupt mortality of young bivalves (spat) is observed due to the large population at this stage of reproduction followed by a relatively high survival rate (Cadée, 1988; Noble and Logan, 1981; Thayer, 1975). The asymmetric right-skewed distribution indicates that the deposition outcomes are influenced by the presence of strong currents (Fagerstrom, 1964). The symmetrical distributions of *C. glaucum* at Tsoukalio lagoon and *P. aureus* at both lagoons indicate either the presence of residual deposition or that the accumulations originate from the transport of shells.

A normal distribution cannot be considered without the existence of a right asymmetric distribution so as to ensure that accumulation represents a residual deposition or a result of transport. This occurred as the small individuals may have been removed under the influence of external factors (i.e. currents or predation) and not calculated in the distribution ratio (Thayer, 1975, 1977). Noble and Logan (1981), however, by comparing living populations with fossil of brachiopods, found a similar right asymmetric distribution of length size, despite the existence of relatively strong currents, thus supporting and demonstrating high juvenile mortality of invertebrate species. The high rate of mortality of young individuals indicates species that originated in muddy environments, as their small size is associated with the burial caused by the shift of concentrated organic sediments (Richards and Bambach, 1975). From the above, it is understood that deposited accumulations at Logarou lagoon sandy barrier with regard to *C. glaucum* is due to the transport by currents (right asymmetric distribution) while the Tsoukalio lagoon's deposited accumulations can be attributed to both the currents and the shell production of the Amvrakikos Gulf. With regard to *P. aureus*, the distribution of length sizes cannot support the conclusion that the cause of their concentration is due to the presence of currents, and its populations can only be assumed to be derived directly from the production of the Amvrakikos Gulf for both lagoons. Furthermore, the length size distributions are 2 mm larger for both bivalve individuals at Tsoukalio lagoon compared to those of the Logarou lagoon, which may be due to the different current intensity resulting in the relocation of the smaller shells and/or the enhancement of shell breakage and therefore in the loss of specimens. Frequencies of length size distributions and survivorship curves alone cannot explain the pattern of accumulations as they involve numerous factors that have to do with their burial, and consequently, they have to be considered along with taphonomic features analysis during their interpretation (Callender and Powell, 1992; Cummins et al., 1986).

4.3. Taphonomy of *Cerastoderma glaucum* and *Polititapes aureus*

The analysis of the deposited materials shows that the Logarou lagoon contains larger quantities of fine-grained material as a result of the long presence in the berm/swash zone of the sandy barrier. On the contrary, the Tsoukalio lagoon's accumulations are located at the edge of the sandy barrier and their deposits consist of the heavier shell of *C. glaucum*. The accumulations of both bivalves (*C. glaucum*, *P. aureus*) originate from the continuous production in the Amvrakikos Gulf, which is then transported and deposited on the lagoons' sandy barriers by the currents.

Abrasion of the shell is the most intensive taphonomic feature for both species. The more durable shells of *C. glaucum* are the ones with the most extensive damage in the deposits of the Logarou lagoon, as illustrated in the Kowalewski taphograms. Abrasion and fragmentation as reported by Meldahl and Flessa (1990) allow interpret the higher intensities of water movement in coastal deposit. Therefore, shells are considered to have been exposed for longer periods of time to external environmental conditions either by moving over longer distances or by remaining in the accumulation for a longer period of time.

The two-fold higher intensity of fragmentation of *C. glaucum* as well as the larger collected quantities at sampling station S1, in conjunction with the topography of the station area, suggest that the accumulated depositions at station S1 are a result of the intense effect of currents in contrast to the other less exposed stations. In addition, the rest of the taphonomic features at sampling station S1 show lower intensities than at the other stations, which is confirmed by the presence of better-preserved specimens. The coexistence of both pristine bivalve specimens and highly affected specimens in the accumulated depositions indicates that they are shallow species and have been transported together (Flessa, 1998), from a close distance from the adjacent wetland (Schneider-Storz et al., 2008).

Encrustation and bioerosion as biological mechanisms of shell destruction appear to be greater when the shell projects from the substrate or has moved away from the soft substrate from which it originated (Kowalewski et al., 1994). The low intensity of encrustation is furthermore indicated by the fact that the encrusting organisms are detached from the shell during the long period of transport/movement, which was observed in the specimens as the encrustation marks were obvious on the shell's outer surface (Schneider-Storz et al., 2008).

The microbial attacks, on the other hand, that cause the bioerosion to the shells do not stop even after the mollusc dies and therefore microbial erosion continues during deposition. The intensity of bioerosion probably depends on: (1) the late burial or more often due to the shell's removal from the sediment, as well as (2) the rapid and more constant coverage from mud in the soft sediment environments. It is clear that bioerosion is totally dependent on shell's exposure to the external environmental conditions (Best and Kidwell, 2000a, 2000b; Kidwell et al., 1991).

The Tsoukalio lagoon shows higher intensity of encrustation for both species compared to the Logarou lagoon, which increases with shell size as a result of the bigger surface area (Schneider-Storz et al., 2008). Consequently, the shells in the deposited accumulations have been exposed to the environmental conditions for a longer period of time, and due to the hydrodynamic pressures they have subsequently lost all of the encrusting organisms. Considering that bioerosion is more intensive for both species at Logarou lagoon, it is clear that the deposited accumulations have remained exposed for longer periods than those of the Tsoukalio lagoon.

The correlation of abrasion and encrustation with all taphonomic features, according to Schneider-Storz et al., (2008) suggests that shell preservation is dependent on the exposure of the accumulated depositions. In the present study the abrasion was related to bioerosion. This could be attributed to the removal (abrasion) of the periostracum and the mantle (outer layers of the shell with a higher tolerance to microbial attacks than the inner layer) which exposes the shell to the microscopic endobionts. Fragmentation is not notably correlated to other taphonomic features for *C. glaucum*, as it is controlled by the robustness of the valves and the influence of the currents' turbulence (Fürsich and Flessa, 1987). The different shell morphologies of the two bivalve species also support the highest concentration of lighter *P. aureus* as found at Logarou lagoon. The thin shells are more fragile, likely to break under hydrodynamic pressures and thus can be transported much easier. Freshwater inputs in both lagoons contain oxidants that enhance bioaccumulation and bio-stimulation, reinforcing penetration and the development of premature bioerosion (Best and Kidwell, 2000a; Walter and Burton, 1990). Shell bioerosion is more intensive at Logarou rather than at Tsoukalio lagoon due to the longer period of shells' presence in the deposited accumulations. Shells accumulations at Tsoukalio sandy barriers are fueled by the production of bivalves in front of the lagoon, i.e. the northwestern part of the Amvrakikos Gulf, where they are transferred and deposited by the influence of the currents.

It is suggested that the continuous deposition of shells' accumulations at Tsoukalio lagoon sandy barriers should be monitored at least every 5 years, an indicative period based on the bivalve's growth rate, in order to confirm their preservation status. However, the shell accumulations at Logarou lagoon sandy barriers should be seasonally monitored, especially in cases of natural disasters, due to their enrichment with organic and inorganic materials which are restrained by vegetation constituting in this way a protective fence for the lagoon.

5. Conclusions

(1) The difference between the accumulated shell's depositions at the sandy barriers of the two lagoons lies in the continuous deposition of shells at Tsoukalio lagoon probably provided by the ongoing gulf's production, in contrast to the long-term deposition at Logarou lagoon where either gulf's production is lower or shells are transported from farther locations.
(2) Living bivalve populations preserve the accumulations at Tsoukalio lagoon sandy barriers. Logarou lagoon's accumulations partially originate from the living populations located in front of the lagoon sandy barrier, and partially from the currents which transport these lighter bivalves.
(3) Mollusc shell accumulations are an integral part of the composition and structure of vulnerable Amvrakikos lagoon's sandy barriers and should be monitored in order to take appropriate management protective measures in due time, ensuring the high productivity and lagoon biodiversity of these priority habitats.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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