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Citation style: Salamon Mariusz A., Leśko Katarzyna, Gorzelak Przemysław. (2018). Experimental tumbling of *Dreissena polymorpha* : implications for recognizing durophagous predation in the fossil record. "Plant Journal" (Vol. 64, iss. 2 (2018), art. no. 10), doi 10.1007/s10347-018-0522-7



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Experimental tumbling of *Dreissena polymorpha*: implications for recognizing durophagous predation in the fossil record

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Received: 2 November 2017 / Accepted: 15 January 2018 / Published online: 7 February 2018
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Abstract

Shell damage left by predators constitutes an important source of information on predator–prey interactions. However, recognition of the origins of shell damage can often be controversial, and needs to be assessed cautiously. More specifically, differentiation between predation- and abiotic-induced shell damage remains challenging. Here, we show the results of tumbling experiments using a bivalve species *Dreissena polymorpha* in order to determine rates and patterns of shell damage induced by physical forces in high-energy conditions. It is demonstrated that, in contrast to durophagous fish and crab predation, abiotic-induced fragmentation and damage are typically characterized by the presence of distinct abrasive scratches and wear scars on the surface of shell fragments. Furthermore, fragmented shells typically reveal a wide size distribution, and a different degree of sphericity and roundness resulting from abrasion. Importantly, large shell fragments commonly display smooth edges. These data suggest that durophagous predation, which typically induces fragmentation into large and angular shell fragments bearing no wear scars, can be reliably recognized both in present-day environments and in the fossil record.

Keywords Tumbling · Fragmentation · Experiments · Predation · *Dreissena polymorpha*

Introduction

Regurgitalites are fossilized materials consisting of undigested, broken fragments of skeletons that were ejected from the upper alimentary canal (mouth, pharynx, or esophagus). They are an invaluable source of information about predator–prey interactions in the fossil record (e.g., Zatoń and Salamon 2008; Salamon et al. 2014). However, in contrast to coprolites, which are relatively easy to recognize in the fossil record (from the external spiral folding and/or vascular markings reflecting the morphology of the predator intestine, and containing the skeletal particles partly affected by digestion that are usually dispersed within calcium phosphate matrix, e.g., Pollard 1990), the identification of regurgitalites is very difficult. In particular, the distinction between abiotic

and biotic factors causing shell damage remains challenging (e.g., Cadée 1994; Zuschin et al. 2003).

Among the factors inducing shell breakage, compaction is relatively easily recognizable in the fossil record. Extensive experimental data revealed that this process induces characteristic brittle fractures in the skeletons due to the overburden pressure (e.g., Zuschin and Stanton 2001; Zuschin et al. 2003). The resulting fragments of broken fossils are not intermingled and are still close together.

Various types of shell damage due to water agitation (such as near-shore waves, currents, and tidal action) have been studied both in natural environments (e.g., Walther 1910; Kidwell and Bosence 1991; Cadée 1968, 1994, 1995, 2016; Leighton et al. 2016) and in laboratory conditions (e.g., Müller 1951, 1976; Kuenen 1966a, b; Chave 1964; Driscoll 1967, 1970; Oji et al. 2003; Chojnacki and Leighton 2013; Gorzelak et al. 2013; Salamon et al. 2014). In general, it has been argued that transported shells are infrequently broken and possess abraded surfaces and rounded margins.

In contrast, angular shell fragments with sharp margins are typically considered a good proxy for durophagous predation (e.g., Cintra-Buenrostro 2007; Salamon et al. 2014). Interestingly, Oji et al. (2003) have argued that durophagous predation intensity, as measured by the frequency of

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occurrences of angular shell fragments in fossil shell beds, increased during the early Cenozoic, coinciding with the radiation of durophagous teleost fish and decapod crustaceans. Likewise, Salamon et al. (2012) documented numerous regurgitalites from the Middle Triassic and suggested that many morphological and behavioral innovations in the Triassic benthic fauna are escalation-related adaptations to durophagous predators. Using angular shell fragments as a predation proxy, Salamon et al. (2014) also analyzed data from many European Paleozoic localities spanning the Ordovician to the Carboniferous. The results of the latter authors showed a significant increase in angular shell fragments of molluscs and brachiopods in the Mississippian. Notably, the timing of this increase is coincident with the radiation of durophagous predators as well as with the occurrence of anti-predatory traits in many invertebrates.

As highlighted above, the proper recognition of the origin of shell accumulations, including detection of the predation traces in the fossil record, is a prerequisite for accurate interpretation of macroevolutionary trends. However, criteria for distinguishing shell fragments produced by physical processes are still not well understood. For this purpose, we performed a number of tumbling experiments using a rotary barrel simulating the hydrodynamic processes taking place in shallow-water high-energy siliciclastic environments.

Methods

Taphonomic experiments using a commercially available unprotected bivalve species *Dreissena polymorpha* were conducted at the Faculty of Earth Sciences, Laboratory of Palaeontology and Biostratigraphy of the University of Silesia with the aid of a rotating barrel LPM-20 (Glass GmbH & Co. KG Spezialmaschinen) (for details see Gorzelak and Salamon 2013). This freshwater species belongs to the Dreissenidae family and exhibits a crossed-lamellar/complex crossed-lamellar microstructure typical of several heterodont bivalves.

To assess whether differences in size and/or presence of soft tissues may affect shell fragmentation rates, two size classes (about 1.3 and 2 cm and having about 0.4 and

0.6 mm thick shells, respectively) of bivalves were used, with and without soft tissues. Before the beginning of each experiment, the bivalves were killed by immersion into formalin solution.

The specimens were tumbled at 30 revolutions per minute [rpm] for up to 63 days in a 27-cm-diameter barrel (the tumbling speed = 0.135 m/s; a time equivalent to ~ 0.5 km of transport or in-place tumbling within the surf zone per 1 h) containing 4 l of fresh water (Przeclzyce Lake) and 0.5 kg quartz gravel with a maximum diameter of 2 cm, 0.5 kg fine-sized sand (\varnothing 0.3–0.5 mm) or 0.5 kg medium-sized sand (\varnothing 0.5–1.0 mm) (Table 1).

All experiments were performed at room temperature (about 21 °C). During the experiments, the pH (~ 8) was measured every day using the inoLab® pH 7310 pH meter. A slight decrease in pH during the experiments was compensated by the addition of sodium bicarbonate.

Depending on the type of sediment in the barrel, the experiment was suspended and shell fragments were systematically removed, photographed, and subjected to various observations. During the experiment, from time to time, shell-size analysis, as well as sphericity and roundness of shell fragments, following the scales by Krumbein and Sloss (1963) and Pilkey et al. (1967) (Figs. 1, 2), were evaluated semi-quantitatively.

For comparison purposes, we also photographed regurgitates produced by the durophagous freshwater fish *Cyprinus carpio* and marine predatory crab *Eriphia verrucosa* that are incubated in the aquaria at the Faculty of Earth Sciences, Laboratory of Palaeontology and Biostratigraphy of the University of Silesia.

Results

Experiment no. 1 (gravel + shells without soft tissues)

The first significant traces of shell fragmentation were observed after 15 min. We observed only larger (> 1 mm) shell fragments displaying a high degree of sphericity

Table 1 Experimental design. Each treatment was repeated three times

No. of experiment	Type of sediment	Type of bivalves	Bivalve size (cm)	Duration (min.)
1	Gravel	Bivalve without soft tissues	2–2.1	90
2	Gravel	Bivalve with soft tissues	1.8–1.9	90
3	Gravel	Bivalve without soft tissues	1.2–1.3	135
4	Gravel	Bivalve with soft tissues	1.3–1.4	135
5	Fine-sized sand	Bivalve without soft tissues	1.8–1.9	90, 720
6	Fine-sized sand	Bivalve with soft tissues	1.2–1.3	87, 840
7	Gravel + medium-sized sand	Bivalve with soft tissues	1.8–1.9	285

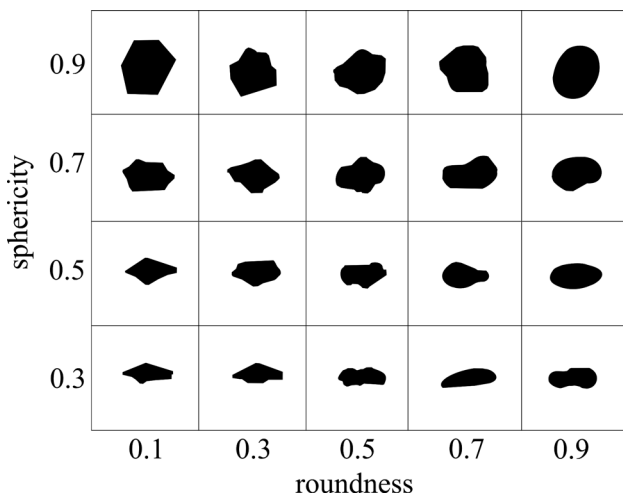
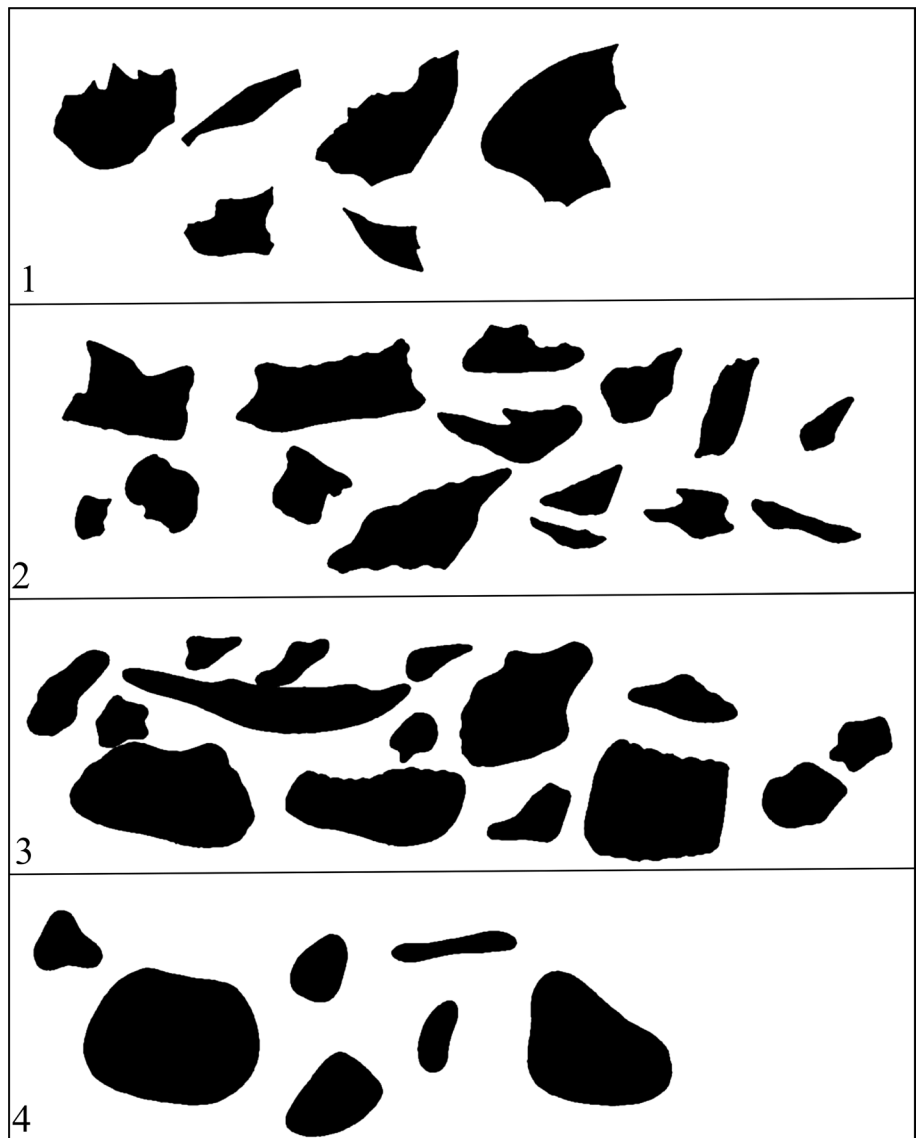


Fig. 1 Krumbein–Schloss chart to quantify sphericity and roundness

(0.7–0.9; Figs. 3, 4, and 5), but usually a low degree of roundness (0.1–0.3; Fig. 3a). However, on the surface of these shell fragments, numerous abrasive cracks and crescentic chips removed from the shell margin (Fig. 5b) were observed. The rate of shell fragmentation increased rapidly, reaching a maximum after 45 min (Fig. 4). After 30 and 45 min, fine fragments ($1\text{ mm} > x > 0.315\text{ mm}$ and $0.315\text{ mm} > x > 0.1\text{ mm}$, respectively), appeared. At this stage, the edges of the larger ($> 1\text{ mm}$) fragments became slightly more rounded. After 60 min, larger ($> 1\text{ mm}$) elements were not observed, and the total number of elements above 0.1 mm decreased (Fig. 4). At this stage, fine fragments ($< 0.315\text{ mm}$) were usually moderately smoothed and slightly elongated. After 90 min, fragmentation of the shell was complete, i.e., no fragments above 0.1 mm fraction were observed. Throughout the experiment, it was observed that the sphericity of the fragments

Fig. 2 Comparison chart for describing the roundness of carbonate bioclasts (after Pilkey et al. 1967)



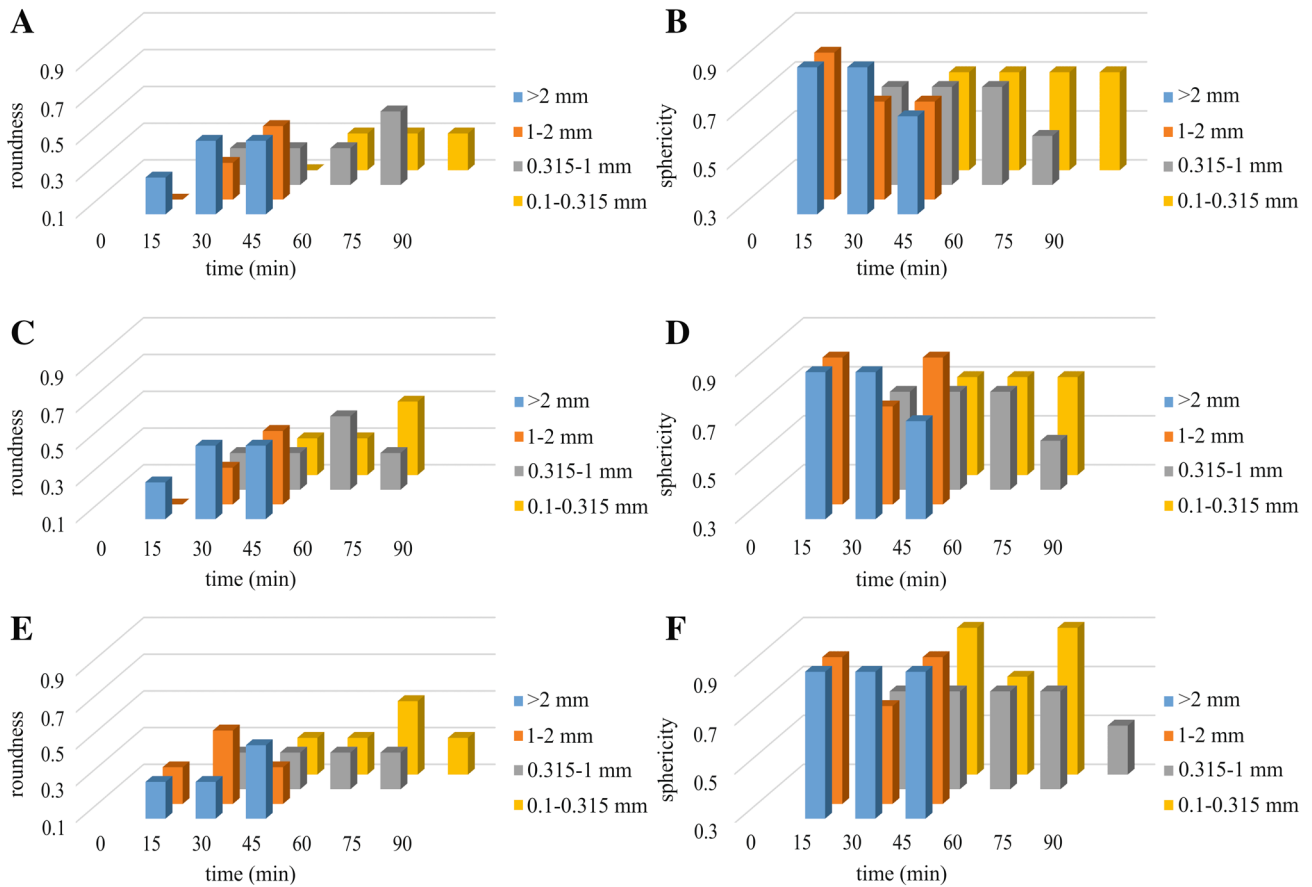


Fig. 3 a, c, e Variation of the degree of roundness of shell fragments during experiment no. 1. b, d, f Variation of the degree of sphericity of shell fragments during experiment no. 1

of a given fraction slightly decreased, while their roundness increased. However, this usually happened with the larger elements (Fig. 5). In other words, the larger elements from angular discoid or spherical became slightly more elongate but smooth (Fig. 5).

According to the roundness classification of shell fragments by Pilkey et al. (1967), the larger shell fragments gradually passed through the first three stages of rounding (Fig. 5). In the next two replicates of the experiment, a very similar pattern of shell fragmentation/abrasion was observed, as described above (Figs. 3c–f, 4c–f).

Experiment no. 2 (gravel + bivalves with soft tissues)

The pattern of fragmentation/abrasion of bivalves containing soft tissues in this experiment was very similar to that observed on naked shells. After 15 min of tumbling, only larger fractions (> 2 and $2 > x > 1$ mm) of shell fragments with a high degree of sphericity (0.7–0.9) and low degree of roundness (0.1) were observed (Figs. 6, 8). At this stage, however, numerous cracks, abrasive scratches, and marginal crescentic chips (Fig. 8b) were noted on the surface of these fragments. Throughout the experiment, the fragments became increasingly fragmented, reaching a maximum at 45 min (Fig. 7). After 30 and 45 min, fragments of finer fraction ($1 > x > 0.315$ mm

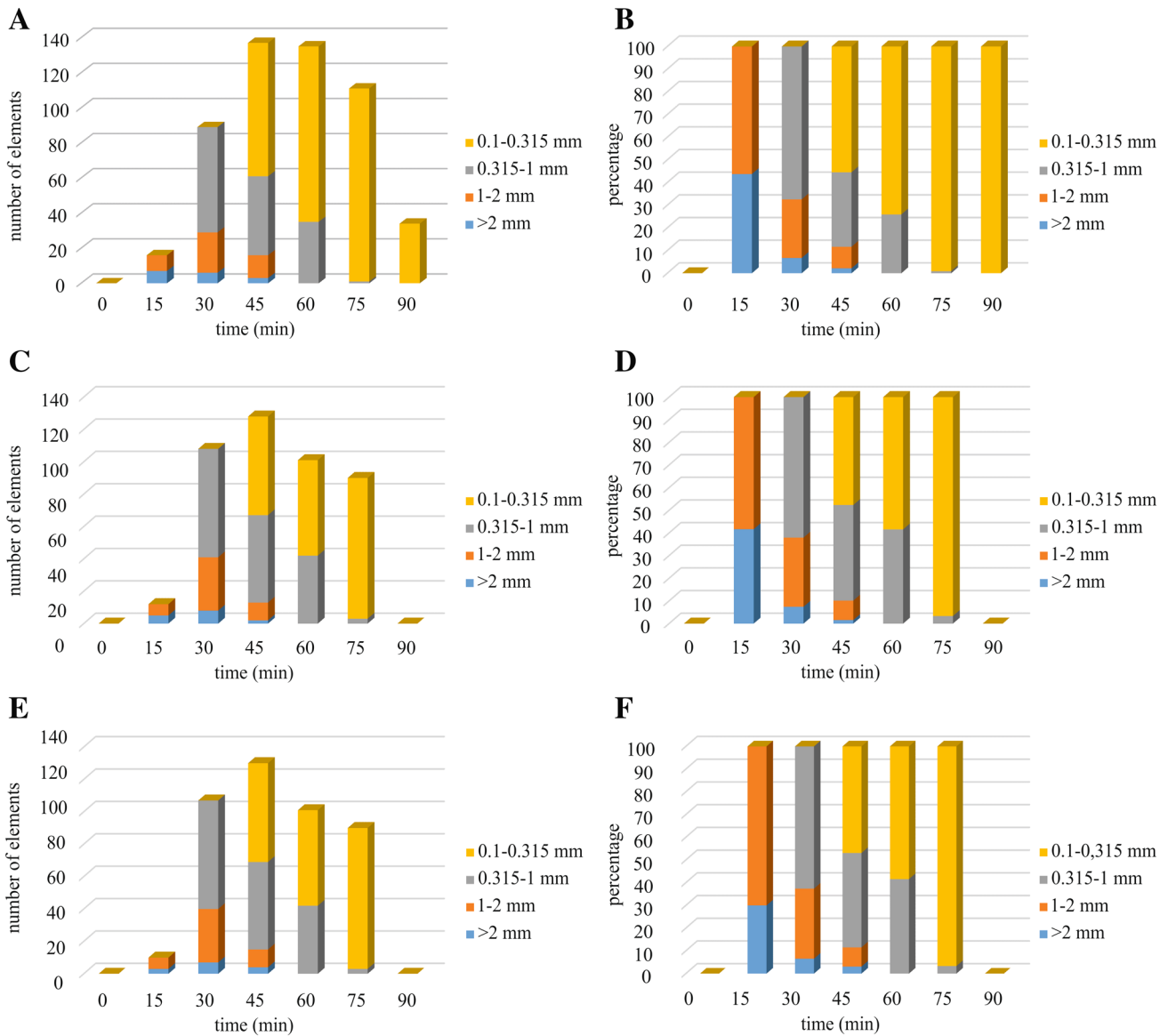


Fig. 4 a, c, e Distribution of the number of shell fragments during experiment no. 1. b, d, f Changes of percentage of each shell fraction during experiment no. 1

and 0.315 mm > x > 0.1 mm, respectively) appeared and since then represented a dominant fraction (Fig. 7). The edges of larger fragments (> 1 mm) were slightly rounded (Fig. 8b, c). After 75 min, no larger fractions (> 2 mm) were observed, and the total number of elements of all fractions above 0.1 mm decreased. The edges of small shell fragments (< 0.315 mm) were usually moderately smooth and slightly elongate. After 90 min, only fragments of 0.315–0.1 mm and rare elements of 1–0.315 mm were observed (Fig. 7). Throughout the experiment, the degree of sphericity of larger shell fragments usually decreased

slightly, whereas their roundness slightly increased (Fig. 6).

According to the roundness classification of shell fragments by Pilkey et al. (1967), elements of the larger fraction gradually passed through the first three phases of rounding (Fig. 8). In the next two replicates of the experiment, a very similar fragmentation/abrasion pattern was observed as described above (Figs. 6c–f, 7c–f).

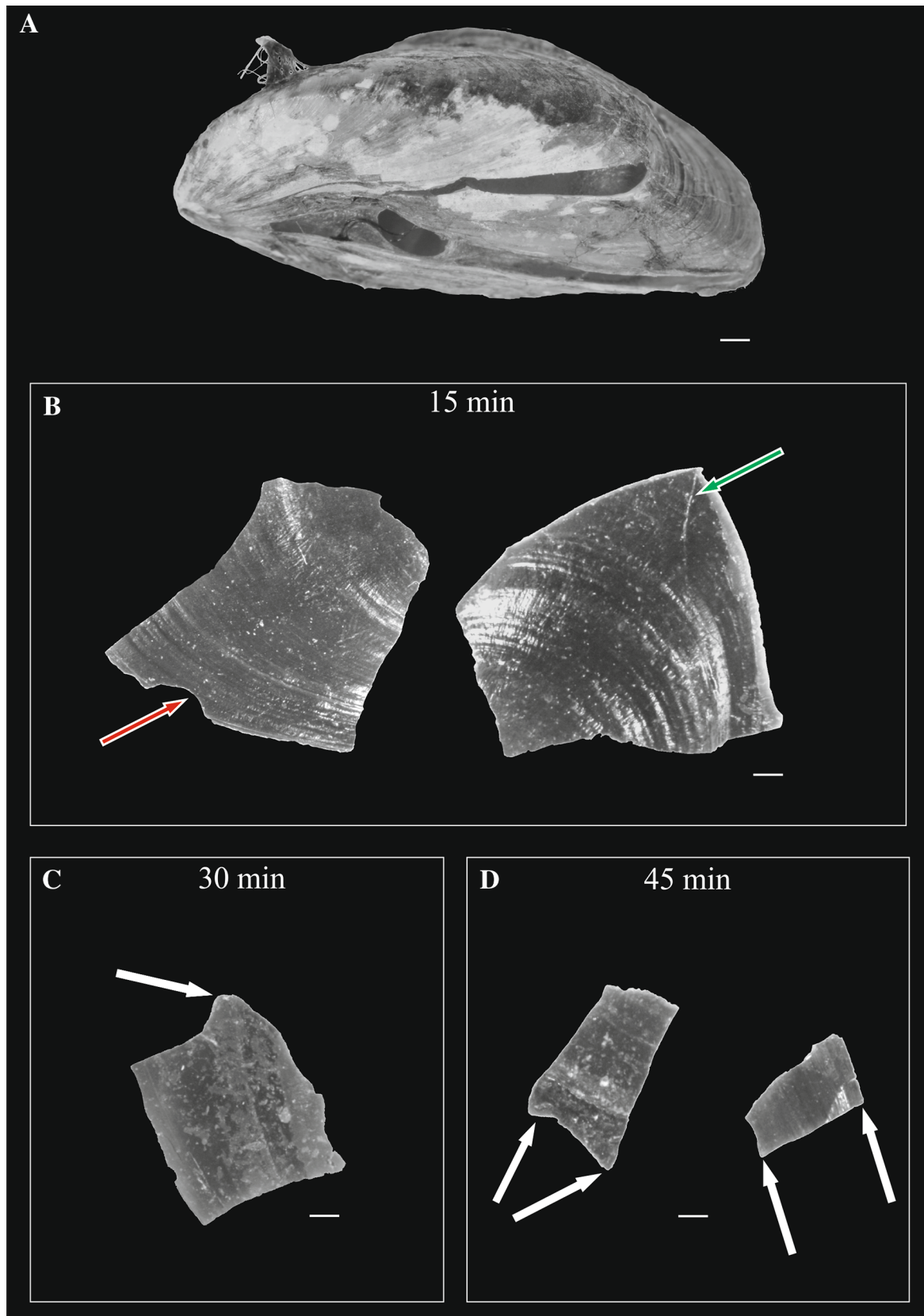


Fig. 5 Patterns of shell fragmentation (a–d) during experiment no 1. Red arrow crescentic chips, green arrow abrasive scratches, white arrow rounded edges. Scale bar = 1 mm

Experiment no. 3 (gravel + small shells without soft tissues)

Three replicates of the experiment revealed a very similar pattern of fragmentation/abrasion (Figs. 9, 10). After 15 min of tumbling, only larger fractions (> 2 and $2 > x > 1$ mm) of shell fragments were noted. They displayed a high degree of sphericity (0.9) and low roundness (0.1–0.3) (Figs. 9, 11). As in the previous experiments, abrasive cracks and semicircular marginal chips (Fig. 11b) were

observed on the surface of the shell fragments. Shell fragmentation increased rapidly, reaching a maximum, depending on the repetition, in about 90 or 75 min (Fig. 10). After 45 and 60 min of tumbling, fine fractions appeared (1.0–0.315 and 0.315–0.1 mm, respectively) (Fig. 10). No larger (> 1 mm) fragments were observed after 105 min. At this stage, the total number of fractions above 0.1 mm decreased. Fragments of the fine fraction (< 0.315 mm) were usually moderately smooth and slightly elongate. After 135 min, the fragmentation of shells was complete (no

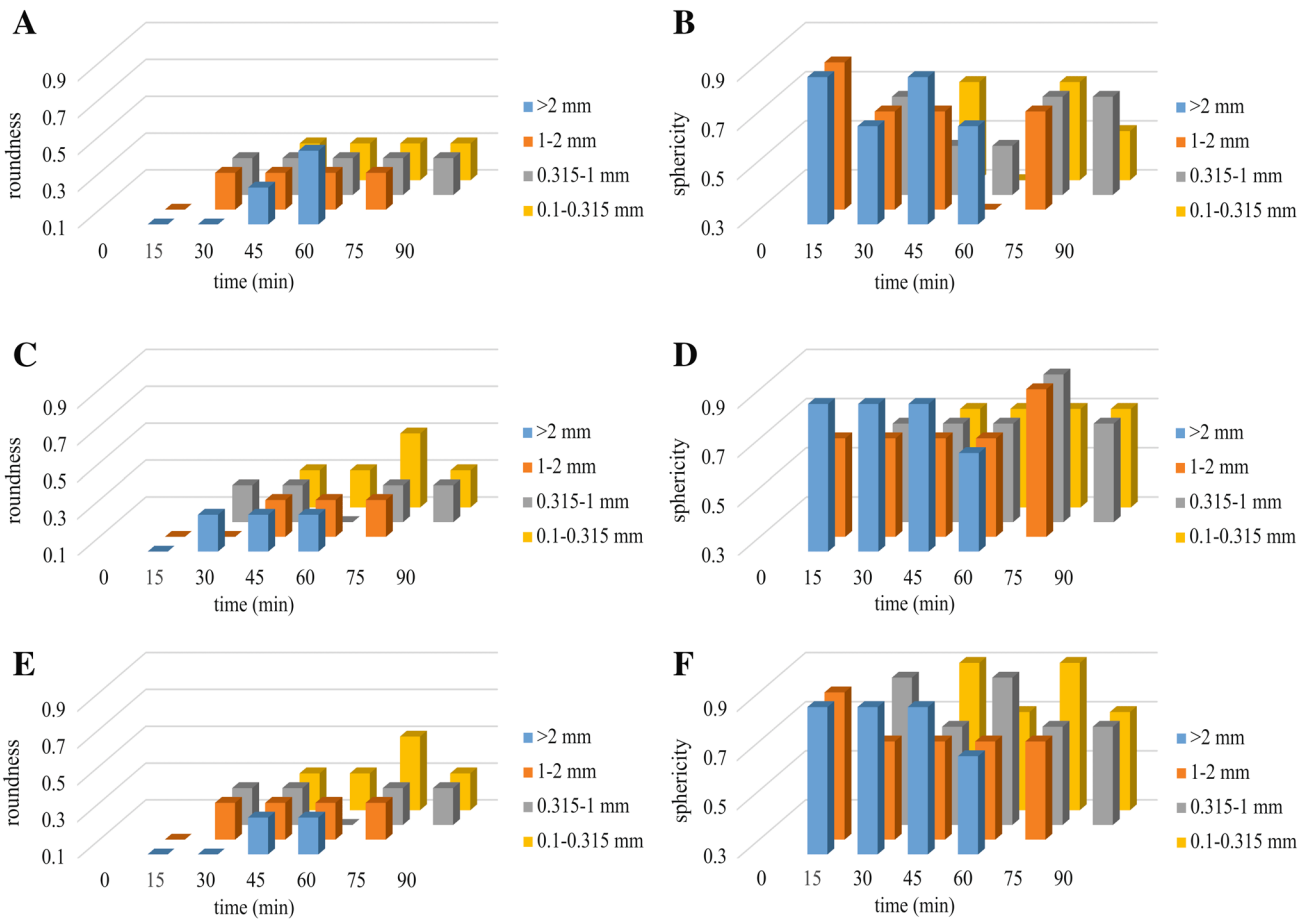


Fig. 6 a, c, e Variation of the degree of roundness of shell fragments during experiment no. 2. b, d, f Variation of the degree of sphericity of shell fragments during experiment no. 2

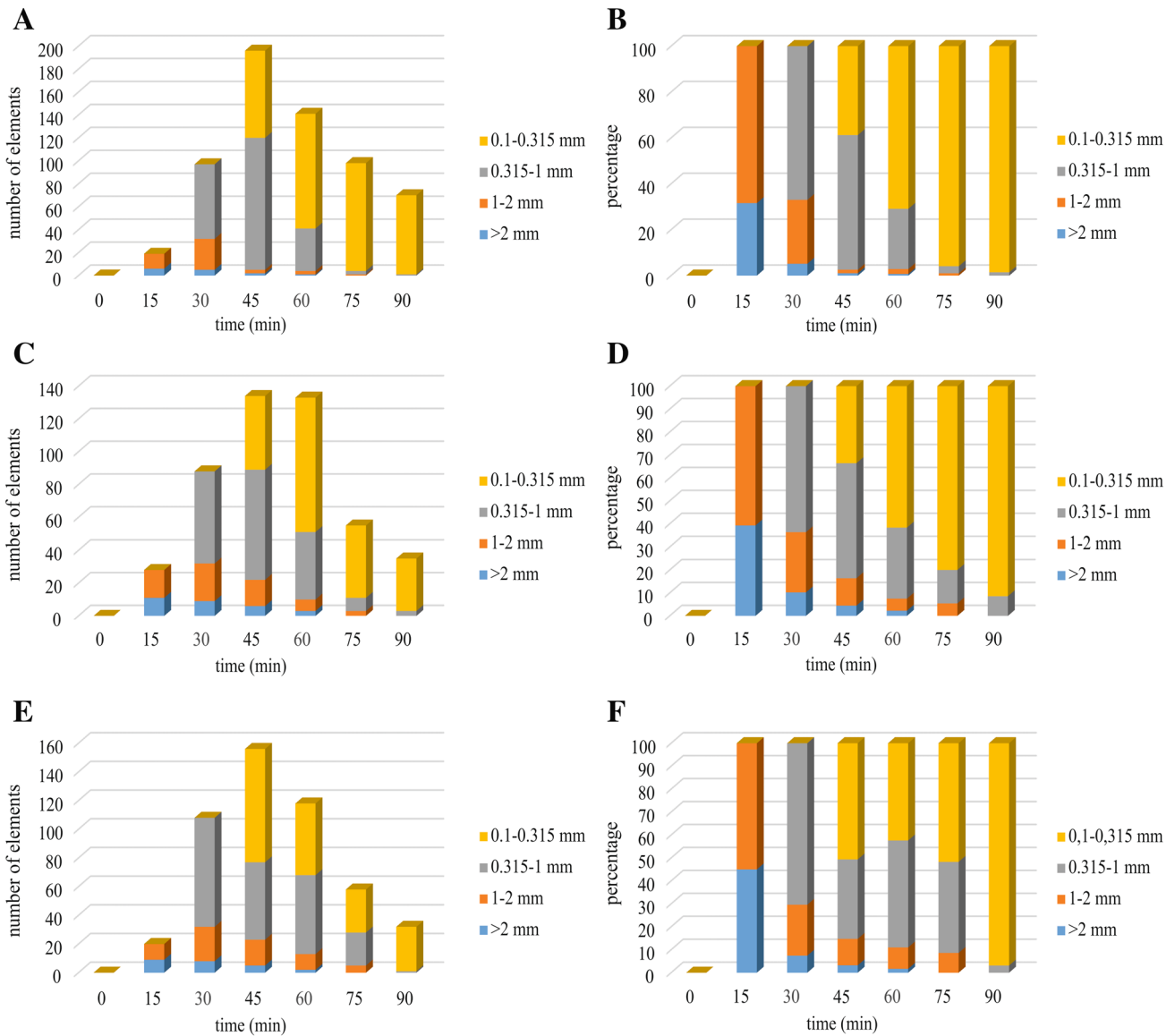


Fig. 7 a, c, e Distribution of the number of shell fragments during experiment no. 2. b, d, f Changes of percentage of each shell fraction during experiment no. 2

fragments > 0.1 mm were recorded). Throughout the experiment, larger fractions (> 2 mm) usually underwent slight elongation and rounding (Fig. 9). The larger shell fragments passed through the first three stages of the rounding scale by Pilkey et al. (1967) (Fig. 11). The degree of roundness of the smaller fractions became generally unchanged, whereas their sphericity varied considerably (Fig. 9).

Experiment no. 4 (gravel + small bivalves with soft tissues)

The pattern of fragmentation/abrasion of small bivalves with soft tissues in this experiment is comparable to that observed on naked shells. After 15 min of tumbling, only larger fragments (> 2 and 1.0–2.0 mm) with a high degree of sphericity (0.7–0.9) and usually low roundness (0.1–0.3) were recorded

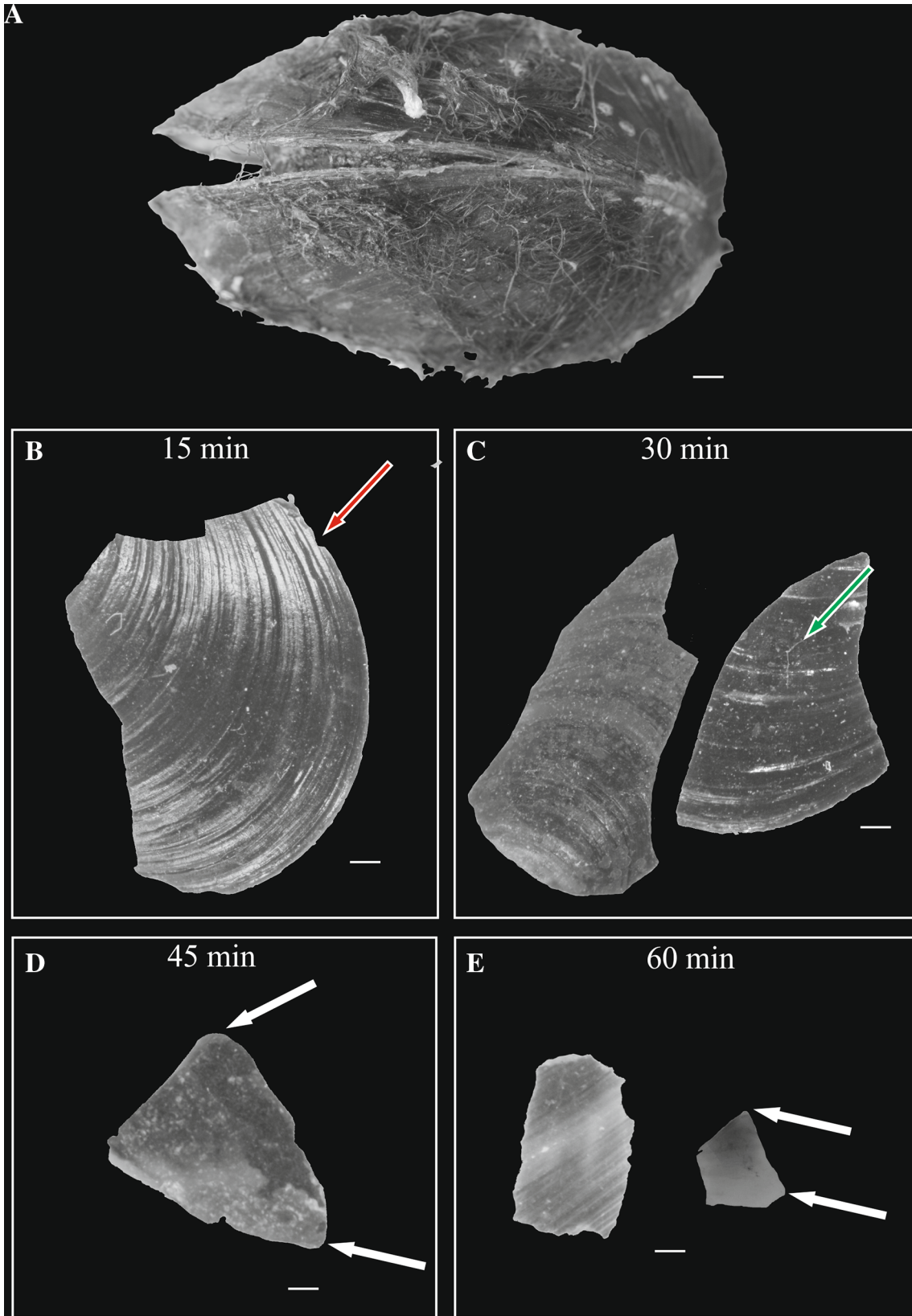


Fig. 8 Patterns of shell fragmentation (a–e) during experiment no 2. Red arrow crescentic chips, green arrow abrasive scratches, white arrow rounded edges. Scale bar = 1 mm

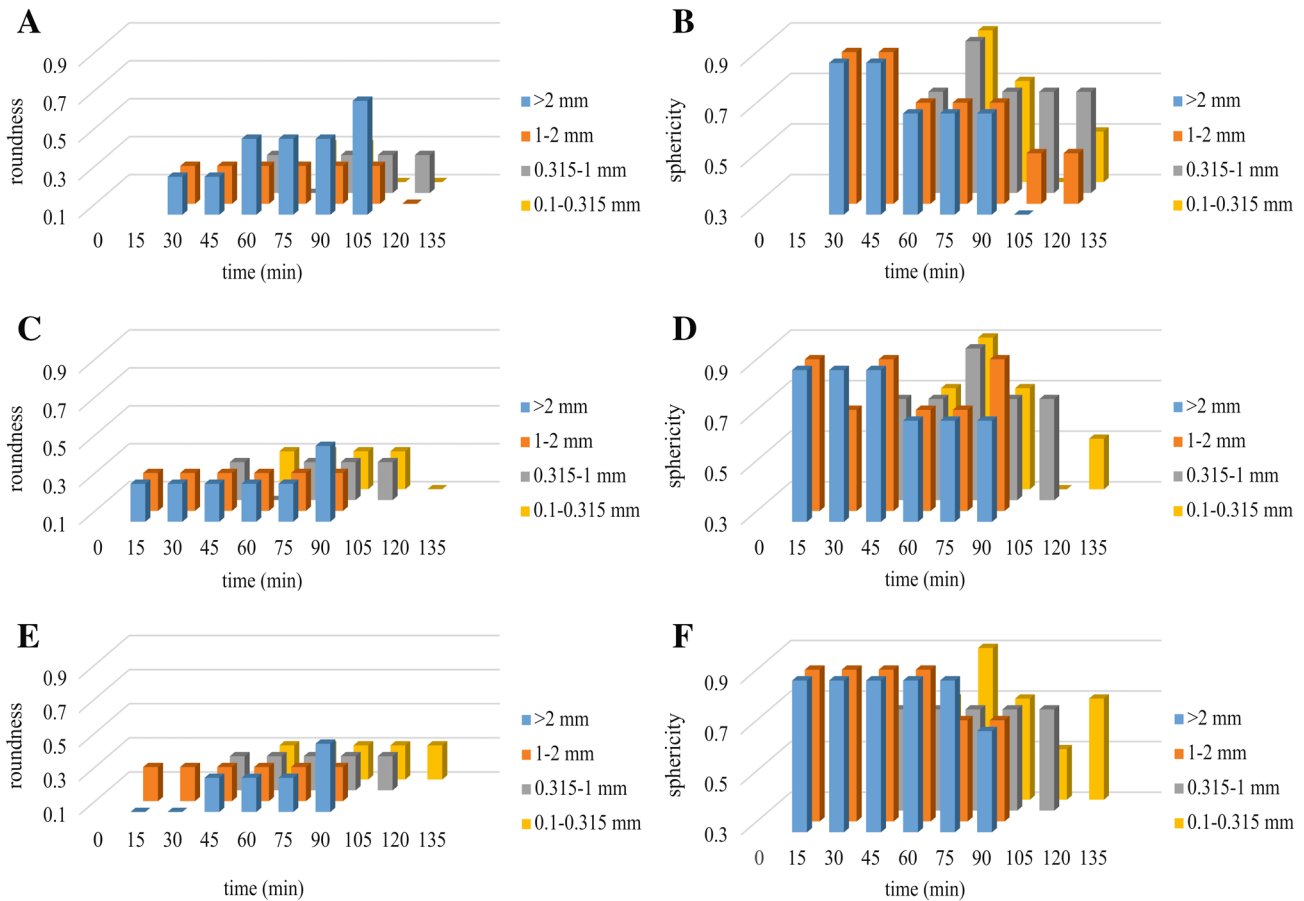


Fig. 9 a, c, e Variation of the degree of roundness of shell fragments during experiment no. 3. b, d, f Variation of the degree of sphericity of shell fragments during experiment no. 3

(Figs. 12, 13). On the surfaces of these fragments, semicircular chips and abrasive irregular cracks were noted (Fig. 14). Fragmentation of the shells increased rapidly, reaching a maximum, depending on the repetition, after 90 or 60 min. After 30 min, fragments of the finer fraction (1.0–0.315 mm) appeared and became dominant (Fig. 13). At this stage, no larger fractions (> 1 mm) were observed, and the total number of fractions above 0.1 mm was greatly reduced. At this stage, fragments of fine fraction (< 0.315 mm) were usually moderately smoothed and slightly spherical. After 120–135 min of tumbling, the fragmentation to the fraction below 0.1 mm was complete. Throughout the experiment, it was noted that the roundness of larger fragments (> 2 mm) usually increased slightly (Fig. 12a). These fragments can be classified into the second and third roundness scale by Pilkey et al. (1967) (Fig. 14). The sphericity and roundness of other elements varied significantly (Fig. 12c–f). The results of the three repetitions of the same experiment varied slightly from

each other; for instance, a slightly different rate of fragmentation of the larger fraction was noted (Fig. 13c–f).

Experiment no. 5 (sand + shells without soft tissues)

In three replicates of this experiment, a very similar pattern of fragmentation/abrasion was observed. After about 17.5 days (420 h) of tumbling, shells were still not fragmented, but displayed a single hole, abrasive cracks and marginal chips (Fig. 15b). After 30 days (720 h) of tumbling, fragmentation of shells was still negligible and limited to a few larger (> 2 mm) triangular elements with strongly rounded edges (Fig. 15c). After 41 days (984 h), elements of the larger fraction were still only observed, all characterized by extremely high roundness and sphericity (0.9) (Fig. 15d). According to the roundness classification of shell fragments by Pilkey et al. (1967), the larger shell fragments rapidly reached the highest phase of the rounding (Fig. 15). After

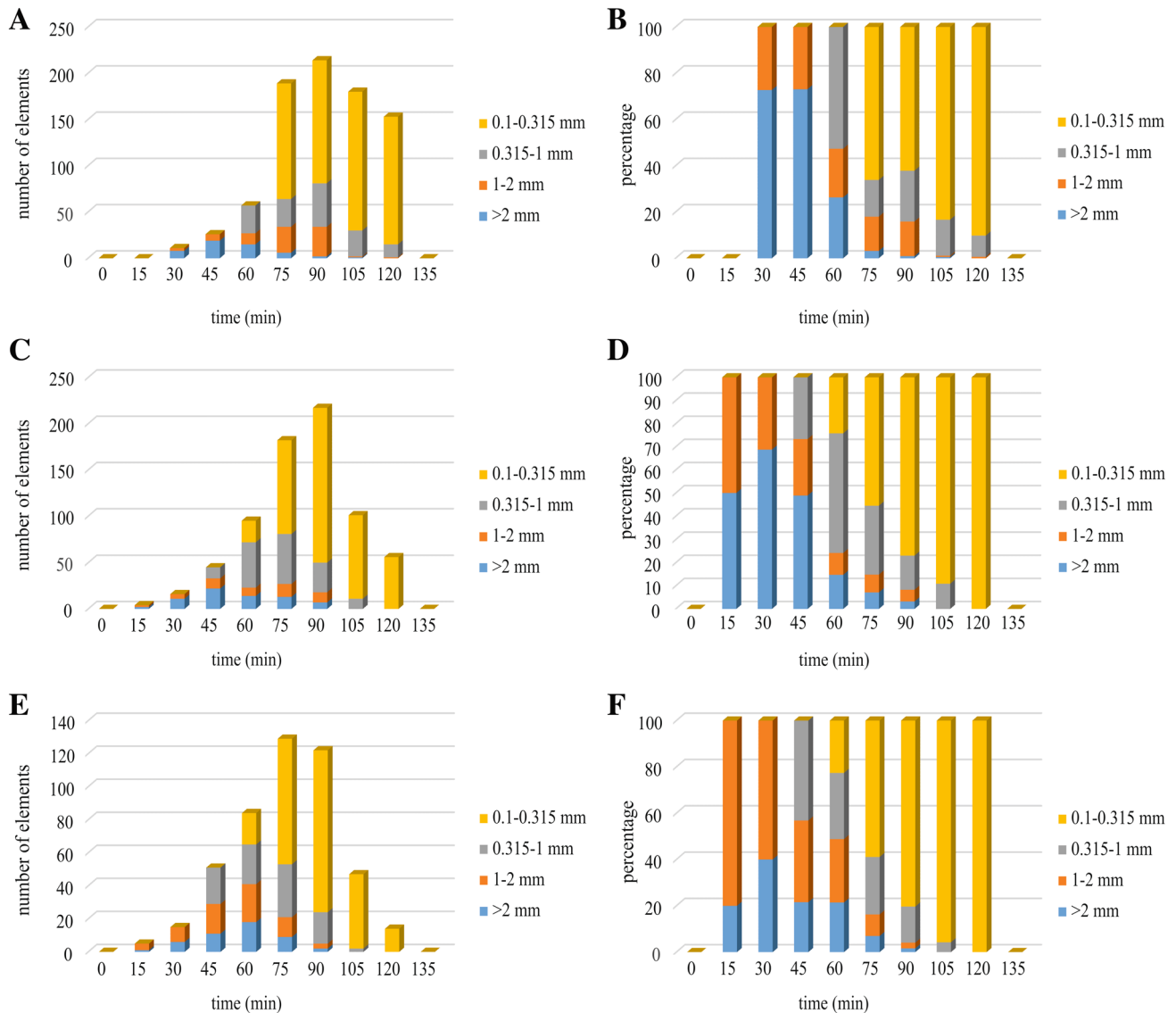


Fig. 10 a, c, e Distribution of the number of shell fragments during experiment no. 3. b, d, f Changes of percentage of each shell fraction during experiment no. 3

63 days (1512 h), fragmentation (below 0.1 mm fraction) was complete.

Experiment no. 6 (sand + bivalves with soft tissue)

The pattern of fragmentation/abrasion of bivalves with soft tissue in this experiment was comparable to that observed on the naked shells. In general, the rate of fragmentation was very slow. Clearly visible single holes, cracks, and abrasive crescentic chips (Fig. 16b, c) were observed after 30 days (720 h). Significant fragmentation was observed only after 41 days (984 h), when several larger elements displaying

an extremely high degree of roundness and sphericity were noted (0.9) (Fig. 16d). These elements could be classified into the highest grade of rounding by Pilkey et al. (1967). Complete damage of the shell (below 0.1 mm fraction) was observed after 61 days (1464 h). In the next two replicates, a very similar pattern of fragmentation/abrasion was observed.

Experiment no. 7 (gravel and sand + bivalves with soft tissues)

The results of the three replications of the experiment varied from one another, mainly in the rate of fragmentation of the

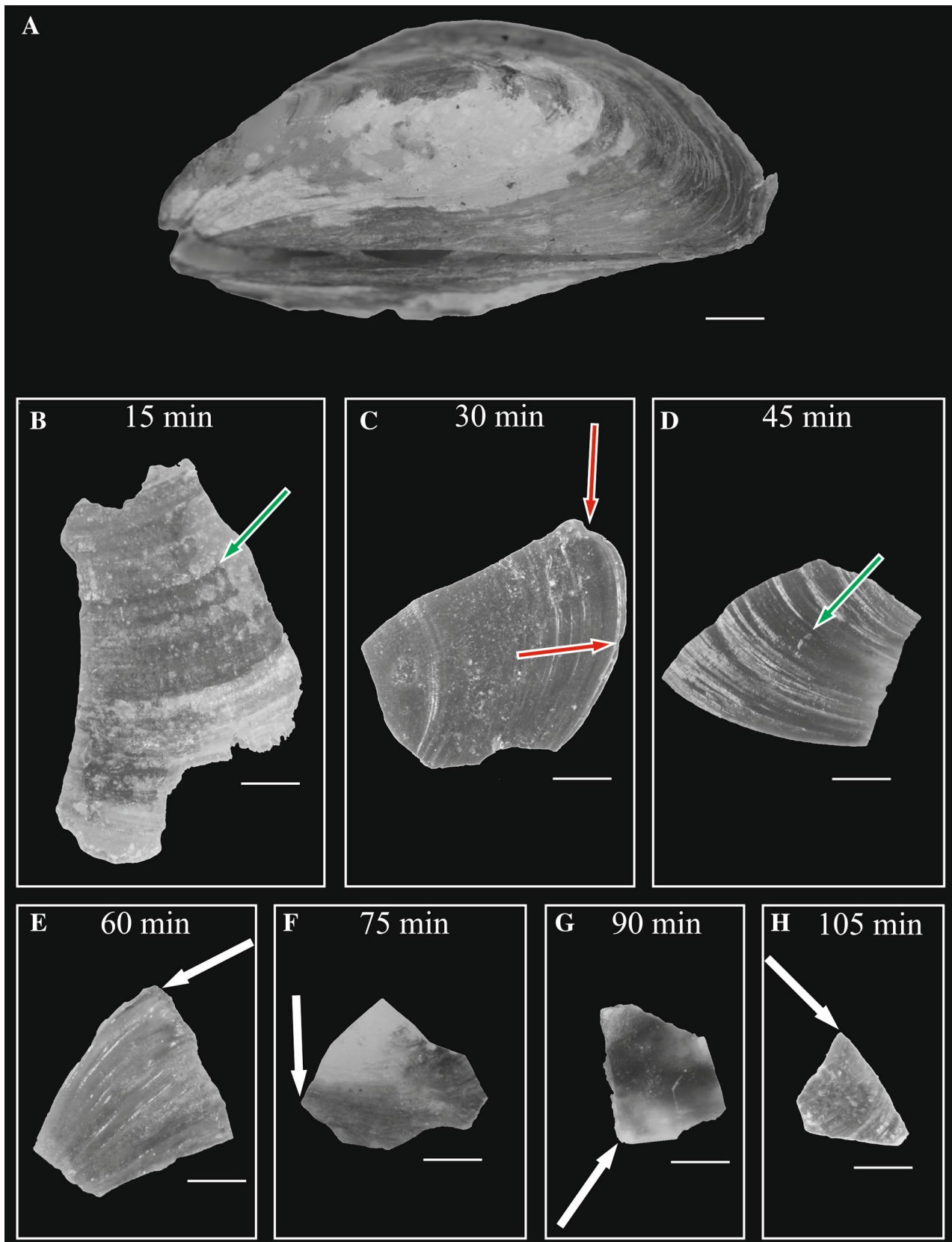


Fig. 11 Patterns of shell fragmentation (a–h) during experiment no. 3. Red arrow crescentic chips, green arrow abrasive scratches, white arrow rounded edges. Scale bar = 1 mm

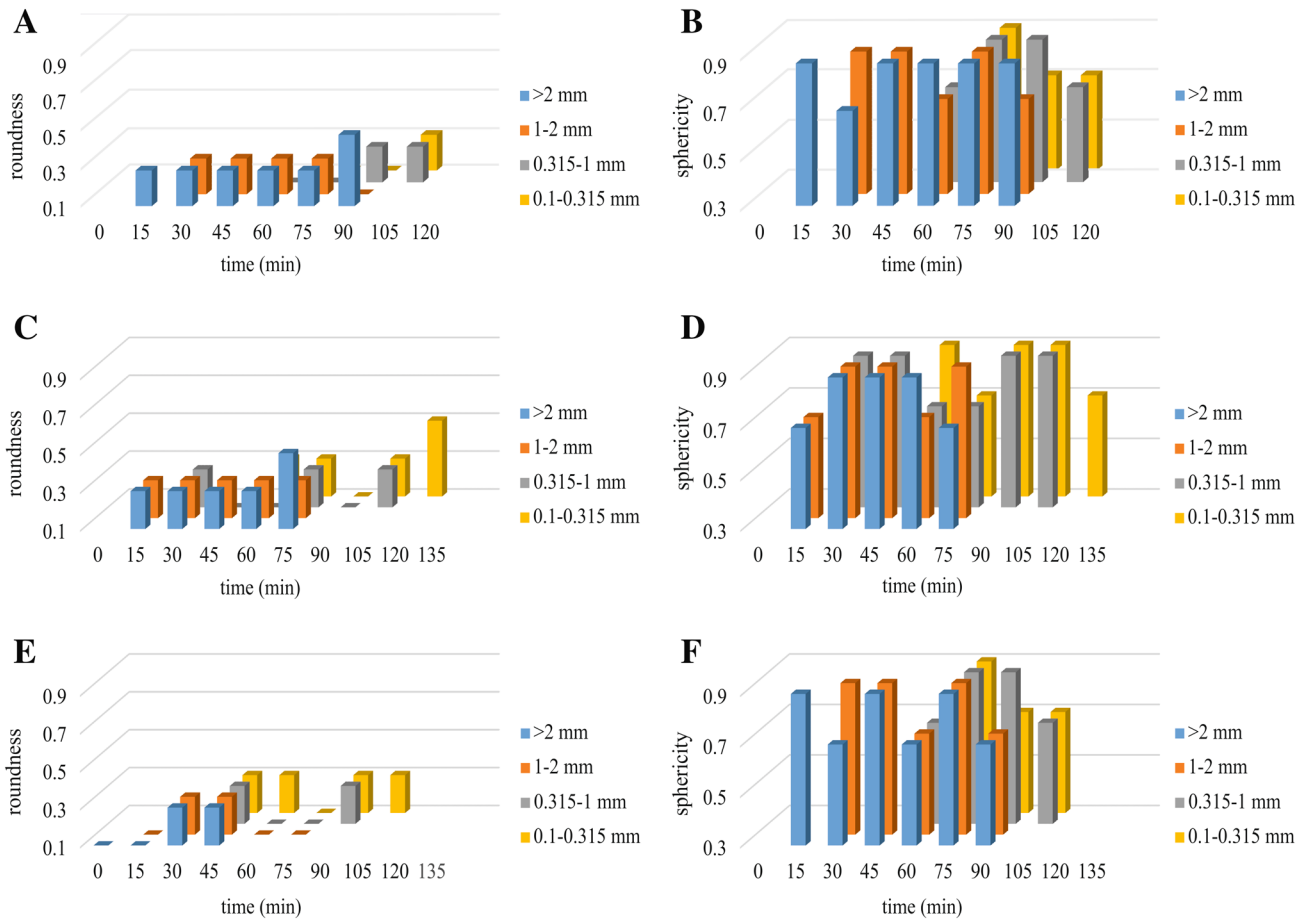


Fig. 12 a, c, e Variation of the degree of roundness of shell fragments during experiment no. 4. b, d, f Variation of the degree of sphericity of shell fragments during experiment no. 4

larger fractions (Figs. 17, 18). Depending on the repetition of the experiment, the first evidence of significant fragmentation was observed after 45, 75, or 90 min of tumbling. At the initial stage, only larger fractions (> 2 mm) with a moderate degree of sphericity (0.3–0.7) and low or moderate degree of rounding (0.1–0.5) were noted. However, semi-circular chips in the shell margin, abrasive scratches, and cracks were also observed (Fig. 19b). Fragmentation of shells increased, reaching a maximum after 210 or 225 min. After 120 or 135 min fine fragments (1.0–0.315 mm) began to appear, and after 195 min the smallest fraction (0.315–0.1 mm) was noticed. After 210 min, no larger fractions (> 1 mm) were recorded. Throughout the experiment, the roundness of larger fraction (> 2 mm) increased slightly (Fig. 17). The

degree of sphericity of all elements varied within a wide range without clear pattern (Fig. 17b, d, f). According to the classification of the roundness of shell fragments by Pilkey et al. (1967), larger shells gradually passed through all four stages (Fig. 19).

Experiment no. 8 (fragmentation by predators)

Aquarium experiments using predatory fish (*Cyprinus carpio*; cf. Salamon et al. 2014) and crabs (*Eriphia verrucosa*) feeding on *Dreissena polymorpha* and *Mytilus* sp. respectively, revealed that these predators induce fragmentation into larger (> 2 mm) sharp-edged shell pieces displaying extremely low roundness and varying degree of sphericity (Fig. 20).

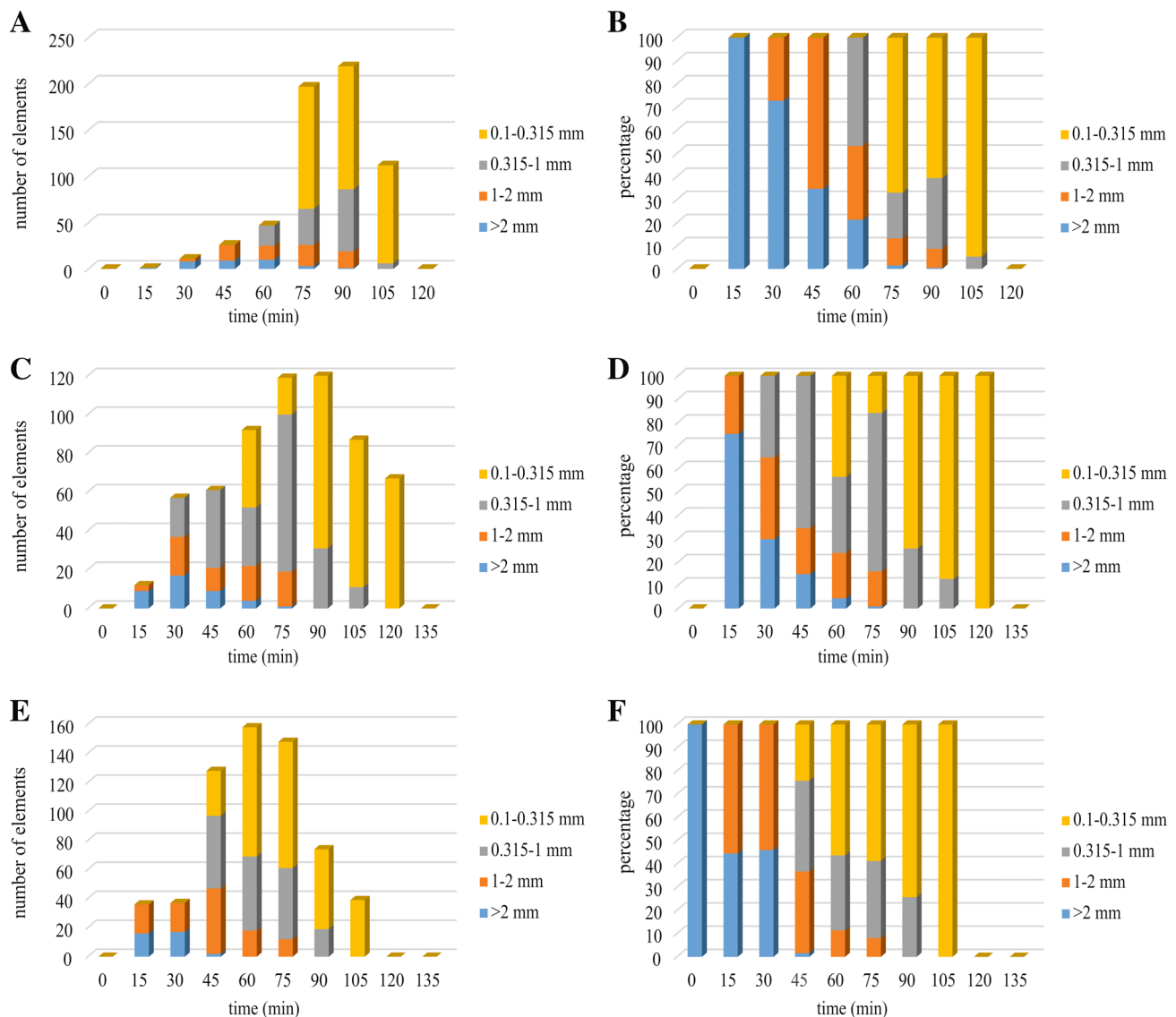


Fig. 13 a, c, e Distribution of the number of shell fragments during experiment no. 4. b, d, f Changes of percentage of each shell fraction during experiment no. 4

Discussion

Some recent literature data based on taphonomic analyses of fossil assemblages have supported an earlier hypothesis that increased durophagous (shell-crushing) predation pressure may have significantly driven macroevolutionary and macroecological changes in the Phanerozoic (e.g., Vermeij 1987; Oji et al. 2003; Salamon et al. 2014). However, evidence of durophagous predation is difficult to determine in Recent marine environments and even more so in the fossil

record. Indeed, although fragmentation of benthic invertebrates by shell-crushing predators is a common phenomenon in Recent environments (e.g., Cate and Evans 1994; Cadée 1994; see Fig. 20), differentiating shell breakages caused by durophagous predators from those caused by physical factors is difficult. Experimental studies on shell fragmentation (Cintra-Buenrostro 2007; Salamon et al. 2014) revealed that shell-crushing predators produce angular shell fragments. Likewise, it has been recently shown that angular shell fragments are much more abundant at high-predation localities

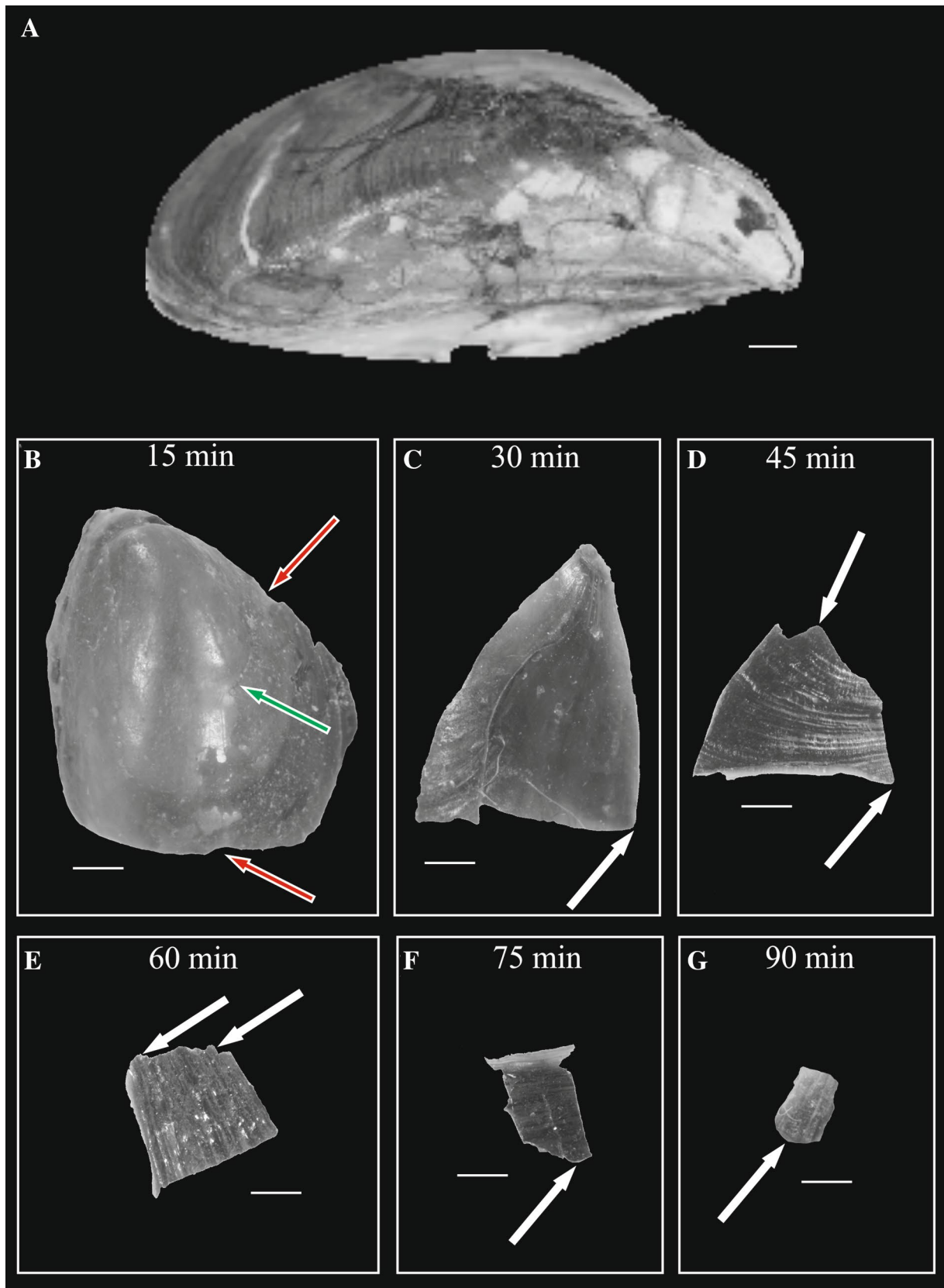


Fig. 14 Patterns of shell fragmentation (a–g) during experiment no. 4. Red arrow crescentic chips, green arrow abrasive scratches, white arrow rounded edges. Scale bar = 1 mm

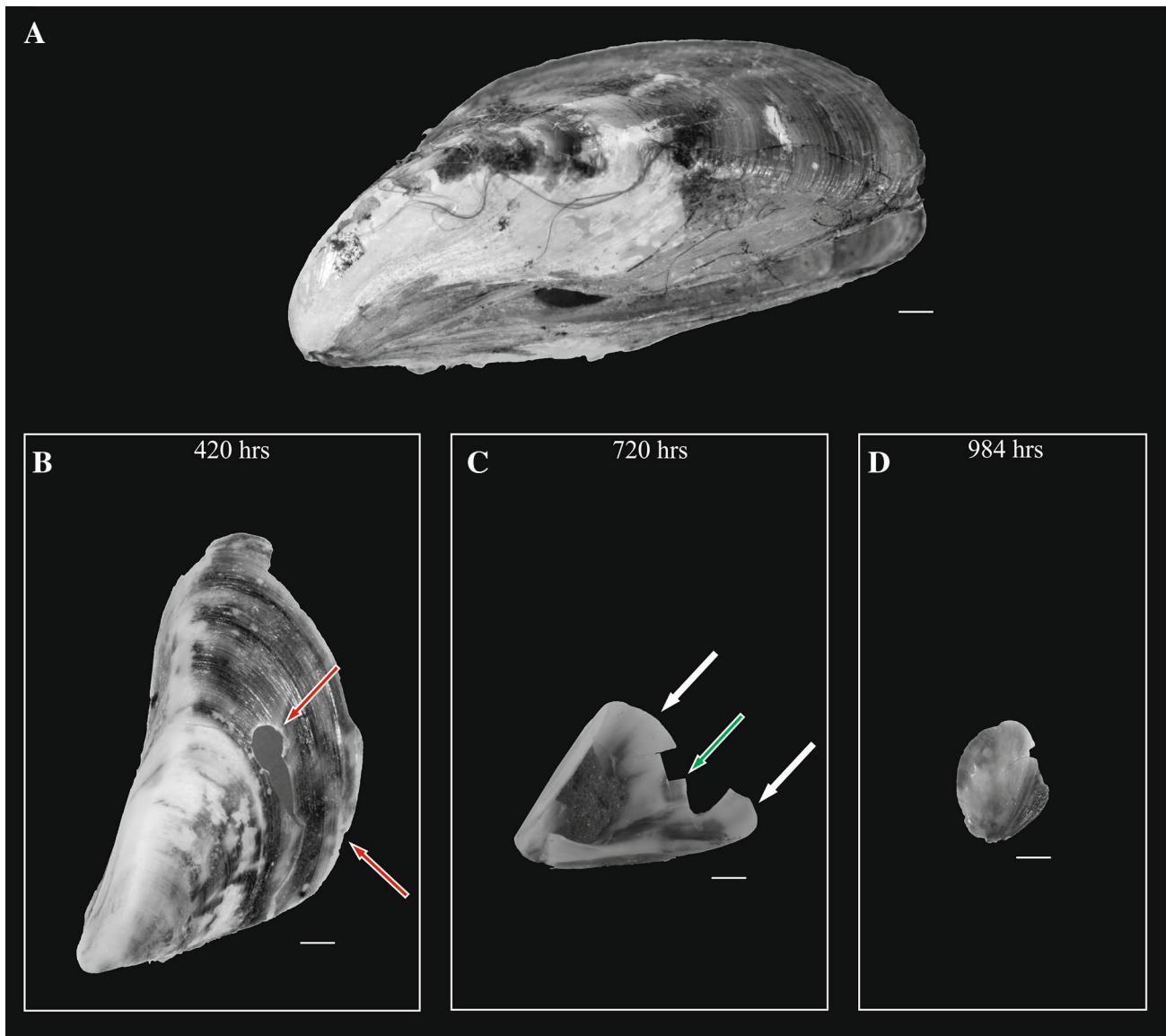


Fig. 15 Patterns of shell fragmentation (**a–d**) during experiment no 5. Red arrow crescentic chips, white arrow rounded edges. Scale bar = 1 mm

(Stafford et al. 2012; Leighton et al. 2016). In contrast, published experimental results have shown that shells become quickly abraded and rounded when tumbled (Oji et al. 2003). Indeed, shell fragments from wave-exposed natural environments are mostly characterized by rounded edges (Leighton et al. 2016).

To date, however, qualitative and semi-quantitative (e.g., size of fragmentation, the degree of roundness and sphericity, the presence of distinct abrasive cracks/holes/chips on the surface/edges) criteria for differentiating skeletal damage caused by abiotic factors have not been well established. In our tumbling experiments, we showed that bivalve shells

from high-energy environments, characterized by the presence of gravels, can be rapidly fragmented (usually within 15 min). Although fragmented shells may reveal angular margins, their surfaces bear characteristic abrasive cracks/wear scars. Total fragmentation (below 0.1 mm fraction) may typically proceed within 2 h. The degree of sphericity of the fragments of a given fraction may vary widely or slightly decrease in time, whereas their roundness usually slightly increases; this is especially true for larger fractions, which are becoming more smooth. In our tumbling experiments with sand, fragmentation of shells proceeded very slowly. The first signs of fragmentation appeared after

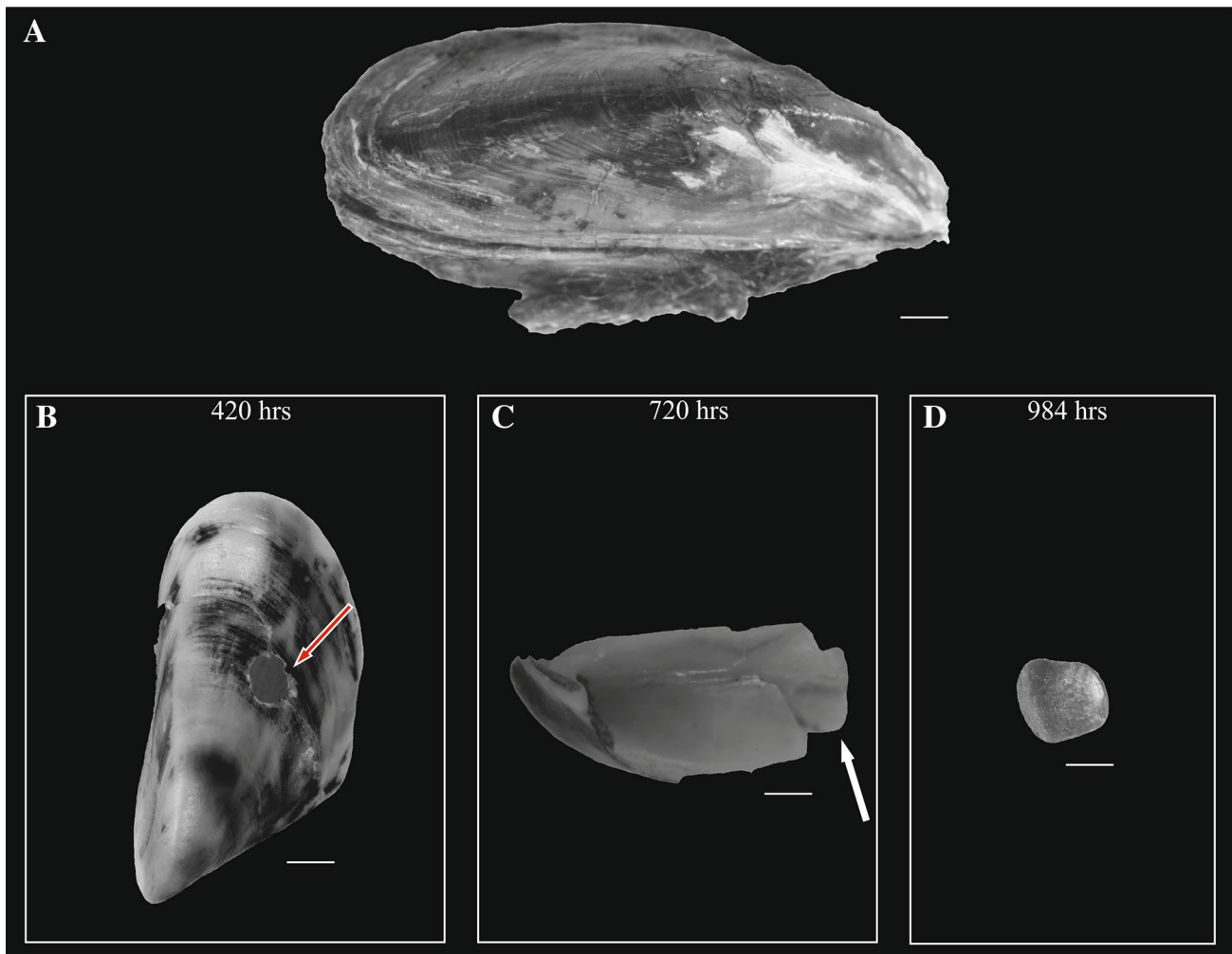


Fig. 16 Patterns of shell fragmentation (a–d) during experiment no 6. Red arrow crescentic chips, white arrow rounded edges. Scale bar = 1 mm

30 days. Fragmented shells, however, were always characterized by a large size and displayed a high degree of sphericity and roundness. Prior fragmentation, abrasive scratches, single holes, and marginal chips were observed on the shell surface.

The results of our experiments clearly showed that the degree of sphericity of shell fragments is not a good proxy of hydrodynamic abrasion. This may be related to the macro- and micro- morphology of the shell and its different susceptibility to abrasion (e.g., Flügel 2004). The degree of rounding of shell fragments, however, seems to be closely related to the abrasion intensity. However, this usually applies to larger elements that have become more smooth throughout the experiment. In the case of small fragments, no consistent pattern was observed. The same trend was observed in the case of bioclasts from recent shallow-water environments (Pilkey et al. 1967). This phenomenon is attributed to the

fact that larger shell fragments are usually more prone to abrasion and rolling due to their greater surface area, and they have a lower tendency to be held in suspension (Folk 1965). In the case of smaller fractions, a dominant process affecting the degree of sphericity is not related to abrasion, as in the case of fragments displaying a larger size, but to their progressive and continuous fragmentation (e.g., Chave 1960).

As mentioned above, in experiments using gravel and with an admixture of sand, shells may be fragmented rapidly. The time-frame to observe angular shell fragments, which may be eventually confused with predation, is very short (up to several dozen minutes), hardly to be registered on the geological time-scale. Moreover, such abrasion-induced angular fragments can be expected only in high-energy environments in lithofacies dominated with gravel (e.g., tidal zone). However, even such elements reveal the

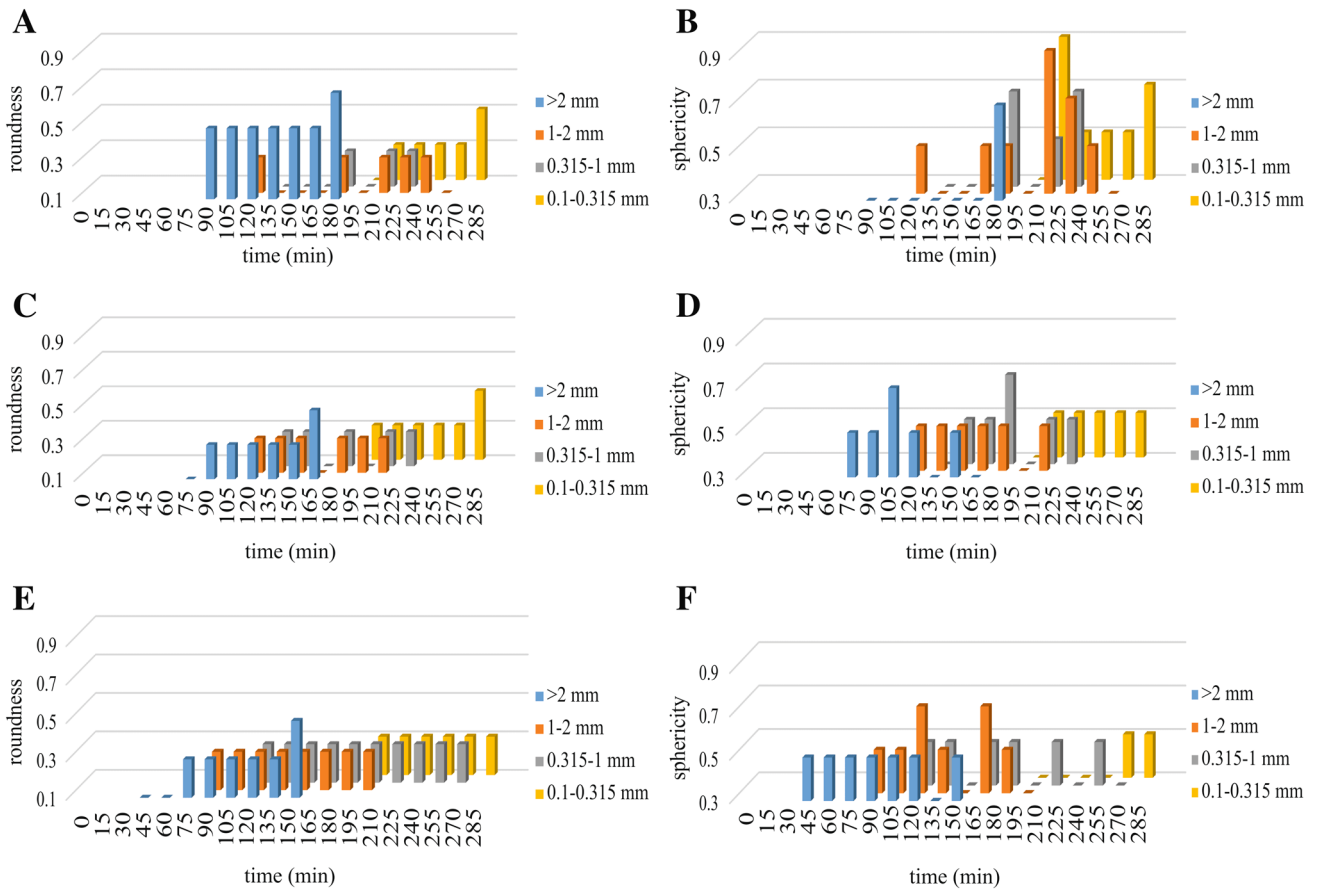


Fig. 17 a, c, e Variation of the degree of roundness of shell fragments during experiment no. 7. b, d, f Variation of the degree of sphericity of shell fragments during experiment no. 7

presence of abrasive scratches and cracks on their surfaces. In low-energy environments dominated by the presence of fine deposits, destruction of shells proceeds very slowly. Hydrodynamic destruction of shells in such environments is easy to identify by the presence of characteristic abrasive scratches, cracks, and holes (Table 2). Furthermore, fragmented shells in such environments usually have a high degree of sphericity and roundness.

Interestingly, our experiments showed that various holes and crescentic marginal chips, which are usually indicative of predation, may also be formed as a result of abiotic

processes (see also Cintra-Buenrostro 2007; Gorzelak et al. 2013). Nevertheless, it must be clearly emphasized that the distinction between these abrasive-induced features from those generated by predators may be possible because these abrasion-induced structures are always associated with characteristic scratches and cracks on the surface of disarticulated valves (Table 2). This distinction, however, can be complicated by the fact that shell fragments produced by predators can be subsequently abraded by physical factors and vice versa, i.e., some abrasion-induced damage on shell surface of bivalves may be formed during life and they

Table 2 Features characteristic for accumulations of shell fragments produced by biotic (fish and crab predation-induced) and abiotic (hydrodynamic, abrasion-induced) factors

Predatory origins	Abiotic origins
Predominance of large shell fragments	Different size classes of fragments, with dominance of finer fractions
Different degree of sphericity but very low degree of roundness (angular shell edges)	Different degree of sphericity but high degree of roundness in larger fragments (smooth shell edges)
Lack of scratches on the shell surface	Numerous scratches on the shell surface

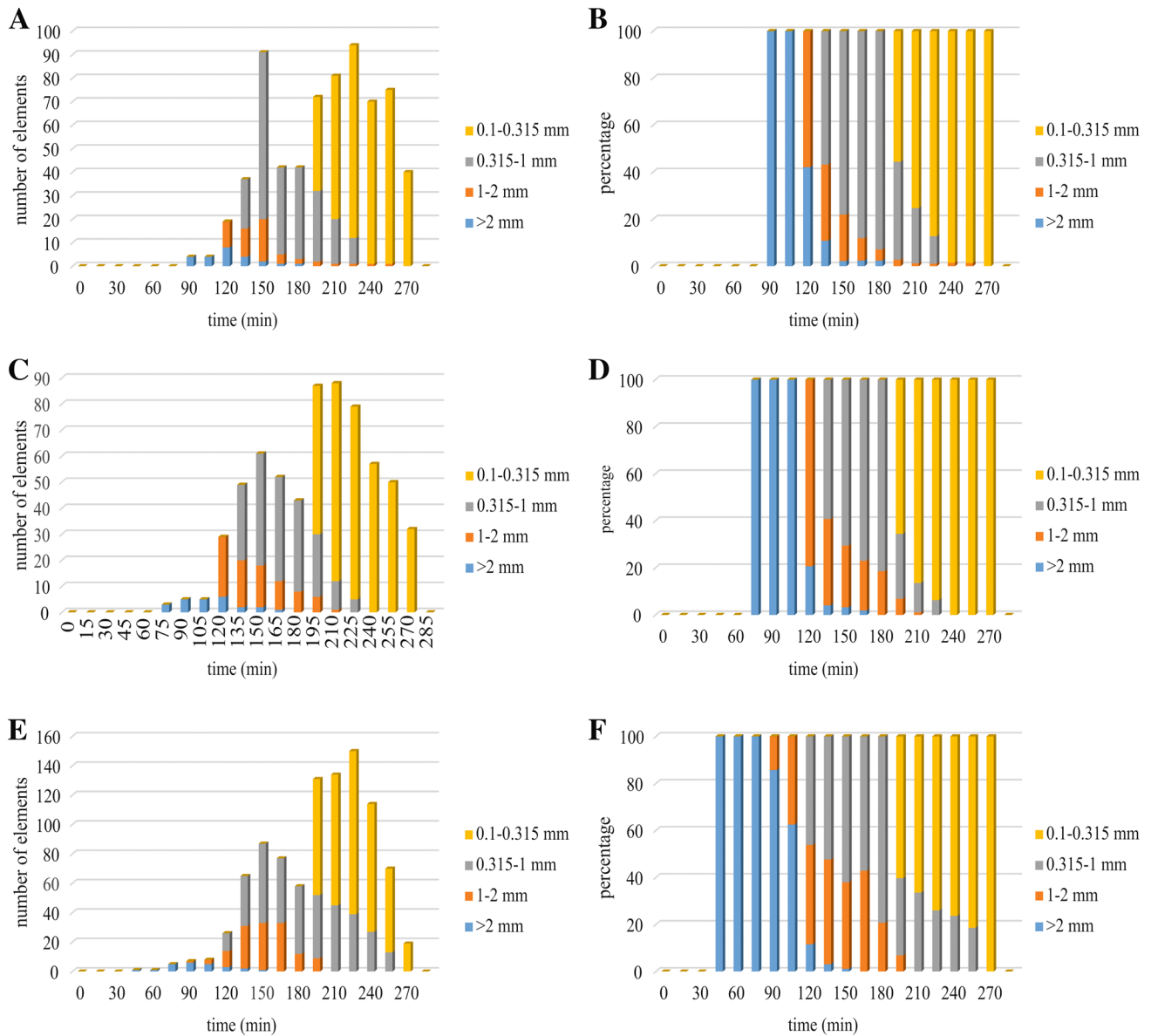


Fig. 18 a, c, e Distribution of the number of shell fragments during experiment no. 7. b, d, f Changes of percentage of each shell fraction during experiment no. 7

can be subsequently fragmented by predators. Nevertheless, as stressed by Salamon et al. (2014) still a scenario where a physical process leads to abrasion only, without acting further to fragment and round the edges, is improbable.

Conclusions

Despite the difficulties in distinguishing features of shell damage and fragmentation produced by predators from those induced by hydrodynamic factors, there are some particular features that might be useful. Durophagous fish predators,

which are able to consume bivalves > 1 cm in size, usually induce fragmentation into larger (> 2 mm) shell pieces (note that this may not apply to predatory birds; cf. Cadée 1994, 1995). These elements are always sharp-edged, and display extremely low roundness and varying degrees of sphericity. Abiotic fragmentation in high-energy siliciclastic environments, in turn, is typically characterized by the presence of shell fragments of different size, shape, and degree of roundness. It is noteworthy that fragments of the larger fraction tend to become more elongate and smooth in time. Complete fragmentation of shells (below 0.1 mm fraction) in such conditions can take place within a few hours. At each stage of

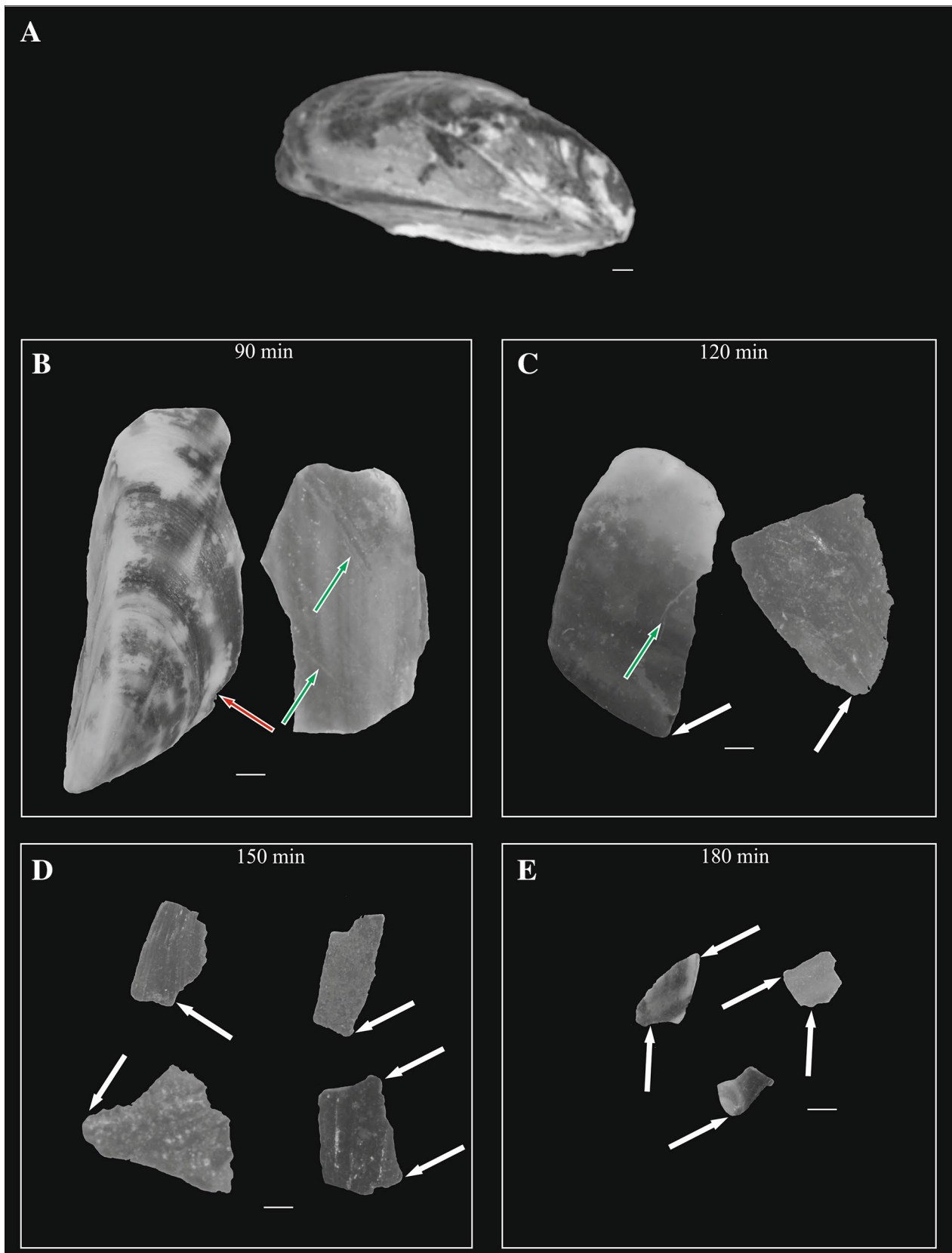


Fig. 19 Patterns of shell fragmentation (a–e) during experiment no 7. Red arrow crescentic chips, green arrow abrasive scratches, white arrow rounded edges. Scale bar equals 1 mm

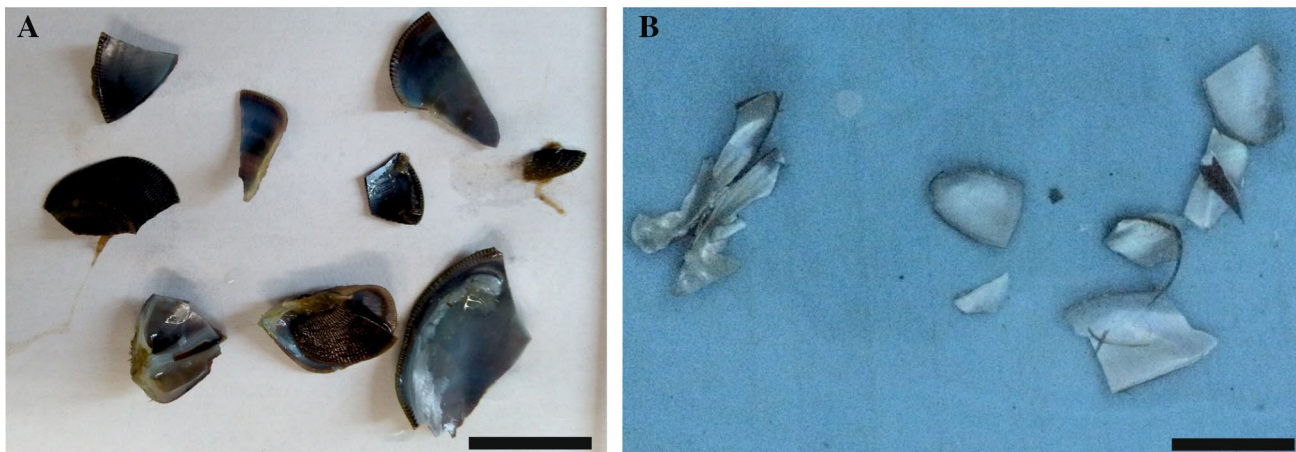


Fig. 20 Examples of predation-induced damage on bivalve shells. **a** Crushed shell by predatory crab *Eriphia verrucosa*. **b** Crushed shell by predatory fish *Cyprinus carpio* (cf. Salamon et al. 2014). Scale bars = 10 mm

the hydrodynamic processing of the shell, distinct abrasive features can be observed on the shell surfaces.

Although tumbling experiments may not ideally imitate the hydrodynamic conditions in the natural environments (e.g., Kuenen 1966a, b; Nichols et al. 2000), it is worth emphasizing that the pattern of shell fragmentation and abrasion is similar to that found in natural habitats (e.g., Pilkey et al. 1967; Cadée 2016; Leighton et al. 2016). It should also be pointed out that due to the large variety of macro- and micro- morphological features of mollusc shells, extrapolation of results of the present study to all molluscs should be undertaken with some caution. Nevertheless, our results are consistent with previously published studies conducted on other mollusc species, such that such a generalization may be justified.

Acknowledgements The authors are greatly indebted to Gerhard C. Cadée (NIOZ Texel) and Tatsuo Oji (Nagoya University) for their constructive reviews. Thanks are also due to Dr. Wojciech Krawczyński (University of Sielsia) for taking photographs. This project was supported by NCN Grant no. 2015/19/B/ST10/01470.

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