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Rolling cockles: shell abrasion and repair in a living bivalve *Cerastoderma edule* L.

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Abstract

Live cockles were eroded from a tidal flat by a storm event and naturally transported to a nearby dike and beach. Their fate was observed regularly for two months. Some died from desiccation high on the shore, and some were consumed by oystercatchers. Others were caught by the byssus threads of mussels inhabiting the intertidal area, while a few tried to re-burrow high on the shore. These cockles were supposedly rolled while being transported to the beach and were later observed being rolled by the waves just below the high water line. Hence, it was concluded that the shells were subjected to abrasion and that this was the cause of the holes that some individuals developed near the umbo of one or both of their (still articulated) valves. A few had repaired such holes, supporting the hypothesis that these holes were made during rolling transportation. Similar shell assemblages of articulated cockleshells partly with subumbonal; holes were later found elsewhere on the Wadden Sea coast of Texel. This 'natural' experiment and the repair indicated that this abrasion occurred while the cockles were still alive, and not after their death. It may also help to better discriminate between biologically and physically produced traces on shells.

Introduction

The biological and mechanical abrasion and fragmentation of shells in modern marine environments has long interested paleontologists, as it may help in the interpretation of the environmental conditions of ancient marine environments (e.g. Alexander an Dietl, 2003; Zuschin et al., 2003; Rogalla and Amler, 2007). This applies both for studies of recent habitats (e.g. Walther, 1910; Schäfer, 1962; review in Kidwell and Bosence, 1991) and experimental work (Chave, 1964, Driscoll, 1967, 1970; Koslosky, 2011; Gorzalek et al. 2013). Most of these studies started in the 1930s in Germany. Müller (1951, 1976) summarized them in German and Seilacher (1973) did an excellent job in giving an overview in English.

The cockle *Cerastoderma edule* L. (in older literature *Cardium edule*) is one of the best-studied Recent bivalves with respect to physical abrasion and fragmentation (Pratje, 1929; Klähn, 1932; Papp, 1941; Hollmann, 1968a,b; Rogalla and Amler, 2003). Its fragmentation due to consumption by birds is also well-studied (Drinnan, 1957; Cadée, 1994). *C. edule* occurs in western Atlantic coastal waters from Senegal to the Barents Sea and in the Mediterranean, the Black, and the Caspian Seas (Tebble, 1966). In the Wadden Sea, where many of such studies were carried out, it is common, occurring at high densities on tidal flats.

The provenance of holes in articulated and non-articulated cockleshells has long been debated. One of the first to mention them was Othenio Abel (1912), the founder of paleobiology, and interest continues to the present day (Brom, 2014). After such a long period of studies, one would think little could be added to the knowledge already gained. However, most of the older studies dealt with holes in shells collected in the field or produced during tumbling-experiments in the laboratory. I had the opportunity to study a ‘natural’ experiment with cockleshells on a tidal flat on Texel. In early May 2013 on an almost daily basis over a period of several months, I followed the fate of living cockles which had been eroded from a tidal flat near the Royal Netherlands Institute for Sea Research (NIOZ), and transported to a nearby beach (map Fig. 1).

The observations

On May 3rd, 2013 I discovered thousands of live 2-year old cockles, which had drifted to the beach near the NIOZ harbor on Texel (Fig. 2). Apparently, they had been dislodged from the nearby tidal flat after a recent strong eastern wind, which had also caused an extra low low tide. Many of these cockles died in the following weeks.

Those too high on the beach desiccated, they remained articulated, with their shells gaping ‘butterflied’, (Fig. 3). A small proportion of these, however, remained closed, with their valves glued together by the dried flesh inside (Fig. 4). This was good confirmation that this can indeed occur in the field, as I had previously suggested when explaining observations of closed articulated bivalves in drift-lines high on Texel’s coast (Cadée, 2002).

Of those that remained in contact with the water at high tide, some had tried to re-burrow themselves but could not dig far enough into the shell-rich sand to become completely covered (Fig. 5). Others could not dig because they were captured and fastened by mussel byssus threads present in the littoral zone (Fig. 6). A large proportion remained in the surf zone. At high tide they were being continuously rolled by the waves up and down the beach, over small distances of one to several dm. The waves at this beach, which is sheltered from northern and westerly winds, are typically small (maximum several dm). (I made a short video of the cockles rolling in the waves). This rolling in the waves suggests that they also had been transported rolling over the tidal flat to this location.

On my first visit, birds had already discovered these cockles. Oystercatchers did not open the shells in their normal way of prying their beaks between the valves at the posterior end of the cockle (Drinnan, 1957), but entered at the ventral side which was apparently easier, because the cockles had started gaping (Fig. 7). Turnstones also discovered this rich spread, but were only feeding on cockles that had recently died and were gaping, and on what was left of the specimens consumed by the oystercatchers.

From the start but part of the now empty but still articulated cockles showed abrasion of the umbonal and subumbonal shell area, even leading to holes in one or both valves (Fig. 8). There were no active microboring organisms observed in any of the shells, which might have softened the shells making abrasion easier. I relate this abrasion purely to their rolling transport while these individuals were still alive. As evidence, I found a few articulated cockles (some alive, some dead), that showed repair of such a hole (Fig. 9). Most, however, had not survived long enough to repair their holes and remained in the high-water drift line as empty, mostly articulated shells. And even more than two years later (August 2015), I observed articulated cockleshells with umbonal holes still present at this location.

Apparently this hole-generation process is not rare in articulated cockleshells, but has never previously been studied in the field. Pratje (1929) does suggest holes may be formed when valves are still articulated, but does not imply how this can occur. In 2014 I observed similar densities of articulated cockleshells on two separate occasions along the Wadden Sea coast of the northern part of Texel (Fig. 10). In both cases, the cockles were high on the shore, most likely above the high water line. A number of individuals showed similar abrasion holes in both valves near the umbo. These holes were most probably due to their having been rolled alive over the tidal flat they had inhabited towards the shore, and not due to rolling with the waves where they were now deposited.

Discussion

Holes in shells

Holes in shells are produced in different ways. Best known are those made by shell-drilling predators such as boring gastropods (review in Kelley & Hansen, 2003); less studied are the irregular holes made by shell-smashing stomatopods (Baluk and Radwanski, 1996; Alexander and Dietl, 2003). Herring gulls have been observed making holes in bivalves stranded on the beach, very similar in size and shape to those of stomatopods (Cadée and De Wolf, 2012). Microborers have also been found to produce holes in shells (Papp, 1941), but they most likely rely on the help of herbivorous gastropods and chitons grazing on these microborers (Cadée, 2013a).

Physical abrasion of shells has interested paleontologists since the early paper by Pratje (1929); see Rogalla and Amler (2007) for a summary of its history. Most studies concern abrasion in shallow water and in particular in the surf zone. On a sandy beach on the southern tip of Texel I observed holes generated by aeolien abrasion on the exposed part of disarticulated cockle valves lying in their stable convex upward position (Cadée, 2012). The impact of sand grains was likely more effective here than under water.

Over this extended period of study history, (sub)umbonal holes in cockleshells have also been considered. Several explanations have been offered for their formation. Pratje (1929) thought he could distinguish holes in cockleshells made in tidal seas from those made in non-tidal seas However, this could not be confirmed by later studies (Klähn, 1932: p. 410). Earlier, Abel (1912: p. 47, fig. 16) had suggested such holes in cockleshells were boreholes produced by whelks *Buccinum undatum*, but Pratje (1929) corrected him and in Abel's later work (1935), the whelk was omitted from the chapter on boring gastropods. Whelks do not open bivalves by boring holes, but by prying their shell lip between the valves (Nielsen, 1975).

Articulated cockles with umbonal holes have been pictured in Papp (1941: p. 235) and studied in detail by Hollmann (1968b). Papp's material originated from Wilhelmshaven (German Wadden

Sea) and he suggested the holes were due to corrosion by boring microalgae. This was also the explanation given by Hollmann (1968b) for his ‘Modus 6’ holes in articulated cockles. Hollmann’s cockles were collected from the naturally inhabited position on the tidal flat (Tonnenlegerbucht, Sylt), but they were already dead, filled with clay, and infested with microboring organisms.

Schneider-Storz et al. (2008) studied shells in mass accumulations (shell banks) with ‘stacked’ valves, including (non-articulated) cockle valves from Würster Watt in the German Wadden Sea. They observed that abrasion first resulted in the softening of the valve rib contours and that it could later also cause a hole near the umbo. They concluded that more studies were needed to analyze the role of various factors in the loss of surface shell material, including grain agitation, microboring activity, and dissolution.

The current observation, that sub-umbonal holes can result from abrasion of live cockles during rolling transport, without the help of microboring organisms, is new. It demonstrates the value of studying a ‘natural’ experiment in the field. Laboratory (tumbling) experiments can never entirely replicate what occurs in the field. This was also the conclusion of Newell et al. (2007). Nevertheless, the lengthwise rocking trough used by Kuenen (1964) seems a better apparatus to mimic abrasion in the surf zone than the more commonly used tumbler. Kuenen also mentioned that fieldwork was needed to properly understand abrasion in the surf.

It will be clear that in such a ‘natural’ experiment one cannot give exact numbers for example of shells showing umbonal holes. I can only state that repair of such a hole was very rare, less than 10 repaired specimens were found.

Shell transport

The bulbous shaped living *C. edule* proves to be easy to roll over the seabed. The fact that storms can dislodge the near-surface living one year and older cockles has long been known. Linke (1939: p. 277) writes that they can easily be transported towards the high-water line, where they usually die. He also reports a case of ~5 million cockles transported from a tidal flat in the Jadebusen to a creek where they died. Although this appeared to be a mass-mortality, it was later confirmed to be only 1-2% of the tidal flat population. Kreger (1940) documented that entire cockle beds can disappear from a tidal flat during a storm and that the cockles can then be transported alive to a nearby creek or shore. This was also observed by Kristensen (1957) who mentions that transport of living cockles occurs in the very small spat (<2 mm) and in the cockles of 3 years and older, because the digging-in speed decreases as the animals get older. The digging-in speed was also many times more slowly in winter at low temperatures than in summer. Schäfer (1980; fig. 80) photographed such a transported cockle mass. In such cockle masses they usually die because they cannot re-enter the sediment and are unable to feed when deposited in thick layers. Such shell concentrations are event concentrations sensu Kidwell (1991).

Shell repair

Shell repair in bivalves is often related to failed predation, but it may also result from non-predatory sub lethal shell breakage (Alexander and Dietl, 2003). Damage may occur while bivalves are digging (Checa, 1993) or due to impact of rolling boulders and ice blocks in the intertidal (Bulkley, 1968; Rafaelli, 1978; Cadée, 1999). Alexander and Dietl (2003: p. 158, fig. 8A.) suggested that the repaired damage in *Dinocardium robustum* was related to failed stomatopod impact. However, Dietl (e-mail 24.12.2013) now suggests that this could also be due to a similar process as described for cockles in the current study. Earlier, we reported on a *Mactra corallina* (Cadée and Checa, 1997) and a *Cerastoderma edule* valve (Cadée, 1997), both with a similarly repaired hole. At the time we were puzzled by their origins and suggested that the mechanical abrasion was responsible during temporary exposure of the animal by submarine erosion, a theory now made more likely by this study.

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Figures

Fig. 1 Map of Texel indicating (A) where all observations were made and (B) where some additional observations were made.

Fig. 2 Still articulated cockles transported alive from the tidal flat to the nearby beach during a storm, May 2013.

Fig. 3 Gaping dead cockles on the beach,

Fig. 4 Desiccated articulated still closed cockle shells high on the shore.

Fig. 5 Cockles tried to dig in the shell-rich beach sediment.

Fig. 6 Cockles caught and attached by mussel byssus threads.

Fig. 7 a,b Articulated cockleshells slightly damaged ventrally due to consumption by oystercatchers.

Fig. 8 Subumbonal abrasion of articulated cockleshells due to rolling transport over the tidal flat.

Fig. 9a,b Repaired subumbonal holes in articulated cockle shells.

Fig. 10 A comparable drift line with cockles transported alive to Texel's shore more to the North in August 2014 (B in Fig. 1).