Variability of Jurassic hardground faunas: pitfalls in studies of community evolution

Hardgrounds possess an outstanding potential for palaeoecological studies as part of their fauna, that is the boring and encrusting organisms, are always preserved in situ. They therefore appear as an ideal object for the study of community evolution. In the following condensed account the validity of this assumption is tested. As an ecological study of Jurassic hardgrounds and their fauna clearly showed (FüRSICH, in press) there are several factors which, despite these ideal prerequisites, severely hamper the validity of ecological interpretation.

Jurassic hardgrounds do not represent a uniform environment, but occur from the supratidal (beach rocks) down to shallow shelf regions and on pelagic seamounts (Fig. 1). Frequently, they are associated with carbonate platforms which covered large parts of the European shelf, especially during Middle and Upper Jurassic times. Prerequisites for their occurrence were long periods of omission which favoured synsedimentary cementation processes within the uppermost sediment layers.
Environmental control of faunal composition and diversity (Fig. 1)

Faunal composition and diversity are strongly influenced by factors such as turbulence, food supply, light intensity, etc. as well as by the stability of these factors in a specific environment. Many of these factors are related to depth and increasing distance from the land. Hardgrounds which formed in an intertidal or supratidal environment can, therefore, be expected to support a fauna of differing diversity and composition from that of shallow submarine or even pelagic hardgrounds. In the Jurassic, intertidal and supratidal hardgrounds carry a fauna of only very low diversity such as thin algal crusts and endolithic algae, whereas submarine shelf hardgrounds are colonized by a low to highly diverse fauna of ectoprocts, serpulids, encrusting and boring bivalves, and calcisponges. Pelagic hardgrounds in turn exhibit low faunal diversity and density and are dominated by endolithic algae and encrusting foraminifera.

Thus, when studying the evolution of hardground communities care must be taken that faunas from the same environment are compared. However, faunal composition and diversity on hardgrounds not only vary according to environmental setting, but are also influenced by a number of other factors.

**Fig. 1. Environments of Jurassic hardgrounds**

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**Fig. 1. Environments and faunal distribution on Jurassic hardgrounds (from Försich, in press).**
Additional factors (Fig. 2)

Hardground morphology

Hardgrounds with a pronounced relief usually offer a larger number of microhabitats than do smooth surfaces, and therefore exhibit a higher faunal diversity. This is particularly the case where empty burrow systems or erosively enlarged cavities are present which support a fauna different from that on the upper surface (Palmer & Fürsich, 1974).

Degree of erosion

Except for pelagic hardgrounds, scour frequently plays an important role in hardground formation and usually occurs intermittently until the onset of renewed sedimentation. The effect of scouring is drastically increased when lag deposits are present. On hardgrounds, they result from a high production rate of organic hardparts combined with non-sedimentation. When such lag deposits are moved across the hardground surface by currents they frequently abrade the encrusting hardground fauna, especially small elements with a weak skeleton (compare Palmer & Palmer, 1977). This easily leads to bias in faunal composition and diversity.

The lack of abrasion in most pelagic hardgrounds might be due to the low bioproduction rate in this biotope which did not lead to formation of lag deposits and therefore reduced the degree of scour.

Time

Another factor influencing faunal diversity is the length of time available for colonization, since pioneer colonization stages exhibit considerably lower diversity than the climax community. The time available for colonization, however, is primarily governed by the frequency of erosive phases which interrupt the colonization stages.

Position of the hardground within the depositional sequence

The fossilization potential of hardground faunas largely depends on the environment in which and the length of time after which the hardground is finally buried. Most hardgrounds are found on top of regressive sequences and are consequently followed by transgressive sediments. A relatively rapid transgression and quick burial of the fauna
reduced post-mortem disturbance to a minimum (e.g., the Bathonian hardground described by Palmer & Fursich, 1974). Furthermore, the degree of the transgressive event plays an important role: Many hardgrounds, formed on oolite shoals in very shallow water, are followed by similar sediments which implies only a slight shift of the facies pattern. In this case, frequently large parts of the hardground fauna were removed during the deposition of the high energy post-erosion sediments. This explains the observed wide range of faunal diversity on very shallow hardgrounds.

Fig. 2. Main factors influencing diversity and faunal composition of hardgrounds.
Biological factors

Elements of the hardground fauna increase by their presence or activity the number of niches within the hardground biotope and thus the species richness. For example, nestling bivalves or certain *Serpula* species preferentially settle in empty bivalve borings. Meadows of silvide ectoprocts, common on some Middle Jurassic hardgrounds, probably created a low turbulence zone immediately above the hardground surface, enabling the growth of delicate and less scour resistant organisms.

Conclusions

Faunal composition and diversity of hardgrounds thus depend on a number of biotic and abiotic factors. When studying the evolution of hardground palaeocommunities, not only their exact environmental setting has to be determined, but also the genesis of the hardgrounds, their position within the depositional sequence, and biostratinomic processes, which commonly alter faunal composition and diversity, have to be studied.

If, despite these difficulties, community evolution studies on hardgrounds are attempted, then only hardgrounds that carry the most diverse fauna from corresponding environments should be compared, since only in this way can errors, introduced by the processes discussed above, be minimized.

Literature


Разнообразие юрской фауны твердого дна: западня в изучении эволюции донных сообществ.

Изучение населения ископаемого твердого дна открывает большие возможности для познания эволюции донных сообществ, поскольку селившиеся здесь сверлящие и инкрустирующие организмы сохраняются.

На систематическом составе населения твердого дна отчетливо сказывалось влияние гидродинамического режима придонных вод, обилие пищи, интенсивность освещения, а также степень стабильности перечисленных факторов. Литоральная и супралиторальная фауна твердого дна юрских морей отличалась бедностью в качественном и количественном отношении и состояла из корковых и эндолитных водорослей. Подводное твердое дно шельфа характеризовалось различной степенью разнообразия и было населено мшанками-септороктами, серпиллами, инкрустирующими и обрастывающими двустворками и кальциспонгиями. Твердое дно подводных гор делагиали отличалось чрезвычайно малым разнообразием, малой плотностью сообществ и преобладанием эндолитических водорослей и инкрустирующих формамифера. При изучении палеосообществ твердого дна необходимо
учитывать селективное диагенетическое растворение скелетных остатков, биостратономические процессы, положение остатков в геологическом разрезе, степень размыва, морфологию и историю развития твердого дна, время, необходимое для заселения, скорость осадконакопления, частоту размывов и др. Только благодаря учёту всех перечисленных факторов возможные ошибки будут сведены до минимума. Библ. 3. В.А. Собецкий.