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# Predation scar frequencies in chemosymbiotic bivalves at an Oligocene seep deposit and their potential relation to inferred sulfide tolerances

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ABSTRACT

Three species of chemosymbiotic bivalves with different inferred sulfide tolerances and life habits from a lower Oligocene seep deposit in eastern Hokkaido, Japan, were investigated for drill holes and scars of durophagous predation. The thyasirid *Conchocele bisecta* had the lowest inferred sulfide tolerance and showed the highest frequencies of repair (0.4) and drilling predation (0.1), and specimens with drill holes were on average smaller than non-drilled specimens, indicating that large size is a refuge from drilling predation in this species. The bathymodiolin *Bathymodiolus inouei* and the vesicomyid *Hubertschenckia ezoensis* are inferred to have lived at higher sulfide concentrations than *C. bisecta* based on comparisons to their living relatives, and show lower repair frequencies (0.24 in *B. inouei* and 0.17 in *H. ezoensis*). Based on the assumption that increased sulfide concentrations are increasingly toxic to predators, we conclude that the frequency of shell injuries in the three investigated species is inversely related to the sulfide concentrations that these species are able to tolerate. Thus when applied carefully, the frequency of shell injuries among shelled invertebrates at fossil seeps may be used to infer their relative tolerances toward sulfide, and may thus represent a tool to assess the life habits of extinct invertebrates that inhabited methane seeps in the geologic past.



## 1. Introduction

Hydrothermal vents and methane seeps on the deep-sea seafloor are places where fluids rich in reduced compounds, such as hydrogen sulfide or methane, reach the seabed. These sites harbor lush faunal communities that derive most of their nutrients from chemoautotrophic bacteria, which use the reduced compounds to fix organic carbon. Due to their in situ food source, these faunas appear to have an independent evolutionary history and may be buffered from perturbation of the photosynthesis-based food chains of the rest of the global biosphere (Tunnicliffe, 1992; McArthur and Tunnicliffe, 1998; Van Dover et al., 2002; Kiel and Little, 2006). The presence and abundance of sulfide play a major role in shaping these communities, from evolutionary patterns on geologic time scales (Kiel, 2015) to small-scale distributions at individual sites (Olu et al., 1996). On local scales, the different adaptations, requirements and tolerances toward sulfide and other reduced compounds result in distinct faunal distributions along geochemical gradients (Barry et al., 1997; Sahling et al., 2002; Cordes et al., 2010). While these adaptations and distributions are well known in the modern ocean, it remains a major challenge to understand such adaptations and distributions in the fossil record, especially in the more distant geologic past when extinct taxa are concerned that lack modern analogs (Campbell and Bottjer, 1995; Jenkins et al., 2013; Kiel et al., 2014).

Fossil seep deposits with distinctive faunal distributions are known and have in some cases been linked to sulfide concentrations. Concentric distribution of different bivalves around a central edifice was reported from the Late Cretaceous Tepee Buttes seep deposits in the Western Interior Seaway, USA (Kauffman et al., 1996) and from the Early Cretaceous seep deposits on Greenland (Kelly et al., 2000), and sulfide concentrations were considered to decrease from the center outward. At a Late Cretaceous seep deposit in Hokkaido, Japan, distinct faunal distributions were noted to correspond to proxies for seepage intensity, namely carbon and sulfur isotopes (Jenkins et al., 2007). Here, taxa known to require or tolerate higher sulfide concentrations were found in areas where the proxies indicated higher sulfide and methane flux than in the marginal parts of the deposit that were inhabited by taxa with lower sulfide requirements (Jenkins et al., 2007). Additional proxies for seepage intensity include biomarkers and the petrography of the seep carbonates. Seep deposits with large amounts of authigenic cements such as banded and botryoidal rim cements are mostly characterized by biomarkers for microbes adapted to high flux rates, whereas mostly micritic seep carbonates tend to be characterized by biomarkers of microbes adapted to low, diffuse sulfide flux (Peckmann et al., 2009). Using this approach, it was shown that the large, seep-inhabiting brachiopod *Peregrinella* had a preference for seeps with low sulfide flux (Kiel et al., 2014).

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Here we investigate the paleoecologic implications of repair scar and drill hole frequencies in three species of fossil chemosymbiotic bivalves with different sulfide-flux requirements. Repair scars and cases of drilling predation have been reported from the fossil record of seeps and cognate habitats (Amano, 2003; Kiel, 2006; Amano and Jenkins, 2007; Amano and Kiel, 2007; Kiel et al., 2008; Peckmann et al., 2013; Kiel et al., 2014). However, these reports were either descriptive or focused on the potential drilling predators, but repair scars have not been systematically assessed in the light of the life-habits of the attacked organisms. The results of our study may allow inferences about the relative sulfide tolerances of now extinct seep inhabitants in the older geologic record.

## 2. Material and methods

All investigated specimens are from a single, early Oligocene seep deposit from the Nuibetsu Formation in Hokkaido, northern Japan. It crops out along the Atsunai River, 1.5 km east of the Kami-Atsunai railway station in Urahora-cho in eastern Hokkaido (Amano and Jenkins, 2011). The three investigated species of chemosymbiotic bivalves are: (i) 24 specimens of the vesicomyid *H. ezoensis* (Yokoyama, 1890), (ii) 88 specimens of the mytilid *B.* (s.l.) *inouei* Amano and Jenkins, 2011, and (iii) 135 specimens of the thyasirid *Conchocele bisecta* (Conrad, 1849). Shells of these three species were found in mass accumulations, suggesting that they lived gregariously like their relatives at modern seep sites. Additional taxa were extremely rare and were found scattered throughout the deposit; they include the solemyid bivalve *Acharax* aff. *gigas* (Kanno, 1960), the naticid gastropod *Euspira meisensis* (Makiyama, 1926), and the buccinid *Colus* cf. *fujimotoi* Hirayama, 1955 (Amano and Jenkins, 2011). All investigated specimens are housed at Joetsu University of Education (Joetsu City, Japan).

The vast majority of specimens from the Nuibetsu seep deposit are articulated and the valves are cemented to each other by the carbonate cement within them. Virtually all specimens of *B. inouei* had most of the shell material preserved, the two other species were either preserved with shell material, or as internal molds, or as combinations thereof. The specimens investigated for shell injuries and drill holes had at least half a valve sufficiently well preserved and included specimens with either preserved shell material or with a well-preserved mold of the internal surface. Specimens with less surface area preserved or with chalky surfaces were excluded. Using only half a preserved shell may seem little, but we feel that it is a good compromise between the need for having complete shells and the need for a large sample size sufficient for robust statistical analysis. Each specimen was measured along its anterior–posterior axis and in the case of specimens with broken shell, the 'missing' length was not interpolated; just the actual specimen was measured. The not observable parts of the shells were either broken off (mostly in the elongate *B. inouei*), were abraded or chalky, or were covered with unremovable rock matrix. In the case of the abraded or chalky specimens, drill holes, if they had been present, would have been mostly observable, but the often more subtle or less distinctive scars due to durophagous predation were not detectable. Thus even in cases where parts of the shell could not be screened for predation scars (and thus inducing some bias in our analysis), the outline of the shell could mostly be recognized and thus our measurements of shell lengths are mostly accurate. The least accurate are those of the elongate *B. inouei*, which sometimes had pieces of the shell missing, the most accurate are those of *C. bisecta* with its roundish to quadrate shell outline. Relationships between shell size and predation scar frequencies were therefore only investigated in *C. bisecta*.

Measurements were taken with a digital caliper (Mitutoyo Absolute Digimatic Caliper 500-152-20) and were rounded to the first decimal place. Data on drill holes and repair scars were kept separately, because complete drill holes were fatal for the bivalve, whereas repair scars are healed injuries and hence did not cause the (immediate) death of the bivalve. Small irregularities of the growth lines (Fig. 1D) are assumed to be the result of shell crowding and were not considered further. We assume that all injuries were caused by biotic interactions rather than physical processes. Wave action can be discounted at the inferred upper slope setting of the Atsunai River seep deposit (Amano and Jenkins, 2011). Jumbling and collisions of (epifaunal) specimens due to turbidity currents may cause shell injuries but neither the seep carbonate itself, nor the monotonous mudstone surrounding the seep deposit showed any signs of turbidity currents; hence we also ignore this possibility. Statistical analyses were carried out with the software package PAST version 2.17c (Hammer et al., 2001).

Repair frequencies are given as the percentage of specimens with scars, independent of the number of scars on the individuals (Alexander and Dietl, 2001). We did not analyze the number of scars per shell because of the incompleteness of many specimens, although multiple scars (when seen) are mentioned in the supplemental material. Drilling frequencies were calculated as the number of drilled specimens divided by the total number of specimens. All specimens were articulated and often both valves could be investigated for drill holes, thus no correction to infer the number of individuals from the number of single valves was needed.

## 3. Results

### 3.1. Drill holes

Drill holes were not seen in any of the 24 specimens of *H. ezoensis* (drilling frequency = 0), a single drill hole was seen in the 88 specimens of *B. inouei* (drilling frequency $\approx$ 0.01), and 14 out of 135 specimens of *C. bisecta* had drill holes, including two specimens with multiple holes (drilling frequency $\approx$ 0.1) (Fig. 1; Table 1). In *C. bisecta*, more than half of all drill holes are found in the dorsal third of the shell; the remaining ones are located either centrally on the shell or close to the ventral shell margin. Specimens with drill holes had significantly smaller median sizes than non-drilled specimens (Table 2, Fig. 2); the largest drilled specimen was 22.5 mm in length.

### 3.2. Repair scars

Specimens of all three species showed a variety of repair scars (Fig. 1) that could be classified as scallops, clefts, and divots, in the terminology of previous authors (Alexander, 1986; Alexander and Dietl, 2001). *C. bisecta* shows a repair frequency of 0.4; most repair scars were seen along the ventral shell margin, and to a lesser extent along the posterior sulcus. The three injured specimens of *H. ezoensis* had the repair scars on the posterior shell margin (repair frequency = 0.17). In *B. inouei* most injured specimens have the repair scars in the posterior part of the shell, both on the dorsal and ventral sides, but repair scars on the anterior side of the shell were also seen (repair frequency = 0.24). Injured specimens of *C. bisecta* were on average larger than non-injured specimens (Tables 1 and 2).

## 4. Discussion

### 4.1. Drilling predation

The morphology of the drill holes seen in *C. bisecta* from the Atsunai River seep deposit suggest that they were most likely made by naticid gastropods (Kitchell et al., 1981; Kabat, 1990), and indeed, a few naticid gastropods were found at this seep deposit. Similar holes have been found in *C. bisecta* shells from the upper Eocene Poronai Formation and the upper Miocene Morai Formation in Hokkaido, Japan, probably drilled by the associated naticids (Amano, 2003; Amano and Jenkins, 2007). The smaller than average size of the drilled *C. bisecta* shells from the Atsunai River seep deposit suggests that large size represents a refuge from drilling predation for *C. bisecta*, as known from many shallow-water bivalves, too (Leonard-Pingel and Jackson, 2013). Larger