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Reviews and syntheses: Sediment-stressed reefs over the past 420 Myr

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Abstract. The evolution of reefs over geologic time is diverse and includes a range of different builders. An understanding of the consequences of natural and anthropogenically-driven sediment influx to reef systems is crucial to planning future protection and mitigation strategies. Most reef systems are associated with clear water settings, however, many reef communities have evolved in turbid water environments stressed by high rates of sediment influx. Conventionally, these mixed carbonate-clastic environments have been considered unfavourable to reef organisms. Utilising case-studies of sediment-stressed reefs from the Devonian to Recent, we clearly demonstrate that reef organisms can survive, and even thrive, under the influence of clastic sediment influx. Ten case-studies were selected on the basis of: i) the presence of a mixed carbonate-clastic matrix, and ii) the existence of a coral framework. For each example, the system was characterised in terms of sediment input, organism growth forms (with a focus on corals) and the overall reef morphology. The host sediment from Cenozoic reefs was found to be typically better-described than that within Paleozoic and Mesozoic communities. This may be due to the closer affinity between Cenozoic communities and recent species when compared to more ancient systems. The same reasoning accounts for the paucity of data describing the internal structure of many fossil reefs, a feature also related to outcrop quality. This study clearly demonstrates that, while reefs in sediment-impacted environments are common, there is no general developmental model that can be applied to all reefs. No relationship was identified between the nature of the reef builders, the character of the siliciclastic component and the reef structure. We demonstrate that, in the majority of cases, the clastic matrix within reefs, both ancient and recent, is insufficiently described – this inhibits understanding of mixed carbonate-clastic reef systems and significantly compromising forecasts of future reef development.

1. Introduction

Throughout Earth's history, reef ecosystems have formed complex environments including soft and hard substrates (Wood, 2011; Lipps and Stanley, 2016). The oldest reef-like structures date from the Archean (Wood, 1999; Lipps and Stanley, 2016). Over geological time, the main reef builders have changed from photosynthetic cyanobacteria during the Precambrian (Allwood et al., 2007) to scleractinian corals and photosynthetic coralline algae in modern reefs (Stanley, 2003; Wood, 2011). The history of reefs is a story of booms and collapses (Jury and Jokiel, 2016). Interestingly, many examples of reefal systems in Earth's history have developed despite suboptimal conditions, such as turbid waters and sediment-loaded (often argillaceous or clastic material) environments (e.g., Lokier et al., 2009; Santodomingo et al., 2016; Zweifler et al., 2021). Classically, these sediment-loaded (or stressed) environments have been regarded as hostile to reefal organisms (Rogers, 1990; Jones et al., 2015; Ricardo et al., 2015). More recently, a number of studies have demonstrated that reefal organisms can indeed survive, and even flourish, under clastic sediment influx in a range of depositional environments (Woolfe and Larcombe, 1999; Wilson and Lokier, 2002; Lokier et al., 2009; Zapalski et al., 2021; Unger et al., 2023). The processes that allow recent reefal organisms to inhabit such environments are still poorly understood (Zweifler et al., 2021). This fact is largely due to a lack of detailed studies of such mixed carbonate-clastic reefal ecosystems throughout much of Earth's history (Wilson, 2005). Studying ancient reefal systems is important to understanding modern coral communities and their possible reactions to anthropogenically-induced climate change or ocean acidification (Kleypas et al., 2001; Santodomingo et al., 2016).

In this paper, 10 case examples of sediment-stressed coral reefs described in the literature are compared. While any comparisons between Phanerozoic reefs must fully consider the palaeoecological, palaeobiological and palaeoceanographic limitations of the main reef builders at the time of reef construction (e.g., May, 1997; Wood, 1999), it is still possible to undertake an overall analysis of broad-scale organism response and reef morphology to siliciclastic sediment influx.

The main aims of this study are to undertake environmental analysis, considering sediment influx, organism growth forms (particularly those of corals) and species diversity with reference to case examples spanning the Devonian to Recent. General conclusions for diagnosing reefs in sediment-stressed environments and the current state of research are drawn.

1.1 Reefs in the course of time

Numerous scholarly papers and books have summarised the evolution of reefal ecosystems through geological time. Here, only a condensed summary of those aspects most relevant to understanding the concepts and principles discussed in this paper is presented. Please refer to cited references for more detail.

During the Great Ordovician Biodiversification Event, metazoan reefs replaced the early microbial reefs typical for the middle and late Cambrian (e.g., stromatolites, thrombolites etc; Grotzinger, 1990; Webby, 2002; Adachi et al., 2011). Metazoan associations of stromatoporoid sponges, corals and calcified algae dominated the middle Palaeozoic seas (; Copper, 1994; Wood, 1999; Stanley, 2001) and the resultant structures had characteristics

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similar to those known of modern reefal systems (Copper, 2002). Tabulate and rugose corals building these reefs biomineralized calcitic skeletons (Sandberg, 1975), and some authors describe tabulate corals as photosymbiotic (Copper, 2002; Zapalski, 2013). The mass extinction at the end of the Ordovician had only a subordinate influence on these reefal ecosystems (Stanley, 2001). During the Silurian and, even more importantly, during the Devonian, coral-stromatoporoid reefs dominated the tropical shallow water platforms but these reef associations collapsed during the Frasnian-Famennian crisis (McGhee, 1996). After the Devonian acme, framework reefs were rare (Wood, 1999; Webby, 2002), and reefal buildups were dominated by bryozoans, calcified algae and sponges (Fagerstrom, 1987). The early Carboniferous is described as a period of recovery of shallow marine reefal assemblages, while microbial mud mounds developed in platform to open marine settings (Yao et al., 2020). Until the mass extinction at the end of the Permian, organisms producing aragonite and high-Mg calcite, such as various sponges and algae, dominated the reef structure during the Pennsylvanian and Permian (Jury and Jokiel, 2016).

Palaeozoic reef builders (including tabulate and rugose corals) became extinct during the end Permian mass extinctions (Benton, 2003). Several million years later, during the Middle Triassic, the first scleractinian corals are documented (Stanley, 1981). Their relationship to the Paleozoic ‘ancestors’ is widely discussed (e.g., Oliver, 1996). Nevertheless, scleractinian corals did not directly evolve from the tabulate nor the rugose corals and are thus regarded as a separate clade (Hill, 1981). Reef-building during the Mesozoic differs from that typical of the middle Paleozoic reef acme. Scleractinian corals replaced the rugose and tabulate corals, and different calcifying sponges and calcifying algae contributed to reef formation (Fig. 1; Stanley, 2003; Kiessling, 2009). Scleractinians persisted as successful reef builders during the Middle and Late Triassic. Suffering severe extinction, no excessive reefal buildups developed during the Early Jurassic. In the Late Jurassic to Early Cretaceous, reef-building regenerated, reached and even transcended modern rates of reef formation (Flügel and Kiessling, 2002; Stanley, 2003; Kiessling, 2009). Cretaceous rudists evolved as a primary contributor to reef construction and competitively replaced coral-algae reefs (Kauffman and Johnson, 1988). Rarely, coral reefal buildups are described during the Cretaceous and many Mesozoic reef builders vanished during the end Maastrichtian extinction (Kiessling, 2009).

Following the end Maastrichtian extinction, coral diversity was low during the Paleocene (Lipps and Stanley, 2016). The Cenozoic Era was dominated by large and sudden climate changes associated with warming and cooling cycles (Zachos et al., 2001). Symbiont-bearing coral species evolved and corals developed the capability of rapid linear extension and quick recovery even under the influence of stressors. Simultaneously, reef frameworks were strengthened by coralline algae (Lipps and Stanley, 2016). During the middle Paleocene, some coral-algal barrier reefs and patch reefs adapted to the greenhouse period but declined during short warming pulses (Zamagni et al., 2012; Lipps and Stanley, 2016). Reef-building decreased significantly at the Paleocene-Eocene Thermal Maximum (ca. 65 Ma, Fig. 1; Kiessling and Baron-Szabo, 2004). This event is currently discussed and proposed as an analogue for modern climate change, ocean acidification and future global warming (Zachos et al., 2005; Lipps and Stanley, 2016). Reefs and photosymbiotic corals generally changed, thrived and suffered in concert with climate fluctuations throughout the Cenozoic (Perrin, 2002; Kiessling, 2006; Lipps and Stanley, 2016).

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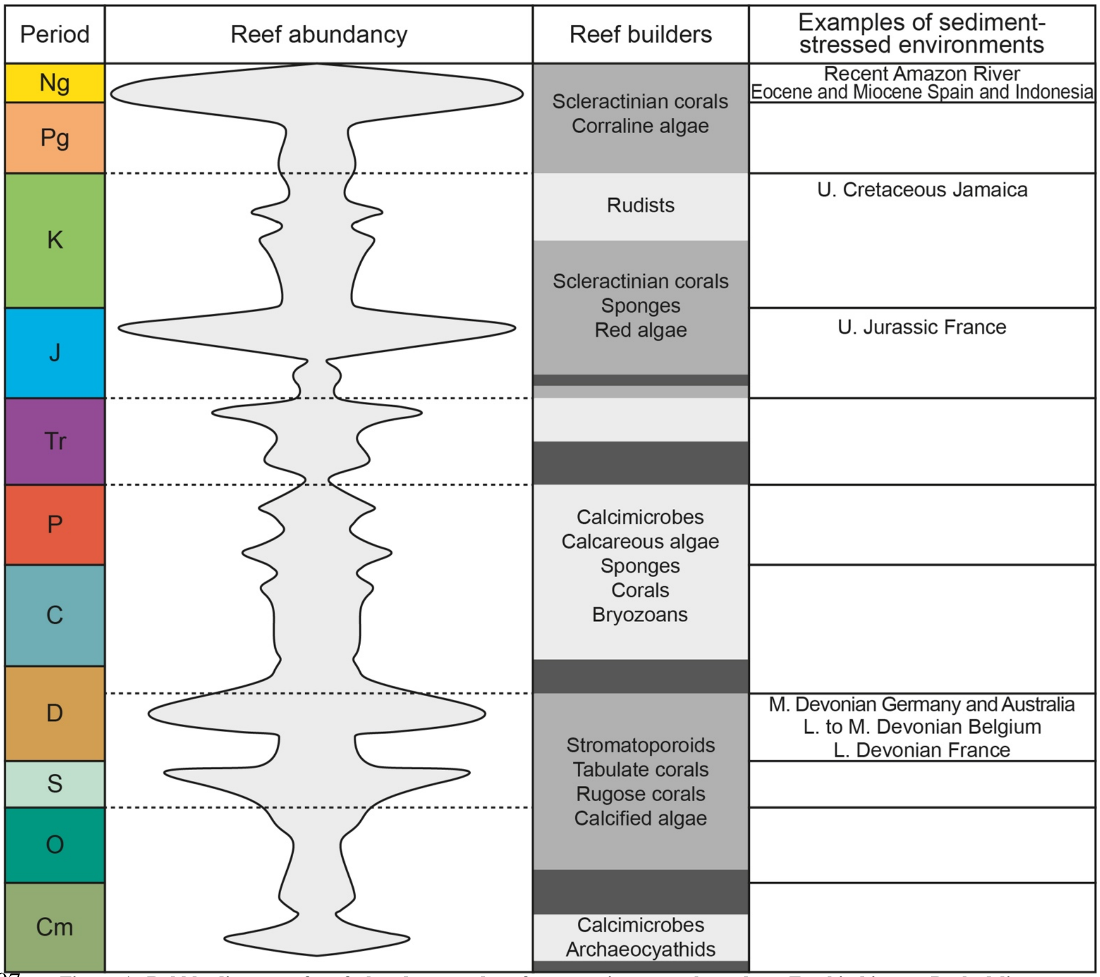

Figure 1: Bubble diagram of reef abundance and reef community types throughout Earth's history. Dashed lines represent mass extinctions. Dark areas represent periods of reef decline or poor reef development in general. The here compared examples of reefs in sediment-stressed environments are known from the Devonian, Jurassic, Cretaceous and Neogene (based on Langenstrassen, 1982; Fagerstrom, 1987; Braga and Martín, 1988; Kaufmann and Johnson, 1988; Robardet et al., 1994; Wood, 1999; Mitchell, 2002b; Wilson and Lokier, 2002; Olivier et al., 2004; Mabille et al., 2008; Kiessling, 2009; Lokier et al., 2009; Lipps and Stanley, 2016; Moura et al., 2016; Zapalski et al., 2021, with modifications).

1.2 Sediment-impacted environments – hostile or opportunity?

Reefs represent habitats that are exposed to a range of different intense physical and biological processes (Wood, 2011). Changes in physical, chemical and biological patterns are seen as endangering the ecosystem (Graham et al., 2006). Studying stressors, such as high turbidity, low levels of incident light, high (or low) seawater temperatures, and low pH or salinity, is important to understanding modern and ancient reefal communities and their responses to environmental changes (Kleypas et al., 2001; Hahn et al., 2012; Santodomingo et al., 2016; Zweifler et al., 2021). Traditionally, excessive sediment influx is considered to be unfavourable to the reef ecosystem. Modern scleractinian coral reefs react to sediment stress with lower growth rates, a reduced number of species, declining calcification, a greater number of branching forms, fewer living corals and, consequently, slower reef accretion (Rogers, 1990; Jones et al., 2015).

Conversely, several studies have demonstrated that turbid waters do not inhibit coral growth *per se* (Roy and Smith, 1971) and that reefal communities can flourish and even display great diversity in such an environment (Johnson et al., 2015; Santodomingo et al., 2016). Inhabiting turbid water environments or settings with high sedimentation rates is possible via a range of passive and active survival strategies. Due to water circulation through waves and currents, fine-grained sediment is flushed from the feeding surface of reef organisms. In addition, the accumulation of sediment and, thus, the burial of reef organisms is prevented where the sediment is entrained and transported to deeper waters (e.g., Woolfe and Larcombe, 1999; Wolanski et al., 2005). The morphology of reef organisms can also cause sediment to slide off due to gravity (Stafford-Smith, 1993).

In some cases, organisms may respond to sediment inundation with active self-cleaning, as observed in modern reefs (Rogers, 1990; Stafford-Smith and Ormond, 1992; Bell, 2004). Other examples show the preferential development of reefs on topographic elevations where the effects of high sediment influx are less substantial than adjacent deeper water settings (Gong et al., 1998). Even though reefs in unfavourable environments have received little attention so far, the case studies known today show how important it is to better understand these ecosystems (Wilson and Lokier, 2002; Zweifler et al., 2021).

2. Methods

To examine the characteristics of coral reefs impacted by argillaceous and siliciclastic material and to highlight the state of research, 10 case examples of coral reefs exposed to sediment-stressed environments throughout Earth's history were chosen for this literature-based study. As data was limited, these examples only had to fulfil two selection criteria: i) have corals as the primary reef constructing agent and, ii) presenting a mixed clastic-carbonated matrix. Under these criteria, rudist reefs, for example, were not considered as viable candidates for discussion. Particular focus was given to the reef type and its size, the internal structure, the fossil assemblage, coral diversity, the type of sediment-stressed environment and the grain size of the preserved sediments within the reef. Both siliciclastic and volcanoclastic environments were considered on an equal basis, as comparable grain sizes affect the reefs in the same way (Wilson and Lokier, 2002).

3. Case examples

3.1 Palaeozoic

3.1.1. Lower Devonian reefs of NW France

At Point d'Amérique in northwestern France (Fig. 2), a succession of Lochkovian strata gives insights into a series of reefal buildups embedded in muddy, siliciclastic facies on the northern Gondwana shelf (Pelhate and Plusquellec, 1980; Robardet et al., 1994). Initially, a metre-scale coral-dominated buildup developed in a low-energy environment (Fig. 3) before being smothered and terminated by an influx of siliciclastic sediment. The succeeding bioherm (metre to 10s of metre scale) was constructed by corals and stromatoporoids building contemporaneously with clastic sediment influx into a low-energy environment. The predominantly bulbous morphology of the stromatoporoids has been interpreted as evidencing growth in a sediment-stressed environment (Pelhate and Plusquellec, 1980). However, the characteristics of the siliciclastic host sediments are not described in detail.

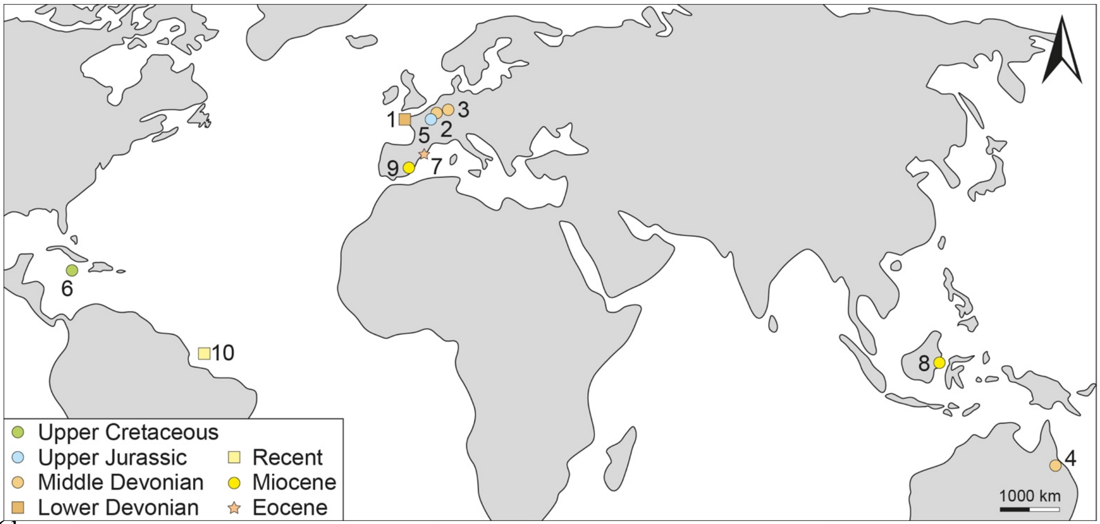

Figure 2: Map of the Earth (recent times) with localities of the here compared examples of sediment-stressed reefs. Many reefs are located in today's Europe. Age of each site is indicated by the colour of the symbol that marks the position. Sites: 1) Lower Devonian reef of France; 2) Lower to Middle Devonian reef of Belgium; 3) Middle Devonian reef of Germany; 4) Middle Devonian reef of Australia; 5) Upper Jurassic reefs of France; 6) Upper Cretaceous reefs of Jamaica; 7) Eocene reefs of Spain; 8) Miocene reefs of Indonesia; 9) Miocene reefs of Spain; 10) Recent Amazon River mouth reefs.

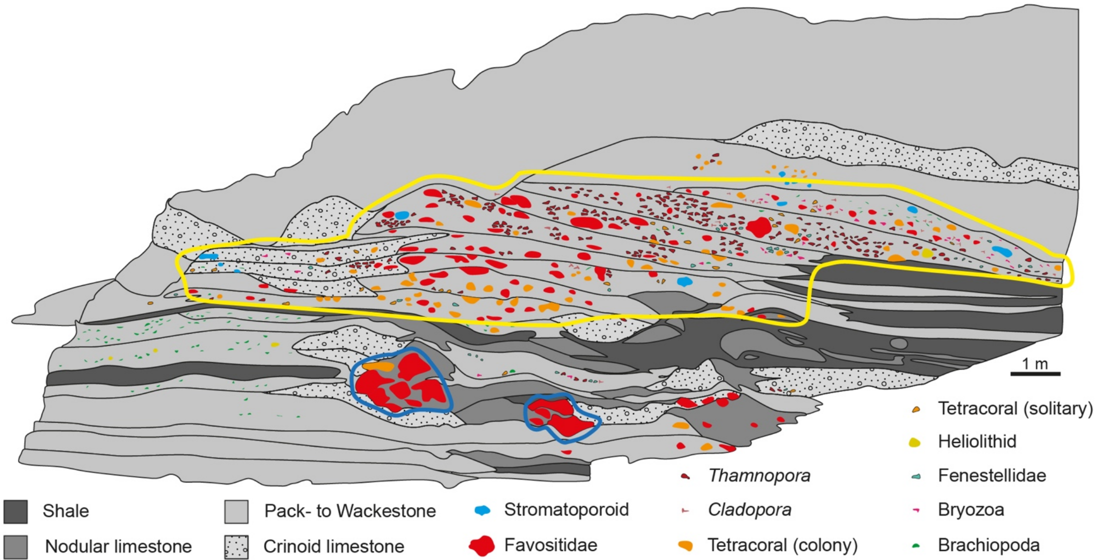

Figure 3: Sketch of the outcrop at Point d'Amérique. The blue lines mark the first reefal build-ups. The yellow line indicates the boundary of the succeeding biostrome (modified from Pelhate and Plusquellec, 1980).

3.1.2. Middle Devonian reef of Belgium

In the Namur-Dinant Basin (Fig. 2), a southwards-facing ramp system developed into a carbonate-rimmed carbonate shelf during the early Givetian. The Marenne Member (upper Eifelian to lower Givetian) is the regional equivalent to crinoidal shoals and biostromal units of the lower Trois-Fontaines Formation (Bultynck and DeJonghe, 2001; Mabille et al., 2008). The Marenne Member comprises a mixed siliciclastic-carbonate succession composed of up to metre scale beds of argillaceous and sandy limestones intercalated with claystone and siltstone.

A 10 m thick reefal buildup, fringed by open marine facies, is documented at the Marenne Quarry (Mabille et al., 2008; Boulvain et al., 2009). Here, a mud- to sand-grade siliciclastic component typically contributes up to 20% (locally up to 50%) of the matrix volume. The presences of this detrital component, even in the limestone beds of the Marenne Member, significantly influenced bioherm development (Mabille et al., 2008; pers. comm. Denayer, 2022). Fauna, dominated by well-preserved (*in situ*) branching tabulate corals, fasciculate rugose corals, crinoids, brachiopods, massive stromatoporoids and bryozoans, was concentrated at the fair-weather wave base (Mabille et al., 2008). In more sandy areas, tabulate and rugose corals dominate and appear to have developed as well as, if not better than, in areas where stromatoporoids dominate (pers. comm. Denayer, 2022).

3.1.3 Middle Devonian reef of Germany

The Middle Devonian Klutert biostrome (carpet-reef) is accessible in Ennepetal, Germany, via a series of cave passages (Fig. 2; Unger et al., 2023). This biostrome formed on the southeastern shelf of Laurussia during the early Givetian (Middle Devonian). The reef represents a biostrome that developed in a mixed carbonate-siliciclastic deltaic environment (Langenstrassen, 1982; Basse et al., 2016) during a period of decreasing siliciclastic influx.

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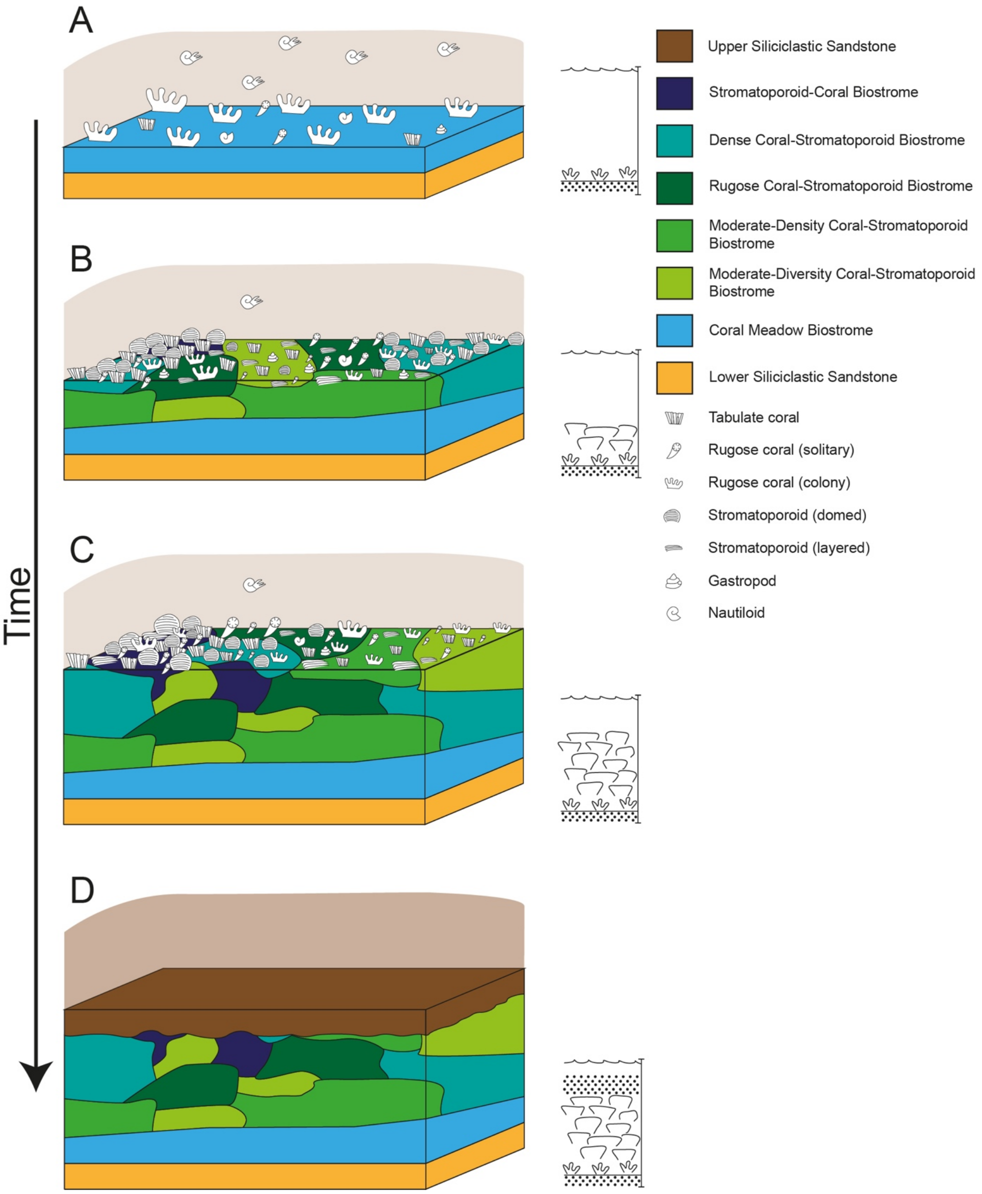

Figure 4: (A to D) Spatial model of the Klutert biostrome, not to scale. The thickness of the fully developed Klutert biostrome reaches a maximum of 12 m. Biostromal patches vary between 1 and 3 m in thickness and lateral between several metres to 10's metres. (A) Initial reef settlement (= Coral Meadow Biostrome) is dominated by phaceloid rugose corals. (B) Patches of different subunits of the Coral-Stromatoporoid Biostrome developed on top of the Coral Meadow Biostrome Unit. The individual subunits gradually merge into each other and are not separated by a sharp transition to a siliciclastic matrix. (C) The spatially complex clusters of the subunits vary in size (metres to 10's of metres) and arrange vertically and horizontally with no preferred direction. (D) Burial and demise of the Klutert biostrome (modified from Unger et al., 2023).

This biostrome classifies as an autoparabiostrome (*sensu* Kershaw, 1994) with a maximum stratigraphic thickness of ca. 12 m. Silt- to sand-grade clastic material (clay and quartz) contributes between 20 and 99 wt.-% of the matrix of the biostrome.

As sediment input declined (20 wt.-% siliciclastics in the matrix), an initial coral meadow (dominated by phaceloid rugose corals) developed (Fig. 4 A). This primary settlement was followed by the development of a Coral-Stromatoporoid Biostrome Unit that can be subdivided into five subunits (Fig. 4 B; for detailed descriptions of the subunits see Unger et al., 2023). These subunits expand laterally from a few metres to several tens of metres, reaching thicknesses of up to three metres, and are arranged as spatially complex clusters of smaller biostromes that define the internal structure of the carpet-reef (Fig. 4 C). The main reef builders are rugose and tabulate corals (10 species) and stromatoporoids, associated with crinoids (mainly trochites), brachiopods, gastropods and nautiloids. Although the siliciclastic component of the matrix was described in detail, no clear relationship between siliciclastic influx and the negative performance of reefal organisms was discerned. In fact, the intervals with the highest concentration of reef builders may yield the highest proportion of siliciclastic sediments. Reef builders were initially able to tolerate the muddy environments, however, a combination of decreasing siliciclastic grain size, decreasing water energy and increasing siliciclastic sediment load eventually overwhelmed the organisms and resulted in reef decline (Fig. 4 D; Unger et al., 2023).

3.1.4 Middle Devonian reef of Australia

The Fanning River inshore coral reef biostrome (Fig. 2) formed during the Givetian in a shallow, turbid, partially protected environment with significant clastic input (Cook, 1995; Zapalski et al., 2021). This reef overgrew a 20 to 40-cm thick stromatoporoid biostrome (Zapalski et al., 2021), with nearby river mouths providing siliciclastic material sourced from a granitoid hinterland (Cook, 1995). The auto- to autoparabiostrome of massive, branching, and encrusting tabulate corals and solitary and rarely colonial, massive rugose corals is traceable over 300 m laterally (Zhen, 1996; Zapalski et al., 2021). Rarely, stromatoporoids and brachiopods are observed, while other typical Devonian invertebrates, such as crinoids, are absent. An internal lateral variation is described based on a range of assemblages, dominated by foliaceous and encrusting tabulates, branching tabulates and either massive or solitary rugose corals (Zapalski et al., 2021). The siliciclastic component of the sediments has not been described. The palaeo-ecological mechanisms that caused this internal zonation are not understood.

3.2 Mesozoic

3.2.1 Upper Jurassic reefs of northern France

In the Pagny-sur-Meuse area in northern France (Fig. 2), various reefal buildups developed on a platform along the northern margin of the Tethys during Oxfordian times (Late Jurassic; Olivier et al., 2004).

The middle to upper Oxfordian units record the onset of siliciclastic influx into a formerly clear water setting. Prior to the influx of siliciclastic sediments, a large (>100 m wide, 15 m thick) biostrome developed in a low-turbidity setting. With the influx of siliciclastic sediments, sourced from the erosion of the Brabant-Ardennes Massif to the

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north (Ziegler, 1990), there was a sharp increase in turbidity with an associated transition in reefal communities and morphologies. Within the new mixed carbonate-siliciclastic depositional environment, coral-microbial reefs developed as metre to decametre scale buildups, irregularly shaped buildups, decametre-sized bioherms or small (metre-scale) patch reefs. Corals are observed throughout the section, with a range of growth forms including phaceloid, lamellar, dome-shaped, ramose and irregularly shaped morphologies.

Five different types of reefal buildups have been identified and described, each with a distinct coral assemblage and exhibiting a positive relationship between the volume of siliciclastic material and microbialites. The inter-reef sediments were only described in two cases – from clear water reefs lacking siliciclastic sediment, and for the mixed carbonate-siliciclastic reefs where siliciclastic sediment contributed up to 5% of the total reef volume. Relatively high coral diversity was observed in both clear water and mixed carbonate-siliciclastic reefs (15 and 16 genera respectively). The lowest diversity coral assemblage (six genera) was observed in mixed carbonate-siliciclastic reefs that had developed in deeper water settings.

Under clear water conditions, corals thrived yet with the onset of siliciclastic influx, the primary control on assemblage development was water depth and the resulting hydrodynamic levels. Even under significant siliciclastic influx, reefs with diverse coral assemblages were still able to develop in shallow-water settings flushed by strong currents or storms. However, where the influx of siliciclastic sediment crossed a critical threshold corals are absent and oyster reefs developed (Olivier et al., 2004).

3.2.2 Upper Cretaceous reefs of Jamaica

During the late Campanian? to Maastrichtian (Cretaceous), small coral patch reefs developed under open marine conditions in association with an island arc setting (Fig. 2). Patch reefs developed during infrequent periods of reduced sedimentation in a setting otherwise dominated by the influx of silt grade volcaniclastic material (Coates,1965; Mitchell, 2002b). The relative contribution of volcaniclastic material is not recorded.

Dense frameworks were constructed and dominated by branching ramose scleractinian corals, and debris contains further encrusting-lamellose scleractinian corals of moderate diversity. Coralline algae, bryozoans, serpulid worms and brachiopods contribute secondarily to the framework. The patch reefs are surrounded by reef-derived debris with beds reaching thicknesses of up to 1.5 m (Mitchell, 2002a).

3.3 Cenozoic

3.3.1. Eocene reefs of Spain

Middle to upper Eocene shallow marine carbonates at the Calders Section in NE Spain (Fig. 2) show the transition from marine to fluviatile sedimentation (Santisteban and Taberner, 1988; Hendry et al., 1999). A prograding siliciclastic shelf was dominated by constant clay and silt input, with carbonates developing during periods of reduced siliciclastic influx (Cavagnetto and Anadón, 1996; Hendry et al., 1999). With decreasing siliciclastic material (<65 wt.-%), benthic foraminifera and coralline algae dominated, while corals replaced the foraminifera where the siliciclastic component falls below 38 wt.-%.

Within coral rubble, patches of a coral framework (<100 m in diameter) are observed. Robust branching corals and solitary corals dominate the shallow high-energy settings influenced by sand-grade siliciclastics (<27 wt.-%), while delicate branching forms dominate protected settings with a high clay-grade siliciclastic content (<39 wt.-%). These buildups were buried during renewed progradation of the siliciclastic dune foresets (Lokier et al., 2009).

3.3.2 Miocene reefs of Indonesia

During the Miocene, several patch reefs developed in front of the Mahakam Delta, Kalimantan, Indonesia (Fig. 2). Several studies have focused on the so-called 'coral triangle' region (Wilson and Lokier, 2002; Wilson, 2005; Santodomingo et al., 2015, 2016) as these patch reefs provide a good analogue for reefs forming in turbid habitats (Wilson and Lokier, 2002). For the Mahakam Delta, recent observations indicate a tide-dominated environment and a significant influx of silt and clay (Storms et al., 2005). The Miocene patch reefs formed in low-energy environments (Allen et al., 1976) and extend between 2 to 4 km laterally with a thickness of up to 40 m (Wilson and Lokier, 2002). Reefal organisms are represented by coralline algae, large benthic foraminifera, echinoids, various molluscs and scleractinian corals (Wilson and Lokier, 2002; Santodomingo et al., 2015). The internal organization of the different patch reefs is relatively simple; a well-ordered sequence of different packstone units referred to as coral sheetstones and platestones (Wilson and Lokier, 2002; Santodomingo et al., 2016). A relationship between coral morphologies and the siliciclastic content is observed, as the number of branching corals increases when the siliciclastic content (up to 20 wt.-% and 10 wt.-%) decreases. Platy corals, for example, are more abundant in fine-grained siliciclastics (up to 60 wt.-%; Wilson and Lokier, 2002).

Even though the environment may be considered as less than favourable, these patch reefs represent the origins of the 'biodiversity hotspot' of corals from the Miocene (Johnson et al., 2015; Santodomingo et al., 2016). It is proposed that these challenging environments may have been important to the development of corals able to tolerate a diverse range of settings and, thus, were able to migrate into a range of habitats (Santodomingo et al., 2016).

3.3.3 Miocene reefs of Spain

During the late Tortonian (Miocene), several different types of coral reefs developed in the Almanzora River Corridor in southeastern Spain (Fig. 2). Reef formation in this siliciclastic-dominated succession occurred during times of lower siliciclastic sediment influx. Reefs developed on fan deltas (patch reefs), at the margins of delta lobes (patch to barrier reefs) and on coastal platforms (barrier reefs; Braga and Martín, 1988; Martín et al., 1989). All of these reef types colonised on either silt or conglomerate substrates and are intercalated with silt layers (Martín et al., 1989). Internal structures are dominated by cyclic successions of beds dominated by two main faunal associations of different corals and, occasionally, coralline algae. The only exemption is represented by the patch reefs in the fan delta setting. In these settings, the central portions of the patches are dominated by a single coral species (*Tarbellastraea*) that is fringed by the bedded succession of siltstones (Fig. 5; Braga and Martín, 1988; Martín et al., 1989). The species diversity of these reefs is comparatively low, with only 7 coral genera observed in the different reefal buildups. Previous studies did not find a connection between species morphology and sediment load. Conversely, a trend with more densely packed colonial structures in deeper waters was observed (Martín et al., 1989).

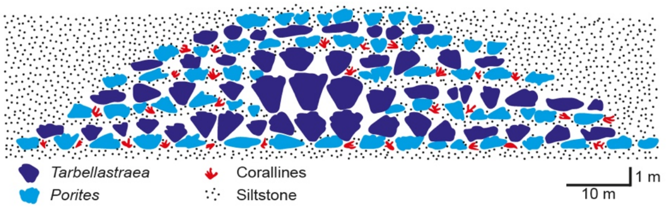

Figure 5: Internal structure of the Miocene patch reefs located at the fan delta area of the Almanzora River. One single coral species (*Tarbellastraea*) dominates the centre and is surrounded by bedded corals (modified from Martín et al., 1989).

3.3.4 Recent Amazon River mouth reefs

The Great Amazon Reef System spans over 9,500 km^2 at depths ranging from 70 to 220 m (Moura et al., 2016; Francini-Filho et al., 2018) on the outer shelf in front of the delta of the Amazon River (Fig. 2; Moura et al., 2016). Turbidity is high due to the sediment-loaded Amazon plume that seasonally influences the northern and central parts of the reef system (Moura et al., 2016; Francini-Filho et al., 2018). The high turbidity and resulting low illumination do not appear to be limiting factors to reef development (Francini-Filho et al., 2018). Internal variation is high and includes areas of rhodolith beds, patch and ridge-like reefs (mainly sponges, black corals and octocorals) and so-called sponge bottoms.

Less than 5% of the reef system has been studied to date (Francini-Filho et al., 2018) and little quantitative data is available in relation to the associated siliciclastic sediments. Based on limited data, reefs and sponge bottoms are more commonly described in the central and southern sections (Moura et al., 2016; Francini-Filho et al., 2018) while reefs with nearly 100% live coverage are predominantly described from the deepest parts (Francini-Filho et al., 2018).

4. Discussion

The analysis of data from the accessible literature clearly reveals that sediment-impacted reefs that have developed in environmentally comparable settings do not necessarily record the same characteristics throughout the stratigraphic record (Table 1). Beyond the comparably well-studied examples, there are other ancient reef systems that were only superficially described (Esteban, 1980; pers. comm. Denayer, 2022).

Table 1: Comparison of the selected examples of reefs in sediment-stressed environments. Abbreviations used: stromatoporoids (strom.); tabulate corals (tc.); rugose corals (rc.); scleractinian corals (sc.).

Age and locality	Type	Dimensions	Internal structure	Environment	Sediment impact	(Fossil) assamblage	Response?	Citation
Lower Devonian France	1. small build-up 2. flank of bioherm			muddy flat shelf	1. grew, then sediment influx 2. simultaniously (not classified nor quantified)	1. corals 2. corals and strom.	bulborous strom. due to sediment impact	Pelhate & Plusquellec, 1980
Lower to Middle Devonian Belgium		10 m thickness		ramp, around Fair Weather Wave Base	detrital-rich, up to 20%, rarely up to 50 %	*in situ* branching tc., fasciculate rc., crinoids, brachiopods, massive strom., bryozoans	especially in sandy areas, normal to even better development of corals	Mabille et al., 2008; pers comm. Denayer, 2022
Middle Devonian Germany	auto- to autoparabiostrome	1 m^2 lateral max 12 m thickness	highly complex internal patchy arrangement of facies clusters	inner shelf	grew synsedimentarily, 20 to 99 wt.% siliciclastic rich matrix	corals and strom.	no connection between growth forms and sediment impact observable	Unger et al., 2023
Middle Devonian Australia	auto- to autoparabiostrome	>300 m lateral	lateral variation of different assamblages	inshore, shallow, turbid, partially protected	significant from nearby river	massive, branching & encrusting tc., solitary & rarely colonial, massive rc., rarely strom.		Zapalski et al., 2021
Upper Jurassic France	1. irregular shaped 2. bioherms 3. patch-reefs	1. metre to decametre 2. decametre 3. metre		shallow platform, moderate energies, frequent storm events	constant from erosion of Brabant-Ardennes Massif	dominated by corals (phaceloid, lamellar, ramose, irregular dome-shaped) and microbialite; coral diversity: 1. eleven genera 2. 16 genera 3. six genera	1) high sediment influx, more microbialites 2) too heavy sediment influx, no reef 3) corals abundand everywhere, flourish in reefs	Olivier et al., 2004
Upper Cretaceous Jamaica	patch-reefs	up to 1.5 m thickness	patch-reefs of dense framework surrounded by debris	open marine, island arc system	fine-grained (silt) volcanoclastics	dense framework of branching ramose sc. debris: encrsuting-lamellose sc. of moderate diversity; secondary: red calcerous algae, bryozoans, serpulid worms, brachiopods	grew in infrequent periods of low sedimentation	Mitchell, 2002a, b
Eocene Spain	*in situ* patches between coral rubble	<100 m diameter		1. shallow, high-energy settings 2. protected settings	1. <27 wt.-% sand-sized siliciclastics 2. <39 wt.-% clay-sized siliciclastics	1. robust branching and solitary corals 2. delicate branching corals	growth form related to energetic environment and grain size	Lokier et al., 2009
Miocene Indonesia	patch-reefs	2 to 4 km lateral up to 40 m thickness	simple, sequence of different pack. sheet- and plate stones	low energy, turbid habitat	high silt and clay sedimentation from deltaic system	coralline algae, benthic foram. echinoids, molluscs and corals	biodiversity hotspot, challenging environment triggers diversification?	Wilson & Lokier, 2002; Santodomingo et al., 2015, 2016
Miocene Spain	1. patch-reefs 2. patch to barrier reefs 3. barrier reefs		1. center one dominant coral species, surrounded by bedded succession 2. & 3. cyclic succession of beds of two main fossil assamblages	1. fan delta 2. margins of delta lobes 3. coastal platform	intercalated silt(layers), settled on silt or conglomerate	corals (diversity comparativly low), ocassionally corraline algae	1) deep water, tighter colonial structures 2) low diversity due to isolated environment	Braga & Martín, 1988; Martín et al., 1989
Recent Amazon River	Great Amazon River System (GARS): patch- & ridge-llike reefs; sponge bottoms	GARS >9,500 km^2 lateral	high variation	high turbidity, depths 70 to 220 m	Amazon plume shifts seasonally	mainly sponges, black corals and octocorals		Moura et al., 2016; Francini-Filho et al., 2018

4.1 Characterising the siliciclastic component

As with any other reef system, turbid water reefs are typically described either in relation to their location (e.g., nearshore, distal), in the context of the energy system (e.g., sheltered, wave influenced), in terms of the water depth (e.g., shallow, deep) or as a combination of these adjectives (e.g. shallow, low energy, lagoonal). However, this study clearly demonstrates that, in the majority of cases, there is a severe paucity of detailed data describing the siliciclastic component that is found in association with these reefs (Table 2). In many cases, the presence or absence of a siliciclastic component is not explicitly stated (e.g., Hayward, 1982; Mitchell et al., 2001; Yue et al., 2004). Even where a reef is described from a mixed carbonate-siliciclastic environment, this does not conclusively prove the presence of siliciclastic material within the reef matrix, for example in cases where the reef is sheltered from turbid environments (Kershaw, 1981; Méndez-Bedia and Soto, 1984). While reference may be made to the presence of siliciclastic material, a detailed quantitative description of the volume, distribution and nature of the siliciclastic grains is relatively rare (e.g., Godefroid, 1968; Pelhate and Plusquellec, 1980; Nield, 1982; Braga and Martín, 1988; Mabille et al., 2008; Moura et al., 2016; Francini-Filho et al., 2018; Denayer, 2019; Zapalski et al., 2021). Where these sediments are described, the description is often incomplete – particularly with reference to any relationship to reef builders. A further difficulty is establishing the temporal relationship between reef growth and siliciclastic influx – was reef growth contemporaneous with siliciclastic input or were these sediments deposited after the reef growth?

Table 2: Overview of the here compared mixed siliciclastic reefal settings. The traffic light system highlights whether and how detailed information on the siliciclastic content and relation to the internal structure are provided for each study. Green: detailed information; Orange: some information; Red: no information provided.

Age and locality	Internal structure	Sediment impact	Sediment qualification	Sediment quantification	Response
Lower Devonian France	🔴	🟢	🔴	🔴	🟢
Lower to Middle Devonian Belgium	🔴	🟢	🟠	🟠	🟠
Middle Devonian Germany	🟢	🟢	🟢	🟢	🟢
Middle Devonian Australia	🟠	🟢	🟠	🔴	🟠
Upper Jurassic France	🔴	🟢	🔴	🟠	🟢
Upper Cretaceous Jamaica	🟠	🟢	🟠	🔴	🟠
Eocene Spain	🔴	🟢	🟠	🟢	🟢
Miocene Indonesia	🟢	🟢	🟠	🟢	🟢
Miocene Spain	🟢	🟢	🟠	🔴	🟠
Recent Amazon River	🟠	🟢	🔴	🟠	🟠

4.2 Reef morphology

The reefs described here are ridge-like, barrier, patch or biostromal reefs. All of these units have a limited (metre to decametre) thicknesses (e.g., Pelhate and Plusquellec, 1980; Mitchell., 2002a, b; Olivier et al., 2004) and lateral extent – only rarely reaching hundreds of metres (Wilson and Lokier, 2002; Zapalski et al., 2021; Unger et al., 2023). In addition to corals, numerous other biota (e.g., microbial communities, serpulids) have been documented as forming patch reefs in argillaceous settings – again, these reefs are of limited extent (metre to decametre; e.g., Berra and Jadoul, 1996). Regardless of the nature of the reef-forming organism, all of the described siliciclastic-associated reefs form sedimentary bodies that are significantly thinner and with a smaller footprint than contemporaneous reefs that formed in 'blue water' settings.

The examples in this study clearly demonstrate that siliciclastic-sediment hosted reefs can and do develop and thrive under significant sediment influx (e.g., Unger et al., 2023) and in constantly turbid waters (e.g., Santodomingo et al., 2015, 2016; Reuter et al., 2019) – this is counter to the widely held notion that sediment particles will, by default, smother and kill reefal organisms (Rogers, 1990; Jones et al., 2015; Ricardo et al., 2015). However, the observation that siliciclastic-hosted reefs are typically considerably smaller than their blue water counterparts, implies that siliciclastic sediment does impact reef morphology by limiting both the vertical and lateral extent of reef development. This conclusion is supported by the observation that, in siliciclastic settings, reef size is related to the volume of siliciclastics within the reef matrix as a proportion of the total reef volume. Larger reefs yield relatively small amounts of clastics from their matrix while smaller reefs typically display a higher volume of siliciclastic matrix (e.g., Olivier et al., 2004). In other words, higher volumes of clastic influx result in smaller reefal bodies.

4.3 Coral growth morphology

It is hypothesised that, during the Paleozoic, massive and platy-foliose tabulate coral forms evolved in turbid shallow water environments (Zapalski et al., 2021). By contrast, Mesozoic to Recent, scleractinian corals with branching frameworks have been associated with significant sediment influx (Rogers, 1990; Mitchell, 2002a, b; Lokier et al., 2009; Jones et al., 2015). Yet such relationships are not universal, scleractinian corals from the Miocene of Indonesia exhibit a strong, converse, relationship between growth form and siliciclastic influx with branching forms dominating during periods of low influx and platy forms where rates are high (Wilson and Lokier, 2002). A further complication arises in that numerous studies have recorded that there is no discernible relationship between siliciclastic sediment influx and coral growth morphology (Mabille et al., 2008; Unger et al., 2023). Clearly, associating coral morphology with siliciclastic sediment influx is highly problematical – particularly for ancient ecosystems where the nature of the associated siliciclastic material is poorly documented, and the rate of sediment influx is unknown.

4.4 Internal organisation

Normal marine reef communities have been described as 'highly patchy' in terms of both the distribution of organisms and growth morphology (Hubbard, 2006; Wood, 2011); this axiom holds true for the majority of the sediment-stressed examples discussed here.

Reefs developing in sediment-stressed settings clearly exhibit lateral and vertical variability at a range of scales from metre (Zapalski et al., 2021; Unger et al., 2023) to many tens or even hundreds of kilometres (Francini-Filho et al., 2018). Internal organisation of facies and biotic assemblages may appear random, as observed in the Middle Devonian auto- to autoparabiostromes documented from Australia and Germany (Zapalski et al., 2021; Unger et al., 2023). Alternatively, discernible cyclical stacking patterns may be observed, as is the case for the Miocene examples from Spain and Indonesia (Braga and Martín, 1988; Martín et al., 1989; Wilson and Lokier, 2002).

Several of the studied examples lacked any definitive information pertaining to the internal organisation of the reef system (e.g., Pelhate and Plusquellec, 1980; Olivier et al., 2004; Mabille et al., 2008). Such a paucity of data may result from the nature of the outcrops, with poor or insufficient exposure prohibiting the elucidation of three-dimensional and, in some case, even two-dimensional architectures. Establishing internal organisation can also be significantly compromised where post depositional (diagenetic) processes have overprinted primary depositional fabrics. In conclusion, no discernible relationship was established between the internal organisation of the reef and its depositional context.

As has been demonstrated, reefs are able to develop and even thrive under conditions of elevated siliciclastic influx, and increased turbidity, particularly for short durations. However, periods of prolonged sediment influx or episodic large scale sedimentation, particularly in combination with other stressing factors, will either smother and kill most reefal organisms or induce a change in the reefal community (van Woesik and Done, 1997; Jordán-Dahlgren and Rodríguez-Martínez, 2003; Januchowski-Hartley et al., 2020; Lokier, 2021).

Where reefs are observed in naturally turbid settings, this is usually in association with relatively high hydrodynamic energies where waves and currents constantly remobilise sediments to limit the duration and, therefore, effects of smothering (e.g., Larcombe et al., 2001; Richards et al., 2018). In cases where a pre-existing reef is affected by anthropogenically-induced siliciclastic influx then, depending on the rate and volume of sediment influx, we can expect to see either the burial and demise of the reef or a switch in the composition of the reef building community.

Documenting and understanding the relationships between siliciclastic influx and the development of ancient reefs offers an opportunity to predict the responses of recent reefs to future anthropogenically-driven stress and climate change (Kleypas et al., 2001; Santodomingo et al., 2016; Zweifler et al., 2021). Present-day reefs developing under a range of environmental stresses, including turbid-water environments, have been cited as possible refugia from which the evolutionary selection of more stress-resistant communities may be utilised to repopulate damaged reefs in the future (Cacciapaglia and van Woesik, 2015; Morgan et al., 2016).

5. Conclusions

Reefs have occurred in sediment-stressed environments throughout the Phanerozoic, yet, beyond some broad-scale generalisations, our understanding of these systems remains hamstringed by a lack of the quantitative data that is necessary to undertake relational analysis. In order to fully elucidate the relationship between siliciclastic sedimentation and reef development, there needs to be a significant step-change in how we routinely record ancient and recent reefal systems. It is only through the collection of constrained quantative data that we can progress beyond the largely conjectural associations postulated for many ancient reefal systems.

Where a reef has developed in relation to siliciclastic sediments, it is necessary to discern if the influx of siliciclastic material was contemporaneous with reef growth or occurred after the development of the reef, for example through the infiltration of siliciclastic material into the reef framework (Lafuste et al., 1991; Fernandez et al., 2006; Huang et al., 2022). Stratigraphic relationships between the siliciclastic sediments and the reef should be detailed, particular attention must be paid to contact relationships. All sedimentary structures, including bioturbation, should be fully documented. A quantitative analysis of the mineralogy and textural properties of the siliciclastic grains should be undertaken. The carbonate component of the matrix should be similarly documented in detail. Any relationships between bioclasts and siliciclastic components (incorporation, overgrowth, abrasion, etc.) needs to be recorded. The morphologies of the skeletal components should be described in detail. Where a reef has developed in a siliciclastic dominated setting, but the reef lacks a siliciclastic component, then an attempt should be made to discern the reason for the lack of siliciclastics.

Under a trajectory of accumulative anthropogenically-driven reef stress, there is an increasing urgency to study and understand these systems that, potentially, offer refugia for those hardy and tolerant corals species that are preadapted to environmental stressors.

Authorship contribution

The study was designed by TU, MA and AI. Interpretations and implications developed from discussions with SL, MA, MS and AI. The manuscript was prepared with input from all co-authors.

Conflict of interest

The authors declare that they have no conflict of interest

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