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Unravelling the paleoecology of flat clams: new insights from an Upper Triassic halobiid bivalve

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Abstract

Flat clams are ubiquitous in marine Triassic and Jurassic deep-water environments, where they are often recovered as mono- or pauci-specific assemblages. Their abundance in deep-water facies deposited under oxygen-depleted conditions suggests a potentially unique, but nevertheless debated, paleoecology. The distribution of *Halobia cordillerana* in an Upper Triassic hemipelagic succession outcropping at Tsiko Lake, Vancouver Island, Canada, serves as a revealing case study. There, deep-water deposits were investigated using a multi-disciplinary approach including facies description (mineralogical, fossil and organic content), taphonomy, morphometry, microscopy (cathodoluminescence, scanning-electron microscope) and independent paleo-redox proxy constraints (framboidal pyrite distributions, Fe speciation). Overall, halobiids' taphonomy at Tsiko Lake is indicative of *in situ* accumulations with little or no reworking. Among the hemipelagic deposits, three major litho-biofacies (BFC 1, 2, 3) were identified; paleo-redox proxies indicate that these litho-biofacies were deposited under different oxygen conditions ranging from extreme dysoxic (BFC 1) to dominantly euxinic (BFC 3). The distribution of *H. cordillerana* is shown to be directly influenced by bottom water oxygenation with this organism peaking both in abundance and dimensions under extreme dysoxic to anoxic conditions (i.e. BFC 1 & 2). Conversely, under prevailing euxinic conditions (i.e. BFC 3), the population of *H. cordillerana* is dominated by forms at larval or post-larval stage which were presumably killed by water-column euxinia. Thus, although the species is here shown to have lived most likely as an epibenthic recliner, an early (larval) planktonic/nektonic stage is needed to explain its mode of occurrence during dominantly euxinic conditions (i.e. BFC 3), and its wide distribution and rapid expansion. Finally, this study highlights the colonizing capacity of halobiids in case of restored oxygen conditions, stressing the potential significance of flat clams for paleoenvironmental reconstruction.

Keywords: #Upper Triassic #flat clams #halobiid bivalves #paleoecology #paleo-redox #paleoenvironment

1. Introduction

Flat clams are bivalves that are characterized by extremely thin shells and low valves convexity. They were ubiquitous in rocks of Devonian to Jurassic age (Jefferies and Minton, 1965). Sporadically found in (possibly) shallower environments (Miroshnikov and Burii, 1969; Hatleberg and Clark, 1984; Ando, 1987; Campbell, 1994), they thrived in deep-water deposits where they often form the main biogenic component. During the Middle-Upper Triassic, genera such as *Daonella* and *Halobia* were incredibly widespread. This fact, along with a fast species turnover, has made them powerful biostratigraphic tools, with an average species duration similar to that of coeval ammonoid species (e.g. around 1-2 Ma: McRoberts, 2010).

Since the early works of Mojsisovics (1869, 1874), flat clams-bearing sedimentary beds of different ages have drawn the attention of a great number of researchers with different backgrounds. Paleontologists, geochemists and sedimentologists have investigated the peculiar distribution of these organisms. However, environmental interpretations often diverge dramatically. Integrated and multi-approach studies investigating the paleoecology of these organisms are lacking, and, too often, interpretations have been made taking into account only a few sets of parameters.

Through a multi-disciplinary approach, this work aims to better characterize the paleoecology, lifestyle and habitat of these conspicuously flat, deep-water Triassic-Jurassic bivalves, highlighting their potential for paleo-environmental reconstruction. We initially provide a summary of current understanding of the mode of life of “flat clams” (Fig. 1) from different ages, with a focus on mostly Triassic and Jurassic forms, which are summarized, discussed, and compared to possible extant counterparts. The second part of the manuscript is a case study of an Upper Triassic, *Halobia*-rich, deep-water succession exposed near Tsiko Lake, Vancouver Island, Canada. There, the sequence was investigated by means of a multi-disciplinary approach including sedimentology, taphonomy, morphometry, microscopy, and geochemistry.

2. Flat clams’ mode of life: a review

2.1 Living on, near, or in the seabed: Benthic

Several authors see the lowered volume/surface ratio of flat clams as an adaptation to soft substratum and low oxygen levels in bottom waters (Rhoads & Morse, 1971; Savrda et al., 1984; Thompson et al., 1985; Fürsich et al., 1991; Kelly and Doyle, 1991; Savrda and Bottjer, 1991; Hollingworth and Wignall, 1992; Wignall, 1993; Wignall and Pickering, 1993; Wignall 1994; Etter, 1995, 1996; Röhl et al., 2001; Harzhauser and Mandic, 2004; Waller and Stanley, 2005; Schatz, 2005; Bakke, 2017; Onoue et al., 2019). However, interpretations of their lifestyle diverge. In Wignall (1994), *Daonella vaceki* was interpreted as a semi-infaunal mud sticker (see Fig. 3.17 in Wignall, 1994). Recent mud stickers, mostly belonging to the families Pinnidae or Mytilidae, do indeed tend to have elongated and thin shells, with a byssus that helps them fix into the substrate (2B in Fig. 1). Conversely, Campbell (1985, 1994) proposed for *Halobia* an epiphytic, attached lifestyle to benthic marine plants (2C in Fig. 1), and therefore a light dependent habitat. Conversely, Doyle and Whitham (1991) suggested an epibenthic recliner mode of life (2A in Fig. 1) for the Jurassic form *Aulacomyella*. They noted that specimens of the buchiid bivalve *Buchia* from the Upper Jurassic of Antarctica routinely occurred on top of *Aulacomyella* pavements: according to these authors the presence of multiple individuals of *Aulacomyella* would have been sufficient to stabilize fine-grained substrates, making them suitable to other organisms as well.

Several investigations of Upper Triassic Halobidae and Monotidae have been carried out on Austrian and Canadian paleo-communities (McRoberts et al., 2008; McRoberts, 2010, 2011). In these localities, “flat clams” are a major component of deep-water filamentous facies (Hallstatt facies) thought to have been deposited under different oxygen conditions [(i.e well-oxygenated basin in Austria (Krystyn and Piller, 2000) and oxygen-poor conditions in Canada (McRoberts, 2011)] . Facies distribution, shell-bed attributes and size-frequency distribution led the authors to suggest that these occurrences were most likely the result of *in situ* biogenic accumulations of benthic populations.

Nowadays, only a few species of bivalves are considered fully benthic recliners: the best modern example for this lifestyle is probably *Placuna placenta*. This species, inequivalve and characterized by an extremely thin shell, is found resting unattached above soft muddy sediments where it often forms dense communities (Yonge, 1977).

2.1.2 Epibenthic chemosymbionts

Chemosymbiosis is a well-known biological process in which bacteria provide chemically-derived nutrients, mostly by the oxidation of hydrogen sulfide or methane, to a higher organism. Cavanaugh et al. (1981) were the first to notice the presence of prokaryotic cells in the hydrothermal vent tube worm *Riftia pachyptila.* Since then, many other chemosymbiont organisms have been discovered and their metabolisms have been subject to intensive research (see Cavanaugh et al., 2006 for a summary).

Chemosymbiont molluscs are not restricted to hydrothermal vents, they are also known from other environments ranging from reducing sediments, cold seeps, sewage outfalls, pulpmill effluent zones, through to seagrass beds (Cavanaugh, 1983; Felbeck, 1983; Fisher and Hand, 1984; Schweimanns and Felbeck, 1985; Dando and Southward, 1986; Dufour and Felbeck, 2003). The principal factor controlling their distribution is the availability of reduced compounds (often hydrogen sulfide). Dufour and Felbeck (2003) demonstrated that bivalves can mine H_2S by extending their feet deep into the sediment to form elongated burrows up to 30 times their contracted lengths, depending on sulphide availability.

Seilacher (1990) reviewed suspected fossil examples of chemosymbiont bivalves, and among these, included *Halobia* (3 in Fig. 1). According to the author, the tube located along the hinge line (referred as the byssal tube by Campbell, 1985 or lower anterior auricle by

McRoberts, 2000) could testify an adaptation to a chemosymbiont mode of life. This neomorphic feature, non-inherited from its ancestors *Daonella* and/or *Aparimella* (McRoberts, 2000), would then have an H_2S pump function. Ward (2006) also speculated that Triassic flat clams such as *Halobia* and *Monotis* were probably chemosynthetic, taking energy from chemical compounds in the anoxic mud they lived in.

2.2 Living in the water column (planktonic, nektonic or pseudoplanktonic)

A wide range of completely different modes of life, independent from the seabed, have been favored by multiple authors in order to explain the high abundance and widespread distribution of these thin-shelled bivalves. Hayami (1969) (for posidoniids and halobiids) and Jefferies and Minton (1965) (for the Jurassic bivalves *Bositra buchii* and *Posidonia radiata*) pointed out how morphological features, such as the size and the negative allometry of the shell, would be indicative of a nektonic/planktonic mode of life (1A in Fig. 1). Parrish et al. (2001), studying the Triassic Shublik Formation of Northern Alaska, came up with the same conclusion, since no articulated valves of halobiids were found and the specimen showed optimal preservation both in hand and thin section. Similarly, Xiaofeng et al. (2008) interpreted the halobiid bivalves found in black shales of the lower Xiaowa Formation of South China as pelagic, because bottom waters were inferred to be anoxic.

Oschmann (1991, 1993, 1994) proposed an adaptation to an holopelagic lifestyle (1B in Fig.1) from a normal pelago-benthic life cycle for the Jurassic form *Bositra,* in order to survive extended periods of anoxia. This type of adaptation, achieved through a delayed metamorphosis and early sexual maturity, is well known in pteropod gastropods, but unknown in bivalves (Oschmann, 1993). The only extant bivalve initially thought to be holoplanktonic is *Planktomya hensemi,* but Allen and Scheltema (1972), after detailed morphological observations and since no specimens showed sexual maturity during any time of the year, inferred that *P. Hensemi* may not be holoplanktonic but most likely was a teleplanic larva of a shallow water bivalve species. In extant adult bivalves, true swimming is only seen in the family Pectinidae, but this ability is mostly used to escape from predators [although free-swimming is common in modern bivalves where larvae (veligers) swim by means of a ciliated velum (Barnes, 1987)].

A more byssus-relying mode of life has instead been postulated by Hayami (1969) for *Monotis,* who considered that its byssal notches might indicate attachment to floating objects (1C in Fig. 1). Also, monotid bivalves have thicker shells and often occur in near shore and coarser sediments, in contrast to *Daonella* and *Halobia*. Tozer (1982) strongly supported the idea of Hayami (1969), that *Monotis* was pseudoplanktonic (probably attached to floating seaweeds in a Sargasso-like situation). An attached mode of life to drifting objects (pseudoplanktonic) was also advocated by Campbell (1985, 1994) for *Halobia*, where the neomorphic feature present in *Halobia* was interpreted as a tube which would house the byssus. Other authors who have proposed a pseudoplanktonic mode of life for flat clams include Rieber (1968), for *Daonella* in the Middle Triassic of Monte San Giorgio (Switzerland), and Duff (1975) for the Jurassic *Bositra*.

3. A case-study from Vancouver Island

3.1 Geological context

The bedrock geology of Vancouver Island is principally formed by a thick Late Paleozoic to Early Mesozoic volcano-sedimentary succession regarded as being part of the tectonostratigraphic Wrangellia terrane (Jones et al., 1977). Wrangellia, which stretches north into southern Alaska via the Haida Gwaii Islands (Wheeler and McFeeely, 1991), is inferred to have collided with the Alexander terrane to form the Insular belt in the Late Carboniferous

(Gardner et al., 1988), and merged to inboard terranes during mid-Cretaceous (Monger et al., 1982) or mid-Jurassic times (van der Heyden, 1991; Monger and Journeay, 1994). The ante-accretion path of these accreted terranes (Wheeler and McFeeely, 1991) relative to the North American craton remains a matter of discussion (Belasky et al., 2002; Colpron et al., 2007; Beranek and Mortensen, 2011). However, recent work on paleobiogeography would suggest a location in the northeastern Panthalassa for Wrangellia during the Early Jurassic (Smith, 2006). In the northern part of Vancouver Island, the stratigraphy is dominated by a Triassic succession formed by volcanics of the Karmutsen Formation, carbonates of the Quatsino Formation and deep-water impure limestones and siliciclastic rocks of the Parson Bay Formation (Fig. 2A). This Triassic sequence, a signature of Wrangellia, is found throughout the terrane, from Vancouver Island all the way up to southern Alaska (Jones et al., 1977).

The Quatsino Formation is a relatively thick (up to 750 m) carbonate succession which remains understudied on Vancouver Island, its facies and sedimentology can be partially correlated with strata of the better studied Kunga Group in the Haida Gwaii Islands (Desrochers, 1988, 1989; Orchard, 1991; Orchard and Desrochers, 1993). At its lower contact, the Quatsino Formation is found lying non-conformably on volcanic deposits of the Karmutsen Formation (Muller et al., 1974). According to Desrochers (1989), the first phase of carbonate sedimentation records the deposition of shallow-water open-platform facies on a relatively flat volcanic basement, just after the end of the volcanism in the Carnian. A second phase registers a gradual change toward a sedimentology which was most likely controlled by tectonic activity within Wrangellia. Here, the switch to a more bank to basin topography is witnessed by the deposition of shallow-water inner-platform, lagoonal and tidal flat facies coeval with deep-water hemipelagic deposits, calciturbidites and gravity flows (Desrochers, 1989). Finally, the gentle upward transition into deep water impure limestones and siliciclastic rocks of the Pearson Bay Formation records the drowning of the platform and the end of carbonate production, along with a gradual increase in siliciclastic input (Muller *et al.*, 1974; Orchard and Desrochers, 1993). This transition, thought to be regionally diachronous, is inferred to have occurred between the Late Carnian and the late Early Norian (Muller et al., 1974; Nixon et al., 2000, 2006).

The Tsiko Lake outcrop (50°14’6.96” N, 126°51’48.98” W; Fig.3) was accessed along a logging road departing from the Zeballos road near Tsiko Lake. There, a recent landslide partially exposed a 7 m sedimentary package (Figs. 2 A, B and 3) of medium-bedded limestones, shales, bituminous dolomitic shales, calcareous shales and carbonate gravity flow deposits.

3.2 Material and methods

A total of 70 samples were collected at the Tsiko Lake locality (Figs. 2A, B and 3) during two distinct field excursions (summer months of 2017 and 2018). Fossil collection for paleontological analysis was mostly made on two different (particularly rich and more fissile) beds occurring at different levels along the section (Fig. 3). The specimens of *Halobia* examined in this study are stored in the Natural History Museum of Geneva under the name “Del Piero et al. 2020”. Samples for geochemical and sedimentological analyses were taken from different beds throughout the section (Fig. 3); since facies variation is very often observed at intrabed level, several samples per bed were collected (i.e. lettering).

3.2.1 Thin section, cathodoluminescence, mineralogy and organic content

Normal and polished thin sections (n= 16) were prepared at the thin section laboratory of the Department of Earth Sciences, University of Geneva. Sedimentological observations in the field were coupled with the study of microfacies assemblages, which were observed under a normal petrological microscope. Cathodoluminescence analyses were obtained using a CITL 8200 Mk 5-1-optical cathodoluminescence microscope with a cold cathode mounted on a Leitz petrological microscope at the Department of Earth Sciences, University of Geneva. Beam conditions were 15-18 kv and 100-210 mA.

Automated petrographic analyses were performed using carbon-coated polished thin sections in the QEMSCAN® (**Q**uantitative **E**valuation of **M**inerals by **SCAN**ning electron microscopy) laboratory at the University of Geneva. The energy-dispersive X-ray signal (EDS) was acquired at 200 pixels/second with a point-spacing of 1 μm. Subsequently, mineral-phase identification was achieved by comparing the acquired EDS spectra for each pixel with a database of standard spectra provided by the manufacturer (FEI company).

Total organic carbon (TOC) content was determined by Rock-Eval analysis (Behar et al., 2001) at the University of Lausanne. About 50-70 mg of sample powder underwent pyrolysis, followed by the complete oxidation of residual material (Espitalié et al., 1985; Lafargue et al., 1998). During analyses, samples were calibrated using the IFP 160000 standard, with an analytical precision of <2%.

3.2.2 Paleontology, taphonomy and morphometry of Halobiids

For this study, 27 specimens (molds and altered shell surfaces) were selected for paleontological determination. The two beds where the fossil collection was made are 5 to 10 cm in thickness, they are tabular in shape and look continuous at outcrop scale (10-15 mtr; see Fig. 2 C). Specimens were coated using heated ammonium chloride, a technique that accentuates the morphological features of *Halobia* specimens (see Hegna, 2010 for the full procedure). Specimens were studied and identified taking into account different shell parameters (see McRoberts, 1993, 2007, 2011 for more details).

Halobia shell thickness was measured on carbon-coated polished thin section under backscatter mode on a JEOL JSM7001F scanning electron microscope (SEM) at the

University of Geneva: conditions were 15 kV and 3.5 nA. Juvenile *Halobia* are tinier and thinner than adults and *Halobia* shells are notably thicker in the central part (i.e. the hinge area) and along the costae. In order to limit potential bias caused by the preferential selection of measured specimens (i.e. juvenile or adults) and/or portion of the shell, measurements were obtained by pre-setting a random vertical line along each thin section at the SEM and taking the measurements at the crossing point of this line with each shell (Fig. 4). In this way, any potential bias that might arise from this type of 2D analysis (which might preclude the comparison between these 2D data with other 3D population analyses such as size-frequency distributions) is equally applicable to all our dataset thus allowing for an internal comparison of our samples. For the taphonomic study of halobiid bivalves, macroscopic (hand specimens) and microscopic (thin sections) observations were made taking into considerations specimens occurring in beds inferred to be the result of autochthonous pelagic/hemipelagic sedimentation only. No specimens from graded beds and/or beds with erosive bases were studied.

3.2.3 Redox proxies

Framboidal pyrite (Fig. 5 B) dimensions were measured by SEM with the same settings as for halobiid shells. This kind of measurement normally tends to underestimate the real dimensions of a framboid whenever the section is not median, nonetheless it has been shown that the difference is rarely >10% (Wilkin et al., 1996). At least 100 framboids were measured for each sample (Tab. 3).

Iron speciation was analyzed at the University of Leeds, UK, on a set of samples covering the different litho-biofacies formed by the autochthonous hemipelagic/pelagic sedimentation. This technique (see Poulton and Canfield, 2005) targets iron phases that are considered highly reactive (Fe_{HR}) towards dissolved sulfide in near-surface environments. The pool of

Fe_{HR} dominantly comprises iron carbonates (Fe_{CARB}; including siderite and ankerite), ferric iron (oxyhydr)oxide minerals (Fe_{OX}; including hematite and goethite), magnetite (Fe_{MAG}), and iron sulfide phases (Fe_{PY}; dominantly pyrite). A sequential extraction targeting Fe_{CARB}, Fe_{OX} and Fe_{MAG} was performed on a sub-sample of 0.07-0.09 g of powdered sample. Fe_{CARB} was first extracted using Na-acetate at pH 4.5 and 50 °C for 48 hours, followed by Fe_{OX} using Na-dithionite for two hours at room temperature, and finally Fe_{MAG} was determined with an ammonium oxalate extraction for six hours. Total iron (Fe_T) was determined on ashed (550 °C for 8 hours) sample aliquots after a HNO_3-HF-$HClO_4$-H_3BO_3 mixed-acid digestion. Dissolved iron concentrations (Fe_{CARB}, Fe_{OX}, Fe_{MAG}, and Fe_T) were measured by an atomic adsorption spectrometry (Thermo ice 3000 at the School of Earth and Environment, University of Leeds). Replicate extractions of an internal standard gave a RSD of <5% for every Fe pool analyzed.

Pyrite iron (Fe_{PY}) was determined stoichiometrically by weight from an Ag_2S precipitate formed after a HCl and chromous chloride distillation (Canfield et al., 1986; Poulton and Canfield, 2005). All samples were tested for the presence of acid volatile sulfide (AVS; predominantly FeS) via an initial 6 M HCl distillation, but in all cases AVS was below detection. Replicate extractions gave a RSD of <5%.

3.3 Lithological and microfacies characteristics

The 7 m package of deep-water sediments exposed at Tsiko Lake is part of the Quatsino Formation (Cui et al., 2017). The sequence is limited to the uppermost part by a fault contact separating it from an olistostrome containing platform-derived carbonate material and capped by 40 cm of shales; the lower contact is covered by vegetation (Fig. 3). The succession consists in alternations of hemipelagic/pelagic beds and re-sedimented layers. While hemipelagic/pelagic beds are generally tabular in shape with thicknesses ranging from a few cm to 30 cm, reworked layers are tabular to lenticular in form and their thickness varies between 10 cm and 60 cm; in the latter, erosive bases and graded beds are commonly observed. Reworked beds range in coarseness from fine sand-sized to gravel-sized carbonate gravitational flow beds. The matrix of these gravitational flows is made up by sand-sized carbonate material composed mostly of radial ooids and peloids; among the coarser material are gravel-sized fragments of silicified shallow water (euphotic) fauna, including fragments of corals, calcifying cyanobacteria, solenoporacean red algae, echinoderms, sponges and molluscs (Figs. 5 C, D). Some bioclasts are heavily microbially encrusted (cortoids, formed prior to down-slope transportation; Fig. 5 D).

Hemipelagic/pelagic beds are commonly 5 to 20 cm thick; bedding is mostly given by thin layers (less than 1 cm) of weathered shale interfingering with bituminous shales and hemipelagic limestones. Three main litho-biofacies dominate the autochtonous sedimentation; changes between them occur both at inter- and intra-bed (laminations) level. Litho-biofacies 1 (BFC 1; Fig. 6 A) is a limestone, consisting of a slightly macro to microbioturbated (even though the sediment is never completely homogenized) wackestone to packstone (rarely floatstone), rich in coproliths, radiolarians (Spumellarians; Fig. 5 F), fish otoliths (Fig. 5 G), moderately fragmented halobiid shells, crinoids (Fig. 5 H), and other unidentified molluscs (gastropods and possibly nuculid bivalves; Fig. 5 G). Litho-biofacies 2 (BFC 2; Fig. 6 B), the most abundant, is also a limestone. It consists of a laminated to microbioturbated *Halobia* floatstone, with a wackestone matrix rich in calcified radiolarians, generally unfragmented halobiid shells, small ammonites, ellipsoidal fish otoliths and small nodosariid foraminifera (Fig. 5 C). In BFC 2, coproliths are rare with the exception of the infilling of articulated halobiids (Fig. 5 A). In BFC 1 and 2, *Phycosiphon* sp. (Fig. 5 I) is the most frequent ichnotaxon; other undetermined ichnotaxa are also common (possible occurrence of *Nereites sp.*; see Fig. 5 I & J). The intensity of bioturbation at the macroscale reflects what is seen at thin section level, with BFC 1 being more affected than BCF 2. Lastly, litho-biofacies 3 (BFC 3; Fig. 6 C), consists of a dark wavy-laminated bituminous dolomitic shale. It occurs either as 5 to 15 cm-thick tabular beds, or as intrabed alternations with the other two facies. It is generally constituted of abundant tiny halobiid shells and few pyritized radiolarian shells. In this litho-biofacies, the planktonic fraction (spumellarian radiolarians) seems to decrease when compared to BFC 1 and 2. Sometimes in BFC 3 we observed 5-10 mm thick areas where the main fabric changes. These areas include generally thicker halobiid shells along with few additional benthic microorganisms (e.g. foraminifera). We also observed rare flattened *Chondrites* sp. burrows (Fig. 5 K), where the burrowing seems to be very shallow, and is limited to the bedding planes or semi-horizontal. *Chondrites* sp. burrows look darker than the rest of the sample due to their higher infill of solid bitumen.

3.4 Results

3.4.1 Petrography and organic content

QEMSCAN analyses are fundamental to investigate the mineralogy of organic-rich horizons and their relationships with other facies: bitumen staining makes normal microscopic observation in this litho-biofacies difficult. As a general rule, BFC 3 received lower biogenic input compared to microfacies 1 and 2 (Fig. 6 E). It contains a fair amount of chlorite, probably derived from the diagenetic alteration of volcanic material [according to Muller (1970) the Upper Triassic sediments were deposited on the west flank of a volcanic plateau] or less stable clay minerals, with a much higher content of fine-grained, microcrystalline to cryptocrystalline, silica, mostly occurring in the rock matrix (Figs. 6 E, F). Since the radiolarians in these facies are preserved with pyrite substituting the original skeleton, the microcrystalline silica making up the matrix of this facies may have been sourced from the biogenic fraction, as a product of early diagenesis. Dolomitization widely affects these organic-rich horizons: dolomite, making up sometimes almost 20% of the rock, occurs as 40-50 μm euhedral displacive crystals scattered in the matrix. Dolomite crystals are zoned and present in at least three different growth stages (Fig. 6 D). Their way of occurrence, mostly found within the most organic-rich horizons, suggests that dolomite is a diagenetic by-product of either bacterial or thermochemical sulphate reduction, linked to organic matter decomposition (see Machel, 2001).

Total organic carbon (TOC) content in the hemipelagic facies (Tab. 1) varies between 0.53 and 2.71%. In general, BFC 1 and 2 have similar TOC contents, ranging from 0.53% to 0.82%, whereas BFC 3 has a much higher organic content, from 1.47% to 2.71%. The thermal maturation of the sequence cannot be clearly revealed through rock-eval, since most samples provided multiple small or plateau-like S2 peaks preventing a clear identification of T_{max} (the pyrolysis temperature with the maximum amount of hydrocarbon released from the organic matter). Nonetheless, various lines of evidence suggest a high level of maturity. Firstly, the S2 peak configuration is typically found in well mature samples, and secondly, most of the organic carbon is in the form of residual carbon with values of pyrolyzable carbon being very low, thus indicating that the rock has undergone the main phase of hydrocarbon generation. In view of the data, original values of total organic carbon in the rock prior to thermal maturation must have been greater; in the case of hydrocarbon migration, the estimated loss of organic carbon by the stage of full maturity varies between 66% and 20% depending on the original type of organic matter [(i.e. loss of organic carbon is higher in case of type 1 kerogen than in case of type 3 kerogen (Daly and Edman (2019)].

Samples	Biofacies type	PC [%]	RC [%]	TOC [%]	MINC [%]	HI [mg HC/g TOC]	OI [mg CO2/g TOC]	Tmax [°C]	S1 [mg HC/g]	S2 [mg HC/g]	S3	PI
VI 63 B	1	0.08	0.47	0.55	9.49	116	54	317	0.20	0.64	0.30	0.24
VI 64 A	3	0.03	2.03	2.06	5.88	3	34	334	0.06	0.05	0.71	0.55
VI 65 C	2	0.02	0.50	0.53	9.64	20	81	442	0.03	0.11	0.43	0.23
VI 66 A 1	3	0.10	1.37	1.47	4.99	59	40	446	0.15	0.87	0.59	0.14

VI 66 B 1	1	0.11	0.71	0.82	8.34	93	106	308	0.26	0.76	0.87	0.25
VI 68 A 1	1	0.07	0.49	0.57	8.50	86	140	318	0.14	0.48	0.79	0.22
VI 69 A	2	0.08	0.74	0.82	4.84	76	63	435	0.15	0.62	0.52	0.19
VI 317 A	3	0.08	2.63	2.71	4.54	22	24	446	0.12	0.61	0.64	0.17

Table 1

Rock eval data for selected samples from Tsiko Lake.

3.4.2 Taphonomy of Halobiids, paleontological determinations and morphometry

The state of preservation of bivalves at Tsiko Lake is generally fair to good. The specimens, generally slightly flattened by compaction, are found preserved in various ways, including simple molds, either internal or external, or as partly recrystallized shells. In the two layers where fossil collection for paleontological determination was made, halobiid shells, rarely in life position (Fig. 5 A), are commonly unbroken (Fig. 7 A), and butterfly preservation (i.e., typical of shells that have not been disturbed after death) as described by Allmon (1985) is quite common (Figs. 7 B, D, E). The beds sampled for fossils yielded a monospecific assemblage of *Halobia cordillerana* Smith, 1927 (identification confirmed by Christopher McRoberts, pers. comm. 14/11/2018). This indicates an upper Lower Norian-lower Middle Norian age in North America, according to Orchard and Tozer (1997).

Overall, specimens with closed articulated shells are very rare, but when present the valve at the bottom seems to have more concavity (inferring their precise original morphology is made difficult by the fact that specimens were taphonomically deformed by compaction and/or other processes), which indicates the life position (Fig. 5 A). In thin section, in all the above-mentioned facies, halobiid valves are found dispersed in the matrix and rarely overlap: none of the accumulations seem to result from mass transport (for comparison see Fig. 5 in Silberling et al., 1988). Valves show a slight preferential concave-upward orientation in most of the samples (see supplementary data). The almost equal distribution of concave upwards vs concave downwards valves means that, firstly, no bottom currents modified the original depositional orientation of the valves (otherwise they would be oriented in the more stable concave downwards position), and secondly, that the accumulations did not derive from single (or opened articulated) valves settling through the water column (which would have resulted in a preferential concave upward orientation). Both inner and outer layers are preserved, indicating that no preferential dissolution occurred (Fig. 6 D).

Since paleontological identifications revealed the presence of only *Halobia cordillerana,* the following observations are made assuming this species is the only one present in transversal cuts in thin section as well. Generally, shell thicknesses for *Halobia cordillerana* ranges from a few µm, up to 72 µm (Tab. 2). In BFC 2, the mean thickness of halobiid shells ranges from 14.33 to 24.67 µm, with a SD (standard deviation) in the range of 6.84 to 15.14. In comparison, BFC 3 bears shells with a smaller mean thickness, from 9.15 to 15.22 µm, and a lower SD varying from 4.38 to 6.84 µm. Finally, shell thicknesses measured on BFC 1 yielded average values spanning from 15.69 to 21.13 µm, with SD spanning from 9.46 to 11.66. As a general rule, BFC 3, the less diversified and most organic-rich litho-biofacies, holds the smallest *Halobia cordillerana* specimens.

Samples	Biofacies type	N. of measurements	Mean (µm)	S.D.	Min thickness (µm)	Max thickness (µm)
VI 317 A	3	45	11.17	5.85	2.88	26.64
VI 317 B	3	71	11.95	5.98	2.15	24.16
VI 63 A	2	62	14.33	6.84	3.35	24.22
VI 63 B	1	no measurements				
VI 64 A	3	86	10.29	6.59	2.27	45.78
VI 64 B	3	90	12.36	5.84	3.12	29.38
VI 64 C	3	85	13.22	6.21	2.15	25.27
VI 65 A	3	31	12.85	5.83	2.4	27.44
VI 65 B	3	36	11.45	6.09	2.29	24.11
VI 65 C	2	33	16.2	9.5	2.14	3.34
VI 66 A 1	3	91	9.15	4.38	4.01	29.56
VI 66 A 2	3	87	15.22	8.59	2.22	39.61
VI 66 B 1	1	11	15.69	9.46	5.24	25.89
VI 66 B 2	1	48	21.13	11.66	2.94	52.65
VI 68 A 1	1	no measurements				

VI 68 A 2	2	47	24.67	15.14	4.92	57.98
VI 68 B 1	2	51	14.13	8.18	1.99	32.30
VI 68 B 2	2	45	15.22	8.41	2.56	33.05
VI 68 B 3	2	50	18.05	10.24	2.46	44.52
VI 69 A	2	150	16.55	10.38	2.45	71.46
Vi 69 B	2	76	15.37	7.15	2.42	31.01
VI 69 C	2	81	15.1	8.16	2.14	40.00

Table 2

Shell thickness data for Tsiko Lake samples.

3.4.3 Redox proxies

Framboidal pyrite dimension is a widely used paleo-redox proxy (Wilkin et al., 1996; Wignall and Newton, 1998; Bond et al., 2004; Wignall and Bond, 2010). Generally, populations of framboidal pyrites having small average size (3 to 6 µm) and narrow size range indicate euxinic to anoxic bottom waters conditions (Bond et al., 2004; Wignall and Bond, 2010). Strongly dysoxic bottom waters conditions are characterized by populations of framboids having small dimensions (< 5 µm) with the addition of larger framboids; when compared to framboids populations formed under euxinic or anoxic conditions, lower dysoxic populations have a larger average size (6 to 10 µm) and larger size-range (Bond et al., 2004). Finally, in the case of weakly dysoxic-oxic conditions, framboidal pyrite tends to be much rarer or absent (Bond et al., 2004; Wignall and Bond, 2010). Under these conditions, when framboidal pyrite is present it shows populations marked by a broad range of sizes with only a small proportion having small dimensions (< 5 µm; Bond et al., 2004; Wignall and Bond, 2010). In most of the studied samples, framboidal pyrite is quite common and is often the most abundant form of pyrite in the sample (Tab. 3). In BFC 2, framboidal pyrite is the most common form of pyrite, and its average dimensions range from 4.98 to 6.05 µm, a size-range that is generally high, with a SD as high as 3.66 and maximum framboid dimensions around 26 µm. BFC 3, if compared to BFC 2, bears a population of smaller sized framboidal pyrites with mean dimensions between 3.97 and 4.81, and with a smaller SD. In contrast, in BFC 1, framboidal pyrite is either not present or rare, with diagenetic euhedral pyrite being the most abundant form. When present, the population of framboids shows larger-sized individuals, up to 33.33 μm, with higher mean and SD, ranging from 6.67 to 6.77 and 4.36 and 4.79, respectively. To summarize, different background oxygen conditions for the three different biofacies can be inferred from the distribution of framboidal pyrite: strongly dysoxic to oxic conditions for BFC 1, anoxic to strongly dysoxic conditions for BFC 2, and euxinic to anoxic conditions for BFC 3.

Samples	Biofacies type	N. of measurements	Mean (μm)	S.D.	Min dimensions (μm)	Max dimensions (μm)
VI 317 A	3	100	4.31	1.99	1.86	9.51
VI 317 B	3	102	4.75	2.05	1.59	13.55
VI 63 A	2	35	5.51	3.66	1.18	15.81
VI 63 B	1	Rare				
VI 64 A	3	150	4.36	1.7	1.54	10.36
VI 64 B	3	100	4.19	1.95	1.63	10.13
VI 64 C	3	110	4.23	1.91	1.73	10.45
VI 65 A	3	105	4.81	1.51	1.82	9.5
VI 65 B	3	87	4.18	1.37	2.04	9.27
VI 65 C	2	95	4.98	2.24	1.75	14.08
VI 66 A 1	3	100	3.97	1.39	1.33	7.5
VI 66 A 2	3	100	4.42	1.42	1.91	8.1
VI 66 B 1	1	101	6.67	4.79	2.68	33.33
VI 66 B 2	1	95	6.77	4.36	2.42	31.26
VI 68 A 1	1	Rare				
VI 68 A 2	2	100	4.76	2.39	1.87	17.46
VI 68 B 1	2	101	5.94	3.18	2.23	26.78
VI 68 B 2	2	90	5.98	3.26	2.36	23.45
VI 68 B 3	2	111	6.5	3.12	2.7	25.89
VI 69 A	2	152	4.99	3.4	2.13	15.35
VI 69 B	2	100	5.72	3.28	1.87	14.54
VI 69 C	2	104	5.25	2.85	2.11	15.35

Table 3
Framboidal pyrite data for Tsiko Lake samples.

The Fe speciation proxy has been extensively calibrated in a wide range of modern and ancient marine sediments (Raiswell and Canfield, 1998; Poulton and Raiswell, 2002; Clarkson et al., 2014). In general, sediments deposited under oxic conditions rarely have Fe_{HR}/Fe_T exceeding 0.38, whereas sediments deposited under anoxic conditions commonly have Fe_{HR}/Fe_T values above this threshold. However, 0.38 is as an extreme upper value, and Poulton and Raiswell (2002) showed that Fe_{HR}/Fe_T ratios in Phanerozoic shales deposited under oxic water column conditions is commonly lower (0.14 ± 0.08). Thus, oxic depositional conditions are inferred from ratios of $Fe_{HR}/Fe_T \leq 0.22$, whereas anoxic conditions are inferred from $Fe_{HR}/Fe_T \geq 0.38$ (Poulton and Canfield, 2011). Intermediate values ($22 < Fe_{HR}/Fe_T > 38$) are considered equivocal, and might represent oxic or anoxic conditions. Where anoxic conditions are inferred, the proxy can be used to further discriminate between ferruginous and euxinic conditions, by the extent of pyritization of the highly reactive Fe pool (Fe_{PY}/Fe_{HR}). The transition from ferruginous to euxinic conditions generally occurs at Fe_{PY}/Fe_{HR} ratios between 0.7 and 0.8 (Anderson and Raiswell, 2004; März et al., 2008). Although this proxy has been established mainly studying siliciclastic sediments, Clarkson et al. (2014) tested its reliability when applied to carbonate deposits. The authors concluded that the proxy is applicable to carbonate rocks when Fe_T is above 0.5%, and when samples have not been subjected to deep burial dolomitization. All samples from Tsiko Lake have values of total Fe above 0.5%, with only one exception (VI 63 B).

Hemipelagic/pelagic samples from Tsiko Lake have high Fe_{HR}/Fe_T ratios, consistently above the 0.38 threshold (Tab. 4; Fig. 8), suggesting deposition under anoxic bottom water conditions. When we look at the distribution of the Fe_{HR}/Fe_T ratio, there is an increase in Fe_{HR} enrichment from BFC 1, through BFC 2, to BFC 3. The same trend is observed in terms of the extent of pyritisation of highly reactive Fe, whereby BFC 1 has Fe_{PY}/Fe_{HR} ratios as low as 0.38, followed by BFC 2 at 0.51, and finally BFC 3 with values up to 0.79. The only exception is VI 317 A (BFC 3), with a Fe_{PY}/Fe_{HR} ratio of 0.05. However, a detailed examination suggests that the pyrite fraction in VI 317 A has been oxidized during weathering (see supplementary data). For this sample, even though the shapes of pyrite grains have been preserved (thus allowing the measurement of framboid dimensions), the mineral has been entirely replaced by iron oxides, as shown by EDX analyses on the SEM. As a consequence, most of Fe_{PY} pool has been transferred to the Fe_{OX} pool (with $Fe_{OX} = 0.64\%$ being much higher than all the other samples). Most likely, the original depositional values of Fe_{PY} in VI 317 A were thus originally in the same range as other BFC 3 samples. Overall, Fe_{PY}/Fe_{HR} values tend to indicate anoxic ferruginous conditions for BFC 1 and 2 (values ranging from 0.38 to 0.64) whereas anoxic euxinic conditions (values >0.7) are suggested during deposition of BFC 3.

		Wt.%							Fe_x/Fe_{HR}			
Samples	Biofacies type	Fe_T	Fe_{ox}	Fe_{carb}	Fe_{mag}	Fe_{pyr}	Fe_{HR}	Fe_{HR}/Fe_T	Fe_{carb}	Fe_{ox}	Fe_{mag}	Fe_{pyr}
VI 63 B *	1	0.199	ND	0.057	0.001	0.104	0.162	0.81	0.35	ND	0.01	0.64
VI 64 A	3	0.861	0.067	0.156	0.004	0.657	0.884	1.03	0.18	0.08	0.00	0.74
VI 65 B	3	2.605	0.189	0.354	0.007	1.942	2.492	0.96	0.14	0.08	0.00	0.78
VI 66 A 1	3	0.741	0.006	0.147	0.006	0.614	0.772	1.04	0.19	0.01	0.01	0.79
VI 66 A 2	3	0.905	0.003	0.174	0.001	0.667	0.843	0.93	0.21	0.00	0.00	0.79
VI 68 A 1	1	0.811	0.162	0.145	0.003	0.188	0.498	0.61	0.29	0.33	0.01	0.38
VI 69 A	2	0.708	0.113	0.174	0.000	0.305	0.594	0.84	0.29	0.19	0.00	0.51
VI 317 A	3	0.778	0.635	0.017	0.011	0.038	0.701	0.90	0.02	0.91	0.02	0.05

* suspected samples

Table 4

Fe-speciation data for selected sample from Tsiko Lake.

4. Discussion

4.1.1 Depositional environments

The succession comprises sediments deposited in a slope to basinal setting, above the CCD (or ACD if the inner layer of *Halobia* was originally made of aragonite as suggested by Carter, 1990), in a low-energy environment, well below the storm wave base, with disturbance only at irregular times by the gravitational re-deposition of sediments reworked from the outer platform. These alternations of hemipelagic sediments and platform to slope-derived sediments are similar to the depositional sequences of the Carnian-Norian Peril Formation on QCI (Orchard and Desrochers, 1993). There, medium-bedded deposits of the Peril Formation document the drowning of the platform and the transition to the hemipelagic/pelagic sedimentation on QCI during the Upper Carnian.

4.1.2 Paleo-redox

The redox proxies used in this study document average redox conditions over a relatively long time-span (likely hundreds of years, depending on the sedimentation rate) since the material analysed consisted of 1-2 cm thick sediment intervals. Nevertheless, framboidal pyrite distributions and iron speciation, coupled with sedimentological and ichnofacies observations, allow us to interpret the background conditions under which each litho-biofacies was deposited. With sedimentological and microfacies data alone, the relative degree of oxygenation of each of the three litho-biofacies can initially be deduced. In this regard, BFC 1 experienced the least severe degree of oxygen depletion. Here, the original fabric is at times obscured (even though it is never completely homogenized) by micro to macro bioturbation, coupled with the presence of a rather diverse and abundant benthic fauna (for a low diversity assemblage), indicating only moderate oxygen depletion. In contrast, in BFC 2, the original lamination is largely preserved and macrobioturbation slightly alters the original fabric only sporadically. The presence of benthos is restricted to a few microbenthic body fossils (e.g. foraminifera). This dearth of macrobenthos, if compared to BFC 1, likely indicates a lower degree of oxygenation. The facies that experienced the most severe oxygen depletion during deposition is BFC 3. Here, the undisturbed laminations imply that oxygen levels were too low even for microbioturbating organisms, which includes soft bodied organisms that are able to cope with extremely low oxygen levels (Levin et al., 2003). However, even if the background oxygen conditions where most likely restricted during most of BFC 3 deposition, several lines of evidence point towards less austere conditions at least during short periods. For example, the rare microlaminae where thicker *Halobia* shells, rare bioturbation and foraminifera fossil occurrences are present indicate that, at least temporarily, the oxygen level of bottom waters improved slightly (but oxygenation was still lower than during BFC 2). In general, TOC values confirm these sedimentological interpretations, as we observe an increase toward higher values from BCF 1, through BFC 2, to BFC 3.

To better constrain levels of oxygen depletion at Tsiko Lake section we combine the redox proxy data with the observations on sediment fabric and benthic communities (Tab. 5). A complication when interpreting oxygenation arises from the fact that different authors often use a different oxygen zonation classification (e.g. limits between zones) and/or nomenclature (e.g. for different redox proxies). Hereafter, we will refer to the oxygen zonation proposed by Tyson and Pearson (1991), which was mostly established according to modern changes in sediment fabrics, as well as the response of benthic biota, to different oxygen levels. These authors established four major oxygen regimes with four related biofacies: oxic (aerobic biofacies), dysoxic (moderate, severe, extreme; dysaerobic biofacies), suboxic (quasi-anaerobic biofacies), and anoxic (anaerobic biofacies). In BFC 1, extreme dysoxic-oxic conditions can be inferred from the pyrite proxy, whereas Fe speciation points to a greater degree of oxygen depletion (anoxic ferruginous). Oxic conditions can be excluded as the sediment is never completely homogenized and the scattered reworking of the sediments by bioturbation is typical of upper dysoxic conditions [Bond and Wignall, 2010; i.e. moderate to severe dysoxic conditions of Tyson and Pearson (1991)]. Moreover, the benthic community in BFC 1 already shows signs of impoverishment [for comparison see the oxic associations in Oschmann (1988)], with only a few specimens of crinoids and molluscs being present.

For BFC 2, the framboidal pyrite distribution indicates anoxic to extreme dysoxic conditions, which is generally consistent with the Fe speciation data, which suggest anoxic ferruginous conditions. In Tyson and Pearson (1991), the limit between suboxic and dysoxic is placed at 0.2 ml/L, because in modern environments this value corresponds to the limit that generally marks the end of macrobioturbation (in Savrda et al. (1984) this limit is placed at 0.1 ml/L). In BFC 2, the intensity of macrobioturbation is generally quite low when compared to BFC 1, and the laminated fabric in this litho-biofacies is usually only disturbed by microbioturbation. Therefore, dominantly anoxic conditions, with intervals of strong dysoxia, is the most likely interpretation for BFC 2. Finally, all proxies suggest anoxic, dominantly euxinic conditions during deposition of BCF 3, with the disappearance of most benthics (or all benthics if we consider that the halobiid bivalves found are larval planktonic-nektonic individuals that settled on the sea-bottom after death; see below) and microbioturbation.

	Framboidal pyrite	**Fe speciation**	**Sediment fabric and benthic biotic components**	**Interpreted background oxygen conditions**
BFC 1	Extreme dysoxic to oxic	Anoxic ferruginous	Original laminated fabric moderately biorturbated Low diversity benthic assemblages (echinoderms, molluscs and foraminifera)	**Severe/moderate dysoxic conditions**
BFC 2	Anoxic to extreme dysoxic	Anoxic ferruginous	Lamination disturbed by microbioturbation and only rarely by macrobiortubation Very low diversity in benthics (foraminifera)	**Dominantly anoxic conditions, with extreme dysoxic intervals**

BFC 3	Euxinic to anoxic	Anoxic Ferruginous/ possibly euxinic	Laminated No benthics	**Anoxic, dominantly euxinic conditions**

Table 5

Interpreted oxygen conditions from redox proxy and sediment fabric.

The above discussion highlights that autochthonous sedimentation at Tsiko Lake was generally characterized by restricted oxygen conditions. The varying physico-chemical characteristics of the hemipelagic/pelagic facies are a sign of varying oxygen conditions with the chemocline [or RPD as defined by Rhoads and Morse (1971)] fluctuating from shallow sediments into the water column. During the dysoxic to anoxic deposition of BFC 1 and 2, we can interpret the position of the chemocline as being located at different depths (Fig. 9 A and B respectively) within the sediment. In the case of BFC 3, oxygen deficiency was probably not only confined to the sea bottom, but most likely led to euxinic conditions in the water column (Fig. 9 C): when compared to BFC 1 and 2, BFC 3, besides being completely devoid of epi- and endobenthic organisms, also shows a decrease in part of the nektonic/planktonic biogenic fractions (e.g. no more fish otoliths and much less radiolarians). As discussed above, anoxic conditions in BFC 3 were only interrupted at times by temporally limited re-oxygenation events. The characteristics of these episodes indicate particular conditions during formation, whereby the lack of bioturbation below these horizons and the almost zero depth penetration of *Chondrites* suggest a sharp change in oxygen conditions just below the sediment/water interface (Fig. 9 D). Similar circumstances were developed at times in sediments of the Miocene Monterey Formation of California and were described as exaerobic conditions (see Savrda and Bottjer, 1987, 1991). According to these authors, exaerobic conditions (dissolved oxygen around 0.1 to 0.2 ml L^{-1}) develop when the RPD is at the sediment surface: these settings prevent the sediments from being burrowed, but allow extremely resistant benthos to habitat the sediment surface (Tyson and Pearson (1991) partially correlated the exaerobic facies with their quasi-anaerobic biofacies). These conditions are thought to be facilitated by microbial mats forming on the sediment surface (Jørgensen et al., 1979; O'Brien, 1990), which favor the development of a sharp oxygen gradient at the surface. To conclude, in BFC 3, prevailing anoxic sulfidic conditions were interrupted at times by short, low oxygenation episodes where conditions similar to the exaerobic facies of Savrda and Bottjer (1987, 1991) developed.

4.1.3 Paleoecology of *Halobia cordillerana* at Tsiko Lake

To better understand the relationship between litho-biofacies, shell thickness and oxygen levels we plotted average shell thickness vs average framboid dimensions (Fig. 10). The data show a moderate positive correlation (r= 0.79) which suggests the existence of a relationship between the two variables. As a general trend, lower values of bottom water oxygenation coincide with an average reduction in shell thickness. This suggests a direct influence of bottom water conditions on the life and growth of halobiid bivalves. At Tsiko Lake, the highest abundance and average shell thickness of halobiids are seen in dysoxic to anoxic facies (BFC 1 & 2). In contrast, under dominantly euxinic conditions (i.e. in BFC 3), halobiid bivalves are present, but only as very small specimens that rarely exceed 15 μm in thickness. These forms probably represent halobiids at larval or post-larval stages that, due to unfavorable conditions, died in the water column or tried to settle down but failed. As the small valves are never found attached or closely overlapping during anoxic periods in BFC 3, it is more likely that these juvenile bivalves died before reaching the sea-bottom (due to water column euxinia). During euxinic periods when bottom waters were inhospitable, it is very improbable that spawning occurred in the area but instead, likely happened elsewhere were conditions were more favorable for halobiids' life and reproduction (e.g. other shallower areas of the basin where oxygen depletion was less severe). Our work therefore suggests that these organisms had an initial pelagic-nektonic larval stage (as alluded by Campbell, 1994 and McRoberts, 1997, 2000), but their adult lifestyle was linked to the sea bottom, as demonstrated by their valves position and distribution and their strong relationship to bottom water redox conditions.

The opportunistic nature of these organisms can be further evaluated in relation to the distribution of the oxygenation episodes in BFC 3. Unfortunately, our data do not allow a detailed examination of the cause(s) of oxygen depletion at Tsiko Lake, since very little is known about the paleogeographic location and the basin configuration of Wrangellia. However, in terms of trace metal data, the anoxic biofacies (BFC 3) is characterized by low Mo enrichment factors and high U enrichment factors, thus suggesting that the formation of these strata possibly occurred in a closed restricted basin setting (see supplementary data; Algeo and Tribovillard, 2009; Algeo and Rowe, 2012; Tribovillard et al., 2012). These repeated black shale appearances imply the creation of closed or semi-closed basinal conditions, possibly caused by sea-level changes due to eustatism or tectonics. Making some assumptions, we can estimate the duration of anoxic periods at Tsiko Lake. For instance, accounting for sedimentation rates of 0.03 mm y^{-1} [e.g. a similar modern environment could be the New Georgia Sound in the Solomon Islands volcanic arc which has hemipelagic sedimentation rates in the order of 0.03 mm y^{-1} (Colwell and Exon, 1988)] and a compaction factor of 60% for hemipelagic oozes (Moore, 1989 pp. 247-251), every mm of actual sediment thickness would record ca. 55 years of sedimentation (0.018 mm y^{-1}), a time period which would have been much longer in the case of lower sedimentation rates (likely the case since biogenic planktonic production would have been lower in the Triassic). Considering that often the anoxic lamination of BFC 3 reaches 4-5 cm in thickness before any macro or microscopic sign of improved conditions is evident, complete oxygen restriction likely persisted for up to hundreds of years, making it impossible for halobiid bivalves to successfully colonize the sea floor for long periods of time. Nonetheless, small oxygenation events at Tsiko Lake are persistently recorded by the settling and partial growth of *H. cordillerana,* which testifies to their rapid dispersal and settling strategies. Hence, looking at their distribution at Tsiko Lake, we support the idea that thin-shelled bivalves are a classic example of r-strategist blooming during time windows of restored biological conditions (Kelly and Doyle, 1991; Conti and Monari, 1992; Wignall, 1993; Etter, 1995, 1996; Harzhauser and Mandic, 2004; Schatz, 2005; Waller and Stanley, 2005). In addition, it is also possible that, under certain circumstances, species turnover was directly influenced by local environmental changes. On this point, Onoue et al. (2019), studying the environmental perturbations at two Carnian/Norian boundary sections (e.g. Pizzo Mondello, Italy, and Black Bear Ridge, Canada), found out that, in both localities, the appearance of *Halobia austriaca* was associated with a change to more oxygen-depleted conditions in the basin (happening asynchronously in the two localities); this led the authors to conclude that this species was particularly adapted to oxygen-depleted environments.

Considering the relationships between adult halobiid bivalves and bottom water conditions (presence of specimens in life position, relationships between bottom water oxygenation levels and the life style and growth of halobiids), we now compare the different benthic living scenarios. An epiphytic mode of life attached to benthic marine plants, suggested by Campbell (1994) is not supported, since the water depth at Tsiko Lake was surely deeper than the photic zone, where such plants live. In the three different litho-biofacies, macro and micro burrows are well preserved, indicating that the sediment was sticky (cohesive) enough to preserve burrowing. Especially observing the oxygenation events in BFC 3, an infaunal mode of life can be ruled out since no vertically-preserved specimens were found and no vertical disruption of the laminated sediment was noticed. As previously discussed, most of the present-day chemosymbiont bivalves living in sediments are known to mine reduced compounds, with burrows extending up to 30 times the length of the shell (Dando and Southward, 1986; Seilacher, 1990; Dufour and Felbeck, 2003). No such burrowing is found at Tsiko Lake. For example, in BFC 3, the only macro burrowing associated with the exaerobic levels is that of *Chondrites,* and this burrowing is only observed subparallel to the bedding plane and in very low frequency. Modern chemosymbionts are generally found in the proximity of the RPD-layer (Schweimanns and Felbeck, 1995), and conditions that are found in the oxygenation events in BFC 3 would theoretically be optimal for chemosymbiosis. However, during these episodes, populations of halobiid bivalves never reached dimensions such as those observed in the other litho-biofacies. Indeed, at Tsiko Lake, the maximum valve thickness of *Halobia cordillerana,* 71.46 µm, is reached in dysoxic to anoxic facies (BFC 1 & 2), whereas the maximum shell thickness reached in the more oxygenated laminae of BFC 3 is 45.78 µm. This difference could be due to the fact that conditions were likely not as optimal as during the deposition of BFC 1 & 2. Another line of evidence against possible chemosymbiosis in halobiids comes from the distribution and shape of halobiid-rich beds. In modern deep-water chemosynthetic environments, similar abundances are only reached in cold seeps and hydrothermal vents. Fossil examples of these environments show very localized chemosynthetic production resulting in lenticular chemoherms [sensu Aharon, 1994; e.g. the Miocene “Calcari a Lucina” of the Italian Appennines (Taviani, 2011)]. At Tsiko Lake, however, halobiid-rich beds are tabular in shape and no data suggest a peculiar distribution influenced by zoned methane seepage. Moreover, the fauna recently described from Upper Triassic hydrocarbon-seep deposits from Turkey (Kiel et al., 2017), although being molluscs-dominated, did not show any presence of halobiid bivalves.

Following these lines of evidence, we conclude that chemosymbiosis was not achieved in *H. cordillerana*. Therefore, our data do not support the interpretations of Seilacher (1990), who linked the “tube” present in *Halobia* to possible chemosymbiosis, although in the case of *H. cordillerana*, this feature is quite developed (see McRoberts, 2011). This neomorphic feature, not inherited from its ancestors (Waller and Stanley 2005), could have a completely different purpose. In any case, it is very unlikely that its function was vital for the life of *Halobia,* since it has been demonstrated that the dimensions of this “tube” vary consistently within the genus, from being scarcely developed to having high amplitude (Waller and Stanley 2005).

Ideally, a paleoecologic interpretation should be supported by modern data and should be able to explain their recurrent presence in oxygen-depleted environments, widespread distribution, morphology and structure, and high turnover rates, which make halobiid bivalves valuable biostratigraphic markers. According to their distribution and life position at Tsiko Lake, these organisms were likely filter feeding, epibenthic recliners. Thanks to their pelagic larval stage, they were endowed with rapid dispersal and re-settling capacities. Once settling occurred, they had the possibility to grow and reach the adult stage under minimal oxygen values (extreme dysoxic to anoxic zone), but not under dominantly euxinic conditions. Their shell morphology clearly reflects the adaptation to low-oxygen, inhospitable environments: the extremely flat and thin shell (maximum thickness 71.46 μm) of *H. cordillerana* at Tsiko Lake can be seen as the need of *Halobia* to minimize energy consumption during shell secretion (Rhoads and Morse, 1971) and the necessity to have light shells which would allow flotation even on soft hemipelagic substrates (Waller and Stanley, 2005; Schatz, 2005).

4.2 Paleoecology of Triassic flat clams and their importance for reconstructing past environments

Apart from the neomorphic and highly variable "tube" present in *Halobia*, Triassic flat clams share several morphological features (Waller and Stanley, 2005), supporting the idea that the benthic mode of life of *Halobia* was inherited from its ancestors (genera: *Enteropleura, Aparimella* and *Daonella*). A shared mode of life is also suggested by their common occurrence, especially *Halobia* and *Daonella,* which except for a few presumably shallow water occurrences (Miroshnikov and Burii, 1969; Hatleberg and Clark, 1984; Campbel, 1994), normally occur in similar deep-water settings (Schatz, 2005; McRoberts et al., 2008; McRoberts, 2011). Therefore, we propose that our model for the mode of life of *H. cordillerana* at Tsiko Lake could be transposed (generalized) to other halobiid species and halobiid-like genera of the Triassic group. Further studies should provide confirmation that these flat clams are benthic recliners, but their relation to oxygenation levels cannot be asserted.

In Triassic hemipelagic settings where flat clams are widely diffused, they could be extremely useful as paleoenvironmental indicators. *H. cordillerana*, fully epibenthic, required lower dysoxic sea bottom conditions to thrive. In successions in which oxygen-depleted conditions are inferred, the study of their vertical (stratigraphic) distribution, both at the macro and microscale, has the potential to elucidate temporal variations in bottom water oxygenation. The analysis of the frequency and length (thickness) of the oxygenation episodes can be very useful when trying to reconstruct the causes and the development of anoxia in a determinate area. This work at Tsiko Lake, once again underlines that great care must be taken when dealing with paleo-redox reconstructions, since, even at the very small scale, changes could be important and changing conditions can be rapidly registered even in successions marked as fully anoxic or euxinic.

5. Conclusions

Flat clams-bearing hemipelagic litho-biofacies at Tsiko Lake were deposited under generally restricted oxygen conditions. The entire halobiid assemblage is monospecific and consists of specimens of *Halobia cordillerana*: the abundance and dimensions (represented by their shell thickness) of these halobiids correlate with bottom water redox conditions inferred from redox proxies and paleontological and ichnofacies data. Based on different lines of evidence, we suggest an epibenthic recliner mode of life for *H. cordillerana*. In layers deposited during anoxic periods, populations of halobiids are only represented by specimens at larval stage, which likely perished due to oxygen deficiency before settling on the sea-bottom. During anoxia, spawning of *H. cordillerana* likely occurred elsewhere, where oxygen conditions were more favorable and adult specimens were present. *H. cordillerana* proliferated under dysoxic conditions but was able to live also under exaerobic conditions. The paleoecology of *Halobia cordillerana* can be used as a starting point to compare the mode of life of other flat clams. It could serve as a reference for the paleoecological reconstructions of similar forms, and stresses the importance of flat clams in reconstructing paleo-oxygenation levels.

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Appendix A. Supplementary data

Supplementary data to this article can be found online.

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